Are changes in predatory species composition and breeding performance responsible for the decline of Coots *Fulica atra* in Milicz Ponds Reserve (SW Poland)?

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Abstract. Both native and non-native predators should strongly affect resident fauna. Nevertheless, because of a lack of defensive mechanisms in potential prey, the influence of non-native predators should have longer-lasting and more deleterious repercussions. The breeding ecology of the Coot was studied in the Milicz Ponds reserve and compared with data from 20 years earlier. In the meantime, non-native, mammalian predators (American Mink *Mustela vison*, Raccoon Dog *Nyctereutes procyonoides* and Raccoon *Procyon lotor*) turned up in this area, while the numbers of Hooded Crow *Corvus cornix*, the main predator of Coot nests, decreased. Compared with 1980–1982, the number of Coots in 2002–2003 dropped by more than half and mean clutch size decreased. Breeding success and the number of hatchlings per pair remained unchanged; in the 1980s, however, Coots renested more frequently, there was greater nesting synchrony and breeding seasons were demonstrably shorter. Moreover, although predation still remained the main cause of losses, its numbers were decreasing. Coots nesting on islands were the most successful, which was due to the weaker predation on the part of Crows. In contrast, the mammalian (non-native) predators did not appear to play a significant role in the breeding success in 2002–2003. Nevertheless, taking into account the breeding parameters of the Coot population and the nature of the relationship between mammalian/bird predators and Coots, it does seem that the low density of Coots in 2002–2003 was a reaction to the pressure of mammalian predators.

Key words: Coot, *Fulica atra*, nest predation, breeding success, population trends, Milicz Ponds

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INTRODUCTION

In the last 20 years, the number and composition of predatory species in Poland has changed markedly (Tomiałojć & Stawarczyk 2003, Osojca 2005). New species, such as the American Mink *Mustela vison*, Raccoon Dog *Nyctereutes procyonoides* and Raccoon *Procyon lotor* have appeared and/or have been spreading their ranges (Brzeziński & Marzec 2003, Głowaciński et al. 2008). Conversely, the numbers of many native predators, e.g. the Hooded Crow *Corvus cornix* or Raven *Corvus corax*, have changed perceptibly (Tomiałojć & Stawarczyk 2003). Mammalian predators and the corvids, having a wide food spectrum and low ecological requirements, can significantly change population sizes of waterfowl (Ferreras & Macdonald 1999, Kauhala & Auniola 2001, Clode & Macdonald 2002). Such changes, in turn, can be used to test hypotheses concerning long-term relationships between the populations of predators and their prey.

Both increases and decreases of population sizes of waterfowl have been observed during 1980s and 1990s in Europe (e.g. Cramp & Perrins 1994, Musil & Fuchs 1994, Rönkä et al. 2005). Some species, e.g. the Great Egret *Ardea alba*, have considerably extended their ranges. As for the majority of species there is no sufficient data to assess the changes in population sizes. Clearly negative changes have been noted, however, in areas where non-native predatory species appeared (Côté & Sutherland 1997, Nordström et al. 2002, Kauhala 2004). This indicates high vulnerability and/or low adaptability of native avifauna to changes in predatory species composition.

Leaving aside the quantitative relationship, the character of the influence and reaction of waterbirds to changes in the number and species composition of predators deserve similar attention. Waterbirds can reveal many adaptations, helping them to reduce the influence of predators, e.g. nesting in lower density (Page et al. 1983), increasing breeding synchrony (Ims 1990), or

choosing certain, more save nesting places like islands, or more concealed locations (Peluc et. al 2008). Page et al. (1983) showed that predators can decrease the density of their prey nests by choosing the hunting places in which they already succeeded and/or selecting the type of prey they already hunted. By contrast it was shown (MacDonald & Bolton 2008) that some species breed in higher densities in order to defend cooperatively their nests from predators. The difference between both effects can result from two reasons: 1) depending on predator species, birds may be unable to defend their nests, even in a group, and 2) the predator may be dangerous not only for broods but for adults as well. As a result, depending on how predators affect their prey we may expect different reactions.

The Coot *Fulica atra* is a species whose number has decreased during the last 20 years in Central Europe (Houdková & Musil 2003), and this trend has been particularly visible in areas where Coots were common (Musil & Fuchs 1994, Houdková & Musil 2003). Such a decline was noted in SW Poland, in the Barycz river valley; however, apart from unpublished reports, this information has not been confirmed. Despite the lack of long-term data, in 1980–1982 a detailed research was conducted in the same area (Jankowski 1985). This enabled me both to assess the change in the number of Coots between two periods as well as to connect this data with the appearance of non-native predators and changes in the number of resident predators. During 1980–1982 non-native mammal predators were not observed and Hooded Crows were several times more numerous than in 2002–2003 (Grabiński 1996). The Raccoon Dog and American Mink probably appeared at the end of the 1980s, and the Raccoon appeared after 2000 (personal observation in 2003).

Research to date showed that the American Mink is dangerous to Coots (Bartoszewicz & Zalewski 2003); however, it is equally dangerous to eggs and nestlings as to adult birds (Ferreras & Macdonald 1999, Brzeziński 2007). Therefore, because Coots neither are able to actively defend their nests nor themselves from mammalian predators, they should nest in lower densities in order to increase the chances of success or at least for their own safety. Conversely, the influence of the Hooded Crow, the main predator of Coot nests, is limited mainly to egg robbery (Jankowski 1985, Zduniak 2006). Because Coots can collectively defend nests from Crows (personal observation),

they should nest in higher densities. As a result, I expect that because of a smaller number of Hooded Crows and the appearance of mammalian predators the density of the Coot breeding population will be lower. Except for the influence on density, predators should also affect the production of hatchlings and breeding success of Coots — both negatively. Nevertheless, the effect of lower density may compensate or even counterbalance the influence of predation (Page et al. 1983) e.g. through lower intra-specific competition. Further, if predation indeed strongly affects the population of Coots, then, despite the cause, I expected clearly uneven nest distribution to the advantage of more inaccessible areas (i.e. islands).

In this paper I focused on the factors affecting the persistence of the population of Coots inhabiting a semi-natural fish pond. There were two main aims: 1) a comparison of population parameters from the 2002–2003 and 1980–1982 breeding seasons (Jankowski 1985) and 2) an analysis of the number and density of Coots in both periods in the context of the change of the number and species composition of predators.

STUDY AREA

Data on the Coot come from a study carried out between April and July in 2002 and 2003 at the „Słoneczny Górny" pond, located in the Milicz Ponds reserve (SW Poland). This is one of the largest nature reserves in Poland (51°33′N, 17°21′E) and a very important breeding area for waterbirds in Central Europe, protected in the RAMSAR convention and being one of 13 unique water areas in the world, qualified for the ONZ Living Lakes program. The reserve consists of several clusters of ponds, of which „Stawno" is the wildest and the most valuable part. The whole cluster consists of 30 ponds with an area of less than one hectare to 270 ha. The „Słoneczny Górny" pond (170 ha) (a part of the „Stawno" cluster) has 13–15 reed islands, of which only 5 have solid ground and trees. Nevertheless, except for one island (without Coot nests) these trees (mainly willows) were low and sparse. Along the SW shore the reeds grow in a strip of up to 200 m wide. Along other shores they grow irregularly in strips of up to 20 m wide (Fig. 1). The pond area was split into three distinctive sub-areas: the main strip of reeds (MS) (along the SW shore), a narrow strip of reeds (NS) (along other shores) and islands (I) (Fig. 1). These areas differed mostly in
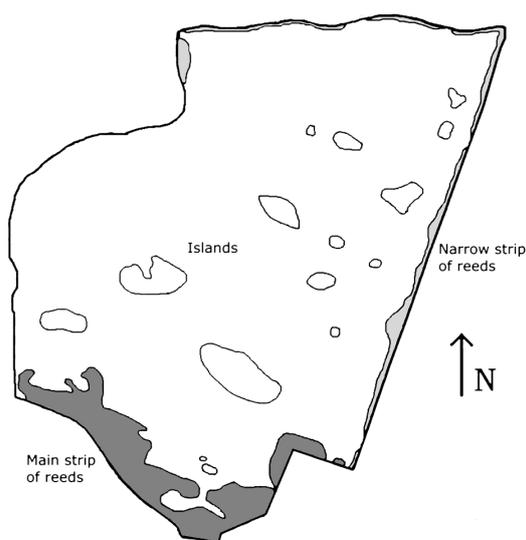
Fig. 1. Pond „Słoneczny Górny" in the Stawno cluster of the Milicz Pond reserve.

their distance to the bank of the pond, which is overgrown with tall trees (mainly oaks, alders and ashes), so they differed in penetrability. As a result, nests built in the NS were discernible from the trees and the most easily accessible.

METHODS

In 2002–2003 nests were searched starting in early spring, i.e. as soon as the Coots started to pair and form territories. Despite the fact that the Coots did not start their second broods, nest searching was continued until the end of July. Coots are highly territorial birds, building big nests usually about 5 meters from the edge of reeds (or other water plants) (mean 5.1 m, SD = 3.51). Therefore, the chance of oversight or any other mistake while defining territory boundaries and nest positions was very small. Moreover, because Coots only sporadically venture deep into the reeds, their density was calculated in relation to the length of the waterline (water/reeds ecotone). The birds were not individually marked. Therefore, if a pair failed and a new nest was found in the same territory such nest was considered as belonging to the same pair (renesting). No pair tried to renest two times. If a pair failed and renested successfully, it was considered successful. Nevertheless, the success and losses of first broods only is also presented separately.

In all nests the eggs were individually marked with a waterproof pen in the order of appearance.

In nests where eggs had already been found the method of follicle age assessment, by sinking the eggs in water (so called egg flotation test) (Walter & Rusch 1997), was used to assess their age and order of laying. The laying date was counted by subtracting one day for each egg laid in unfinished clutches. Besides, in case of any uncertainty, 23 days were subtracted from the hatching date in nests of 7 eggs or fewer and 24 days in nests of 8 or more. A clutch was considered complete if, during two consecutive visits, the number of marked eggs had not changed and if during the second inspection (no later than 2 days after the first visit) the nest had not been deserted. The nests were always controlled after thunderstorms to detect flooding. Adult Coots continually modify their nests and, except for the first few days of laying, keep the eggs warm. Hence, a brood was considered deserted if the eggs were left cold and the nest did not bear any traces of use. Nest controls were continued until the end of hatching.

Dumped eggs were not counted in clutch sizes. Nest parasitism was detected with the use of several criteria, in the order: more than one egg a day, a new egg laid two or more days after clutch completion, the distinctiveness of egg features (color of the background, spotting, size and shape). In such cases hatching date delay (three days or more) might be used as another probability determinant of parasitism. Such techniques, with small modifications, had been used effectively in many studies before (e.g. Yom Tov 1980).

Broods with at least one hatchling were regarded as successful. Coots do not remove eggshells but crush them in the nest, incubating other eggs and warming chicks. Therefore, the presence of many small shell fragments crushed inside the nest was sufficient evidence to assume that at least one chick had hatched. The lack of shells or big uncrushed pieces of shells with the rest of the yolk and/or blood in the nest were evidence of a loss. The time span required from laying to hatching was another probability determinant of failure. Moreover, the type of nest destruction and traces on the shells (holes, crushing), regularity of egg robbery, traces in the nest and its surroundings (e.g. hair, feathers) or direct observation were sufficient information to find the culprit.

For a comparison of breeding synchronies between the periods I used an index of breeding synchrony (SI) (Kempenaers 1993), which gives the average percentage of females that are fertile on any given day during the period when all females in a population are fertile. Nevertheless,

Table 1. A comparison of population parameters from the 2002–2003 and 1980–1982 (after Jankowski 1985) breeding seasons. x — means, [a] — including renesting, [b] — excluding renesting.

Parameter	1980–1982	2002–2003	Statistics
No. of pairs	90–180	53–70	$G_1 = 84.35$, $p < 0.001$
Clutch size (x ± SD)	7.0 ± 1.65	6.55 ± 1.49	$t_{468} = 2.61$, $p = 0.009$
Pairs with breeding success [a]	x = 70.6%	x = 73.7%	$\chi^2_1 = 0.028$, $p = 0.87$
Pairs with breeding success [b]	x = 41%	x = 73.7%	$\chi^2_1 = 35.74$, $p < 0.001$
Lost broods [a]	x = 54%	x = 32%	$\chi^2_1 = 20.99$, $p < 0.001$
Lost broods [b]	x = 59%	x = 26%	$\chi^2_1 = 35.74$, $p < 0.001$

because of the lack of complete data from the 1980s I accepted a constant number of 15 fertile days for all females in both periods. This value was counted assuming that the fertility period of females starts 5 days before the first egg is laid (Chu et al. 2002) and finishes when the penultimate egg is laid in the biggest clutches found (i.e. 11 eggs).

All chi-square and G tests with df = 1 are presented with the Yates correction. The requirements of normality and homogeneity of variances were met wherever needed. The data from 1980–1982 come from Ph.D. dissertation of Jankowski (1985). Source data was not used. All values i.e. numbers, means, SDs were copied without changes or counted directly from the data available in the paper. The exception was the analysis of brood synchrony for which the data was read from the graphs.

RESULTS

During 2002–2003 over two times fewer breeding pairs on average were found than during 1980–1982 (Table 1). Also, the average clutch size was smaller (Table 1). At the same time, almost twice as many first broods were successful in the 2000s as in 1980s and, including renesting, a similar number of pairs had breeding success (Table 1). In both periods pairs with success produced on average a similar number of chicks (Table 2) (t = 1.31, p = 0.19, df = 405). Nevertheless, from among the eggs laid in the whole population, more eggs hatched in the 2000s (Table 1)

($\chi^2 = 19.72$, $p < 0.0001$, df = 1). Analogically, the number of lost nests had decreased since the 1980s, both including and excluding renesting (Table 1).

In 2002–2003 laying began on average 9 days later than in 1980–1982 and finished 28 days earlier (Fig. 2). As a result, even considering only the periods of first brood beginnings, the seasons 2002–2003 were much shorter (1980s: mean = 69 days; 2000s: mean = 44 days) and the average breeding synchrony increased (1980s: SI = 21%; 2000s: SI = 37%). During 2002–2003 the highest density was observed on the islands and the lowest in the narrow strip of reeds, though significant variability between the sub-areas was only in 2003 (2002, $\chi^2 = 3.77$, df = 2, p = 0.15; 2003, $\chi^2 = 24.98$, df = 2, p < 0.0001) (Table 4). The location of the nests significantly affected breeding success; however, relatively the most successful pairs were living on islands and the least successful were pairs inhabiting the narrow strip of reeds (Table 3 and 4).

The laying date did not affect significantly breeding success (Table 3). Considering the location of the nests, however, late broods were more vulnerable to predation than the early ones, especially in MS. Nevertheless, this result was marginally insignificant (ANOVA: $F_{2,127} = 14.78$, p = 0.068) (Fig. 3).

In 2002–2003 Hooded Crows were the main Coot predators during incubation. Other predators, such as the Raccoon Dog or American Mink, were of little importance (3 nests). These mammals were absent during the 1980s when predation was twice as intensive ($\chi^2 = 21.65$, p < 0.0001,

Table 2. Hatchling production during 1980s and 2000s. [a] — Jankowski 1985.

Year	No. of eggs	No. of hatchlings		No. of hatchlings /pair	No. of hatchlings /pair with success
		N	%		
1980–1982[a]	3647	2062	56.54	4.68	6.51
2002–2003	756	564	74.6	4.24	6.27
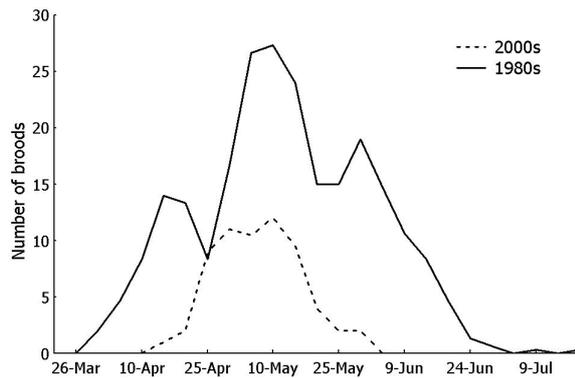
Fig. 2. The breeding phenology of Coots in 1980–1982 (Jankowski 1985) and 2002–2003.

Table 4. The number of pairs with breeding success and the number of pairs per 1000 m of waterline and in three areas of the pond.

Sub-area	Density[a]		Pairs with success	
	2002	2003	2002	2003
Main strip of reeds	6.06	2.83	10	5
Islands	6.10	13.13	22	42
Narrow strip of reeds	2.67	1.56	9	2
All	4.72	6.23	41	49

df = 1; Table 5) and its share in the sum of losses was higher (79% vs. 67%). During the 2000s five nests were lost due to the death of one or both parents. In 2002 four such cases occurred between May 16 and 27, and the nests were less than 100 m from each other. In 2003 two such cases occurred 80 m from each other on the same day. Examination of the dying bird revealed paresis of the neck and wing muscles and movement disorder.

DISCUSSION

Common waterbirds, such as Coots, are suitable subjects for testing hypotheses concerning the state of ecosystems and many types of relationships between species. This study shows how a relatively common species, inhabiting a seemingly stable ecosystem of fish ponds, responds to changes in the number and species composition of predators during two periods separated by a total of 20 years. Despite the fact that the Coot population living in the Milicz Ponds did not

diverge meaningfully in terms of the breeding parameters from other populations (Cramp & Perrins 1994), it had shrunk more than twice since the 1980s.

This change, however, not necessarily must be connected with changes in the ecosystem but it may be a part of a natural fluctuation. Nevertheless, during this time, similar trend has been noted in other Central European areas (Houdková & Musil 2003), and the negative influence of non-native predators (e.g. the American Mink) turned out to be so with reference to all affected water ecosystems in Europe (Nordström et al. 2002). Therefore, the coexistence of both phenomenons: the decrease of the Coot number and changes in the number and species composition of predators deserves special consideration.

In the Barycz Valley predation was the most important factor affecting the breeding success of Coots. Nevertheless, its intensity had decreased since the 1980s (Jankowski 1985), the same as the size of the Coot population. Between the 1980s and the 2000s the number and species composition of predators had changed. Non-native species, such as the Raccoon Dog, American Mink or Raccoon appeared and spread. These mammals are good swimmers and are especially dangerous to waterfowl. In the case of the Coot this is so to such a large extent that the persistence of its

Table 3. Relationship between breeding success and nest location, year and laying date. Table shows parameter estimates of Generalized Linear Model with binomial dependent variable and logistic link function. [a] — this parameter is set to zero because it is redundant.

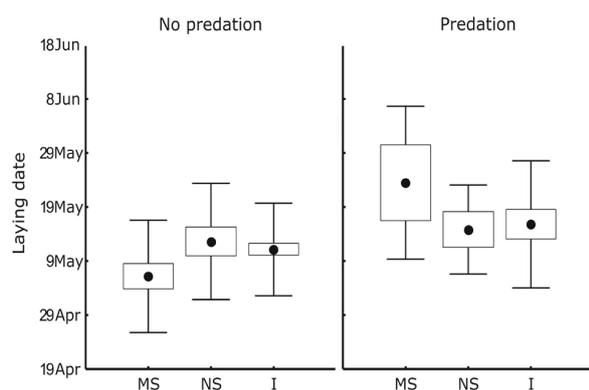| Parameter	B	SE	Test		
			Wald χ^2	df	p
Intercept	10.267	0.5533	50.242	1	0.022
Year 2002	0.936	0.4503	40.323	1	0.038
Year 2003	0[a]				
Location Main strip	-10.256	0.5585	50.059	1	0.025
Location Narrow strip	-10.365	0.4945	70.619	1	0.006
Location Islands	0[a]				
Laying date	-0.070	0.0867	0.657	1	0.418

Fig. 3. Laying dates of broods destroyed and non-destroyed by predators (non-destroyed broods — successful and lost due to other causes) in three sub-areas (MS — main strip of reads, NS — narrow strip of reeds, and I — islands). The chart includes means (dots), standard errors (boxes) and standard deviations (whiskers).

populations can be impossible without immigration (Ferreras & Macdonald 1999). During 2002–2003, however, the influence of the Mink in the studied area was slight, at least in the context of breeding success. This could have resulted from the fact that Minks, just as Raccoon Dogs, are generalists, hunting the most abundant and available prey in the given conditions (Brzeziński 2007). Therefore, the attractiveness of the Coot as potential prey could have decreased since the 1980s as its number had decreased. Consequently, the present level Coot density can be the result of the influence of mammalian predators.

During the period of investigation the number of Hooded Crows had decreased from 51–55 pairs inhabiting the whole Stawno area (Grabiński 1996) and 7–10 pairs living only nearby the Słoneczny Górny pond in 1980–1982 (Jankowski 1985), to fewer than 20 pairs in 2002–2003 in the whole Stawno area. All the same, Crows have remained the main nest destroyers, as other species robbed eggs only accidentally. It seems that the success of the Crows resulted from a high degree of cooperation. For example, in 2002 in only two days they robbed five nests in the narrow strip of reeds in a distance of less than 200 m. Crows were looking out for Coot nests from the trees, thus they seldom robbed nests on the islands. Hence, Coots

breeding on islands were the most successful and this explains why density on the islands increased and in other sub-areas it decreased in 2003. Many studies showed a strong relationship between Coots and crows. In France (Salathe 1987), for example, Carrion Crows *Corvus corone* stole 18% of Coot eggs. In Poland 69% of the shells found in crow nests were Coot eggs (Zduniak 2006). It is surprising why despite a smaller number of Crows and generally a smaller impact of predators on the breeding success of Coots, the breeding success of Coots had not notably increased. The results show that the success of first broods was indeed much higher in the 2000s but higher losses in 1980s were compensated by more frequent renesting. Thus, it appears that renesting in Coots is an adaptation to the predation of Crows. This suggests in turn that Crows could not have contributed significantly to the observed decrease of the Coot population.

Another premise indicating the strong adaptive abilities of Coots to the pressure of predators is the fact that lower density in 2002–2003 was not equivalent to lower but higher nesting synchrony. Besides, in these circumstances the breeding seasons had shortened. Even if delayed season beginnings and higher synchrony could result from low temperatures in the early spring (Wiklund 1984), much earlier endings, the lack of second broods and rare renesting could not. This could result from a more intensified predation among late breeders (Fig. 3), which is frequently connected with an increased demand for food of the growing offspring of predators (Wiklund 1984).

The remaining causes of losses were of marginal significance. Nevertheless, those that stemmed from the deaths of adult birds can have potentially high importance. These birds bore the traces of poisoning. Specific symptoms observed in a dying bird and the lack of any injuries in already dead birds indicate that the cause was botulism (Friend & Franson 1999). The habitat of shallow fish ponds is especially well predestined for the development of this disease, which in some circumstances can result in mass scale mortality of birds (Rocke 2006).

Table 5. The causes and the level of losses during incubation (including renesting). ᵃ — Jankowski 1985, N — the number of nests.

Year	N	All losses	Predation	Waving	Nest desertion	Death of adult
1980–1982[a]	696	54%	43%	5%	6%	–
2002–2003	133	32%	22%	3%	4%	4%

The Coot appears to be a very flexible species. Although there were no second broods and the average clutch size was smaller in the 2000s than in the 1980s, hatchling production per pair was similar and the population as a whole produced more hatchlings relative to the number of eggs laid. Therefore, it seems that despite the fact that the Coot population is smaller today, its productivity is better than 20 years earlier. Future research could explain whether the state observed in 2002–2003 became established or it was only temporary. Because there is no data on adult mortality and the recruitment of the young, such research could explain whether the low density in 2002–2003 was an adaptive reaction to predation or an effect of predation.

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STRESZCZENIE

[Czy spadek liczebności łyski od lat 1980-tych jest powiązany ze zmianami składu gatunkowego drapieżników i pogarszającą się produktywnością lęgów?]

Badano ekologię lęgową łyski na stawie Słoneczny Górny w rezerwacie Stawy Milickie w Dolinie Baryczy (Fig. 1) w latach 2002–2003 i porównywano otrzymane wyniki z wcześniejszymi badaniami (Jankowski 1985) (Tab. 1). W okresie tym zmieniły się zarówno liczebność jak i skład gatunkowy potencjalnych drapieżników łyski. Pojawiły i rozprzestrzeniły się obce gatunki ssaków drapieżnych tj. norka amerykańska, jenot i szop pracz. Jednocześnie liczebność wrony, głównego drapieżnika gniazd łyski, spadła. W porównaniu z latami 1980–1982 liczebność łysek spadła przeszło dwukrotnie (z 90–180 do 53–70 par na rok). Zmniejszeniu uległa także wielkość zniesienia. Sukces lęgowy par (uwzględniając lęgi powtarzane) i liczba piskląt wyklutych na parę pozostały bez zmian, przy czym w latach 1980-tych łyski zdecydowanie częściej powtarzały lęgi. W efekcie, w proporcji do liczby złożonych jaj, w latach 2002–2003 badana populacja łyski produkowała znacznie więcej piskląt (Tab. 2). Długość sezonu lęgowego uległa znacznemu skróceniu (Fig. 2), a synchronizacja lęgów wzrosła. Ponadto w przeciwieństwie do wcześniejszego okresu, w latach 2002–2003 nie notowano drugich lęgów. W latach 2002–2003 poziom drapieżnictwa spadł w porównaniu do lat 1980-tych, jednakże wciąż stanowiło ono główna przyczynę strat w lęgach (Tab. 5). Pojawiła się także inna kategoria strat w lęgach, wynikająca ze śmiertelności ptaków dorosłych (Tab. 5). Łyski gniazdujące na wyspach rzadziej traciły lęgi (Tab. 3, 4), co było związane ze względnie niskim drapieżnictwem wrony. Mniejsze straty notowano także u par przystępujących do lęgów wcześniej (Fig. 3). Drapieżniki czworonożne nie odrywały istotnej roli w sukcesie lęgowym łysek. Niemniej jednak sugeruje się, iż niskie zagęszczenie w latach 2002–2003 mogło być konsekwencją i reakcją na presję tych właśnie drapieżników.

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