

## BREEDING ECOLOGY OF MONTAGU'S HARRIER (*CIRCUS PYGARGUS*) IN MARSHES OF EASTERN POLAND: IMPORTANCE OF AGGREGATED NESTING

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**Abstract.** Breeding success in Montagu's Harrier (*Circus pygargus*) was studied in peat bogs of eastern Poland during the period 1996–2002. Harriers nested only in the area covered with great fen sedge (*Cladium mariscus*). The studied Harriers laid from 1 to 6 eggs, on average 4.09 eggs ( $n = 118$ ). With the progression of the season, no significant decline in clutch size was recorded. The highest values of clutch size were found for pairs nesting in five nest aggregations. Harriers fledged on average 2.49 young per nest and 1.46 young per breeding pair. Early clutches in semicolonies were larger than later ones. Aggregations of five and four nests were found optimal in terms of clutch size, total loss and fledging success. The results of the study agree with the hypothesis that reproductive success may be highest at intermediate colony size.

**Key words:** Montagu's Harrier, *Circus pygargus*, breeding, semicolony size, Poland

### INTRODUCTION

Colonial breeding displays some selective advantages over solitary breeding. So far, the majority of research on different aspects of colonial breeding has been performed on colonial water birds (Yorio & Quintana 1997; Sorokaitė & Budrys 2000; Jakubas 2005). A number of studies were also concerned with other bird species (Inglis & Galeotti 1993; Hoi *et al.* 2002; Stutchbury & Robertson 1988; Brown & Brown 1996). The relationship between colony size and breeding success in colonial raptors remains understudied and poorly understood (Blanco & Tella 1997; Arroyo *et al.* 2001; Serrano *et al.* 2005). Montagu's Harrier (*Circus pygargus*) is a raptor that explores various habitat types: steppes and open marshes, as well as corn fields or young plantations of coniferous trees (Cramp & Simmons 1980; Garcia & Arroyo 2002; Kitowski 2002a). Montagu's Harriers seem to have substituted their original breeding habitats for crops in many countries. In Europe, there is an east-west gradient of crop nesting (Garcia & Arroyo 2002). In such conditions, data on the breeding ecology in marshes of eastern Europe, when Harriers nest in loose aggregations (semicolonies), may also have an important implication for the conservation and management of the species. The presented research was aimed at determining the relationship between nesting aggregation size and breeding success in Montagu's Harrier nesting in marshes of eastern Poland.

### STUDY AREA AND METHODS

Studies were carried out from 1996 to 2002 in the area (1,014 ha) of calcareous marshes near Chełm (Chełm, E Poland: 51°07' – 51°11'N, 23°30' – 23°42'E). These marshes are lowland bogs lying in CaCO<sub>3</sub> beds. They are dominated by the *Cladietum marisci* community. Water table levels fluctuated from 40 to 10 cm in spring and from 20 to 0 cm in summer. Water pH ranged from 7.7 to 8.6 (Buczek 2005).

About from 20 to 50 pairs of Montagu's Harriers regularly nested in the area (Krogulec 1992; Kitowski 2002a). At the beginning of the breeding season in May, nests were located observing prey transfer between mates or nest material supply trips by females. During the egg laying, hatching and fledging periods, nests were visited every 4–7 days to record clutch size, hatching and fledging success. Incubation time of 30 days was assumed for phenological calculations (Cramp & Simmons 1980; Corbacho *et al.* 1997). The nearest neighbouring nest distances (NNNDs) and distances to the marsh edge were measured by means of a theodolite in winter time. Rare cases of clutch replacement were excluded from the calculations covered in this paper. Nests were gathered into particular aggregations according to the NNNDs criteria given by Arroyo (1996). The observed behaviour of Montagu's Harriers (nuptial and territorial, communal defences, cases of kleptoparasitism, etc.) showed that nests with the NNNDs smaller than 400 m

formed one semicolony (aggregation) (Arroyo 1996; Kitowski, unpubl. data). Losses recorded during the study period were of both partial and overall character. Total losses were inflicted by predators. The following were among the predators occurring in the vicinity of colonies and posing a threat to the considered species: Marsh Harrier (*Circus aeruginosus*), a sympatric nesting raptor with approximately 60 breeding pairs (Buczek & Keller 1994), Goshawk (*Accipiter gentilis*), Magpie (*Pica pica*), Raven (*Corvus corax*), Carrion Crow (*Corvus cornix*) and carnivorous mammals: red fox (*Vulpes vulpes*) and racoon dog (*Nyctereutes procyonoides*). Partial breeding losses were recorded as single eggs found with dead embryos or dead fledglings as a result of siblicide (sibling aggression, cannibalism, starvation). Krogulec (1992) and Witkowski (1989) have described detailed methods of distinguishing partial and total brood losses in Harriers. They have also offered methods how to distinguish between losses made by the mentioned three groups of predators. The nest was considered to be successful if at least one nestling fledged. The present study does not deal in detail with prey abundance, parental quality and seasonal effects on breeding. These will be analysed in the coming paper. Frequencies were compared with the  $\chi^2$  test with Yates' correction. Correlations were ascertained using Spearman rank correlation. Differences between the class sizes of colonies were compared with Kruskal-Wallis ANOVA and the Mann-Whitney U test. Results were presented as mean  $\pm$  SD (Fowler & Cohen 1992).

## RESULTS

### Clutch size, colony size and fledging success

During the study, 118 nests were found, of which 111 nests forming 30 aggregations (semicolonies) of 2 to 6 nests were found only in the area covered with great fen sedge (*Cladium mariscus*). The other 7 nests were solitary. The mean size of a semicolony was  $3.7 \pm 1.32$  nests. The studied Montagu's Harriers laid 1–6 eggs. On average,  $4.09 \pm 0.99$  eggs ( $n = 118$ ), with a median value for all the discovered clutches of 4.0, were found (see Table 1). The most numerous clutches had 4 eggs ( $n = 60$ ; 50.8%) and 5 eggs ( $n = 29$ ; 24.6%). Only seven clutches with 6 eggs were found, making up 5.9% of the overall number of clutches. The clutches of Harriers also contained 3 eggs ( $n = 15$ ), i.e. 12.7% of the overall number of clutches. The smallest clutch contained 1 or 2 eggs, which accounted for 2.5% and 3.4% of all clutches, respectively. The increase in semicolony size (5 classes of aggregation size) was accompanied by increase in the mean clutch size, but this trend was

not significant (Spearman  $r = 0.836$ ,  $n = 5$ ,  $p < 0.077$ ). Considering all data (including clutches from 7 solitary nests as another aggregation size class), the trend was significant (Spearman  $r = 0.896$ ,  $n = 6$ ,  $p < 0.02$ ). The maximum value of clutch size of  $4.4 \pm 0.82$  eggs was found in five nest semicolonies (Table 1). The size of the first clutch in colonies, i.e. the one which initiated semicolony forming ( $n = 30$ ), was  $4.63 \pm 0.76$  eggs, and ranged between 3 and 6 eggs. In comparison with later clutches ( $n = 81$ ) with an average of  $3.94 \pm 0.97$  eggs, it ranged from 1 to 6 eggs, the difference was found to be significant ( $Z = 3.20$ ,  $n_1 = 30$ ,  $n_2 = 81$ ,  $p < 0.0014$ ). With the progression of the season, no significant decline in the size of clutch (Spearman  $r = 0.135$ ,  $n = 118$ ,  $p = 0.148$ ) was recorded.

Montagu's Harriers fledged on average  $2.49$  young  $\pm 0.81$  young per nest and  $1.46$  young per breeding pair, the range was from 1 to 4 young. The highest number of fledged young was found in four nest semicolonies, which accounted for  $2.91 \pm 0.65$  fledglings (Table 1). A statistically significant difference in the number of fledged young was found between the studied semicolonies where Harriers happened to nest (Kruskal-Wallis ANOVA:  $H = 11.6$ ,  $df = 4$ ,  $p < 0.021$ ). In the course of the season, the number of fledged young in breeding pairs which had young was found to decline significantly (Spearman  $r = 0.309$ ,  $n = 69$ ,  $p < 0.021$ ).

### Phenology and spatial organisation of aggregations

In the studied period, Harrier females laid eggs between 3 and 30 May, (123<sup>rd</sup> – 149<sup>th</sup> day of the year) (average:  $135^{\text{th}} \pm 7.4$  days, median: 135<sup>th</sup> day, all data in Julian dates). The laying of eggs was found to be highly synchronised. Within the first week (123<sup>rd</sup> – 130<sup>th</sup> day of the year), 25.4% (30 clutches) of all clutches were completed. By the 12<sup>th</sup> day of the laying period, i.e. between 3 and 15 May (123<sup>rd</sup> – 135<sup>th</sup> day in Julian dates), 50% of clutches ( $n = 59$ ) had been laid. Eggs in nests initiating the largest aggregations (4–6 nests), were laid first ( $126.3^{\text{rd}} \pm 2.6$  days, median: 126<sup>st</sup> day, range: 123<sup>rd</sup> – 131<sup>st</sup> day), when compared to those initiating smaller aggregations (2–3 nests) and solitary nests ( $129.8 \pm 2.4$  days, median: 130<sup>st</sup> day, range: 123<sup>rd</sup> – 134<sup>th</sup> day (Mann-Whitney U test:  $Z = 3.13$ ,  $n_1 = 15$ ,  $n_2 = 22$ ,  $p < 0.002$ ).

Harriers tend to build nests at an average distance of  $119.6 \pm 80.0$  m, median: 86.5 m, range: 40–377 m from the marsh edge (Table 1). No correlation between the average size of aggregations and the mean distance from the marsh edge was noted: Spearman  $r = 0.156$ ,  $n = 5$ ,  $p = 0.801$ . Pioneer nests involved in semicolonies ( $n = 30$ ) were located further from the marsh edge ( $189.2 \pm 74.9$  m, median: 200 m, range: 40–339 m) than nests built later ( $n = 81$ ) ( $95.4 \pm 64.3$  m, median: 67 m,

Table 1. Variables describing the breeding ecology of Montagu's Harrier in E Poland. Data are given as mean  $\pm$  SD. \* – distances to nests from other semicolonies. Data for solely nesting pairs are given as (1).

Aggregation size ( <i>n</i> )	(1)	(2)	(3)	(4)	(5)	(6)	Total
Number of studied nests	7	12	27	28	20	24	118
Clutch size (egg number)	3.57 $\pm$ 1.3 1–5	3.58 $\pm$ 1.2 1–5	3.96 $\pm$ 1.1 2–6	4.25 $\pm$ 0.9 2–6	4.40 $\pm$ 0.8 3–6	4.21 $\pm$ 0.8 2–6	4.09 $\pm$ 1.0 1–6
Nearest neighbouring nest distance (m)	326 $\pm$ 32 * (306–394)*	141 $\pm$ 51 (72–206)	157 $\pm$ 76 (64–272)	197 $\pm$ 86 (69–294)	166 $\pm$ 77 (71–284)	148 $\pm$ 61 (57–233)	174.7 $\pm$ 82.5 (57–394)
Nest distance to the marsh edge (m)	93 $\pm$ 63.0 (40–181)	108 $\pm$ 72.0 (49–243)	118 $\pm$ 75.0 (51–280)	124 $\pm$ 82.0 (50–377)	120 $\pm$ 80.0 (54–331)	127 $\pm$ 87.0 (49–339)	119 $\pm$ 78.0 (40–377)
Number of successful nests	3	7	20	22	8	9	69
Number of fledged juveniles	1.7 $\pm$ 0.58 1–2	1.9 $\pm$ 0.55 1–3	2.45 $\pm$ 0.68 1–3	2.91 $\pm$ 0.65 1–4	2.56 $\pm$ 0.73 1–3	2.25 $\pm$ 0.89 1–3	2.49 $\pm$ 0.81 1–4

Table 2. Total loss in nests in relation to semicolony size of Montagu's Harrier. Data for solely nesting pairs are given in column (1).

Aggregation size ( <i>n</i> )	(1)	(2)	(3)	(4)	(5)	(6)	Total
Number of aggregations	7	6	9	7	4	4	37
Total number of nests	7	12	27	28	20	24	118
Incubation loss (predators)	3	3	2	2	2	6	18
Incubation loss (predators, in %)	42.8	25.0	7.4	7.1	10	25.0	15.2
Incubation loss (infertile)	–	–	1	–	1	1	3
Incubation failure (infertile, in %)	–	–	3.7	–	5	4.2	2.6
Total incubation failure (in %)	42.8	25.0	11.1	7.1	15.0	29.2	17.8
Number of nests with nestlings	4	9	24	26	17	17	97
Nestling losses	1	2	4	4	8	9	28
Nestling failure (in %)	25.0	22.0	16.7	15.4	47.1	52.9	28.9
Total number of lost nests	4	5	7	6	11	16	49
Successful nests	3	7	20	22	9	8	69
Total rate of nests failure (in %)	57.1	41.2	25.9	21.4	55.0	66.7	41.5

range: 45–377 m) (Mann-Whitney U test:  $Z = -5.54$ ,  $p < 0.0002$ ). Large clutches were typically found further from the edge ( $r_s = 0.21$ ,  $n = 118$ ,  $p < 0.02$ ). The NNND in the study area was  $174 \pm 82.5$  m, the range was 57–394 m. The shortest NNND of  $141 \pm 51$  m (range: 72–206 m) was found in two nest semicolonies.

#### Nest failure and colony size

Total losses in the studied population resulted mainly from rare cases of death of entire clutches (2.5% of 118 nests). The remaining total losses in incubation resulted from the predation of corvids and mammals (15.3% of 118 nests). Brood losses varied with aggregation size reaching a high percentage of 57% for the recorded single nests. Minimum losses (21.4%) were found in semicolonies containing four nests (Table 2). The data on breeding failure revealed the same regularities both for the incubation and nestling period. The smallest percentage of lost nests for both incubation and nes-

ting periods was found in four nest aggregations. The respective percentage was equal to 7.1% and 15.4% (Table 2). A total number of 49 nests (41.5%,  $n = 118$ ) was lost during the incubation and nestling periods. The other 69 (58.5%,  $n = 118$ ) studied nests produced at least one flying juvenile, whereas 46 broods (38.9%,  $n = 118$ ) were lost in predation. Statistical differences were found analysing the broods lost due to predation between the incubation and the nestling period for all pooled data (15.2% of  $n = 118$  nest vs. 28.9% of  $n = 97$  nest;  $\chi^2 = 5.1$ ,  $df = 1$ ,  $p < 0.024$ ).

Differences between the results of this and earlier studies (1985–1988) conducted at the same place concerning the frequency of loss due to predation during the incubation period were found to be insignificant (15.2% of  $n = 118$  nest vs. 12.8% of  $n = 140$  nest) ( $\chi^2 = 0.14$ ,  $df = 1$ ,  $p < 0.71$ ) (Krogulec 1992). Though the frequency of loss in the nestling period (Table 2) in comparison

with Krogulec's (1992) data was higher, differences were also insignificant (28.9% of  $n = 97$  nest vs. 19.8% of  $n = 116$  nest;  $\chi^2 = 2.36$ ,  $df = 1$ ,  $p < 0.125$ ). The percentage of lost nests was similar to that obtained in previous studies (41.5% of 118 nests vs. 34.2% of 140 nests:  $\chi^2 = 1.14$ ,  $df = 1$ ,  $p < 0.286$ ).

## DISCUSSION

Though the determined average clutch size of Montagu's Harriers in eastern Poland was larger than that reported so far from southern Europe as not exceeding 4.0 eggs (Castano 1989; Corbacho *et al.* 1997), it was similar to the value recorded for other northern populations of Montagu's Harrier (Schipper 1979; Clarke 1996). The experience from earlier studies prompted to link the observed differences to geographically based differences in food content for Montagu's Harriers, whose southern populations take the advantage of a considerable number of insects, whereas the northern ones feed mostly on rodents and birds (mainly passerines) (Schipper 1977; Corbacho *et al.* 1997; Clarke 1996; Arroyo 1997; Krogulec 1992; Salamolard *et al.* 2000). Therefore, geographically oriented differences in the quality of food resources can consequently generate differences in clutch size. Moreover, such a line of reasoning allows to understand why such a high number of clutches including 5 or 6 eggs was recorded (a total of 30.5% of all clutches) in Polish Montagu's Harriers, as well as a higher value of clutch size in 'vole years' detected in some southern populations (Salamolard *et al.* 2000). In some southern and western populations of Harrier clutches, the presence of 6 eggs was very rare or never noted (Corbacho *et al.* 1997; Millon *et al.* 2002). Harriers under consideration highly depend on common vole (*Microtus arvalis*) (Krogulec 1992). The same tendency was also observed in many previously studied European populations of Montagu's Harriers (Schipper 1979; Cormier 1985; Salamolard *et al.* 2000). In eastern Poland, the most frequent clutches were those with 4 eggs. Such high frequency (50.8%) of 4 egg clutches could also determine the lack of clear differences in clutch size between the analysed nesting semicolonies. Since the beginning of the 90's of the last century, Montagu's Harriers in eastern Poland have been breeding in crops. In crop habitats, clutches are smaller (3.8 eggs,  $n = 18$ ) than in marshes and their food contains a larger share of insects when compared to the diet of Harriers nesting in marshes (Wojciechowski 1999).

No statistically significant seasonal decline in clutch size was registered during the study as reported by Schipper (1979) and Corbacho *et al.* (1997), and also by

earlier studies performed in the considered marsh area (Krogulec 1992). It should be noted, however, that such seasonal decline was found to be strongly pronounced in other Harriers such as Hen Harrier (*Circus cyaneus*) and Marsh Harrier (Schipper 1978; Picozzi 1984; Witkowski 1989; Zijlstra *et al.* 1992). Such seasonal decline was reported for Montagu's Harrier, but not for Hen Harrier during the comparative breeding biology studies mentioning the species in northeastern France (Millon *et al.* 2002). The same tendency of seasonal decline was noticed in some other diurnal raptors and other birds (Newton 1979; Korpimäki & Wiehn 1998; Klomp 1970; Birkhead 1991; Briggs 1993; Christians *et al.* 2001). It is also frequently indicated that adaptive values of such phenomenon allow to maximise the probability of breeding success according to the equilibrium between laying date and clutch size (Drent & Daan 1980; Dijkstra 1988).

In this study, seasonal decline in clutch size of Montagu's Harrier was also accompanied by seasonal decline in fledging success. Such seasonal decline was also observed in other Harriers (Schipper 1978). The rate of breeding success of Montagu's Harriers from eastern Poland was low (58.5%) and similar to that of Mediterranean populations strongly affected by farming practices (Corbacho *et al.* 1997). This was due to predation by red foxes and Marsh Harriers, of which the population size has been rapidly increasing in the study area and throughout Poland during the last decades (Buczek & Keller 1994; Bresinski & Panek 2000; Tomialojc & Stawarczyk 2003; Kitowski, unpubl. data).

In some studies (Stutchbury & Robertson 1988; Brown & Brown 1996) there were differences the quality of individuals involved in establishing colonies. Obviously, the costs-to-benefits ratio could be affected then and related to individual bird quality. The date of arrival at the breeding site, similarly as for other birds, can be considered in Montagu's Harrier as an index of quality since it is widely known that weaker, less experienced or younger birds arrive at breeding sites later (Stutchbury & Robertson 1988), thus starting their breeding at a later date. The first (pioneer) clutches in colonies were larger than the later ones, which can be explained by the fact that more experienced birds establishing basic colonies can also display a higher percentage of late settling birds, which in turn contributes to a greater variation in the quality of pairs joining the aggregation.

Brown and Brown (1996) proved that the chances of late (worse quality) breeders to find within the colony a nestling place of better quality are much smaller. In the marshes of eastern Poland, a short distance to the marsh edge is obviously correlated with worse quality of such places exposed a higher predatory pressure (Table 2).

Though this explains why smaller clutches are found closer to the marsh edge, it should not be disregarded that sometimes such 'edge' nesting is beneficial in terms of provisioning food for juveniles (Kitowski 2002b). Serrano and Tella (2007) showed that inexperienced individuals (yearlings and first breeders) of Lesser Kestrel (*Falco naumanni*) often try to settle in large colonies, but they are often relegated to breed solitarily or in small colonies by previous residents, which are generally old and experienced adults. This creates an age-structured distribution of individuals in relation to colony size, with large colonies gathering a much lower proportion of first breeders than small ones (Serrano & Tella 2007). Fitness components (breeding success and survival) increase with colony size in part due to the age-structured distribution. The fact that some surrogates of individual quality or age in Montagu's Harriers, such as clutch size, increase with aggregation size, suggests that similar processes can also take place in this species. The studied Montagu's Harriers nested in aggregations of 2–6 nests. Other studies showed that larger aggregations including 16, 20 or even over 30 nests (Studinka 1942; Leroux & Bretagnolle 1996; Arroyo 1996; Garcia & Arroyo 2002) can be established. In central Spain, most pairs breed in clumps of 2–16 nests. In Montagu's Harriers nesting in crops of eastern Poland, only 1–2 nests are found (Wojciechowski 1999). Previous studies revealed that the rate of nest failure in the nestling period was significantly larger than losses suffered in the incubation period. Predation during incubation in the studied colonies was heavily impacted by corvids foraging on eggs during either short breaks when females deliver nest material or when aerial prey transfers between mates are performed, or incubation was interrupted for any other reason (Kitowski, unpubl. data). Quite a different scenario happened in the late nestling period when the water level was low. Water deficiency, short distance from the nest site to the marsh edge, short NNND and nutritional attractiveness of fledglings (mass approaching 500 g before the nest is left) (Kitowski, unpubl. data), their noisiness and synchronised breeding are the major factors that allow Marsh Harriers and terrestrial mammals to greatly benefit from penetrating semicolonies. Similar observations of Bee Eater (*Merops apiaster*) were performed. One individual of weasel (*Mustela nivalis*) or ladder snake (*Elaphe scalaris*) managed to destroy the entire colony (Lessells *et al.* 1994; Hoi *et al.* 2002). On the other hand, the synchronisation of breeding is used by many bird species as antipredatory strategy (Becker 1995; Brown & Brown 1996, Murphy & Schauer 1996; Stokes & Boersma 2000). The study revealed that for the studied population of Montagu's Harriers the average nearest-neighbour nest distance was

174 m, whereas the average nest distance to the marsh edge was 119.6 m. The values reflect increased distances in comparison with the average results from 1984–1988, which accounted for 160 m and 115 m, respectively (Krogulec 1992). This indicates that Montagu's Harriers responded with a changing spatial distribution of their colonies to a strong growth of the populations of terrestrial predators in the studied area, particularly of foxes, raptors and corvids.

In previous studies on predation, the results concerning coloniality relationships were found to be inconsistent. Many researchers notice that nesting in large colonies brings a series of benefits such as diluting the risk of predation (Wiklund & Andersson 1994), earlier detection of predators (Brown & Brown 1996), reduced need for individual investment in vigilance and antipredator behaviour (Arroyo *et al.* 2001) that limits the risk of losing brood. For some colonies, a 'selfish effect' was reported, i.e. birds tend to place their nests in the centre where the risk of predation is reduced (Becker 1995; Yorio & Quintana 1997). Some studies showed the opposite results, i.e. that densely aggregated nests are more attractive and more frequently visited by predators (Bellinato & Bogliani 1995; Emslie *et al.* 1995; Stokes & Boersma 2000).

The colonies of five and four nest size were found to be optimal in terms of clutch size, total loss, and fledging success. This corresponds to the hypothesis that reproduction increases with colony size, but reproductive success may be the highest at intermediate colony size (Pulliam & Caracao 1984; Rannala & Brown 1994; Brunton 1999).

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**PIEVINĖS LINGĖS (*CIRCUS PYGARGUS*), PERINČIOS RYTŲ LENKIJOS PELKĖSE, VEISIMOSI EKOLOGIJA IR KOLONIJŲ SVARBA**

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**SANTRAUKA**

Per 1996–2002 metų laikotarpį buvo tirtos pievinės lingės (*Circus pygargus*), perinčios kalkingose pelkėse Rytų Lenkijoje. Stebėti paukščiai lizdams sukurti rinkosi vietas, apaugusias šakotosiomis ratainytėmis (*Cladium mariscus*), kur išperėdavo nuo 1 iki 6 kiaušinių (vidutiniškai  $4,09 \pm 0,99$ ;  $n = 118$ ). Perėjimo sezono eigoje statistiškai reikšmingo kiaušinių skaičiaus sumažėjimo dėtyje pastebėta nebuvo. Daugiausia kiaušinių išperėdavo poros, kurios susiburdavo į penkių lizdų kolonijas. Nustatyta perėjimo sėkmė vienam lizdai – vidutiniškai 2,49 išperėti jaunikliai, o vienai paukščių porai – 1,46 jaunikliai. Mažose kolonijose ankstesnės dėtytys buvo didesnės negu vėlesnės. Didžiausia perėjimo sėkmė nustatyta keturių ir penkių lizdų kolonijose, kuriose taip pat susidaro palankiausias sąlygos kiaušiniams perėti ir jaunikliams auginti. Šio tyrimo rezultatai patvirtina hipotezę, kad reprodukcija yra sėkmingiausia vidutinio dydžio kolonijose.

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