Belg. J. Zool., 145(2) : 103-114 July 2015

Long-term changes of breeding success in Montagu's Harrier *Circus pygargus*

Jarosław Wiącek

Department of Nature Conservation, Institute of Biology and Biochemistry, Curie Skłodowska University
Akademicka 19, 20-033 Lublin, Poland, wiacek@hektor.umcs.lublin.pl

ABSTRACT. Over a period of almost twenty years, clutch size and breeding success in the Montagu's Harrier were investigated in the context of changing environmental conditions in the species' natural breeding habitats in eastern Poland. During the study periods (1990-95 and 2003-12) a decline was noted in the number of breeding pairs in the population nesting on the calcareous peat bogs near Chełm, not far from the Polish-Ukrainian border. Statistically significant differences in breeding parameters between the two periods were also observed. In the first period clutch volumes were greater, as the dimensions of the individual eggs were larger; additionally, more eggs hatched and the hatchling survival rate was higher. Some habitat conditions were different in the two periods, with the water level and height of vegetation near the nests being lower in the second period. The harriers' food in the two study periods fluctuated strongly with regard to the content of small mammals and compensatory items. In the second period a distinct increase in predator pressure was noted. Pressure from terrestrial predators diminished whereas that from aerial predators increased. Broods in semi-colonies, where birds actively defended their nests, enjoyed a higher rate of survival, as did nests situated far in from the edge of peat bogs. The results suggest that the decline in breeding numbers was driven by increased predation, which was in turn a consequence of habitat changes in the natural environment of eastern Poland.

KEY WORDS: *Circus pygargus*, breeding success, predation, habitat changes

INTRODUCTION

The Montagu's Harrier *Circus pygargus* is a medium-sized raptor nesting in farmland (Cramp & Simmons, 1980, 2000; Clarke, 1996; Arroyo et al., 2004) and in natural wetlands and peat bogs, the latter particularly in eastern Europe (Krogulec & Leroux, 1994; Wiącek, 2006, 2009). In eastern Poland, declines in populations and breeding success of Montagu's Harrier have been observed in recent decades (Wiącek, 2007). The species shows a tendency to nest semi-colonially throughout its range (Arroyo et al., 2004; Wiącek, 2006b, 2008; Kitowski, 2008; Krupiński et al., 2010). The reproductive success of females in many bird species is partly determined by clutch size and egg size (Blackburn, 1991), and is influenced by food supply (Stearns, 1992; Arroyo, 1998; Arroyo & Garcia 2006; Koks et al., 2007). The availability of food and its fluctuations even during a single season can seriously affect breeding success (Tremblay et al., 2003). Studies on the effect of food on clutch size in Montagu's Harriers confirm this dependence (Salamolard et al., 2000; Millon et al., 2008): for example, young or poorly fed females lay fewer and smaller eggs (Salamolard,1998, Arroyo et al., 2004; Arroyo et al., 2007; Millon et al., 2008). The dependence between food abundance and breeding success is particularly conspicuous in vole-eating predators (Korpimaki, 1990; Brommer et al., 2002).

Being a ground nesting raptor, the Montagu's Harrier is itself vulnerable to predation (Clarke, 1996; Simmons, 2000). Harrier nests – usually situated on the edges of marshes in the natural environment of eastern Poland – are easily detected by terrestrial or aerial predators

(Wiącek, 2007, 2009). Another form of predation pressure is intraguild predation (Sergio & Hiraldo, 2008; Quinn et al., 2008). One way of avoiding or decreasing the predation risk is to breed in semi-colonies (Arroyo et al., 2001, 2004; Wiącek, 2008). Many studies confirm that nesting aggregation is advantageous to breeding success in many avian species (Bertram, 1978; Quinn & Ueta, 2008). Mobbing behaviour is another means of enhancing brood safety in a semi-colony (Arroyo et al.,2001; Kitowski, 2004; Wiącek, 2008). The benefits of this behaviour are evident, because they decrease the predation risk and increase breeding success (Birkhead & Moller, 1992; Brown & Brown, 1996).

A further reason for the decline of harriers may be changes to the wintering habitats in the Sahel and mortality during migration and overwintering. The large-scale conversion of floodplain habitat into desiccated grasslands may lead to decreasing food resources and to sub-optimal environmental conditions for wintering harriers (Liminana et al., 2007; Buij et al., 2012). Changes in climate or land use in wintering areas are important for the survival of harrier species (Liminana et al., 2012). All these limiting factors may have contributed to a distinct decline in the numbers of this raptor nesting on peat bogs in eastern Poland.

The main objective of this paper was to analyse the changes in the breeding parameters of Montagu's Harriers during the last two decades on the calcareous peat bogs near Chełm in eastern Poland, in the context of environmental changes, fluctuating food resources and predator pressure.

STUDY AREA AND METHODS

Montagu's Harriers were monitored on the calcareous peat bogs (4309 ha) near Chełm in eastern Poland (51°10' N, 23°37' E). The study area is part of a Special Protection Area for birds within the NATURA 2000 network, located near the Polish-Ukrainian border (Wilk et al., 2010). The dominant vegetation type is the sedge association based on *Cladietum marisci*. There the Harriers build their nests in clumps of sedges surrounded by water, or in partly paludine areas (Wiącek, 2009). The study area was surrounded by farmland, which constituted the foraging habitat of the harriers (Wiącek, 2006a).

The fieldwork was conducted during two periods, i.e. 1990-95 and 2003-12. Montagu's Harrier nests were mapped and monitored frequently (two or three times a week) from egg laying to fledging (from late April to the end of July). Observations started in the pre-laying period in mid-April. In total, 106 nests with complete clutches were found. Replacement clutches were excluded from the study. All nests were observed before being inspected. The laying date was estimated according to the method described by Arroyo (2002). If a few eggs were found in the nest, it was assumed that an interval of 2 days had elapsed between the laying of consecutive eggs (Arroyo et al., 2004). Eggs from 94 nests were individually marked in laying sequence and their lengths and widths measured (n=405, with callipers to the nearest 0.1 mm). 161 eggs were measured in the first period and 244 in the second. Egg volume was calculated with Hoyt's formula (1979): 0.51 x length x width^2.

Weather data for May were analysed, when harriers started incubating, and all nests were found. The mean temperature during egg laying, maximum and minimum temperature, number of days with rainfall, and wind speed were obtained from www.TuTiempo.net, based on the nearest weather station at Lublin-Radawiec airport. The data given here on the composition of food are derived from several other studies conducted in the same study area: Tabor & Tabor (2005, 262 prey items collected during the incubation and nestling periods), Wiącek & Niedźwiedź (2005, 210 prey items collected during the pre-laying period), Wiącek & Niedźwiedź (2009, 618 prey items) and Zietek (2009, 967 prey items collected during the incubation and nestling periods). In the papers cited above, the

Montagu's Harrier diet was determined on the basis of prey remains in the nests and pellet analysis (TABOR & TABOR, 2005; WIĄCEK & NIEDŹWIEDŹ, 2009; ZIĘTEK, 2009) or from the pellets and observation of birds carrying prey during food transfer WIĄCEK & NIEDŹWIEDŹ (2005). Pellets were collected during nest or perch inspections (two or three times a week).

To assess the effect of predation on Montagu's Harrier clutches, 78 nests of the 106 found were closely monitored: 30 in the first study period and 48 in the second. In the first period 15 adult Montagu's Harriers were caught and individually marked with coloured wing tags (KOCHERT et al., 1983; WIĄCEK, 2008). The presence of young females in the study area was determined from feathers remaining in the nests or in flight by direct observation (MILLON et al., 2008).

Clutch survival was defined as the number of days between the laying of the first egg and the last inspection, when at least one hatchling was alive in the nest. Most of the fieldwork carried out near the Harrier nests was based on the methods described by TYLER et al. (1998) with modifications described by WIĄCEK (2009). Vegetation height, depth of water, internal and external nest diameter were measured accurate to 1 cm in mid-May. Vegetation density was measured near the nest at a distance of 0.5 m in plots of 0.1 m^2. In the second study period additional measurements of vegetation density were made at a distance of 2 m from the nests. The numbers of plants were counted along a 1 m section, 0.5 m above the ground in a few randomly chosen spots in the vicinity of the nest. The measurements were averaged for each nest.

Categorisation of Montagu's Harrier nests as clumped or solitary was based on a behavioural criterion described by WIĄCEK (2008). The distance between nests and the nearby meadows was measured with a tape or GPS receiver. The harriers' brood predators were determined from observations conducted near the nest, tracks (footprints) left near the nest, remains of the victims (bite marks on the feathers or eggs in the nest) or by using digital trail cameras (www.ecotone.pl). Four cameras were used in the last two study seasons.

Data analyses were done using logistic regression and nonparametric statistics (Mann-Whitney test, Kruskal-Wallis test and Spearman correlation). All analyses were carried out using Statistica 8.1. The study was conducted with the permission of the Local Ethics Committee for Animal Experimentation and the Regional Directorate for Environmental Conservation in Lublin.

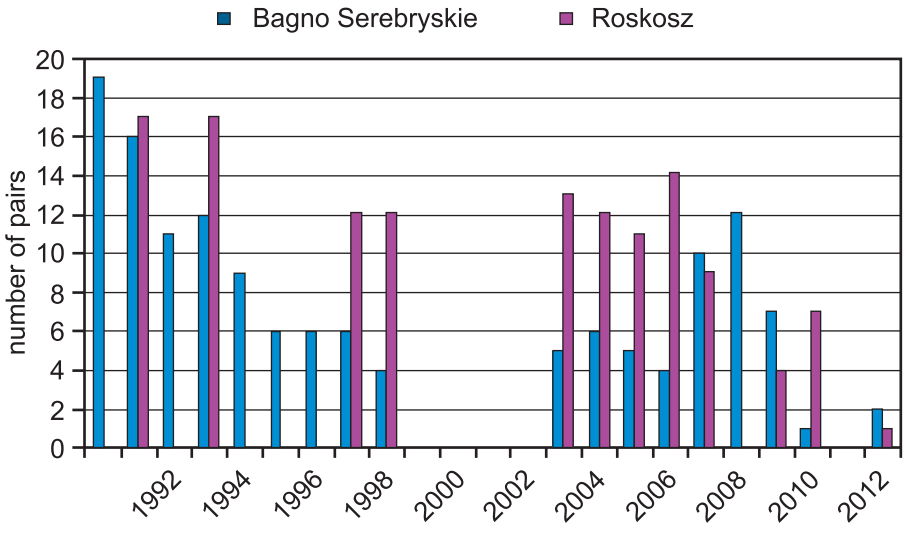

Fig. 1. – Numbers of breeding pairs in two nature reserves in the study area.

RESULTS

Number of breeding pairs

The observations conducted from 1990 to 1998 and from 2003 to 2012 show a significant decrease in the number of pairs nesting in the two peat bog reserves that were studied (Fig. 1): from 17 to 1 pair in the "Roskosz" reserve and from 19 to 2 pairs in the "Bagno Serebryskie" reserve (Table 2).

Eggs, chicks and fledglings

The mean egg volume and the mean clutch volume per female were both larger in the first period than in the second one. There were significant differences between egg volumes in the two study periods (Table 2). The mean dimensions of eggs laid in the 1990s were greater (4.25 x 3.37 cm) than in the second period (4.17 x 3.35 cm). The differences in egg length and width in the two study periods were statistically significant (Table 2). The first and last eggs in a clutch were smaller than those laid in the middle of the sequence (Fig. 2). In the 1990s, 3-, 4- and 5-egg clutches were reported (n=37), whereas after 2003 (n=66), one small clutch of 2 eggs and 2 clutches of 6 eggs were also recorded. The mean clutch size was similar in both periods (Table 2). In the first study period females started laying eggs two days earlier than during the second one. Nonetheless, the overall timing of egg laying did not differ statistically (Table 2). The numbers of chicks hatched were different in the two study periods; in the first, the mean number of nestlings hatched was higher than in the second. The numbers of fledglings in the two study periods were also different: in the first period, the mean number of fledglings in all nests was higher than in the second one (Table 2).

Nest and environmental factors

The nests built by the harriers in the two study periods differed in size. The mean diameter of nests built in the 1990s was smaller than that of the nests in the second period (Table 2). The diameter of the nest was not related to brood size (Mann-Whitney test z=1.603, n=78, p=0.87) or clutch size, but the relationship between diameter and clutch size was near-significant (Mann-Whitney test z=1.94, n=78, p=0.052). Weather conditions in May, when most harriers started incubating were similar in both study periods. There were no differences between them with respect to the following weather parameters: maximum temperature (Mann-Whitney test z=-0.96, n=14,

Fig. 2. – Mean egg volume vs. egg laying order.

Table 1

Changes in food resources of the Montagu's Harrier in the study area (a,d - Wiącek & Niedźwiedź 2009; b-Tabor & Tabor 2005; c-Wiącek & Niedźwiedź 2005, e-Ziętek 2009).

Food categories (%)	Period				
	1985-89 (a)	1988-89 (b)	1992-95 (c)	2004-08 (d)	2007 (e)
mammals	64.2	36.3	56.2	30.3	18.2
birds	27.2	22.5	24.3	33.3	4
birds' eggs	1.1	0	9.5	3	0
amphibians	0.2	0	1.4	0	0
reptiles	1.9	0	8.1	16.2	3.7
invertebrates	5.4	41.2	0	17.2	74
% of Common Vole in mammalian prey	55	29.5	50	23	69

P=0.33), minimum temperature (z=-1.67, n=14, P=0.09), number of days with rainfall (z=-1.69, n=14, P=0.09) and wind speed (z=0.77, n=14, P=0.43). The mean temperature in both periods was also similar (Mann-Whitney test z=-1.42, n=14, P=0.15). The water level on the peat bog where the Montagu's Harriers built their nests was different in the two study periods. During the first period (1992-95) the mean water level was lower than in the second one (Table 2). The mean height of the vegetation near the nests as measured from the nest base were different in the two study periods, being higher in the first period than in the second one. The differences between the two periods were near-significant (Table 2). In 2008-09, the density of the vegetation directly adjoining the nests was measured. Both the nests in semi-colonies (mean density 98.2/0.1m^2, SD=14.95, n=10) and the isolated ones (mean density 97.7/0.1m^2, SD=12.78, n=10) had been built in vegetation patches of similar density (Mann-Whitney test z=0.468, P=0.63, n=20). Investigations of vegetation density at a distance of 2 m from the nest did reveal differences, however (Mann-Whitney test z=2.114, P=0.033, n=20). Measurements in semi-colonies indicated that these nests had been built in larger patches of dense vegetation (on average 24 plants in a 1 m^2 section, SD=4.32, n=10) than were the isolated nests (on average 19.3, SD=5.33, n=10).

Analysis of the food composition in the two study periods (Table 1) reveals strong fluctuations in the numbers of small mammals, birds, reptiles and invertebrates in the harriers' diet. The percentage of common vole (*Microtus arvalis*) in the total mammalian prey also fluctuated strongly.

Brood losses

During the two study periods, 40 of the 78 Montagu's Harrier broods monitored were destroyed by predators and three others were lost for different reasons – in one case the nest was flooded and in the other two the eggs were addled. In the first study period in the 1990s, 20% of broods were destroyed by predators. The perpetrator in five cases was a predatory mammal, probably a fox, and in the sixth case it was a Marsh Harrier. In the second study period, 75% of broods were destroyed (Table 2). The predators in these cases were corvids, which destroyed 19 (52%) broods, Marsh Harriers – 9 (25%) and foxes or other mammals – 6 (16%). All the eggs in two clutches turned out to be addled (5%) and one nest with eggs was flooded following very heavy rainfall (2%). During the first study period, there were also partial losses in 21 successful broods, from which at least one

Table 2

The main results.

	First period	Second period	Differences
Number of breeding pairs	R=0.67; Beta= -0.67; n=19; p=0.001	R=0.84; Beta= -0.84; n=12; p=0.006	Significant decrease in both study periods
Nest diameter	Φ=31.46; SD=53.37 n=30	Φ=34.78; SD=37.32; n=48	Mann-Whitney test z=2.59; n=78; p=0.009
Mean egg volume	24.81; SD=1.85;; n=161	23.74; SD=2.16; n=244	Mann-Whitney test z=5.71; n=161+244; p<0.0001
Mean clutch volume per female	109.27; SD=13.53, n=37	93.53; SD=24.79; n=55	Kruskal-Wallis test H=8.08; n=92; p=0.004
Mean dimension of eggs	4.25 x 3.37 cm;n=161, SD_{length}=0.16, SD_{width}=0.09	4.17 x 3.35 cm; n=244, SD_{length}=0.19, SD_{width}=0.12	Mann-Whitney test (length) z=-2.86, n=92, P=0.004 Mann-Whitney test (width) z=-2.90, n=92, P=0.004
Mean clutch size	4.36; SD=0.54; n=37	4.22; SD=0.79; n=66	Mann-Whitney test z=0.72; n=103; p=0.42
First egg (laying date)	16th of May, 15.38, SD 3.39; n=37	18th of May, 17.36; SD=7.76; n=55	Kruskal-Wallis test H=19.37; n=92; p=0.08
Chicks hatched	3.39; SD=1.33, n=33	2.01; SD=1.88; n=73	Mann-Whitney test z=3.104; n=106; p=0.001
Number of fledglings	2.23; SD=1.1; n=30	0.45; SD=0.95; n=73	Mann-Whitney test z=5.61; n=103; p<0.0005
Water level	3.16cm; SD=2.8; n=30	15.01cm; SD=1.89; n=48	Mann-Whitney test z=5.09; n=78; p=0.0001
Vegetation height	85.16 cm; SD=10.88; n=30	72.4 cm; SD=14.29; n=48	Mann-Whitney test z=1.92; n=78; p=-0.052
Brood losses	20% (6 from 30)	75% (37 out of 48)	
Brood survival	53.3 days SD=42.68; n=30	40.73 days SD=3.51; n=41	Mann-Whitney test z=-3.69; n=71; p=0.0002
Brood survival in a semi-colony or in solitary nests	In a semi-colony 59.36 days SD=2.67; n=19. Solitary nests: 42.9; SD=23; n=11	In a semi-colony: 45.86; SD=16.7; n=30. Solitary nests 26.72 SD=9.85; n=11	First: Mann-Whitney z=1.84; n=30; p=0.06 Second: Mann-Whitney z=3.29; n=41; p=0.0009

nestling fledged. The causes of mortality in the 32 chicks that died were starvation (30 chicks – 94%) and sibling cannibalism (2 chicks – 6%). In addition, six eggs were addled. In the second period, partial losses were recorded in 11 successful broods. Then, the causes of mortality in 20 chicks were starvation (11 chicks – 55%), predation by Marsh Harriers (4 chicks – 20%), sibling cannibalism (3 chicks – 15%), drowning (1 chick- 5%), trampling by wild boar (1 chick – 5%); three eggs were addled.

Brood survival was higher in the 1990s than after the year 2000 (Table 2). In the first period most

of the nests (5 out of 6) destroyed by predators were situated outside the semi-colonies. The time elapsing between the construction of a nest in a semi-colony to its destruction by a predator was longer than if it was isolated, but the differences were not statistically significant (Table 2). In the second period (after 2000), when predator pressure was greater, nests in semi-colonies had a far greater chance of survival than nests built in isolation (Table 2).

In the first period, when water levels near the nests were low, predators destroyed nests situated closed to the edge of the peat bog. This relationship was statistically significant (Mann-Whitney test: z=2.48, P=0.012, n=30). In most cases (5) the predator was a fox or other mammal; only once was a Marsh Harrier the culprit. In the second period, when water levels were higher and it was generally harder for terrestrial predators to gain access to the nests than in the first period, no such relationship could be discerned (Mann-Whitney test: z=1.004, P=0.3, n=48). Interestingly, the water levels in the first period were similar around nests that were successful and those that failed (Mann-Whitney test, z=-0.72, P=0.45, n=30). The critical factors determining the success of a nest and enabling attacks by predators to be foiled was the distance from meadows and nesting in a semi-colony (Table 3). Other parameters measured in the study area did not have any serious effect on brood survival in either of the study periods.

DISCUSSION

Breeding success

Egg sizes in the two study periods were significantly different. In the first one, the size of eggs (42.5 x 33.7 mm) was to my knowledge the largest described in the literature. In the second period, egg sizes (41.7 x 33.5 mm) were similar to those given by other authors monitoring harrier nests (ARROYO et al., 1998; CORBACHO & SANCHEZ, 2000; ARROYO et al., 2004). The differences in egg size between the study periods were probably the result of better food conditions during the first one; associations between the availability of food and breeding parameters of Montagu's Harriers have been found before (SALAMOLARD et al., 2000; MILLON et al., 2008). Alternatively, the smaller egg size in the second study period could have been due to a larger number of young females starting to breed in the second period, because young females produce significantly smaller eggs in comparison with older females (ARROYO & GARCIA, 2006; ARROYO et al., 2007).

Clutch sizes in the Montagu's Harrier populations studied here were similar to the mean results from Europe cited by CRAMP & SIMMONS (1980). They were distinctly larger than in the majority of studies reported from Italy and France. At some sites, clutch sizes were similar to our study, for example, in Charente-Maritime and Deux Sèvres in France or in England. However, in some places in Spain and Portugal these values were lower (ARROYO et al., 2004). The numbers of birds hatching in the two periods we studied were comparatively high, but the number of hatchlings was significantly lower in the second period than in the first one. These differences were due to greater predation pressure in the second study period. Nevertheless, both values were similar to the data obtained in France (ARROYO et al. 2004), the Netherlands (SCHIPPER, 1979), Spain (ARROYO et al., 2004) and England (UNDERHILL-DAY, 1990).

Food

During the two study periods, there were strong fluctuations in the availability of harrier food. The changes in the proportions of small mammals reflected the typical periodic fluctuations in the numbers of these animals (LAMBIN et al., 2006; LIMINANA et al., 2012a). In the periods when small mammals predominated in the harriers' diet (Table 1) the proportion of other prey items decreased. In other periods, when mammalian food was not readily available, the proportion of other prey items compensating for the lack

Table 3

Probability of breeding success in harriers explained by different variables (forward stepwise logistic regression). Only significant variables are shown.

Variable	Estimate	SE	T	P
Constant	4.672	-12.419	-2.658	0.009
Distance to the meadows	1.485	0.015	2.021	0.046
Nesting in semi-colony	1.485	3.935	2.649	0.009

of small mammals, such as reptiles, birds or invertebrates, increased. According to the ornithological literature, mammals and birds are the most important components of the Montagu's Harrier diet (Arroyo et al., 2004; Terraube & Arroyo 2011; Liminana et al. 2012a). This high-energy food is easier to assimilate than other items (Tollan, 1988). A link between the availability of common voles and the breeding parameters of Montagu's Harriers was demonstrated by research done in France (Salamolard et al., 2000; Millon et al., 2008). Analogous relationships were also found for owls (Korpimaki, 1990) and kestrels (Wiebe & Bortolotti 1994; Wiehn & Korpimaki 1997). The proportion of common voles in the harrier diet, recorded in France, fluctuated between 33 and 86% (Millon et al., 2008), values that are similar to those we obtained in our study area (Table 1). However, in comparison with other factors such as predation or age of the females, the food fluctuations observed in the study area in both study periods may have been less important for breeding success.

Predator pressure

The number of fledglings was different in the two study periods, decreasing significantly from 2.5 per successful nest in the first to 1.9 in the second period (from 2.3 to 0.45 in all monitored nests). The main factor limiting the number of fledglings was predator pressure. In the second study period, the mean length of time during which a nest was active was almost two weeks shorter than in the first period. Changes in predator pressure were due to mammalian predators (probably red foxes) and corvids during the incubation stage, and increasing predator pressure from Marsh Harriers in the nestling period (Wiącek, 2007). The main reason for the increase in the red fox population has been the nationwide anti-rabies vaccination programme in Poland, which started just before 2000. The increasing pressure from corvids on Montagu's Harrier broods is due to the high density of Magpies and Ravens breeding in Poland in both study periods (Jerzak, 2005, Bednorz, 2005, Panek, 2005, www.monitoringptakow.gios.gov.pl). An important factor facilitating access to harrier nests in the first study period was the low water level. In such conditions it was quite easy for terrestrial mammalian predators, mostly foxes, but also cats and feral dogs, to gain access to the nests (Tryjanowski et al., 2002, 2009). The first nests to be destroyed were those situated at the edge of the peat bog. Therefore, the distance between the meadows around the marshes and the harrier nests was important for breeding success in both periods. In the second period, the water level was far higher, so access to the nests was much more difficult. As a consequence, nest losses due to terrestrial predators were fewer, but against that there was much greater pressure on the nests from aerial predators like Marsh Harriers and corvids (Wiącek, 2007). The losses caused by predators also depended on other habitat factors. One of these, enabling predators to discover nests in the second period, was the shorter vegetation close to the harriers' nests: this did not provide sufficient cover for incubating

females (Arroyo et al., 2004, Liminiana et al., 2006; Wiącek, 2009). However, the most important factor in the destruction of Montagu's Harrier broods was intraguild predation and the presence of breeding Marsh Harriers in the same area (Buczek & Keller 1994; Wiącek, 2005; Sergio & Hiraldo 2008).

One factor significantly modifying breeding success in the Montagu's Harriers was their nesting in semi-colonies or in isolation. Brood losses from colonial and isolated nests differed significantly: colonial breeding was far safer (Arroyo et al., 2001; Wiącek, 2008). All the nests, whether in semi-colonies or in isolation, were built in patches of denser vegetation (Wiącek, 2009), but the semi-colonial nests were situated in larger patches of optimal habitat. In heterogeneous natural habitats such as bogs or marshland, the size of available patches is more important for semi-colony formation than in fields, which are large, homogeneous habitats. The formation of a semi-colony in a field is probably behaviour-based, since the availability of optimal habitat offering a secure nest site is greater than in a structurally heterogeneous, natural peat bog. Evidence for this is provided by the greater distances between semi-colonial nests in fields in Spain and France than on peat bogs in eastern Poland (Arroyo et al., 2001; Wiącek, 2008). On a peat bog, the "capacity" of the optimal nesting habitat is limited, hence the greater density of nests in semi-colonies. In both variants, the basic factors as regards nesting are the availability of food in the vicinity of the semi-colony and nest security (Arroyo et al., 2001; Wiącek, 2008, 2009). Additionally, the active conservation of some rare bird species, such as Aquatic Warbler *Acrocephalus paludicola* living in the same habitats as the Montagu's Harrier, has contributed to the destruction of the optimum structure of the nesting habitat utilised by this raptor. While mowing the tall vegetation growing on the peat bog optimises the habitat for some species, it destroys the habitat for other species with diametrically opposed habitat requirements (cranes, harriers or bitterns).

CONCLUSIONS

In the 1980s the study area boasted the greatest density of breeding Montagu's Harriers in Europe (Krogulec & Leroux, 1994). Observations conducted in this area over two study periods showed a decrease in the number of pairs nesting there (Fig. 1). This was driven by changes to their traditional breeding habitat (higher water level, shorter vegetation, mowing or burning of sedge beds). This led to a deterioration in a whole range of breeding parameters, not to mention a rapid increase in predation pressure and strong fluctuations in food availability in the study area.

ACKNOWLEDGEMENTS

I am grateful to Beatriz Arroyo and the anonymous referees and editors for their useful suggestions, advice and comments. Peter Senn reviewed the English version of this paper.

REFERENCES

Arroyo B (1998). Effect of diet on the reproductive success of Montagu's Harrier *Circus pygargus*. Ibis 140: 690-693.

Arroyo B (2002). Sex-biased nestling mortality in the Montagu's Harrier *Circus pygargus*. J. Avian Biol. 33: 455-460.

Arroyo B & Garcia J (2006). Diet composition influences annual breeding success of Montagu's harrier *Circus pygargus* feeding on diverse prey. Bird Study 53: 73-78.

Arroyo B, Leroux A & Bretagnolle V (1998). Patterns of egg and clutch size variation in Montagu's Harrier. Journal of Raptor Research 32: 136-42.

Arroyo B, Mougeot F & Bretagnolle V (2001). Colonial breeding and nest defence in Montagu's Harrier. Behav. Ecol. Sociobiol. 50: 109-115.

Arroyo B, Garcia JT & Bretagnolle V (2004). Montagu's Harrier. BWP Update 6: 39-53.

Arroyo B, Bretagnolle V & Leroux A (2007). Interactive effects of food and age on breeding in the Montagu's Harrier *Circus pygargus*. Ibis 149: 806-813.

Bednorz J (2005). Current knowledge about the Raven *Corvus corax* in Poland. In: Jerzak L, Kavanagh B & Tryjanowski P (eds), Corvids of Poland, pp.127-135, Bogucki Wydawnictwo Naukowe, Poznań.

Bertram B (1978). Living in groups: predators and prey. In: Krebs J & Davies N (eds), Behavioural ecology: an evolutionary approach, pp. 64-97, Oxford.

Birkhead T & Moller A (1992). Sperm competition in birds. Academic Press, London.

Blackburn T (1991). An interspecific relationship between egg size and clutch size in birds. Auk 108: 209-211.

Brommer JE, Pietianen H & Kolunen H (2002). Reproduction and survival in a variable environment: Ural owls (*Strix uralensis*) and the three-year vole cycle. Auk 119: 544-550.

Brown C & Brown M (1996). Coloniality in the cliff swallows. University of Chicago Press, Chicago.

Buczek T & Keller M (1994). Breeding ecology of the Marsh harrier *Circus aeruginosus* in eastern Poland. Population numbers and phenology of the onset and laying. Acta Ornithologica 29: 67-80.

Buij R, Van der Goes D, De Jongh H, Gagare S, Haccou P, Komdeur J & De Snoo G (2012). Interspecific and intraspecific differences in habitat use and their conservation implications for Palearctic harriers on Sahelian wintering grounds. Ibis 154: 96-110.

Clarke R (1996). Montagu's Harrier. Arlequin Press, Chelmsford.

Corbacho C, Sanchez J & Sanchez A (1997). Breeding biology of Montagu's harrier *Circus pygargus* in agricultural environments of southwest Spain; comparison with other populations in the western Palearctic. Bird Study 44: 166-175.

Cramp S & Simmons KEL (1980). The birds of the western Palearctic, vol. 2. Oxford University Press, Oxford.

Hoyt D (1979). Practical methods of estimating volume and fresh weight of birds eggs. Auk 96: 73-77.

Jerzak L (2005). Magpie *Pica pica* in Poland – current state of knowledge. In: Jerzak L, Kavanagh B & Tryjanowski P (eds), Corvids of Poland, pp. 35-51, Bogucki Wydawnictwo Naukowe, Poznań.

Kitowski I (2004). Behaviour of Red Foxes *Vulpes vulpes* during of Montagu's harrier *Circus pygargus* social defences – case study from southeast Poland. Acta Biol. Univ. Daugavp. 4(2): 71-76.

Kitowski I (2008). Breeding ecology of Montagu's Harrier *Circus pygargus* in marshes of eastern Poland: importance of aggregated nesting. Acta Zool. Lituanica 18(2): 83-89.

Kochert M, Stenhoof K & Mortish K (1983). Evaluation of patagial markers for raptors and ravens. Wildlife Society Bulletin 11: 271-281.

Koks B, Trierweiler K, Visser E, Dijkstra C &. Komdeur J (2007). Do voles make agricultural habitat attractive to Montagu's Harrier *Circus pygargus*? Ibis 149: 575-586.

Korpimaki E (1990). Low repeatability of laying date and clutch size in Tengmalm's owl: an adaptations to fluctuating food conditions. Ornis Scand. 21: 282-286.

Krogulec J & Leroux A(1994). Breeding ecology of Montagu's Harrier *Circus pygargus* on natural and reclaimed marshes in Poland and France. In: Meyburg B & Chancellor R (eds), Raptor Conservation Today, pp. 151-152, Proceedings of the IV World Conference on Birds of Prey and Owls. Berlin, Germany, 10-17 May 1992, Pica Press, London.

Krupiński D, Lewtak J & Szulak K (2010). Semicolonial nesting and conservation of the Montagu's harrier *Circus pygargus* in rapeseed fields in Southern Podlasie (eastern Poland). Slovak Raptor Journal 4: 37-40.

Krupiński D, Lewtak J, Rzępała M & Szulak K (2012). Breeding biology of the Montagu's harrier *Circus pygargus* in east-central Poland and implications for its conservation. Zoology and Ecology 22(2): 86-92.

Lambin X, Bretagnolle V & Yoccoz G (2006). Vole population cycles in northern and southern Europe: is there a need for different explanations for single pattern. J. Anim. Ecol. 75: 340-349.

Liminana R, Soutullo A, Urios V & Surroca M (2006). Vegetation height selection in Montagu's Harriers *Circus pygargus* breeding in a natural habitat. Ardea 94: 280-284.

Liminana R, Soutullo A & Urios V (2007). Autumn migration of Montagu's harriers *Circus pygargus* tracked by satellite telemetry. J. Ornithol 148: 517-523.

Liminana R, Soutullo A, Urios V & Reig-Ferrer A (2012). Migration and wintering areas of adult Montagu's Harriers *Circus pygargus* breeding in Spain. J Ornithol 153: 85-93.

Liminana R, Javaloyest & Urios V (2012a). Diet of the Montagu's Harrier *Circus pygargus* nesting in natural habitat in Eastern Spain. Ornis Fennica 89: 74-80.

Millon A, Arroyo B & Bretagnolle V (2008). Variable but predictable prey availability affects predator breeding success: natural versus experimental evidence. Journal of Zoology 275: 349-358.

Panek M (2005). Activity of the Raven *Corvus corax* on farmland and an assessment of its predation on Brown Hares *Lepus europaeus* near Czempiń. In: Jerzak L, Kavanagh B & Tryjanowski P (eds), Corvids of Poland, pp. 407-418. Bogucki Wydawnictwo Naukowe, Poznań.

Quinn J& Ueta M (2008). Protective nesting associations in birds. Ibis 150: 146-167.

Quinn J, Renolds J & Bradbury R (2008). Birds as predators and as prey. Ibis 150: 1-8.

Salamolard M (1998). Stratégie d'utilisation des ressources chez une espèce de rapace semi-colonial, le busard cendre (*Circus pygargus*). PhD thesis, Université de Tours.

Salamolard M, Butet A, Leroux A & Bretagnolle V (2000). Responses of an avian predator to variations in prey density at a temperate latitude. Ecology 81: 2428-2441.

Schipper W (1979). A comparison of breeding ecology in three European harriers (*Circus*). Ardea 66: 77-102.

Sergio F & Hiraldo F (2008). Intraguild predation in raptor assemblages: a review. Ibis 150: 132-145.

Simmons R (2000). Harriers of the World. Oxford University Press, New York, United States.

STATSOFT INC(2001). Statistica for Windows (data analysis system).

Stearns S (1992). The evolution of life history. Oxford University Press, Oxford.

Tabor M & Tabor J (2005). Food of the Montagu's harrier *Circus pygargus* in the breeding period on the Calcareous Marshes near Chełm. Kulon 10: 33-42 (in Polish).

Terraube J & Arroyo B (2011). Factors influencing diet variation in a generalist predator across its range distribution. Biodivers. Conserv. 20: 2111-2131.

Tollan A (1988). Maintenance energy requirements and energy assimilation efficiency of the Australasian Harrier. Ardea 76: 181-186.

Tremblay I, Thomas D, Lambrechts M, Blondel J & Perret P (2003). Variations in blue tit breeding performance across gradients in habitat richness. Ecology 84: 3033-3043.

Tryjanowski P, Gołdyn B & Surmacki A (2002). Influence of the red fox *Vulpes vulpes* on the distribution and number of breeding birds in an intensively used farmland. Ecol. Res. 17: 395-399.

Tryjanowski P, Kuźniak S, Kujawa K & Jerzak L (2009). Ekologia ptaków krajobrazu rolniczego. Bogucki Wydawnictwo Naukowe, Poznań (In Polish).

Tyler G, Smith K & Burges D (1998). Reedbed management and breeding Bitterns *Botaurus stellaris* in UK. Biol. Conserv. 86: 257-266.

Underhill-Day J (1990). The status and breeding biology of Marsh Harrier and Montagu's Harrier in Britain since 1900. PhD thesis, CNAA, London, UK.

Wiącek J (2006). The fluctuation in the number of Montagu's Harrier *Circus pygargus* in the context of the change in the protection status and utilization methods on the territory of Chełm's calcareous peat bogs. Polish J. Environ. Stud. 15 (5d): 737-741.

Wiącek J (2006a). Food transfer in Montagu's Harrier *Circus pygargus* during the courtship. Acta Ornithologica 41: 88-91.

Wiącek J (2006b). Behavioural consequences of semi-colonial breeding in Montagu's Harrier in Poland. Journal of Ornithology 5: 271. XXIV International Ornithological Congress, Hamburg.

Wiącek J (2007). Nest predation in the Montagu's Harrier *Circus pygargus* in natural habitats of Eastern Poland. In: Birds as Predators and as Prey. BOU Annual Spring Conference 2007, University of Leicester, England.

Wiącek J (2008). Benefits and costs of semi-colonial breeding in the Montagu's Harrier *Circus pygargus*. Belg. J. Zool. 138(1): 36-40.

Wiącek J (2009). Nest site selection of Montagu's Harrier *Circus pygargus* breeding in natural habitats in eastern Poland. Ardea 97(1): 117-119.

Wiącek J & Niedźwiedź M (2005). The food of Montagu's Harrier *Circus pygargus* in the pre-laying period. Berkut, 14/2: 189-192.

Wiącek J & Niedźwiedź M (2009). Long term changes in the diet of Montagu's Harrier *Circus pygargus* during the nesting period on the Chełm Calcareous Marshes. In: Wiącek J, Polak M, Kucharczyk M, Grzywaczewski G& Jerzak L (eds), Birds-Environment-Threats-Conservation. Selected issues in avian ecology, pp. 309-318. LTO, Lublin, Poland (In Polish, with English summaries).

Wiebe K & Bortolotti G (1994). Food supply and hatching spans of birds: energy constraints or facultative manipulation? Ecology 75: 813-823.

Wiehn J & Korpimaki E (1997). Food limitation on brood size: experimental evidence in the Eurasian kestrel. Ecology 78: 2043-2050.

Wilk T, Jujka M, Krogulec J & Chylarecki P (2010). Important Bird Areas of international importance in Poland. OTOP, Marki. www.monitoringptakow.gios.gov.pl

Ziętek K (2009). Food composition of Kestrel *Falco tinnunculus* and Montagu's harrier *Circus pygargus* in eastern Poland. MSc manuscript, Department of Nature Conservation, Curie-Skłodowska University, Lublin, Poland (in Polish).

Received: April 11th, 2014

Accepted: March 18th, 2015

Branch editor: Diederik Strubbe