

Benefits and costs of semi-colonial breeding in the Montagu's Harrier *Circus pygargus*

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ABSTRACT. A total of 31 pairs of Montagu's Harrier *Circus pygargus* nesting on calcareous marshes near Che³m in eastern Poland were observed from 1991 to 1995 in "Bagno Serebryskie" nature reserve. This area has been included into Nature 2000 network as a special protection area for birds. Total time of observations was 1700 hours. The harriers were caught, ringed and individually marked by special colour wing tags. Observations each year started in April at the beginning of pair formation and continued until the start of post-fledging period in July. The size of a harrier nesting territory varied from 0.42ha to 2.25ha, averaging 1.14ha. Clumped territories were significantly smaller than solitary ones. The clumped territories were occupied earlier (as estimated from egg-laying dates) than solitary ones. Clutch size in clumped nests was larger than in solitary ones and the number of fledglings per nest was also higher in clumped territories. Semi-colonial nesting was safer in terms of predation risk. Copulation frequency was higher in semi-colonial than in solitary nests, suggesting a higher risk for extra-pair copulations. Males from clumped nests spent more time inside territories than males from solitary nests. Most of observed copulations were preceded by food pass.

KEY WORDS : *Circus pygargus*, semi-colonial breeding, copulation, breeding success, predation risk.

INTRODUCTION

Breeding density of the Montagu's Harrier *Circus pygargus* as other birds of prey is strongly dependent on habitat quality and prey availability (NEWTON, 1979). In optimal habitats most harriers' species nest in association or semi-colonies (HAGEMEIJER & BLAIR, 1997; SIMMONS, 2000). Semi-colonial breeding in birds has associated costs and benefits (BIRKHEAD & MOLLER, 1992). Main costs are competition for breeding sites, mates and food but benefits are evident: information about food or mates and decrease of predation risk.

Semi-colonial breeding helps in mate assessment of mates at the time of mate choice (WIĄCEK, 2004). In contrast, the risk of extra-pair copulation (EPC) is higher in semi-colonies than in solitary places (ARROYO, 1999), so cuckoldry may represent a high cost for birds in colonies (BIRKHEAD & LESSELLES, 1988; ARROYO, 1999). Two basic methods of paternity assurance occur in birds. The first method is mate guarding (BIRKHEAD, 1979), but in species such as raptors, with intensive courtship feeding, where females stay at the nest while males hunt far away from it, mate guarding interferes with foraging. The second strategy to decrease the risk of cuckoldry is frequent within-pair copulations (BIRKHEAD et al., 1987). Harrier males, similarly to other birds of prey, increase their paternity assurance by frequent copulations (BIRKHEAD & MOLLER, 1992; MOUGEOT et al., 2001). Therefore semi-colonial breeding birds such as Montagu's Harrier may have high copulation rates in comparison to birds breeding solitary (MOUGEOT, 2004) although KOPIMAKI et al. (1996) found that in some bird of prey species solitary nesting birds copulated more frequently than clumped birds.

In a study with Montagu's Harrier, losses caused by predators were lower in semi-colonies than in isolated nests (ARROYO et al., 2001). Safety of group-living birds depends on individuals participating in group defence of breeding places or nests. One of the ways of defence in semi-colonial breeding birds of prey is mobbing behaviour. Montagu's Harriers are medium-sized birds of prey, defending their breeding places by active antipredator behaviour individually or communally. Communal defence provides benefits to all members of the colony and semi-coloniality decreased the individual's costs of defence (ARROYO et al., 2001). Costs associated with mobbing behaviour include the time spent in the territory, risk of death during attacks or a decrease in physical condition.

This study sought to determine whether nesting in solitary or clumped territories modified harriers behaviour, in such aspects as time spent inside the territory, mate guarding, copulation frequency and breeding success.

STUDY AREA AND METHODS

From 1991 to 1995 aspects of the behaviour of 31 pairs of Montagu's Harrier were observed on calcareous marshes in the nature reserve: "Bagno Serebryskie" near Che³m (51°10'N, 23°37'E) in eastern Poland (Fig.1). This nature reserve is a part of Special Protection Area for birds within Nature 2000 network. The area of the nature reserve was 376.6ha (BUCZEK & BUCZEK, 1996). The Sedge *Cladietum marisci* is the dominant vegetation type (*Cladium mariscus* dominant). The study area was surrounded by agriculture landscape. Over the study years, fifteen harriers (11 females and 4 males) from clumped territories were caught in special ornithological nets

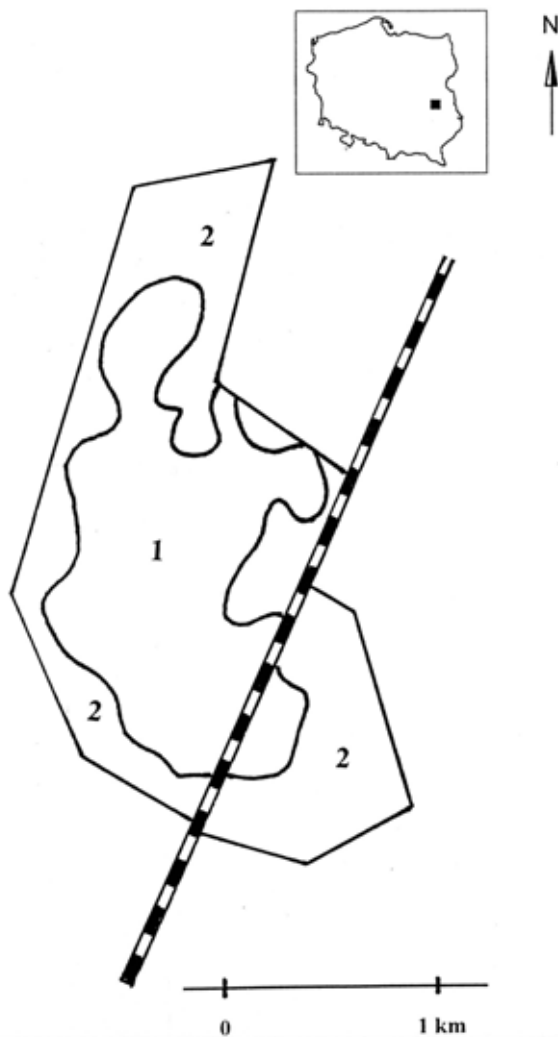


Fig. 1. – Map of the study area and its location in Poland.
 1. Breeding area covered by the sedge *Cladietum marisci*.
 2. Meadows around the marsh; black and white line = railway line along study area.

(BUSSE, 2000) using Eagle Owl *Bubo bubo* as a decoy (Table 1). These birds were ringed and individually marked using special coloured wing tags (KOCHERT et al., 1983). The colour markers did not modify the harriers' behaviour. Some unmarked individuals were individually recognized by differences in their plumage and the moulting stage (gapes in primaries, secondaries or tail feathers).

Observations started each year in the second half of April (between 16th and 20th) after the arrival of harriers at the

breeding places. We recorded first egg laying and hatching dates in the studied pairs through nest visits, as well as number of eggs in each nest and growth rate of nestlings. Nests with fledglings were monitored every week.

Field observations were conducted throughout the pre-laying period, incubation, hatching and nestling periods until the beginning of the post-fledging period in July. The behavioural observations focused on early stages of the breeding season, mainly in the pre-laying period. Total time of observations in this period was 1700h. Observations in later periods of the breeding season were conducted mainly while visiting the nest and nestlings until they started to fly. Observations were performed from 100 to 150m away from nests, using 10x50 binocular and a spotting scope 20x77. Birds were observed from 7 a.m. till sunset (12 hours a day). The size of 27 of the 31 studied territories was estimated through Minimum Convex Polygon method (KENWARD, 1987), using observations of female location as data. We measured the time spent in the territory by both sexes with accuracy to 1s (by the use of a stopwatch). This data were presented as a percent of the time spend within territory. Copulations rates per female were estimated from the total number of copulations observed, whether successful or unsuccessful. Mating was described as successful when duration of copulation was near 5s. Shorter time of copulations with no contact of the cloacae was recorded as unsuccessful. Copulation rates were presented as number of copulations per hour observation. All cases of predator attack, nest detection and nest destruction by predators were also recorded.

The location of the territories, within the marshes during all the years of observation, was uneven. Some of these territories were located in high density, in close proximity to each other so that they bordered with one another, whereas the remaining ones were located within a certain distance from one another. A change in behaviour towards the nearest neighbour was the criterion distinguishing between "clumped" or "solitary" categories. Harriers in solitary territories did not provoke behavioural answers from nearest settled pairs of harriers, in contrast to birds in the clumped category where a reaction was immediate: pursuits, escorts or attacks (WIĄCEK, 2006). The distance between clumped territories was 40 to 146m, on average 78.4m (N=16). Solitary areas (N=15) was placed in the distance from 265 to 655m, on average 368m (Table 2). All the nests and distances between nests were measured by use a measuring tape. Analyses were made with nonparametric statistics (Mann-Whitney test and χ^2 test). All analyses were performed with Statistica 6.1.

TABLE 1

The breeding pairs of the Montagu's Harriers *Circus pygargus* in the nature reserve "Bagno Serebryskie" in the time of study.

Year	nesting pairs	observed pairs	clumped territories / observed/	isolated territories /observed/	marked birds	density per 100ha
1991	16	5	2	3	2♂	4.25
1992	11	7	4	3	5♀+1♂	2.92
1993	12	6	3	3	2♀+1♂	3.19
1994	9	8	4	4	2♀	2.39
1995	6	5	3	2	2♀	1.59

TABLE 2

The distance of the nearest neighbour between breeding pairs of the Montagu's Harrier *Circus pygargus* (CP) in the time of study.

Season	Clumped pairs	Isolated pairs
1991	CPA – 146m	CP1 – 295m
	CPB – 146m	CP4 – 265m
		CP2 – 285m
1992	CP8 – 56m	CPO – 325m
	CP7 – 40m	CP10 – 345m
	CP9 – 40m	CP13 – 325m
	CP3 – 126m	
1993	CPF – 67m	CPM – 275m
	CP£ – 67m	CPK – 310m
	CPT – 75m	CPL – 655m
1994	CP2 – 44m	CP4 – 280m
	CP3 – 64m	CP6 – 610m
	CP8 – 44m	CPZ – 485m
	CP1 – 60m	CPS – 410m
1995	CP4 – 110m	CPC – 335m
	CP13 – 60m	CPW – 320m
	CPU – 110m	

RESULTS

The size of observed territories varied from 0.42 hectares to 2.25 hectares, on average 1.14 hectare (N=27, SD=0.52). Clumped territories were smaller (from 0.42 to 1.4ha, on average 0.92ha, N=16, SD=0.44) than solitary ones (from 0.6 to 2.25ha, on average 1.47ha, N=11, SD=0.47), Mann-Whitney test $Z=-2.76$, $p=0.005$.

The conducted observations and nest monitoring enables to suggest that semi-colonial breeding in Montagu's Harrier provides pairs with higher nest safety. Among 16 observed pairs in clumped territories, only one case of destruction of the nest by a raptor was observed, while there were 5 cases among 15 solitary territories ($\chi^2=43.859$, $df=1$, $p<0.001$).

There were also significant differences in the breeding success of nesting birds in the two types of territories. Number of eggs in nests located in semi-colonies was higher (4.37 eggs per pair, N=16, SD=0.6), than in solitary territories (3.73 eggs per pair, N=15, SD=1.09). Those differences had further consequences in the number of hatched fledglings: 3.43 fledglings in clumped territories (N=16, SD=1.36) and 2.93 in solitary territories (N=15, SD=1.66). The number of flying fledglings in clumped nests was 2.56 per pair (N=16, SD=1.31), while in solitary ones 1.46 per pair (N=15, SD=1.35) and this difference was statistically significant (Mann-Whitney test $Z=2.055$, $p=0.03$). Clumped territories were occupied earlier than solitary ones. The date of laying of the first egg over all study years was six days earlier in clumped than in solitary territories ($Z=1.97$, $p=0.04$).

Overall copulation rate was 0.22 per hour (2.65 copulations a day) but breeding density influence copulation behaviour. Clumped pairs (N=16) had a higher copulation density than those in solitary (N=15) territories ($Z=3.05$, $p=0.002$), (Fig. 2). Two peaks of copulation were

observed: first in mid-morning and second in the afternoon (Fig. 4). Most of 69 observed copulations (62%) were preceded by food pass. Copulation occurred more often after courtship feeding than without food ($\chi^2=4.18$, $p<0.04$).

All observed pairs built nest of similar sizes and located in similar areas and surroundings. Nevertheless, the internal diameter of clumped nests (N=16) was larger than in solitary territories (N=15), this difference was statistically significant ($Z=2.21$, $p=0.03$) and was associated with the higher number of eggs in these nests.

There were also significant differences in time budget for males among clumped and solitary territories (Fig. 3). During the pre-laying period, males (16) in clumped territories spent more time within the territory than did males (15) in solitary territories ($Z=2.303$, $p=0.02$). Additionally, females from solitary territories spent more time in the territory that did females from clumped territories but differences were not statistically significant.

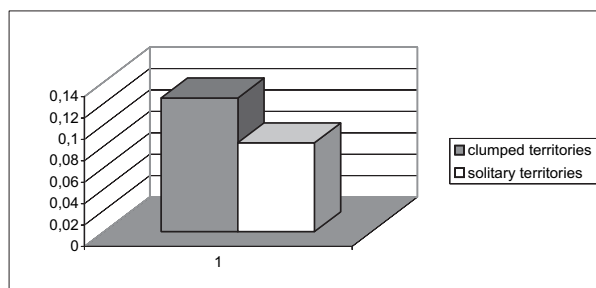


Fig. 2. – The copulation frequency as number copulations per hour observation (as medians)

DISCUSSION

Montagu's Harrier shows a distinct tendency to semi-colonial breeding (CLARKE, 1996) in the whole area of its occurrence (HAGEMEIJER & BLAIR, 1997). Territorial behaviour is mostly observed within the nest area while aggressive behaviour associated with hunting territories is not observed. The size of nesting territories observed in this study was smaller than territories occupied by Montagu's Harrier in an Italian population, where the average size of the territory was approximately 4 hectares (PANDOLFI & PINO D'ASTORE, 1992). However the habitat conditions of the Italian population differed from that in Poland. In Italy, harriers occupied dry habitats with grass and shrubs while in Poland birds were breeding in wet marshes with sedge *Cladium mariscus*. The small marshes in eastern Poland (study area 3.76km²) created optimal breeding conditions for harriers building their nests in high densities (KROGULEC & LEROUX, 1994). Therefore the distance of nearest neighbour on calcareous marshes in eastern Poland was much shorter in comparison with that in most other areas (ARROYO et al., 2004) such as in a big agricultural area in Spain where longest distance between nearest neighbours recorded in clumped category was 600m (ARROYO, 1999).

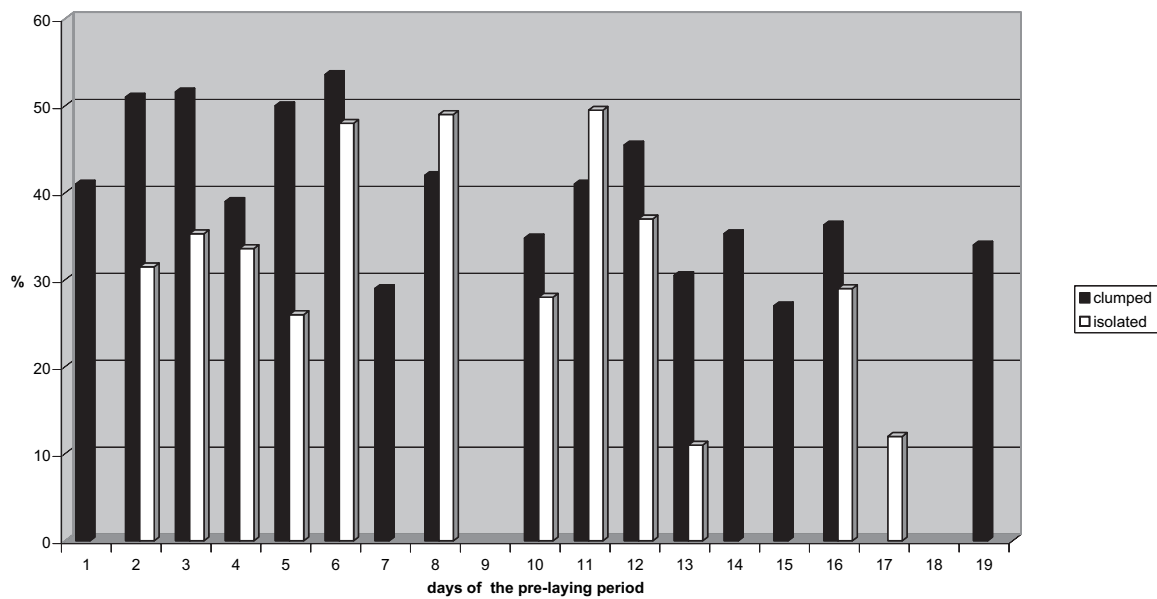


Fig. 3. – Time spend inside the territory by males

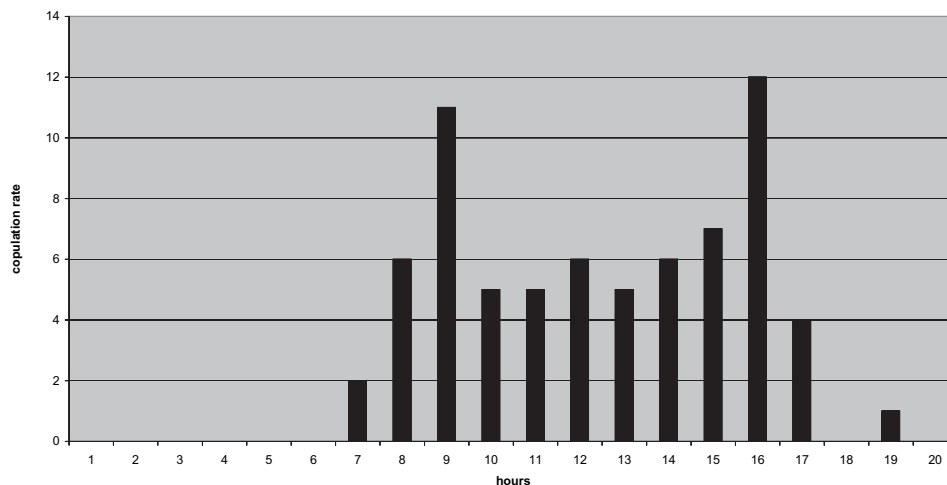


Fig. 4. – Daily pattern of the copulation behaviour

Semi-colonial breeding apparently increases the safety of nests located in close proximity. Based on the result of observations and experiments conducted in Spain and France, semi-colonial breeding decreases individual costs of nest defence and the risk of undertaking such defence (ARROYO *et al.*, 2001). The bigger the colony of birds, the faster the detection of predators so Montagu's Harrier broods is probably safer. My results show that indeed probability of predation by a raptor in tightly clumped nests was significantly lower.

The clumped territories were occupied earlier than solitary ones. Earlier laying occurred in the territories with the most intensively displaying males indicating that males in better physical condition which were chosen first by females (SIMMONS, 1988; 1988a). The high level of sky-dancing points to high genetic quality of these individuals (WIŁCEK, 2004). The breeding place around the best sky-dancers, which are the first ones to settle, is

probably considered as the safest one in the context of possible common defence against the predator and at the same time, it seemed more attractive to neighbouring pairs.

Settling near attractive males may have benefits for female in terms of EPC. Territories, taken the earliest, occupied by birds of the highest genetic quality showed larger clutches than isolated ones. The partners of best males, in good condition, are frequently mature females, usually laying the higher number of eggs (KROGULEC, 1992). The bigger size of these nests was the result of higher number of eggs from these females.

Semi-colonial breeding, and high density of territories in one place, increases the level of safety, but the level of aggression between individuals increase too, especially between females who spent most of the time in the territory (CRAMP & SIMMONS, 1980; CLARKE, 1996). Such situation provokes a lot of aggressive situations among

females settling in semi-colonies (SIMMONS, 2000; MOUGEOT et al., 2001).

Females from solitary territories spent more time in the territory than did females from clumped territories. This difference probably derived from a higher risk of predator attack in solitary territories where birds cannot rely on help in the form of common defence against the intruder. That is why they have to spend more time in the territory in order to defend it against *Corvidae* or a fox, the main predators of Montagu's broods in France and Spain (ARROYO et al., 2001) or Poland (WIĄCEK, 2007).

Semi-colonial breeding of Montagu's Harrier increases the risk of extra-pair copulation, in particular because the males of this species spend the majority of the time outside the territory (MOUGEOT et al., 2001; MOUGEOT, 2004). Mate-guarding and intensive courtship feeding during the female fertile period in Montagu's Harrier are difficult to carry out. Nevertheless, the fact that males from clumped nests spend more time in the territory than males in the separated territories may indicate a certain rudimentary form of mate-guarding. This tendency has been described by other authors as rare occurring in other birds of prey with intensive courtship feeding (PANDOLFI et al., 1998; SIMMONS, 2000), although has already been suggested for semi-colonial Montagu's Harriers (MOUGEOT et al., 2001).

A statistically significant difference in the number of copulations in semi-colonies and solitary territories, indicates that the main protection of the female against another male is frequent-within pair copulation which can dilute sperm from rival males and decrease the risk of cuckoldry (BIRKHEAD et al., 1987). The similar correlation between the number of copulations in separated territories and semi-colonies in a Spanish population of Montagu's Harrier, was described by ARROYO (1999). Copulation behaviour in this study was observed most often after food transfer than without food. The same correlation was observed in Spanish population where harrier copulated in two peaks before and afternoon (ARROYO, 1999).

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