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Nesting success and productivity of the Common Barn-owl *Tyto alba*: results from a nest box installation and long-term breeding monitoring program in Southern Hungary[x]

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Abstract In this study, the results of a long-term nest box installation program of the Common Barn-owl *Tyto alba* (Scopoli, 1769) in Southern Hungary were evaluated, which program was conducted during a 24-year period (1995–2018). The percentages of occupied nest boxes ranged from 9.72 to 73.44% in the first breeding periods while this varied between 0 and 41.46% in the case of repeated clutches in the same nest boxes with second broods. A total of 1,265 breeding attempts were recorded including 1,020 (80.63%) in the first and 245 (19.36%) in the second breeding periods, from which a total of 210 (16.6%) clutches did not produce any fledglings. The modal clutch size was 7 eggs in both first and second annual clutches. However, the value of productivity was higher in the case of larger clutch sizes and we found significant linear relationship between initial clutch size and fledgling production per nesting attempt in both breeding periods. Significant variation of reproductive parameters was observed among the years. The proportion of egg loss showed significant decline, while the change of hatching success and the variation of annual productivity showed significant slight positive linear trend during the 24 years. Our results suggested that despite the outlier values of reproduction characteristics in the extreme years with negative effect, a relatively stable Common Barn-owl population can be maintained by the placement of nest boxes in the investigated region.

Keywords: nest box occupancy, clutch size, eggs and hatching losses, productivity

Összefoglalás Jelen tanulmányban a gyöngybagoly, *Tyto alba* (Scopoli, 1769) 24 év során (1995–2018) Dél-Magyarországon megvalósított hosszú távú költőláda telepítési programjának eredményeit értékeltük. A ládafoglalási arány az első költéseknél 9,72 – 73,44%, míg a másodköltések során ugyanabban a költőládában megismételt fészkelések aránya 0 – 41,46% között változott. Összesen 1265 megkezdett költést, 1020 (80,63%) első és 245 (19,36%) másodköltést regisztráltunk, melyekből összesen 210 (16,6%) költés nem produkált kirepülő fiókát. Mind az első, mind a másodköltéseknél a 7 tojásos fészekalj volt a leggyakoribb. A produktivitás értéke a nagyobb fészekalj méreteknél nagyobb volt, és mindkét költési periódusban szignifikáns lineáris összefüggést találtunk a kezdeti fészekalj méret és a megkezdett fészkelésekre vonatkozatott kirepülő fiókaprodukció között. A szaporodási paraméterek tekintetében évek közötti szignifikáns eltérést figyeltünk meg. A tojás veszteség aránya szignifikáns csökkenő, míg a kelési siker és az éves produktivitás változása enyhe, de szignifikáns pozitív trendet mutatott a 24 év során. Eredményeink azt sugallják, hogy a negatív hatású extrém években a szaporodási karakterisztikák kiugró értékei ellenére a vizsgált régióban a költőládák kihelyezésével viszonylag stabil gyöngybagoly populáció tartható fenn.

Kulcsszavak: költőláda foglalás, fészekalj méret, tojás és fióka veszteség, produktivitás

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Introduction

The Common Barn-owl *(Tyto alba)*, as a cosmopolitan nocturnal raptor is characterized with worldwide distribution because it occurs in all the continents except Antarctica (Bunn *et al*. 1982, Taylor 1994, Gill & Donsker 2018). Within the areas of its range, Common Barn-owl was distributed across many biomes (continental steppes, savannas, pampas, rainforests), especially in preference to open fields and farmlands in the temperate region of South and North America as well as Europa (Taylor 1994, Roulin 2002a). As a secondary cavity-nesting bird, due to the limited availability of natural nesting and roosting sites, Common Barn-owl switched to using the open man-made structures, especially church towers and traditional farm buildings (Taylor 1994, Ramsden 1998, Golawski *et al*. 2003, Meyrom *et al*. 2008, Mainwaring 2015).

Despite the wide distribution and the successful adaptation to the anthropogenic environment, the decline of local populations of Common Barn-owl was reported already from the mid-80s (Colvin 1985, Shawyer 1987, Percival 1991, de Bruijn 1994, Taylor 1994, Heath *et al*. 2000, Toms *et al*. 2001) and was confirmed by a synthesis of its population size data in many regions (BirdLife International 2004). This population decline was caused by several factors such as the loss of suitable roosting and nesting sites (Taylor 1994, Ramsden 1998, Hindmarch *et al*. 2012), the loss of hunting areas especially the grassland due to land use conversions and the increase in agricultural activity which has influenced the available small mammal populations as main prey groups (Colvin 1985, Taylor 1994, Love *et al*. 2000, Askew *et al*. 2007), chemical poisoning by anticoagulant rodenticide (Newton *et al*. 1994, Gray *et al*. 1994, Albert *et al*. 2010, Geduhn *et al*. 2016) as well as the mortality effect of traffic and roads (Fajardo 2001, Boves & Belthoff 2012, Borda-de-Água *et al*. 2014, De Jong *et al.* 2018, Šálek *et al*. 2019).

However, numerous short and long-term studies have demonstrated that the application of nest boxes as artificial cavities is an appropriate practice to compensate for the effect of the factors causing the decrease of the populations and breeding successes (Marti *et al*. 1979, Johnson 1994, Leech *et al*. 2009, Mainwaring 2011), and to increase the pest control effect of Common Barn-owls (Meyrom *et al*. 2009, Kan *et al*. 2013, Paz *et al*. 2013, Kross *et al*. 2016, Wendt & Johnson 2017). The costs and benefits of man-made structures as nesting sites, especially in the case of artificial nest boxes were evaluated and contested (Johnson 1994, Møller 1994, McCafferty *et al*. 2001, Lambrechts *et al.* 2010, 2012, Mainwaring 2011, 2015). Although the earlier studies demonstrated that the application of nest boxes increased the clutch size and breeding success compared to natural nesting sites (Marti *et al*. 1979, Johnson 1994), the advantages of nest boxes were questioned by a Hungarian study, which showed that the survival of owls differed between the artificial nest box and the 'natural' environment of a church tower (Klein *et al*. 2007). Moreover, in the case of the artificial nest box application, more species could occupy the same nest boxes which realise competitive situation or predation (Charter *et al*. 2010a) such as the interspecific offspring killing which was reported in the interaction between Tawny Owl *(Strix aluco)* and Common Barn-owl (Mátics *et al*. 2008).

Nesting and breeding success of Common Barn-owls were investigated from more aspects covering the impact of habitat variability, land-use and landscape context of the hunting area (Martínez & Zuberogoitia 2004, Bond *et al*. 2005, Meek *et al*. 2009, Frey *et al*. 2011, Charter *et al*. 2012), the effect of urbanisation (Salvati *et al*. 2002, Hindmarch *et al*. 2014) and agricultural land use, such as intensive farming practise, restoration of the agricultural sector, ecological compensation areas (Leech *et al*. 2009, Arlettaz *et al*. 2010, Martin *et al*. 2010, Milchev & Gruychev 2014, Almasi *et al*. 2015), as well as the change of population size (Toms *et al*. 2001, Altwegg *et al*. 2006a, De Jong 2009). The studies of Common Barn-owl's breeding ecology demonstrated that the reproductive output and so the local size and survival of its populations were determined basically by habitat and nest-site qualities (Gubanyi *et al*. 1992, Bond *et al*. 2005, Frey *et al.* 2011), food supply, in particular the availability and density fluctuation of main prey species or groups (Taylor 1994, Klok & de Roos 2007, Charter *et al*. 2015, Pavluvčík *et al*. 2015), and weather conditions (Chausson *et al*. 2014a, Charter *et al*. 2017) especially extreme winters (Marti & Wagner 1985, 1997, Taylor 1992, Marti 1994, Altwegg *et al*. 2006b, Chausson *et al*. 2014b). The reproductive success of Common Barn-owls was investigated at the border of its distribution range where the lifetime productivity was determined significantly by winter weather, particularly the additive effect of cold temperature and the higher snow cover (Marti 1994, 1997, Tóth *et al*. 2004). Due to a severe winter, a large decline in the effective number of Common Barn-owls can lead to genetic bottlenecks, which has been investigated in a local population in Hungary (Mátics *et al*. 2017).

Clutch size, as one of the most important life history traits of birds (Lack 1947, Stearns 1976, Price & Liou 1989), has been assessed in detail in the breeding ecology of Common Barn-owls such as the comparison of first, replacement and second clutches (Marti 1994, Martínez & López 1999, Frey *et al.* 2011), seasonal (Baudvin 1986, Marti 1994, Roulin 2002b) and annual variation (Martínez & López 1999, Toms *et al*. 2001), and in relation to the abundance of main prey (Taylor 1994, Pavluvčík *et al.* 2015). Nevertheless, the variation of breeding characteristics related to initial clutch size and relationship between clutch size and productivity were evaluated only in a few studies on Common Barn-owls (Wilson *et al.* 1986, Johnson 1994, Martínez & López 1999). Lack (1947, 1954) proposed that clutch size corresponds to maximum number of young that parents can rear, and as the consequence of natural selection, the most productive clutch size is the most frequent. In contrast, numerous studies of birds demonstrated that the most frequent clutch size is smaller than the most productive which was determined by a trade-off between clutch size and future reproductive success (Stearns 1976, Partridge & Harvey 1988, Godfray *et al*. 1991). However, modal clutch size was the most productive clutch in case of Common Barn-owls in the Mediterranean region, and no significant variation was found between years in the average clutch size (Martínez & López 1999).

Birds of prey and owls, particularly Common Barn-owls were characterised by hatching asynchrony, which is an adaptive breeding strategy for producing marginal offspring (Clark & Wilson 1981, Stoleson & Beissinger 1995) and causes intra-brood size hierarchy and conflict (Viñuela 1999, 2000, Roulin *et al*. 1999, 2004). Numerous hypotheses have been proposed to explain asynchronous hatching (Clark & Wilson 1981, Stenning 1996). According to the 'brood reduction hypothesis' (Lack 1954), hatching asynchrony is an adaptive trait resulted in the mortality of the smallest offspring when food supply is low and not enough for parents to raise all hatchlings. In case of Common Barn-owl, the 'sibling negotiation hypothesis' was developed to understand the mechanism of competition between nestlings of different age, which highlighted the importance of nutritional need asymmetry between siblings (Roulin 2002b, 2004). Although the smaller nestlings can compensate their weaker competitive ability through the negotiation mechanism (Roulin 2004), the occurrence of brood reduction is frequent in the case of Common Barn-owls (Taylor 1994, Roulin 2002c), which can be realised in different behavioural mechanisms, such as lethal attacks on smaller siblings or siblicide (Mock 1985) and cannibalism (Baudvin 1978, Hamilton 1980, Roulin & Dreiss 2012). Furthermore, the results of video observation suggested that the risk of brood reduction increases as the female starts foraging after hatching, since access to food is reduced for the youngest nestling (Durant *et al*. 2004). It has also been proposed that the Common Barn-owl's female adjusts clutch size to the male's efficiency to feed the nestlings and herself in order to optimise fledging success (Durant *et al*. 2010). The level of brood reduction is an important and measurable feature of Common Barn-owls' breeding biology (Hindmarch *et al*. 2014) which can significantly influence reproductive success.

The objectives in this study are to evaluate the results of a long-term Common Barn-owl nest box installation and monitoring program in Southern Hungary, examining the variation of observed and calculated breeding characteristics, comparing first and second annual clutches (1), the relationship between clutch size and breeding success focusing on productivity (2) and the multi-annual change of reproductive output (3).

Material and methods

Study area, nest box installation and control protocol

Nest box installation and the breeding monitoring of Common Barn-owl was carried out in Baranya county (4429.6 km²) (46°04′N, 18°14′ E) which is situated in the south-eastern part of the Transdanubian region in Southern Hungary. The environmental conditions of this county are favourable for Common Barn-owls. The climate is determined by Mediterranean and sub-Mediterranean effect and is characterized by a high number of sunshine hours, relatively low fluctuations of temperatures and mild winters. Due to relatively high winter temperatures, the number of snow-covered days are low. The spatial structure of the county is characterized with a multitude of small villages, with 301 settlements altogether that actually represent 340 separate units of built and populated surface. The average administrative

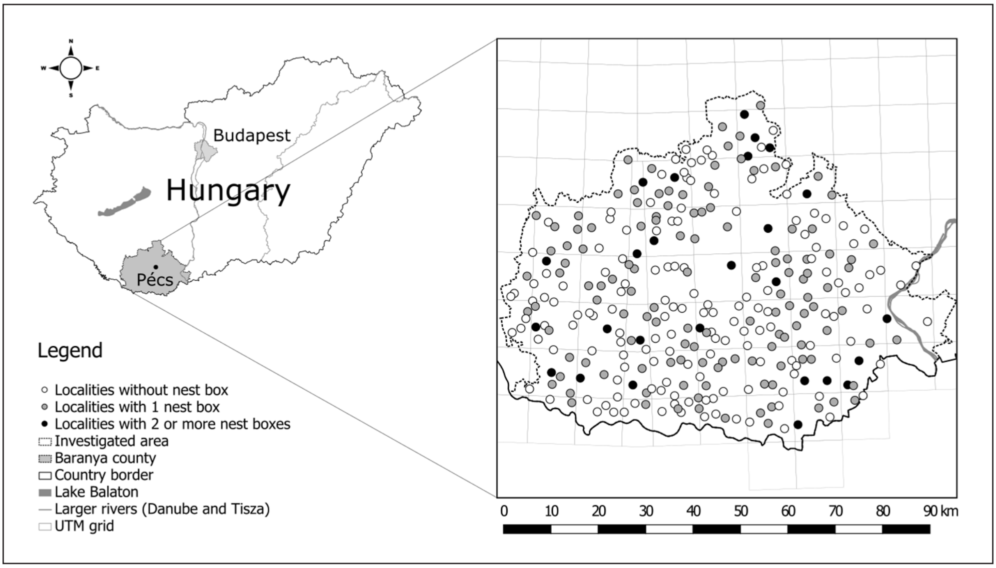

Figure 1. Spatial distribution of installed Common Barn-owl nest boxes in South-Hungary, Baranya County

1. ábra A kihelyezett gyöngybagoly költőládák térbeli eloszlása Dél-Magyarországon, Baranya megyében

area of the villages slightly exceeds 1,500 hectares. In 96% of the settlements, at least one church tower or chapel can be found and 21% have more such buildings.

A total of 163 nest boxes were placed in different buildings (95% in church towers, 5% in chapels and lofts of farm buildings) progressively from 1995 to 2018. The nest boxes were placed in a total of 150 settlements, 82% of which had one and 18% had more than one boxes *(Figure 1)*. The number of available nest boxes for Common Barn-owls in the consecutive years was determined by the number of installed new and removed nest boxes (due to dilapidation of boxes and church tower renovation). During the monitoring period, the number of settlements as nest site localities varied between 41 and 137 (108.16 ± 5.47 per year).

Nest boxes, measuring 100×50×50 cm were made from good quality pine boards, with a 15×15 cm entrance, a partition wall in the middle and a removable roof. The orientation of nest boxes within the towers was determined by the location of bell structures (racks, bins). Depending on these, the direction of east was preferred at the installation of net boxes. If this was not possible, the nest box was placed with western, southern or occasionally northern orientation. In the latter case, a dividing wall was built in the nest box for wind protection. In church towers, chapels and farm buildings nest boxes were placed 20–40 m and 4–10 m high, respectively.

During the 24 years, the nest boxes were regularly visited in the breeding season including first and second annual clutches to determine whether they were occupied or not by breeding pairs. Criterions of controls were determined by climate condition of Baranya county and life-history strategies and traits of Common Barn-owl. During the monitoring periods, the first visits were conducted between 1–15 April. However, the controls were started 8–10 days earlier after a mild winter. In the case of non-occupied nest boxes, controls were carried out until mid-September (4–5 times a year) and in the case of occupied nest boxes until the end of the second clutches, usually until mid-October. During the 24-year monitoring program, nest box checkings were implemented by volunteers (50–60 people) of the Baranya County Group of BirdLife Hungary based on a protocol developed for this purpose. The data were sent to the coordinator after each control. The date of the next visit was determined from the conditions observed at the first occasion (empty nest box, eggs, etc.). In addition, to evaluate the diet composition of Common Barn-owl pairs, pellet samples were collected from the nest boxes each time a control visit was executed.

Observed and calculated breeding parameters

At each sampling locality, the presence/absence of Common Barn-owls and their breeding status were recorded. Nest boxes in which at least one egg was found, were considered 'occupied' (active nest) (Steenhof 1987, Charter *et al*. 2010b, Frey *et al*. 2011). The proportion of nest box occupancy was calculated from the number of occupied nest boxes in the first annual clutches, while in the second annual breeding seasons, this proportion was obtained relative to the occupied nest boxes by breeders of the first annual clutches. Furthermore, occupancy rate was calculated in the case of the breeding pairs which occupied a nest box and laid eggs only in the second annual breeding periods. Based on the total number of breeding attempts, nesting success was calculated as the proportion of pairs that raised at least one fledgling, and the percentage of unsuccessful pairs was also determined (Steenhof & Newton 2007). The following breeding parameters were recorded: clutch size, brood size at hatching and fledging. To determine reproduction loss, two more parameters were calculated: the number and proportion of unhatched eggs and brood reduction. Hatching success was calculated as the percentage of eggs that hatched within each clutch, and fledging success was obtained as the percentage of young that fledged from each brood. Reproductive success was calculated as the percentage of fledged young per eggs from each successful nest. In addition, productivity was defined as the rate of the number of fledglings per nesting attempts (Martínez & López 1999, Steenhof & Newton 2007) or per all observed breeding pairs (including unsuccessful breeders) which, as standardized fledging success value (Sasvári & Hegyi 2011, Hindmarch *et al*. 2014), is suitable for comparing productivity between different clutch sizes and years. In the first step, productivity was calculated from the number of young produced in all successful nests and from the cumulative number of fledglings considering initial clutch size. Secondly, annual productivity was determined from the pooled quantity of fledglings and nesting attempts of different years.

Statistical methods

The results of nest box occupancy and proportion of occupied boxes were presented as range and mean ± SE from the first annual clutches, both in case of occupied nest boxes where the clutches were repeated by the nesting pairs and in case of nest boxes were the clutches were detected only in the second annual breeding periods. To assess the statistical difference of clutch failure and nesting success proportions between the first and second annual clutches, chi-square test was applied in the software R with the command prop.test. As regards all successful nests, the amount of all breeding parameters per nest and per year are presented as range and mean ± SE from the first and second annual clutches as well as from the whole annual breeding period, respectively. The distribution of clutch size, brood size, fledglings and annual productivity were represented with histograms and overlaid smoothed histograms with first and second order smoother in case of first and second annual clutches and total breeding seasons, respectively.

According to initial clutch sizes for which the exact reproductive history was detected, the cumulative number of breeding parameters, the percentage value of different successes and the calculated productivity rate as well as their mean and 95% confidence interval were presented in tables (clutch sizes only occurring once were excluded from the assessment) separately for the first and second annual breeding season. Considering different clutch sizes, the prop.test function was used to evaluate the difference in the proportion of unhatched eggs and brood reduction between the first and second annual breeding season, as well as in comparison of the proportion of egg and nestling losses within the given breeding periods. Boxplots (mean ± SE, lower and upper limits of 95% confidence interval) were used to present the annual variation of observed and calculated breeding parameters. The standard error and 95% confidence interval of mean were calculated in R using the 'Plotrix' (Lemon 2006) and 'Rmisc' (Hope 2016) package.

Mann-Whitney's U-test and the Kruskal-Wallis test (followed by Dunn's post hoc test for multiple comparisons) were used to compare the amount of breeding parameters between the first and second annual clutches and among the different years, respectively (Zar 2010).

Based on the data of all successful nests, linear regression method was used to assess the relationship between clutch size and productivity. Furthermore, linear regression was performed also to analyse the trend of variation of unhatched eggs, hatching success and annual productivity for the period 1995–2018. All statistical analyses were conducted in the R v3.4.0 environment (R Core Team 2017). Statistical tests were considered as significant at the level $P \leq 0.05$ as standard in all analyses (Sokal & Rohlf 1997).

Results

Nest box occupancy, number of breeding attempts and nesting success

During the 24 years, the total number of installed nest boxes varied between 43 and 163 (126.58 ± 6.91 per year) while nest box occupation ranged from 7 to 94 (42.5 ± 4.29 per year) in the first annual clutches. Considering Common Barn-owl pairs which occupied successfully a nest box in the first annual breeding season, the clutches were repeated in 2 to 26 nest boxes (8.37 ± 1.46 per year) in the second nesting periods. The number of boxes where the clutches were produced only in the second annual breeding seasons ranged from 1 to 11 (1.83 ± 0.54 per year). The percentage of occupied nest boxes ranged from 9.72 to 73.44% (34.22 ± 3.37%) in the first breeding periods, while the proportion of occupied nest boxes in the second annual clutches relative to the cumulative number of first nest box occupancy varied between 0% and 41.46% (18.58% ± 2.17%). In the case of breeding pairs for which nesting was detected only in the second annual periods, nest box occupancy rate varied between 0% and 9.02% (1.66% ± 0.47%).

Based on the results of nest box occupancy, 1,265 breeding attempts were recorded including 1,020 (80.63%) nesting attempts in the first and 245 (19.37%) in the second breeding

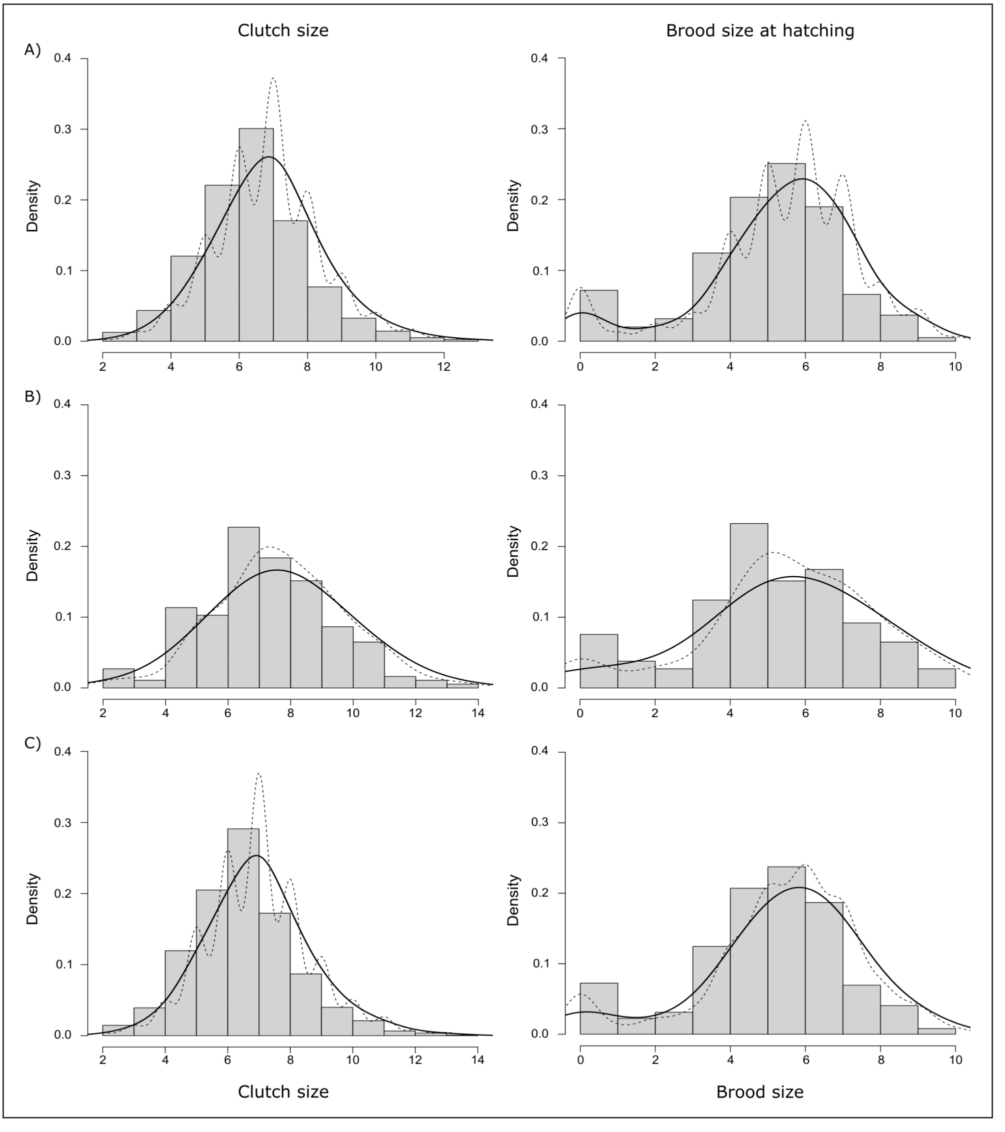

Figure 2. Histograms and smoothed histograms with first (dashed line) and second (solid line) order smoother of clutch size and brood size distribution in the first (A) and second (B) annual clutches as well as in whole breeding period (C)

2. ábra A fészekalj nagyság és a kikelt fiókaszám eloszlásának hisztogramja és simított hisztogramja első (szaggatott vonal) és másodrendű (folytonos vonal) simítással az első- (A) és másodköltés (B) esetén, valamint a teljes szaporodási időszakban (C) periods. From the total number of breeding attempts, 210 (16.6%) clutches did not produce any fledglings. Comparing the two annual nesting periods, the percentage of clutch failure was almost similar: 16.17% (165 out of 1,020 clutches) of the first and 18.37% (45 out of 245 clutches) of the second annual clutches did not produce fledglings. Thus, calculated nesting success was 83.39% (1055 productive clutches out of 1,265 nesting attempts) in the case of the total annual breeding season while 83.82% (855 out of 1,020 nesting attempts) of the first annual clutches and 81.63% (200 out of 245 nesting attempts) of the second annual clutches were successful where at least one young was produced by the breeding pairs. In the case of both successful and failed clutches, the number of nestlings did not differ from a homogeneous distribution in the comparison of the two annual breeding periods ($\chi^2 = 0.53$, $P = 0.464$).

Clutch size, brood size and hatching success

From the total of 1,265 breeding attempts, 982 clutches ($N = 797$ for first and $N = 185$ for second annual clutches) were recorded where the complete reproductive history was known. Based on the sample size, the average size per nest of first clutches was 6.84 ± 0.05 eggs,

Table 1. Cumulative number and percentage value of Common Barn-owl breeding parameters in relation to initial clutch size for clutches where complete reproduction history was detected in the first annual breeding period

1. táblázat A gyöngybagoly költési paramétereinek összesített és százalékos értéke a kezdeti fészekalj méretek függvényében, melyeknél detektáltuk a teljes reprodukciós történetet az első költés időszakában

Clutch size	# of nesting attempts	# of clutches (complete history)	Total eggs	Unhatched eggs		Eggs hatched		Brood reduction		Young fledged		Productivity
				n	%	*n*	%	*n*	%	*n*	%	
2	1	1	2	2	100	0	0	0	0	0	0	0
3	9	7	21	7	33.33	14	66.67	3	21.43	11	78.57	1.56
4	37	36	144	28	19.44	116	80.56	29	25.00	87	75.00	3.14
5	106	97	485	96	19.79	389	80.21	47	12.08	342	87.92	3.67
6	210	184	1104	170	15.40	934	84.60	158	16.92	776	83.08	4.45
7	272	240	1680	338	20.12	1342	79.88	235	17.51	1107	82.49	4.93
8	161	130	1040	221	21.25	819	78.75	156	19.05	663	80.95	5.09
9	77	61	549	110	20.04	439	79.96	82	18.68	357	81.32	5.70
10	32	28	280	88	31.43	192	68.57	23	11.98	169	88.02	6.00
11	8	8	88	37	42.05	51	57.95	5	9.80	46	90.20	6.38
12	4	4	48	29	60.42	19	39.58	3	15.79	16	84.21	4.75
13	1	1	13	4	30.77	9	69.23	0	0	9	100	9

Table 2. Cumulative number and percentage value of Common Barn-owl breeding parameters in relation to initial clutch size for clutches where complete reproduction history was detected in the second annual breeding period

2. táblázat A gyöngybagoly költési paramétereinek összesített és százalékos értéke a kezdeti fészekalj méretek függvényében, melyeknél detektáltuk a teljes reproduckiós történetet a másodköltés időszakában

Clutch size	**# of nesting attempts**	**# of clutches (complete history)**	**Total eggs**	**Unhatched eggs**		**Eggs hatched**		**Brood reduction**		**Young fledged**		**Productivity**
				n	**%**	*n*	**%**	*n*	**%**	*n*	**%**	
2	2	2	4	0	0	4	100	0	0	4	100	2
3	3	3	9	2	22.22	7	77.78	3	42.86	4	57.14	1.33
4	3	2	8	4	50	4	50	1	25	3	75	1
5	22	21	105	31	29.52	74	70.48	18	24.32	56	75.68	2.55
6	23	19	114	21	18.42	93	81.58	20	21.51	73	78.49	3.17
7	51	42	294	99	33.67	195	66.33	65	33.33	130	66.67	2.55
8	40	34	272	59	21.69	213	78.31	44	20.67	169	79.34	4.23
9	30	28	252	77	30.56	175	69.44	36	20.57	139	79.43	4.63
10	18	16	160	45	28.13	115	71.88	23	20	92	80	5.11
11	14	12	132	39	29.55	93	70.45	16	17.2	77	82.8	5.5
12	3	3	36	10	27.78	26	72.22	1	3.85	25	96.15	8.33
13	2	2	26	16	61.54	10	38.46	2	20	8	80	4
14	1	1	14	7	50	7	50	1	14.29	6	85.71	6

7.71 ± 0.15 eggs for second clutches and 7.01 ± 0.05 eggs for the total annual breeding periods. The relative frequency distribution of clutch size and brood sizes at hatching observed during the monitoring period are given in *Figure 2*. Both in first and second clutches as well as in the case of all clutches, modal clutch size was 7 eggs which was detected with highest frequency (first annual clutches: 30.11%, second clutches: 22.7%, the entire annual periods: 28.72% of clutches) *(Figure 2)*. Although modal clutch size was equal in both nesting periods, clutches of 6 eggs were detected with the second highest frequency in the first annual clutches (23.09%), while the clutches of 8 eggs were also characterized with higher proportion in the second clutches (18.38%). The clutches of 6–7 eggs were typical for 53.2% of total clutches in the first and clutches of 7–8 eggs were typical for 41.08% of total clutches in the second nesting periods *(Figure 2)*. As a result we found significant difference in clutch size between first and second annual clutches (Mann-Whitney U-test: $Z = 5.66$, $P < 0.001$).

The numbers of unhatched eggs per nest ranged from 0 to 13 (1.57 ± 0.06) in the total annual breeding season while it changed between 0 and 12 (1.42 ± 0.07) in the first and 0 to 13 (2.22 ± 0.15) in the second annual clutches. The loss of eggs was significantly higher in the first than in the second annual nesting period (Mann-Whitney U-test: $Z = 5.65$, $P < 0.001$). In the case

Table 3. Variation of the main and 95% confidence interval of breeding parameters in relation to initial clutch size for clutches where complete reproduction history was known in the first annual breeding period

3. táblázat A költési paraméterek átlag és 95%-os konfidencia intervallum értékeinek eltérése a kezdeti fészekalj méretek függvényében, melyeknél ismert a teljes reprodukciós történet az első költés időszakában

Clutch size	Unhatched eggs		Eggs hatched		Brood reduction		Young fledged		Reproductive success		Productivity	
	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*
3	1.00	-0.07-2.07	2.00	0.93-3.07	0.43	-0.30-1.16	1.57	0.40-2.75	52.38	13.16-91.61	1.07	0.30-1.85
4	0.78	0.35-1.21	3.22	2.79-3.65	0.81	0.35-1.25	2.42	1.86-2.97	60.42	46.50-74.33	1.89	1.45-2.33
5	0.99	0.69-1.29	4.01	3.71-4.31	0.48	0.28-0.69	3.53	3.19-3.86	70.52	63.83-77.20	2.74	2.47-3.02
6	0.92	0.71-1.13	5.08	4.87-5.29	0.86	0.66-1.06	4.22	3.95-4.49	70.29	65.80-74.78	3.36	3.16-3.59
7	1.41	1.18-1.63	5.59	5.37-5.82	0.98	0.82-1.14	4.61	4.37-4.85	65.89	62.47-69.31	3.66	3.47-3.86
8	1.70	1.38-2.02	6.30	5.98-6.62	1.20	0.94-1.46	5.10	4.75-5.45	63.75	59.42-68.08	4.12	3.83-4.40
9	1.80	1.22-2.39	7.20	6.61-7.78	1.34	0.89-1.80	5.85	5.22-6.49	65.03	57.96-72.09	4.69	4.16-5.22
10	3.14	2.12-4.17	6.86	5.93-7.99	0.82	0.83-1.32	6.04	5.02-7.05	60.36	50.21-70.51	5.11	4.22-5.99
11	4.63	2.06-7.19	6.38	3.81-8.94	0.63	-0.14-1.40	5.75	3.31-8.19	52.27	30.12-74.43	4.51	2.44-6.57
12	7.25	-1.5-16.00	4.75	-4.0-13.50	0.75	-1.64-3.14	4.00	-3.5-11.5	33.33	-28.86-95.5	3.34	-2.90-9.58

$\bar{x}$: mean value, *CI:* 95% Confidence Interval

of different clutch sizes for which the exact reproductive history was detected, the percentage of non-hatched eggs was higher in the case of smaller and larger clutch sizes while it was lower in the case of more frequent clutch sizes (clutches of 4–9 eggs) in the first annual clutches *(Table 1)*. Another type of percentage distribution of egg losses was obtained from the data of second annual clutches: the higher proportion of non-hatched eggs was detected in case of modal clutch size (7 eggs), in addition, the percentage value of egg losses was typically higher likewise in case of larger clutch sizes (13–14 eggs) *(Table 2)*. Considering the initial clutch sizes, the distribution of unhatched eggs' proportion was not homogeneous in the comparison of the first (20.72%, 1,130 non-hatched eggs out of 5,454 total eggs) and the second (28.75%, 410 non-hatched eggs out of 1,426 total eggs) nesting periods ($\chi^2 = 41.53$, $P < 0.001$). As regards the results of all successful nests, the mean of egg losses was higher in the case of larger clutches (9–12 eggs) in the first annual breeding period, however due to an overlap of 95% confidence interval, egg losses did not differ significantly between clutch sizes *(Table 3)*. Although the mean value of egg losses was higher in larger clutch sizes in the second annual

Table 4. Variation of the main and 95% confidence interval of breeding parameters in relation to initial clutch size for clutches where complete reproduction history was known in the second annual breeding period

4. táblázat A költési paraméterek átlag és 95%-os konfidencia intervallum értékeinek eltérése a kezdeti fészekalj méretek függvényében, melyeknél ismert a teljes reprodukciós történet a másodköltés időszakában

Clutch size	Unhatched eggs		Eggs hatched		Brood reduction		Young fledged		Reproductive success		Productivity	
	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*	$\bar{x}$	*CI*
2	0	–	2	–	0	–	2	–	100	–	1.61	1.20-2.02
3	0.67	-0.77-2.10	2.33	0.90-3.77	1	-1.48-3.48	1.33	-0.1-2.77	44.44	-3.36-92.25	0.84	-0.29-1.97
4	2	-	2	-	0.5	-	1.5	-	37.5	-	1.03	-
5	1.48	0.58-2.37	3.52	2.63-4.42	0.86	0.40-1.32	2.67	1.82-3.51	53.33	36.46-70.2	1.97	1.33-2.61
6	1.11	0.45-1.77	4.89	4.23-5.56	1.05	0.53-1.57	3.84	3.19-4.49	64.04	53.24-74.83	2.89	2.41-3.37
7	2.36	1.70-3.02	4.64	3.98-5.30	1.55	1.02-2.08	3.10	2.43-3.76	44.22	34.69-53.74	2.41	1.87-2.95
8	1.74	1.09-2.69	6.26	5.61-6.92	1.29	0.79-1.79	4.97	4.33-5.62	62.13	54.06-70.20	3.81	3.17-4.49
9	2.75	2.11-3.39	6.25	5.61-6.89	1.29	0.74-1.83	4.96	4.28-5.95	55.16	47.52-62.80	4.14	3.46-4.83
10	2.81	1.69-3.93	7.19	6.07-8.31	1.44	0.74-2.14	5.75	4.53-6.97	57.5	45.27-69.73	4.84	3.56-6.12
11	3.25	2.01-4.50	7.75	6.51-8.99	1.33	0.55-2.12	6.42	5.08-7.76	57.33	43.15-70.51	5.17	4.08-6.26
12	3.33	1.90-4.77	8.67	7.23-10.10	0.33	-1.1-1.77	8.33	6.90-9.77	69.44	57.49-81.40	7.44	2.74-12.15
13	8.00	–	5.00	–	1.00	–	4.00	–	30.77	–	3.28	–

$\bar{x}$: mean value, *CI:* 95% Confidence Interval

clutches, the average number of unhatched eggs was more balanced than in the first breeding periods. Due to the overlap between 95% confidence intervals of means we did not find significant difference in the comparison of different clutch sizes *(Table 4)*.

The mean brood size per nest of the first annual clutches was 5.42 ± 0.07, 5.44 ± 0.07 for second clutches, and 5.43 ± 0.07 for the total annual breeding periods. The number of nestlings did not differ between the first and second annual clutches (Mann-Whitney U-test: $Z = 0.9$, $P = 0.771$). In contrast, the mean of hatching success per nest was higher in the first (79.81 ± 0.93%) than in the second clutches (71.86 ± 1.98%) (Mann-Whitney U-test: $Z = 4.9$, $P < 0.001$). The average value of hatching success was 78.31 ± 0.85% for the whole annual breeding periods.

Brood sizes at hatching of 6 (25.72%), 5 (19.95%) and 7 (18.57%) nestlings were observed most frequently in the first annual clutches, the cumulative proportion of these three brood sizes being 64.24% of all clutches. In the case of the second annual clutches, the modal brood size was 5 nestlings which was detected with the highest frequency (23.24%) and the relative frequency of brood size of 7 (16.76%) and 6 (15.14%) nestlings was even higher. Therefore, the cumulative percentage of these three brood sizes was 55.14% of all clutches. In addition, in the case of total annual breeding seasons the brood size of 6 (23.73%), 5 (20.57%) and 7 (18.23%) nestlings were detected with higher frequency, the cumulative percentage of these three brood sizes adding up to 62.53% of the total clutches *(Figure 2)*.

Regarding brood size and hatching success in relation to initial clutch size, the cumulative number of hatchlings was the highest in the case of modal clutch size (7 eggs) in the first annual clutches and the clutch size of 8 eggs in the second clutches *(Table 1–2)*. In contrast, the percentage distribution of hatching success in the first annual clutches was similarly high in the case of more clutch sizes (4–9 eggs), while higher proportion of hatching success was observed not only for the most frequent clutch sizes but also for smaller and larger ones in the second nesting period *(Table 1–2)*. Considering different clutch sizes, the mean of brood size was higher in the case of larger clutch sizes (7–10 eggs) in the first annual breeding period, which average values were significantly higher than the mean of smaller clutch sizes (2–6 eggs), due to the lack of overlapping confidence intervals *(Table 3)*. The mean of nestlings was similarly higher in larger clutch sizes in the second annual breeding season, due to the separation of confidence intervals; the average values of clutch size of 8–12 eggs were significantly higher than in the case of smaller clutch sizes (5–7 eggs) *(Table 4)*.

Brood reduction, young fledged and fledging success

In the case of first annual clutches, the average number of brood reduction per nest was 0.93 ± 0.05, 1.24 ± 0.101 for the second clutches and 0.98 ± 0.04 for the whole annual breeding periods. Brood reduction was higher in the second than the first annual clutches (Mann-Whitney U-test: $Z = 3.41$, $P < 0.001$). Considering the initial clutch sizes, the loss of nestlings was the highest in the case of modal clutch size (7 eggs), but the proportion of brood reduction was also higher in the case of larger (8–9 eggs) and smaller (3–4 eggs) clutch sizes in the first breeding season *(Table 1)*. Similarly, brood reduction was the highest in the case of modal clutch size (7 eggs) in the second annual clutches, but the largest percentage value of brood reduction was typical only for this clutch size *(Table 2)*. The distribution of brood reduction was not homogeneous in the comparison of first (17.14%, 741 out of 4,324 total hatchlings) and second annual breeding periods (22.64%, 230 out of 1,016 total hatchlings) ($\chi^2 = 16.37$, $P < 0.001$), the degree of hatchling losses being higher in the second than the first annual clutches. Comparing egg and hatchling losses, the loss of eggs was larger in both the first ($\chi^2 = 19.77$, $P < 0.001$) and the second ($\chi^2 = 11.15$, $P < 0.001$) annual clutches. Based on data of all successful nests, the mean of brood reduction per different clutch sizes ranged from 0.43 to 1.34 in the first annual clutches, the degree of brood reduction did not differ significantly in the comparison of clutch sizes *(Table 3)*. The average number of hatchling losses per different clutch sizes varied between 0.5 and 1.55 in the second annual breeding period, however due to overlap of the 95% confidence intervals considering the loss of hatchlings we did not find significant difference between clutch sizes *(Table 4)*.

The mean of young fledged per nest varied between 0 and 9 (4.45 ± 0.07) in the total annual breeding season while it varied in the same range in the first (4.49 ± 0.07) and in the second (4.25 ± 0.17) annual clutches. There was no significant difference in the amount of fledglings between the first and second annual breeding season (Mann-Whitney U-test: Z = 1.71, P = 0.088), while fledging success was greater in the first (77.91 ± 1.09%) than in the second (71.47 ± 2.3%) annual clutches (Mann-Whitney U-test: Z = 3.41, P < 0.001).

The distribution of fledglings showed that 4–6 fledged young birds were observed most frequently in the first annual clutches, so the cumulative proportion of these three brood sizes at fledgling was 60.1% of all clutches. In the case of the second annual breeding seasons, 3–6 fledglings were produced by Common Barn-owls most frequently, the cumulative proportion of these four brood sizes at fledging being 61.63% of all breeding pairs. As regards the whole breeding periods, 4–6 fledged young birds were observed most frequently, the cumulative percentage of these three brood sizes at fledging adding up to 57.43% of total clutches *(Figure 3)*.

Regarding brood size at fledging in relation to initial clutch size, the cumulative number of fledglings was the highest in the case of modal clutch size (7 eggs) in the first annual clutches and the clutch size of 8 eggs in the second clutches *(Table 1–2)*. However, the percentage value of fledging success was higher in the clutch size of 5 eggs and other larger clutch sizes (10–13 eggs) in the first breeding period while in the case of the second breeding season, higher degrees of fledging success were detected in larger clutch sizes (8–14 eggs), except for the clutch size of 2 eggs *(Table 1–2)*.

Reproductive success and clutch size productivity

The mean of percentage value of reproductive success per nest of first annual clutches was 66.12 ± 1.05%, 55.09 ± 1.99% for second clutches and 64.04 ± 0.94% for the whole annual breeding periods. There was significant difference in reproductive success between the first and second annual clutches (Mann-Whitney U-test: Z = 5.63, P < 0.001). Considering initial clutch size, the average value of reproductive success was higher in the case of clutch sizes of 5–9 eggs, however, due to the 95% overlapping confidence intervals, it did not significantly differ in the comparison of clutch sizes in the first annual breeding season *(Table 3)*. The mean of reproductive success was the highest in case of clutch size of 12 eggs in the second annual breeding period, but the lack of non-overlapping confidence intervals we did not find significant difference between clutches *(Table 4)*. As regards initial clutch size, calculated productivity rate was not the highest from the pooled data in the case of modal clutch size; productivity showed an increasing trend relative to clutch sizes which was typical in both breeding periods *(Table 1–2)*. According to the results of all successful clutches, the mean of productivity was higher in case of larger clutch sizes (6–11 eggs) thus, the rate of young produced was significantly lower in the clutch size of 3–5 eggs than in case of other larger clutch sizes (6–11 eggs) in the first annual breeding season *(Table 3)*. The calculated productivity value from the second annual clutches similarly increased depending on clutch size, the rate of productivity being significantly lower in clutch sizes of 3–5 eggs than in larger clutch sizes (6–10 eggs), except for the clutch sizes 11 and 12 eggs due to the overlapping of confidence intervals *(Table 4)*.

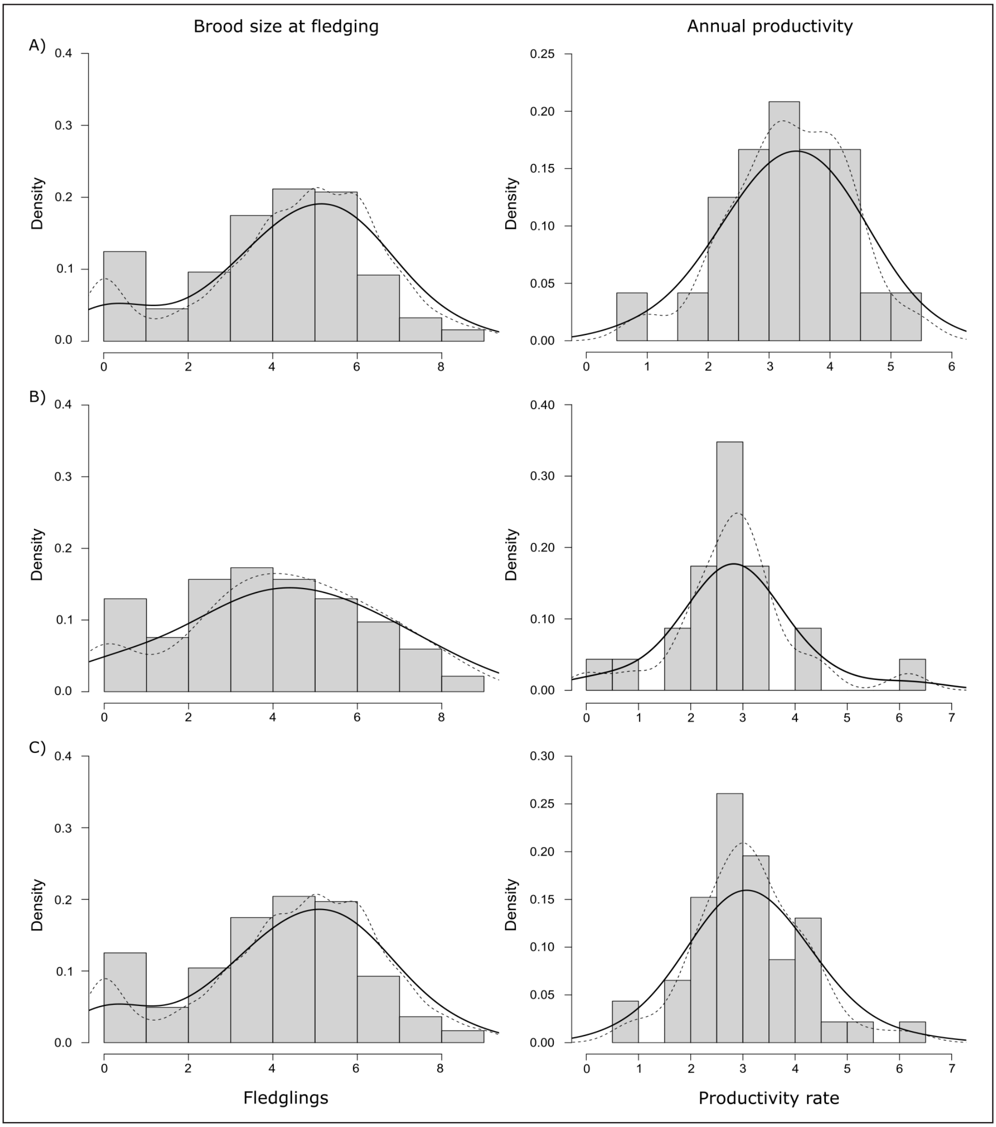

Figure 3. Histograms and smoothed histograms with first (dashed line) and second (solid line) order smoother of fledgling numbers and annual productivity distribution in the first (A) and second (B) annual clutches as well as in whole breeding season (C)

3. ábra A kirepült fiókaszám és az éves produktivitás eloszlásának hisztogramja és simított hisztogramja első- (szaggatott vonal) és másodrendű (folytonos vonal) simítással az első (A) és másodköltés (B), valamint a teljes szaporodási időszakban (C)

Considering all successful clutches we found significant positive linear regression between clutch size and productivity rate in both the first ($R^2 = 0.15$, $F = 142.1$, $P < 0.001$; $B_{slope} = 0.45$, $t = 11.92$, $P < 0.001$) and the second ($R^2 = 0.27$, $F = 66.39$, $P < 0.001$; $B_{slope} = 0.52$, $t = 8.15$, $P < 0.001$) breeding season *(Figure 4)*.

Annual patterns of breeding parameters and productivity

The average number of eggs laid per year of first annual clutches was 227.25 ± 26.31 (range 29 – 518), 64.82 ± 12.36 (range 6 – 206) for second clutches and 149.56 ± 19.11 (range 6 – 518) for the whole annual breeding seasons. The number of eggs per year was significantly different between the two annual breeding periods (Mann-Whitney U-test: $Z = 4.76$, $P < 0.001$). Based on data of complete annual breeding cycles, the variation of clutch size showed fluctuation during the years (Kruskal-Wallis test: $H(23, N = 982) = 144.52$, $P < 0.001$) which was detected at its largest average clutch size value in 2014. It was significantly higher than the clutch size obtained in the other years, except for 1995 (post hoc Dunn test: $z = 4.02 – 9.01$, $P < 0.05$) *(Figure 5A)*.

The average proportion of egg loss per year for first clutches was 21.65 ± 1.74% (range 10.17 – 48.74%), 25.45 ± 2.88% (range 0 – 50%) for second clutches and 23.47 ± 1.66% (range 0 – 50%) for the whole annual breeding periods. Although the higher proportion of non-hatched eggs was observed in the second annual clutches, egg losses did not differ significantly between the two annual breeding seasons (Mann-Whitney U-test: $Z = 0.78$, $P = 0.431$). Considering the whole annual breeding periods, the percentage value of egg loss varied among the years (Kruskal-Wallis test: $H(23, N = 982) = 47.59$, $P < 0.01$), the highest proportion of non-hatched eggs being detected in 2010 *(Figure 5B)*. During the 24 years, the rate of egg loss showed decline with significant negative linear trend ($R^2 = 0.099$, $F = 4.85$, $P < 0.05$; $B_{slope} = – 0.51$, $t = 2.25$, $P < 0.05$) *(Figure 6A)*.

As regards the brood size at hatching, the average number of hatchlings per year of first annual clutches was 180.17 ± 21.91 (range 26 – 419), 46.18 ± 8.88 (range 6 – 146) for the second clutches and 116.08 ± 15.66 (range 6 – 419) for the whole annual breeding periods.

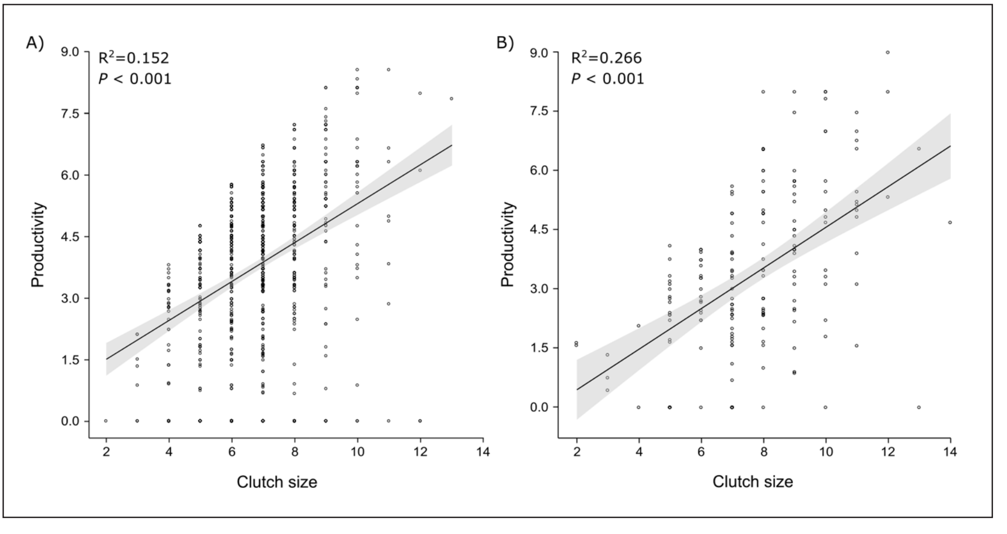

Figure 4. Relationship between clutch size and productivity (fledglings per nesting attempt) in the first (A) and second (B) annual clutches

4. ábra A fészekalj méret és produktivitás (kirepült fiókák/megkezdett fészkelések száma) összefüggése az első (A) és a másodköltés (B) időszakában

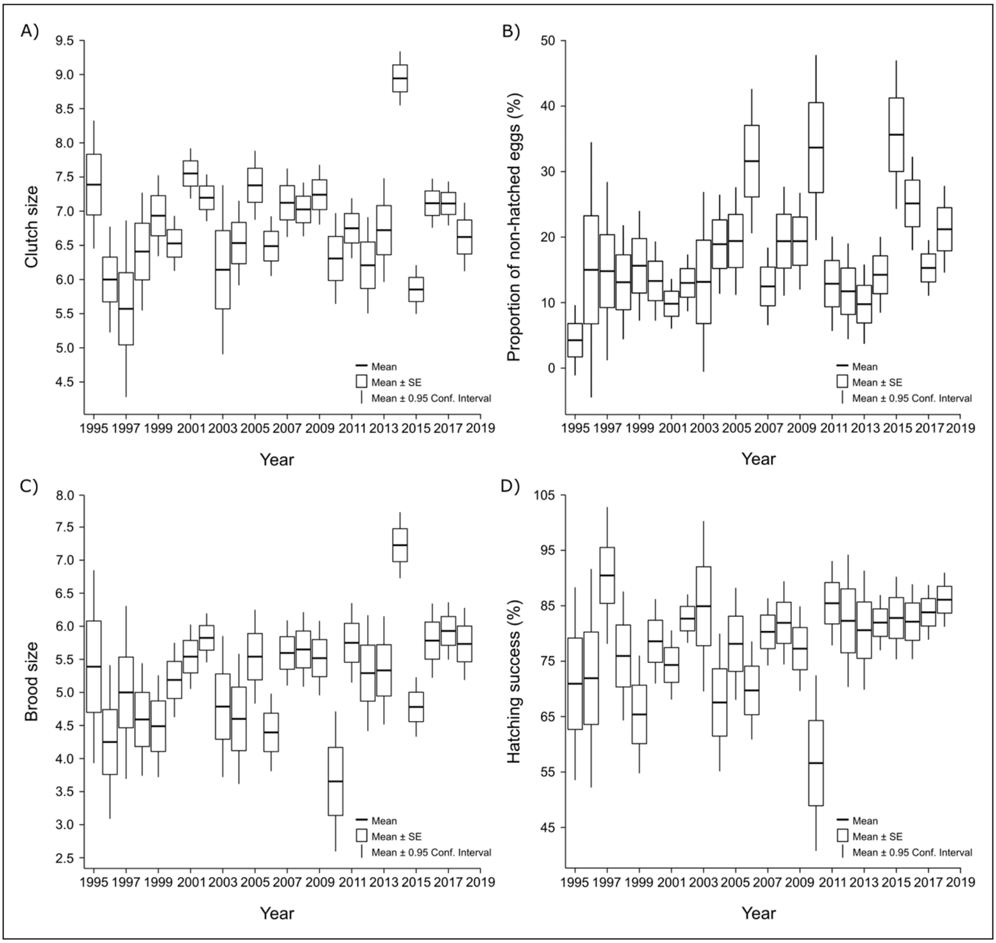

Figure 5. Fluctuation of the annual values (mean ± SE, 95% CI) of clutch size (A), proportion of egg loss (B), brood size (C) and hatching success (D) during the 24 years

5. ábra A fészekalj méret (A), a tojás veszteség arányának (B), a kikelt fiókák számának (C) és a kelési siker (D) éves értékének (átlag ± standard hiba, 95%-as konfidencia intervallum) fluktuációja a 24 év során

A significant difference in hatchling numbers was observed in the comparison of first and second clutches (Mann-Whitney U-test: $Z = 4.76$, $P < 0.001$). Considering the total breeding periods, brood size varied similarly to the amount of eggs laid during the monitoring period and it was significantly different among years (Kruskal-Wallis test: $H(23, N = 982) = 114.11$, $P < 0.001$). The maximum average value of nestlings was detected in 2014 similarly to egg productivity but a significantly lower average value of brood size was observed in 2010 compared to several years (2002, 2014, 2016, 2017) (post hoc test: $z = 3.79 – 6.53$, $P < 0.05$) *(Figure 5C)*.

Taking into account the above, the mean of hatching success per year of the first annual clutches was 78.35 ± 1.74% (range 51.26 – 89.83), 74.08% ± 2.81% (range 50 – 100) for second clutches and 76.31% ± 1.63% (range 50 – 100) for the whole annual breeding seasons.

Significant difference was not observed between two annual breeding periods (Mann-Whitney U-test: Z = 1.53, $P = 0.125$). Considering the whole breeding seasons, despite that the degree of hatching success was less fluctuating during the monitoring period, it differed significantly among years (Kruskal-Wallis test: H(23, $N = 982$) = 47.59, $P < 0.01$). The lowest average rate of hatching success was detected in 2010 *(Figure 5D)*. Despite this minimum value, hatching success increased with significant positive linear trend ($R^2 = 0.091$, F = 4.42, $P < 0.05$; $B_{slope} = 0.48$, t = 2.10, $P < 0.05$) during the 24 years *(Figure 6B)*.

The average proportion of brood reduction per year of the first annual clutches was 18.35 ± 2.08% (range 3.61 – 50.82%), 24.29% ± 2.89% (range 0 – 51.72%) for second clutches and 21.19% ± 1.79% ($N = 46$, range 0 – 51.72%) for the whole annual breeding period. Although the loss of hatchlings was higher in the second annual clutches, significant difference was not found between the two annual breeding seasons (Mann-Whitney U-test: Z =1.35, $P = 0.176$). The percentage value of this parameter from the total annual clutches varied significantly among the years (Kruskal-Wallis test: H(23, $N = 982$) = 69.32, $P < 0.001$). Higher average proportions of brood reduction were observed in three years (2007, 2010, 2015) while the degree of nestling loss was the lowest in 1995 (post hoc test: z = 3.76 – 4.19, $P < 0.05$) *(Figure 7A)*.

Considering brood sizes at fledging, the average number of fledglings per year was 149.29 ± 19.38 (range 21 – 364), 35.5 ± 7.54 (range 6 – 125) for the second clutches and 94.87 ± 13.59 (range 6 – 364) for the whole annual breeding periods. The quantity of fledglings was significantly higher in the first than in the second annual clutches (Mann-Whitney U-test: Z = 4.78, $P < 0.001$). As regards the total breeding seasons, the amount of fledglings significantly differed among the years (Kruskal-Wallis test: H(23, $N = 982$) = 145.46, $P < 0.001$). The greatest number of fledglings was observed in 2014 which was significantly higher compared to other years (post hoc test: z = 3.83 – 7.61, $P < 0.05$). Due to the higher degree of brood reduction, the significantly smaller number of fledglings was also typical in 2010 (post hoc test: z = 3.75 – 7.61, $P < 0.05$) *(Figure 7B)*.

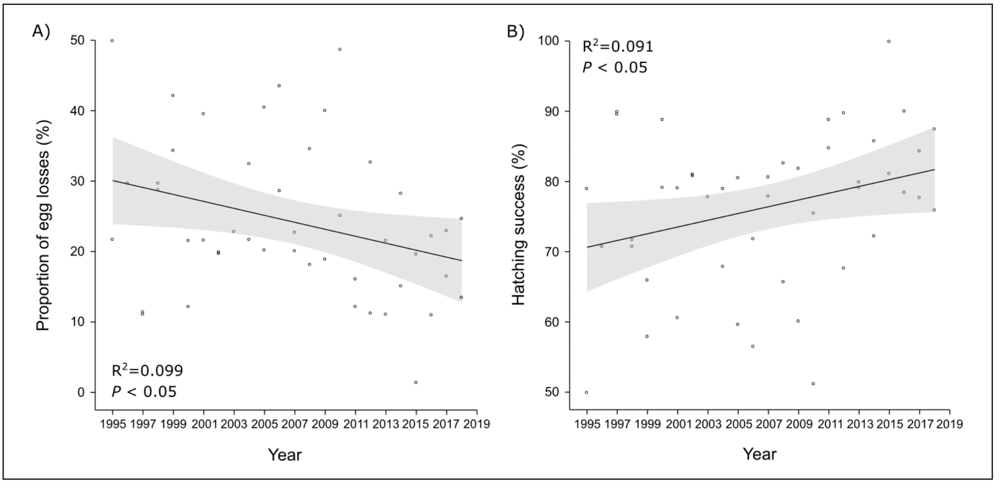

Figure 6. Temporal change of the proportion of egg loss (A) and hatching success (B) during the monitoring period

6. ábra A tojás veszteség (A) és a kelési siker (B) időbeli változása a monitorozási periódus alatt

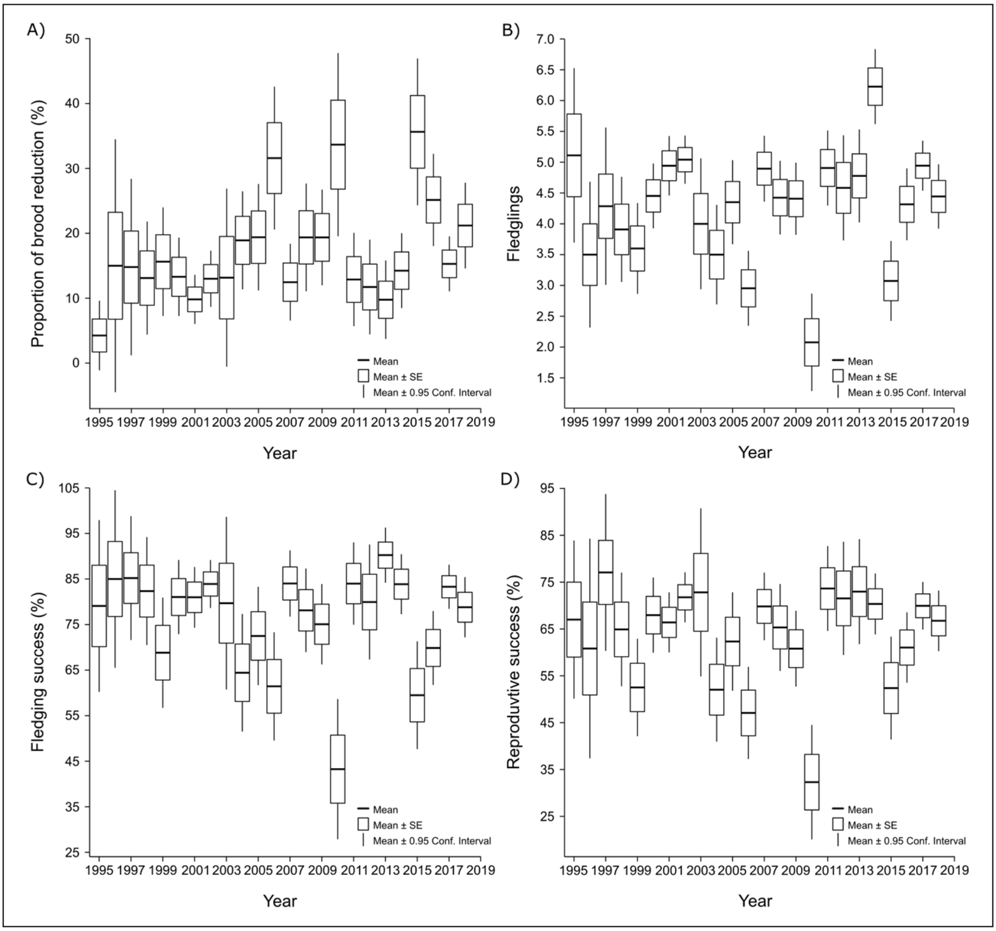

Figure 7. Fluctuation of the annual values (mean ± SE, 95% CI) of brood reduction (A), fledglings (B), fledging success (C) and reproductive success (D) during the 24 years

7. ábra A kikelt fiókák vesztesége (A), a kirepült fiókák számának (B), a kirepülési (C) és a szaporodási siker (D) éves értékének (átlag ± standard hiba, 95%-as konfidencia intervallum) fluktuációja a 24 év során

The mean of fledging success per year varied within the same range (48.27 – 100%) in the first (81.65% ± 2.08%), second (75.70% ± 2.89%) clutches and in the whole annual breeding seasons (78.81% ± 1.79%). As regards the whole annual breeding seasons, the fledging success significantly differed between years (Kruskal-Wallis test: $H(23, N = 982) = 79.97$, $P < 0.001$). Due to the high degree of brood reduction, these results of median test were determined essentially by the lowest rate of fledging success in 2010, which differed significantly in the comparison of several years (post hoc: z = 3.75 – 7.61, $P < 0.05$) *(Figure 7C)*.

The rate of reproductive success per year ranged from 25.21 to 79.66% (64.39 ± 2.38%) in the first, from 28 to 100% (56.40% ± 3.46%) in the second clutches and from 25.21 to 100% (60.57 ± 2.13%) in the total annual breeding seasons. Considering the whole breeding periods, reproductive success showed similar annual fluctuation to fledging success, which

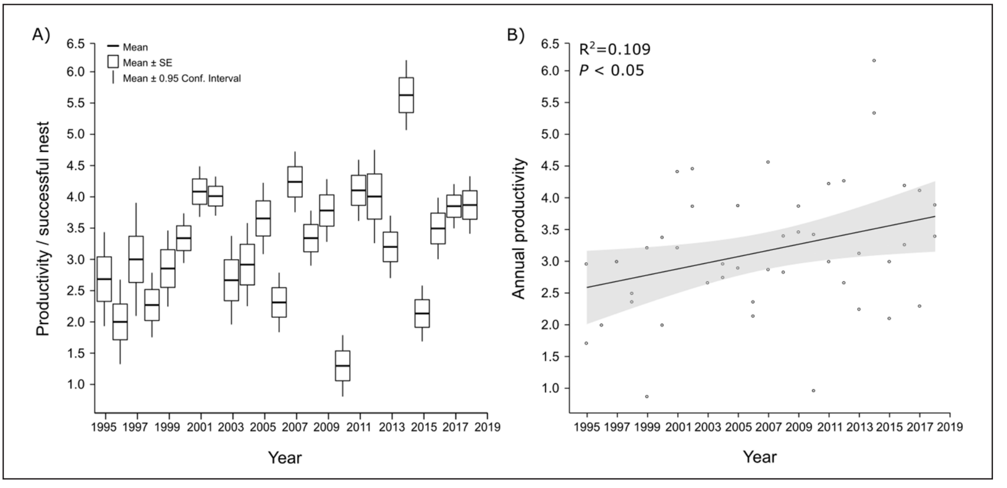

Figure 8. Fluctuation of the annual values (mean ± SE, 95% CI) of productivity per successful nest (A) and the changes of annual productivity of Common Barn-owls (B) during the 24-year monitoring period

8. ábra A sikeres fészkek produktivitás értékének (átlag ± standard hiba, 95%-as konfidencia intervallum) fluktuációja (A) és a gyöngybaglyok éves produktivitásának változása (B) a 24 éves monitoring során

differed among the years (Kruskal-Wallis test: H(23, N = 982) = 81.53, P < 0.001) because a significant yearly decline in reproductive success was observed in 2010 in comparison to several years (post hoc test: z = 3.75 – 4.99, P < 0.05) *(Figure 7D).*

Based on the number of fledglings of successful nests, the mean of annual productivity fluctuated between 0.97 and 5.34 (3.44 ± 0.19) in the first, 0.87 and 6.17 (2.96 ± 0.23) in the second annual clutches, and between 0.87 and 6.17 (3.16 ± 0.15) in the total annual breeding seasons. We did not find significant difference of productivity between the first and second annual clutches (Mann-Whitney U-test: Z = 1.85, P = 0.064). Based on the distribution of annual productivity rate, 2.8 – 4.5 fledglings per nesting attempt were observed most frequently in the first breeding seasons, so this range of productivity was typical in 17 cases out of total sample (72%) *(Figure 3)*.

In case of second clutches, 8 fledglings per nesting attempt were observed most frequently (36%, 8 out of 22 case numbers) while productivity of 2.5 – 3.5 fledglings per nesting attempt was calculated most frequently (46%, 21 out of 46 samples) in the whole annual breeding periods *(Figure 3)*. The annual productivity of Common Barn-owls differed significantly among the years (Kruskal-Wallis test: H(23, N = 982) =223.94, P < 0.001). The greatest productivity rate was observed in 2014 which was significantly higher compared to other years (post hoc test: z = 4.20 – 9.23, P < 0.01). Due to lower fledgling production, the significant low productivity was typical in 2010 (post hoc test: z = 4.42 – 9.23, P < 0.01) *(Figure 8A)*. Considering the complete annual breeding cycles, the annual variation of productivity showed significant slightly positive linear trend (R^2 = 0.109, F = 5.38, P < 0.05; B_{slope} = 0.048, t = 2.32, P < 0.05) during the 24 years *(Figure 8B)*.

Discussion

In this study, we evaluated the results of a long-term Common Barn-owl nest box installation programme in Southern Hungary. The number of placed nest boxes varied from 43 to 163 during the 24-year-long monitoring period, and the average percentage of nest box occupancy per year was 34.22 ± 3.37% (yearly range 9.72 – 73.44%) at the start of first annual clutches which was lower than that reported in other studies. In the USA (northern Utah) 50% of installed nest boxes were occupied in the first and 80% of boxes were used in the second year, which was observed when a low number of boxes were placed ($N = 30$) (Marti *et al*. 1979) and the average percentage of occupied nest boxes was 81.35 ± 6.32% (yearly range 53.3 – 96.7%) during the 6 years (Marti & Wagner 1985). Also during the 6 years, 41 nest boxes were installed in a similar program in the USA, however, the rate of nest box occupancy per year was 65.29 ± 6.41% (Looman *et al*. 1996). In a long-term study (13 breeding seasons), 51.7 ± 3.7% (yearly range = 25.7 – 73.5%) of all placed nest boxes ($N = 309$) per year were occupied by Common Barn-owl pairs in the Middle-East (Beit She'an Valley, Israel) (Charter *et al*. 2017). The first five-year evaluation of this monitoring program is also worth highlighting, when the mean percentage of nest boxes ($N = 248$) occupied was 53.5 ± 2.1% (Meyrom *et al*. 2009). Although the yearly range of nest box occupancy rate was greater according to our results than the occupancy range defined in the Middle East (Charter *et al*. 2017), but the maximum percentage value of occupied nest boxes was very similar in the comparison of the two long-term studies. The lower average proportion of nest box occupancy showed by our results presumably can be traced back to two basic reasons. First, some natural nesting and roosting sites (open church towers, farm buildings and lofts) are still available for the Common Barn-owl in the monitored county which is characterized with a multitude of small villages (Bank 1990). Second, the size of the potential regional population of Common Barn-owl showed several collapses due to the impact of extreme periods during the 24 years, which was indicated by the lowest percentage values of nest box occupancy in 1997 (9.72%), 2003 (16.28%), 2012 (14.57%) and 2013 (14.47%), so these low proportion values influenced the calculated average. Based on the reported nest box occupancy data of Common Barn-owl from Cyprus, the yearly average proportion of occupied nest box was lower (18.58 ± 2.98%) compared to our results (Kassinis & Roulin 2017). Furthermore, a low nest box occupancy rate was also found in the semiarid pampas of Argentina where the Common Barn-owl occupied the nest boxes only occasionally, which was a consequence of the fact that the applied nest boxes were smaller than in other studies focusing specifically on the Common Barn-owl (Liébana *et al*. 2013).

The mean proportion of double brood pairs ranged from 0 to 41.46% in the second annual clutches. This average percentage was higher than that reported by Martínez and Lopez (1999) in the Mediterranean region, where the number of pairs laying a second clutch was 33.3%. The second clutches are frequent in the case of the Common Barn-owl (Roulin *et al.* 1999), which is an adaptive strategy because regarding the whole breeding season the reproductive success of double brooding pairs is higher than of single-brooded owls (Béziers & Roulin 2016).

Although the proportion of occupied nest boxes was lower in the investigated region, nesting success showed higher percentage value in the whole annual breeding season (83.39%), indicating the role of the artificial nest boxes in promoting the Common Barn-owl's nesting efficiency (Marti *et al*. 1979, de Bruijn 1994, Marti 1994, Petty *et a*l. 1994, Taylor 1994, Frey *et al*. 2011, Charter *et al*. 2017), similarly to nest box installation programs implemented in other countries. For example, 71% (Marti 1994) and 85.85% (Looman *et al*. 1996) of nesting attempts was successful in the USA, the yearly range of 73.2 – 93.5% nesting success was detected in the Middle-East (Charter *et al*. 2017), and 87.24% of nesting attempts was successful in western Switzerland based on a 23-year dataset of nest boxes (Frey *et al*. 2011).

According to our results, the average clutch size of first clutch per nest (6.84 ± 0.05, N = 797) was higher than that reported in other countries of Europe such as Netherlands ($\bar{x}$ = 4.0) (Braaksma & de Bruijn 1976), England ($\bar{x}$ = 4.68) (Bunn *et al.* 1982), Scotland ($\bar{x}$ = 4.6, N = 425) (Taylor 1994), France (Burgundy) ($\bar{x}$ = 5.89, N = 765), Czech Republic ($\bar{x}$ = 5.85, N = 193) (Poprach 1996), Spain (Valencia) ($\bar{x}$ = 4.63, N = 30) (Martínez & Lopez 1999) and Switzerland ($\bar{x}$ = 5.85, N = 193) (Frey *et al*. 2011). Furthermore, smaller average clutch size was found in other parts of the world such as Mali ($\bar{x}$ = 6.05, N = 140) (Wilson *et al*. 1986), Pakistan ($\bar{x}$ = 5.83, N = 28) (Mahmood-Ul-Hassan *et al*. 2007), Utah ($\bar{x}$ = 5.8, N = 28) (Looman *et al*. 1996), and even smaller clutch size ($\bar{x}$ = 3.8, N = 17) was reported from Arkansas (Radley & Bednarz 2005). Nevertheless, in the first annual breeding period similarly high average clutch size has already been observed in peninsular Malaysia ($\bar{x}$ = 6.6, N = 36) (Lenton 1984), northern Utah ($\bar{x}$ = 7.17, N = 275) (Marti 1994) and British Columbia ($\bar{x}$ = 6.5, N = 23) (Andrusiak & Cheng 1997). Considering the geographical variation of clutch size, our results confirmed that the first clutch size was larger in Hungary than in Spain, contributing to the earlier observation that the clutch size of Common Barn-owl increase from Spain to Hungary in mainland Europe (Roulin 2002a). We found that size of the second annual clutches of Common Barn-owl was significantly larger than the size of first clutches which is in accordance with the results of other studies (Schönfeld & Gibrig 1975, Kaus 1977, Poprach 1996, Frey *et al*. 2011). Conversely, the mean of clutch size was significantly larger in the first than the second annual clutches in northern Utah (Marti 1994), Scotland (Taylor 1994) and in Spain, but in the latter case the difference of clutch size was not significant between the two breeding seasons (Martínez & Lopez 1999). As regards the variation of Common Barn-owl clutch size, the studies showed that the size of second clutches are larger than the first in case of *Tyto alba guttata* subspecies while that difference is reversed in *Tyto alba alba* population (Roulin 2002a). Modal clutch size was larger (7 eggs) in our study area than that reported by some other studies since it was 5 eggs in Spain (Martínez & Lopez 1999), 6 eggs in Mali (Wilson *et al*. 1986) and in western Switzerland (Chausson *et al*. 2014a). However, clutches of 7 eggs were detected with the highest frequency in USA (Looman *et al*. 1996) and Cyprus (Kassinis & Roulin 2017) which is consistent with our results.

During the 24 years of our study, the average values of unhatched eggs per nest was 1.42 ± 0.07 in the first annual breeding period, and egg losses were significantly higher in the second than in the first clutches. Mean of disappeared eggs was higher ($\bar{x}$ = 1.7) in northern

Utah (USA) (Marti 1994) and smaller in Switzerland ($\bar{x}$ = 0.42) (Chausson *et al*. 2014a). Considering the initial clutch sizes, we found that the percentage of unhatched eggs was higher in the case of smaller and larger clutch sizes, while it was lower in the case of clutch sizes with high frequency in the first annual breeding period. In contrast, a larger proportion of egg losses was typical in the case of modal and larger clutch size in the second clutches. In addition, the higher degree of egg losses in the second clutches was also confirmed by the inhomogeneous distribution of the pooled quantity of unhatched eggs between the two breeding periods. Contrarily to the present study, unhatched eggs were found only in clutches with 4 or more eggs in Spain (Martínez & Lopez 1999). However, our results are consistent with this earlier study in that egg losses were higher in the case of larger clutch size which was mainly typical of the second breeding season in our study area.

Mean brood size per nest was higher ($\bar{x}$ = 5.42 ± 0.07) in the first clutches than that detected in other European countries such as Scotland ($\bar{x}$ = 3.4) (Taylor 1994), Czech Republic ($\bar{x}$ = 3.82) (Poprach 1996), Spain ($\bar{x}$ = 3.32) (Martínez & Lopez 1999) and Slovakia ($\bar{x}$ = 4.5) (Sárossy 2000). This difference also exists in comparison with previous studies since average brood size ranged from 2.4 to 4.3 in Germany (Schönfeld & Gibrig 1975) and from 3.0 to 5.1 in eastern France (Müller 1990). Compared to our results, the mean number of nestlings was also smaller in other continents, such as in Mali ($\bar{x}$ = 4.79) (Wilson *et al*. 1986), in Pakistan ($\bar{x}$ = 4.15) (Mahmood-Ul-Hassan *et al*. 2007), in Malaysia ($\bar{x}$ = 4.6) (Lenton 1984) and in different parts of North America such as north central Utah: $\bar{x}$ = 3.97 (Looman *et al*. 1996), British Columbia: $\bar{x}$ = 3.3 (Andrusiak & Cheng 1997) and Florida: $\bar{x}$ = 2.87 (David 1996). However, a higher average number of nestlings was detected in northern Utah (Marti 1994), thus as regards the brood size at hatching of the Common Barn-owl, our result is consistent with this study. We found that brood size was not significantly different between the first and second annual clutches and it is in accordance with the result which was reported by Marti *et al*. (1994). In contrast, the average number of nestlings was significantly larger in the first than in the second breeding period in Switzerland (Frey *et al*. 2011). According to our results, the mean of hatching success per nest was significantly higher in the first (79.81%) than in the second clutches (71.86%), but these values were lower than it had been reported from the Mediterranean area (Spain) (83%) (Martínez & Lopez 1999).

Several studies pointed out that brood reduction takes place in the first 3 weeks after hatching for various reasons. Nestling losses frequently occur by starvation due to the reduction of food availability, but siblicide and more frequent cannibalism also reduce brood size (Roulin, 2002b). We found that the average number of brood reduction per nest was significantly higher in the second ($\bar{x}$ = 1.24) than in first ($\bar{x}$ = 0.93) clutches. Based on the cumulative number of disappeared nestlings, the proportion of brood reduction was not homogeneous in comparison of the first (17.14%) and the second (22.64%) breeding periods, confirming the higher level of brood reduction in the case of second annual clutches.

Additionally, our results showed that the degree of egg losses before hatching was larger than the loss of nestlings after hatching in both the first and second annual clutches, and this result is in agreement with those reported by Marti (1994) in northern Utah. Considering initial clutch sizes, the proportion of brood reduction was also higher in case of larger and smaller clutch sizes than the modal one, but the degree of brood reduction did not differ significantly in the comparison of initial clutch sizes. Nevertheless, higher level of brood reduction was reported in the case of large than in small brood size (Taylor 1994). Similar to the distribution of egg losses, Martínez and Lopez (1999) found that the partial loss of nestlings was typical in clutches with 4 or more eggs.

We found that, the average number of fledglings per nest varied in the same range in the first ($\bar{x}$ = 4.49) and in the second ($\bar{x}$ = 4.25) annual clutches as well as in the total annual breeding season ($\bar{x}$ = 4.45). The range of average value of fledglings was similar in France (first: $\bar{x}$ = 4.29 and second clutches: $\bar{x}$ = 4.8) (Baudvin & Jouaire 2001), in the Middle-East ($\bar{x}$ = 4.91) (Meyrom *et al*. 2008), in northern Utah (USA) (first: $\bar{x}$ = 5.09 and second clutches: $\bar{x}$ = 4.94), and in north central Utah (USA) ($\bar{x}$ = 4.0) (Looman *et al*. 1996), while it was higher in the Czech Republic (first: $\bar{x}$ = 4.62 and second clutches: $\bar{x}$ = 6.75) (Poprach 1996) and lower in British Columbia ($\bar{x}$ = 3.4) (Andrusiak & Cheng 1997), in Africa ($\bar{x}$ = 3.19) (Wilson *et al*. 1986) and in Malaysia ($\bar{x}$ = 3.7) (Lenton 1984). There was no significant difference in the amount of fledglings between the two annual breeding periods in our investigated area. However, we found that calculated fledging success was greater in the first than in the second annual clutches. The lack of significant difference in the numbers of young fledged between two annual breeding periods was reported from the USA (Marti 1994), however, no significant difference was found in the case of fledging success in the Spanish Mediterranean area (Martínez & Lopez 1999).

Regarding brood size at fledging in relation to initial clutch size, the percentage value of fledging success was lower in modal clutch size while higher values of this breeding parameter were typical in the case of larger clutch sizes in our study area. Our results showed that, larger clutch sizes were more productive than the modal clutch size which in the first approach support the general hypothesis that the most productive clutch size is larger than the most frequent (Klomp 1970, Perrins & Moss 1975, Stearns 1976). In contrast, modal clutch size (5 eggs) was the most productive in the Mediterranean region in Spain (Martínez & Lopez 1999) and in north central Utah (USA) where the modal and most productive clutch size was higher (7 eggs) (Looman *et al*. 1996), the same clutch size having been identified in the present study as the modal, but not the most productive for Southern Hungary. In addition, we found significant linear regression between clutch size and young fledged production per nest attempt. Similarly, the number of fledglings increased with clutch size in Switzerland (Frey *et al*. 2011). The results of these two long-term studies (24- and a 23-year datasets) seemed to support the general hypothesis.

In the case of the Spanish population, the authors suggested that the coincidence of modal and the most productive clutch size may be explained by the alternative hypothesis by Boyce and Perrins (1987) because in terms of adult survival, the reproductive costs were low or were not measurable with owls. According to this alternative hypothesis, the cost of reproduction is not a necessary and sufficient factor for the optimization of clutch size because it is beneficial for the birds in the long term to lay clutches smaller than the most productive clutch size (Boyce & Perrins 1987). The low reproduction costs observed in Spain can be traced back to the lack of fluctuation of environmental variables, such as climate and food resources (availability of rodents) because variation in the reproductive parameters of the Common Barn-owl was not detected during the 7 years, the average laying date and clutch size did not differ between years (Martínez & Lopez 1999). The coincidence of modal and the most productive clutch size was observed in a shorter study (6-year dataset) also in north central Utah (USA). However, this study detected significant variation in clutch size among the years (Looman *et al*. 1996). In contrast, Marti (1994) reported the lack of significant difference of clutch size among years and among nest sites during a 16-year sampling period. Conversely, our results showed that all observed and calculated breeding parameters for the whole annual breeding season varied significantly among the years. As already highlighted above in case of percentage values of nest box occupancy, the impact of extreme years ('good-year' or 'bad-year effect') influenced the reproductive output of the Common Barn-owl during the 24 years. The largest average value of clutch size, brood size, fledglings and productivity rate were detected in 2014, caused by the extreme population outbreak of the Common Vole *(Microtus arvalis)* (Pallas, 1778). The multiannual population cycles of the Common Vole were widely investigated (Jacob *et al*. 2014) and three-year-long population cycles were documented in Europe (Tkadlec & Stenseth 2001, Lambin *et al*. 2006). Predominance of Common Vole was typical in diet of Barn Owls from the pellet analysis which was conducted in Baranya County (Horváth 1999, Horváth *et al*. 2018). The direct monitoring of Common Vole activity in the intensively used alfalfa fields in our investigated area was started in the collapse phase after the 2014 outbreak, based on counting reopened burrow entrances, and detected the next increasing phase of this rodent in 2017 (Somogyi & Horváth 2019). Earlier studies of Common Barn-owl's breeding biology had already reported that the number of nesting and the proportion of double brood pairs as well as the values of reproductive output of owls were larger in the outbreak than in the non-outbreak periods of Common Vole (Schönfeld & Girbig 1975, Kaus 1977, Baudvin 1979, de Brujin 1994). In contrast to this 'good-year effect', due to extreme large participation in the first clutches period, the highest proportion of egg loss, the lowest average value of brood size and hatching success, the higher degree of brood reduction, as well as the lowest rate of fledging success and annual productivity were detected in 2010, as a prominent negative impact ('bad-year effect'). Boyce and Perrins (1987) already emphasized the importance of long-term studies, since the impact of extreme years on clutch size optimization and the variation of reproductive outputs could not be detected without multi-annual dataset, also pointing out the Spanish study in the case of Common Barn-owl clutches. Although we have no data on the reproductive cost of the owls or the lack of it but our data seem to support the hypothesis of Boyce and Perrins (1987), because Common Barn-owls laid more often smaller clutches than most productive ones in our investigated area in South-Hungary where the fluctuating environment was typical. While in the case of Spanish population, due to the more stable environment, the variance of reproductive success was not typical and thus modal clutch size was the same as the most productive clutch size (Martínez & Lopez 1999). In this study, we had no purpose to examine the effect of environmental variables, however, based on our long term dataset, it is necessary to test the impact of weather parameters and small mammals, particularly the Common Vole as the main prey, on the reproductive output of the Common Barn-owl.

Among the breeding parameters, we emphasize the results of three variables such as egg loss, hatching success and annual productivity. During the 24 years, the rate of egg loss showed decline with significant negative linear trend while hatching success increased with significant positive linear trend. Based on the distribution of annual productivity rate 2.5 – 3.5 fledglings per nesting attempt were calculated most frequently for the whole annual breeding periods and we did not find significant difference of productivity between the first and second annual clutches which result is consistent with the study by Martínez and Lopez (1999). Similar productivity rate ($\overline{x}$ = 3.5) was calculated in north central Utah (Looman *et al*. 1996) which average value is equal to the upper limit of the most common annual productivity range of investigated Hungarian Common Barn-owl population. Nevertheless, lower average productivity ($\overline{x}$ = 2.7) was detected in the agricultural landscape of British Columbia (Hindmarch *et al*. 2014), however this value was similar to the lower limit of the most frequent annual productivity range which we calculated in our investigated area. The Canadian study suggested that food availability was reduced in more urbanized landscapes which lead to a higher degree of brood reduction and thus low productivity in Common Barn-owls (Hindmarch *et al*. 2014). Additionally, considering complete annual breeding seasons, the annual variation of productivity showed significant, slightly positive linear trend during the 24 years.

Although the monitoring of the Common Barn-owl's breeding biology was conducted in the continental region of European temperate zone in Southern Hungary, our results were compared to studies of different geographical and climatic zones where the environmental variability and the availability of food resources differs from those found in our study area. Considering all of the above, the comparative evaluation suggested that the optimization of clutch size for the stable or variable environment is an evolutionarily stable strategy of Common Barn-owls to maximize its lifetime reproductive success. In the light of our findings, despite the outlier values of reproduction characteristics in the extreme years with negative effect, a relatively stable regional Common Barn-owl population can be maintained by the placement of nest boxes in the investigated Southern Hungarian region.

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