Breeding ecology of the Mallard on a flooded area of the Warta river mouth, Poland

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Introduction

Mallard *Anas platyrhynchos* are the most common and most hunted ducks in Poland. Extensive drainage, regulation of water courses and increasing human disturbance account for shrinking of the preferred habitats of this species, particularly during the breeding season. However, mallards show a high adaptability to environmental changes; it is thus difficult to state precisely what impact man is having on this species despite the large extent of habitat changes. This species therefore deserves special attention from both a theoretical and practical point of view. An important issue is the management of this species and, in particular, the development of sound regulation for hunting, and plans for habitat improvement.

The objective of this paper is to provide a detailed description of the reproduction of a Mallard population in a river floodplain.

There is a large body of literature on this species in Europe but few papers provide a comprehensive picture of mallard reproduction. Many detailed papers describe selected stages in the reproduction of the species (Eygenraam 1957; Boyd & King 1960; Melde 1963; Hilden 1964; Ogilvie 1964; Fog 1965; Grenquist 1965; Balat 1967; Mednis 1968; Bengtson 1972). North American studies of Mallard reproduction have been reported by Keith (1961), Coulter and Miller (1968) and Dzubin and Gollop (1972).

Study area

The study was carried out on a flooded area at the confluence of the Warta and the Oder rivers in western Poland. This is a combination of the natural river mouth with an artificial reservoir. The reservoir covers an area of about 5000 ha and is bordered by high dikes. It stores the excess of water from the river and collects water from meadows located in the river valley. The reservoir is filled with water for about eight months of the year. Changes in water level are frequent and irregular. Annual differences between lowest and highest water levels can be up to 4 m (Fig. 1). Though irregular, these changes undergo some annual rhythm, the water level being highest in spring and lowest in summer.

In 1977, a waterfowl nature reserve called Slonsk was established in this reservoir. It occupies 4166 ha, including 1100 ha under strict protection.

At a high water level, this area resembles a shallow lake with a few small islands and willow trees and scrub emerging from the water. At low water, the area becomes dominated by meadows and pastures invaded by luxuriant vegetation which is grazed by cattle and geese.

The vegetation consists of relatively few species. Most of them are very abundant and form dense carpets. Characteristic plants include *Rorrippa amphibia, Phalaris arundinacea, Polygonum ssp., Rumex hydrolapathum* and *Oenanthe aquatica.* Willows *Salix ssp.,* in the form of trees and shrubs, are common. The reed *Phragmites communis* occupies only small areas. Dominance structure of the vegetation depends on water level, and year-to-year differences can be very large.

Potential avian predators of Mallard and their nests were Hooded Crow *Corvus corone* (60–100 pairs, and visitors); Magpie *Pica pica* (20–30 pairs); Marsh Harrier *Circus aeruginosus* (10–20 pairs); Goshawk *Accipiter gentilis* (frequent visitors) and White-tailed Eagle *Haliaeetus albicilla* (1 pair, and visitors). Among predatory mammals, there were fox *Vulpes vulpes,* polecat *Mustela putorius,* stoat *Mustela erminea,* pine marten *Martes martes,* beech marten *Martes foina* and *Mustela nivalis.* Amphibious animals were abundantly represented by muskrat *Ondatra zibethica* and water vole *Arvicola terrestris.*

Since 1968, artificial nest baskets were provided for ducks on willow trees. Their total number ranged between 100 to 250 in different years.

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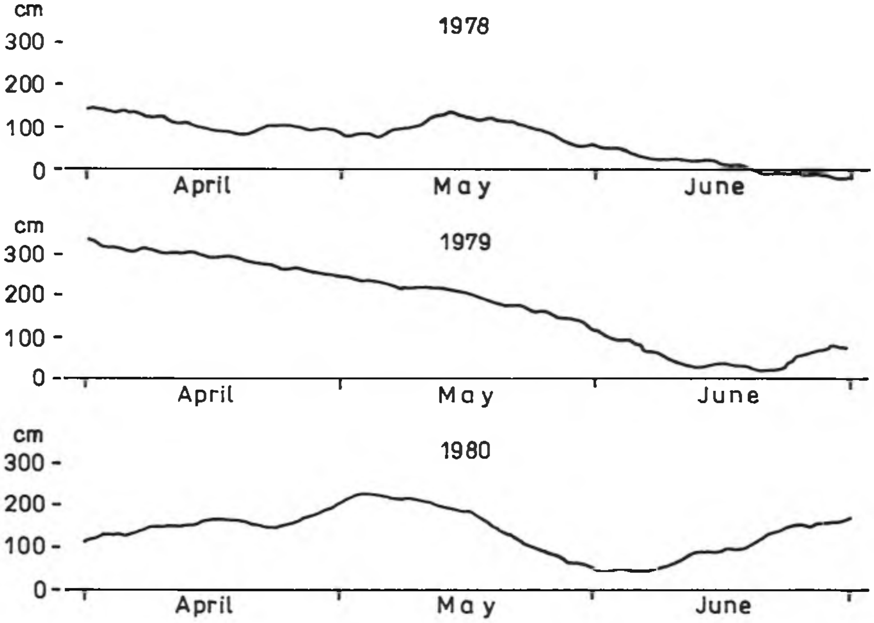


Figure 1. **Changes in the level of water over the breeding season.**

Materials and methods

The study was conducted in 1978–1980, between 1 April and 31 July. The scheme of the study is shown in Fig. 2.

Breeding population

The size of the breeding population of Mallard was assessed using male counts (Dzubin 1969). As the study area was large, sampling plots were used, and the results were extrapolated to the whole study area. Sampling plots covered 20–56% of the study area, depending on the year.

Sex ratio of the breeding population was determined during the first ten days of April – that is, immediately prior to breeding.

Female mortality during the breeding period was estimated using the number of dead birds or their remains found during visits to nests and their proportion to the number of nesting females in the sampling plots.

Nests

To obtain results representative of different habitat conditions, sampling plots were selected so that they differed in nest density, duration of flooding and the accessibility to predators and man. Plots were visited every 12 days on the average and successful nests were visited an average of 3.3 times. A total of 756 nests was found, of which 696 were visited. 191 incubating females were captured and ringed. The date of nest initiation was estimated by direct back-dating of nests found during laying, or by floating eggs in water if nests were discovered during incubation (Mednis 1972; Majewski 1980). Only complete clutches were used to estimate clutch size. Clutches of less than 4 and more than 14 eggs were excluded. The former was considered as partially destroyed and the latter as mixed clutches, following the assumptions made by Bezzel (1966) and Bengtson (1972). Only the nests with known fate were used for the analysis of nest losses. The category of fate unknown included 48 nests. Nest in which at least one egg hatched were considered as successful.

Mortality of young

Survival of ducklings up to the flying stage was estimated from changes in the brood size. The key by Gollop and Marshall (1954)

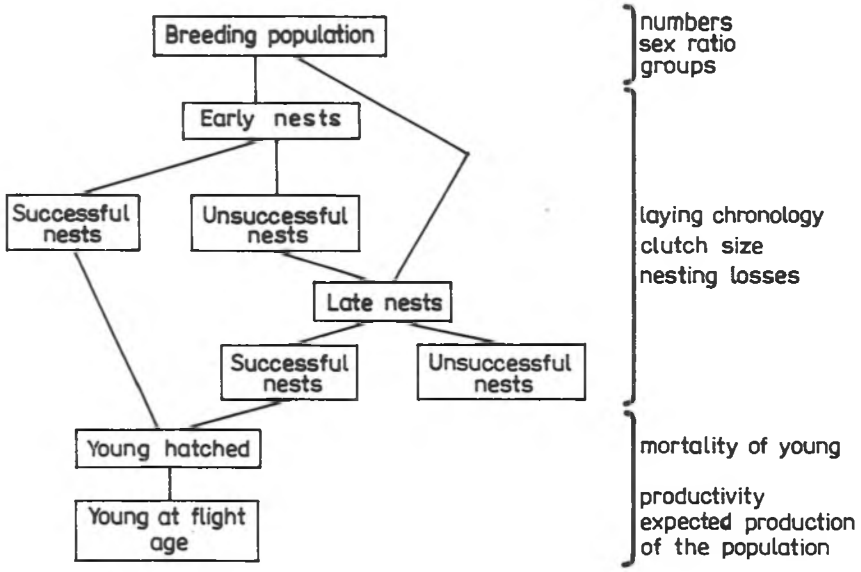


Figure 2. A model for the study.

was used to age ducklings. Because dense vegetation in the study area hampered observations, young 5–8 weeks old were pooled on the assumption that survival of birds in this age group was equivalent to their survival at week 8, the age of flying. Survival until flight age was calculated from the ratio of the mean brood size at an age 5–8 weeks to the mean number of eggs hatched.

Productivity

Productivity was expressed as the number of ducklings reaching flight age per breeding female. It was calculated by measuring successive stages of the reproductive cycle. Two assumptions were made for renests. The first one was that all females that lost their first clutch renested. Literature data on this subject are equivocal. Using the number of breeding pairs, nesting success, and the number of young, Keith (1961) has calculated that all Mallard that lost first nests laid eggs again and, in addition, some of the females that lost replacement eggs renested once more. Coulter and Miller (1968), who marked ducks individually, have found that at least 57% of Mallard renested. According to Bentson (1972), all Mallard that lost first clutches in his study area renested.

The second assumption was that early nests (1 April – 10 May) represent the first nesting attempt and late nests (11 May – 10 June) represent renests. In fact, some renests may be among early clutches, while some first nests may be among late clutches.

Results

Characteristics of the breeding population

Numbers

There were large year-to-year changes in the size of the breeding population from 1820 pairs in 1978 to 395 pairs in 1979 and 580 pairs in 1980. In 1979, when a drastic decline in numbers occurred, the water level in the two rivers was extremely high (Fig. 1). Most suitable nest sites were flooded in April, after a severe winter. This situation lasted until the first days of May. Large areas of meadows and crop fields beyond the reservoir were covered with shallow flood water attractive to ducks, resulting in a higher density of Mallard there than in the study area. Deep water in the reservoir also prevented ducks from foraging there (Fig. 1). An opposite situation was created on shallow waters beyond the reservoir.

In 1980, the water level was normal; thus, breeding and foraging conditions were good in the study area, but the Mallard population did not increase much.

Sex ratio and population components

In the first days of April, prior to the onset of laying, the number of males was higher than that of females in the breeding population. The proportion of males in different years was 56.3%, 55.0% and 55.5% (Table 1). Year-to-year differences were not significant, though the density of the population and habitat conditions differed greatly.

Group structure prior to breeding was very similar from year to year. Pairs of birds predominated, accounting for 82% of the groups, on the average. The other groups were made up of several males with a female, or only of males. In this period, a characteristic feature was lack of lone females, or groups of two or more females (Table 1), which were characteristic of the period of migration in March.

The structure of groups changed over the breeding season (Fig. 3). The apparent number of females declined as they were incubating or rearing young. In the period of peak laying (first half of May), the proportion of lone males was high each year. This was related to the breaking of pair bonds at the beginning of incubation (Coulter & Miller 1968; Dzubin 1969). However, the proportion of pairs in this period was also high, averaging 53% (Table 1). A high proportion of pairs was maintained almost throughout the breeding season (Fig. 3).

Rapid changes in groups were observed in late May and early in June. At that time, males tended to form large groups made up of 10–70 birds, showing no interest in females. Most frequently, they concentrated in the places of their future moulting.

Nesting sites

Although the study area was generally attractive to ducks (many shoals, foraging sites, and no human disturbance), nesting sites were very limited. Ducks occupied old pollarded willow trees, where nests were situated between branches, in rotten depressions, holes, and artificial nest baskets fastened on trees (Fig. 4).

Sparse cover provided by branches and rims of rotten willows did not conceal the nests. Thus, these nests, except for those in holes and baskets, were considered as open and uncovered.

Mallard rarely nested on the ground. The soil surface was either submerged or freshly emerged, covered with mud, with no plant cover. In 1978 and 1980, nesting on the ground was possible, as water dropped early and vegetation appeared. Nonetheless, ducks preferred trees as nesting sites. In the

Table 1. Compositions of groups and their proportion (%) in the groups observed. Sex ratio and number of pairs in the breeding population.

	Pre-laying period 1–10 April			Mid-laying period 1–15 May		
	1978	1979	1980	1978	1979	1980
Type of group:						
1 ♂+ 1 ♀	80	83	83	50	53	56
2 ♂+ 1 ♀	6	6	5	3	3	5
3–5 ♂+ 1 ♀	2	3	1	1	2	3
6–12 ♂+ 1 ♀	–	–	–	–	–	<1
1 ♂	11	7	7	39	40	27
2 ♂	1	1	3	4	2	6
3 ♂	–	–	<1	2	<1	1
4–10 ♂	–	–	–	<1	–	<1
1 ♀	–	–	–	<1	–	1
Number of groups observed	568	217	276	863	230	355
Number of individuals in groups observed	1134	443	553	1477	386	688
:	129:100	122:100	125:100	210:100	190:100	193:100
Number of pairs over the study area	1978:– 1820		1979:– 395		1980:– 580	

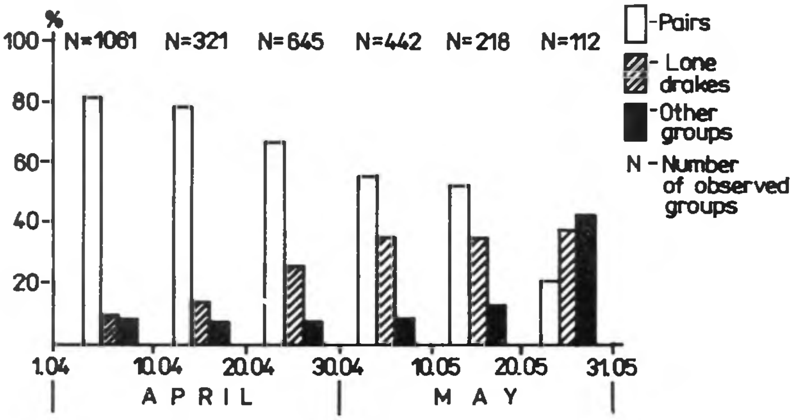


Figure 3. Changes in the proportion of different groups in the breeding population during April and May.

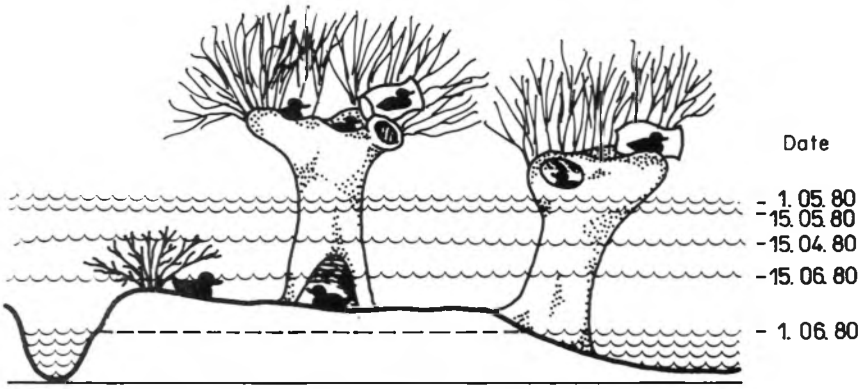


Figure 4. Nesting sites in relation to changes in water level in 1980.

unflooded habitats adjoining the study area, Mallard nested both on willow trees and on the ground.

Mallard eggs were also found in abandoned nests of Greylag Geese *Anser anser,* Coots *Fulica atra,* Crows, Magpies and Cormorants *Phalacrocorax carbo.*

Marked nest sites were used every year by the same or different females. Some nests (17%) were used twice a year (Table 2). The use of nest baskets by Mallard was very high, reaching 80%, 52%, and 61% in successive years. Some (18%) were used twice or even three times a year (Table 2).

Table 2. Use of natural and artificial nesting sites.

Year	Number of natural nests	Mean number of successive clutches in a nest	Number of nest baskets used	Proportion of nest baskets used	Mean number of successive clutches per basket used
1978	95	1.2	181	80%	1.3
1979	14	1.0	115	52%	1.1
1980	79	1.2	143	61%	1.2

Chronology of laying and hatching

The period of egg laying extended from early April to early June (Fig. 5). An important feature was a high proportion of clutches started in the last ten days of May. Probably these were renests, likely to be common because of low nesting success.

Hatching chronology did not precisely reflect laying chronology. Peak hatching occurred from the last ten days of May until 20 June (Fig. 6).

Clutch size

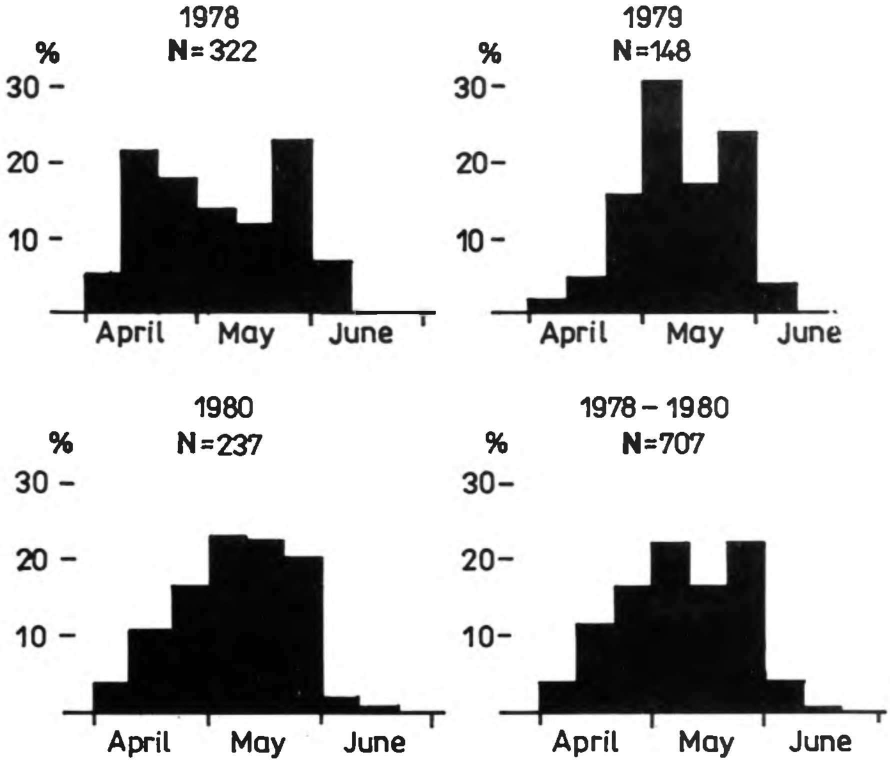
Most frequently (72% of nests), clutch size ranged form 6 to 9 eggs. The mean clutch size in the study period was 7.9 eggs (Fig. 7).

Early clutches were significantly larger than late clutches in 1978 and 1979 (Table 3). Over the breeding season, the mean clutch size dropped from 9.8 eggs at the beginning to 6.5 eggs for the latest clutches (Fig. 8).

Mixed one-species clutches were recorded only in 1978, when the density of breeding pairs was highest. It has been assumed that only clutches of more than 14 eggs are mixed. Smaller clutches could also include mixed ones but it was difficult to distinguish them as the parasitism usually occurred during laying by the primary female. Although the density of nests in the study area was high, mixed clutches by this definition accounted for only 4%. These were clutches containing 15, 17, 17, 18, 19, 19, 29, and 27 eggs.

Nesting losses

Nesting losses varied according to whether the nest was natural or artificial and, to a lesser extent, from year to year. Losses of natural nests in successive years were 79%, 77%, and 76%. Losses of nests in baskets were lower at 60%, 51%, and 69% respectively (Table 4).



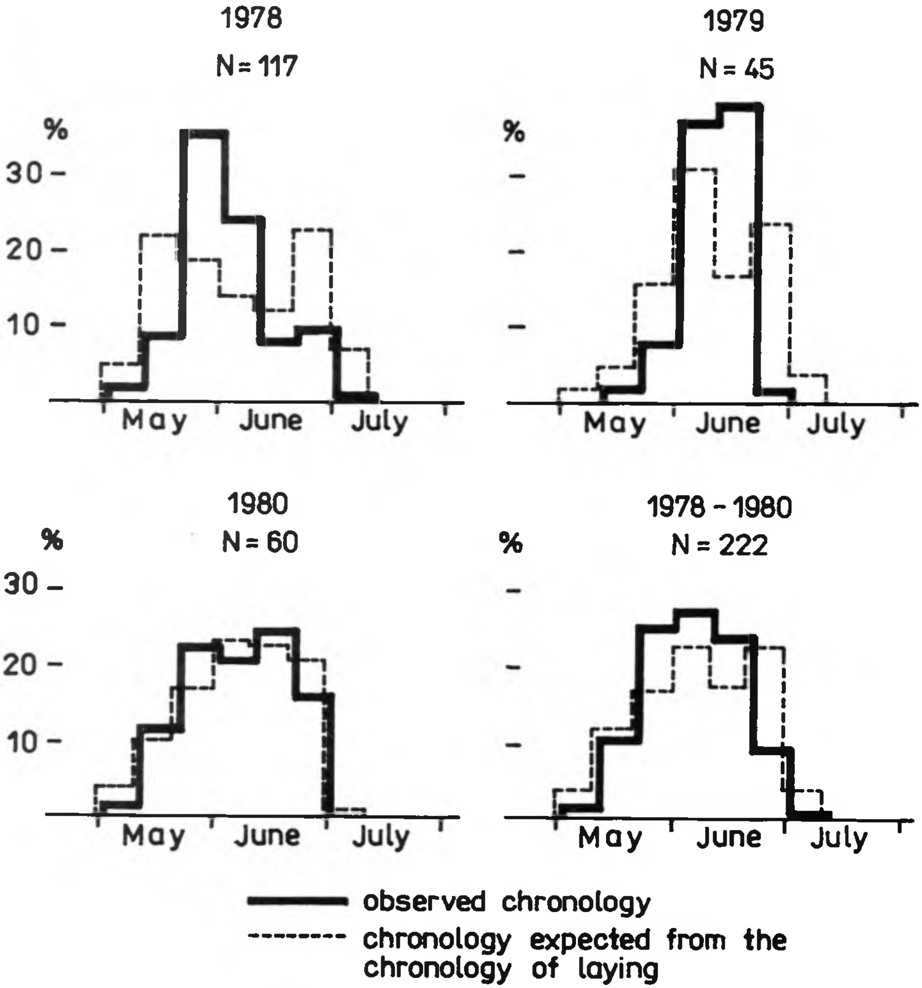


Figure 6. Chronology of hatching.

Table 3. Clutch size in relation to the date of laying within and between years

Year	Laying period*	Number of clutches	Mean clutch size**	SD	Combined mean clutch size***	SD
1978	early nests	137	8.8	2.1	8.3	2.0
	late nests	61	7.1	1.4		
1979	e. n.	49	8.4	2.0	7.6	2.1
	l. n.	40	6.7	1.8		
1980	e. n.	52	7.8	1.7	7.5	1.6
	l. n.	45	7.4	1.3		

* early nests – initiated 1 April – 10 May
late nests – initiated 11 May – 10 June

** differences in clutch size between early and late nests significant ($p<0.001$) except in 1980.

*** mean annual clutch size in 1978 significantly higher than in 1979 ($p<0.05$) and 1980 ($p<0.001$).

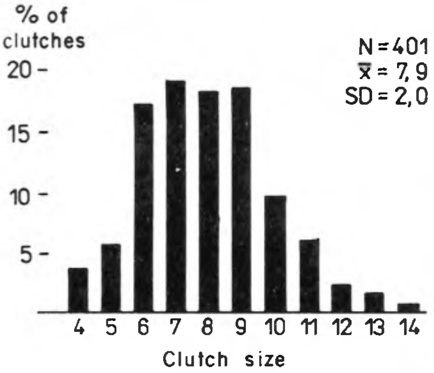


Figure 7. Distribution of clutch sizes.

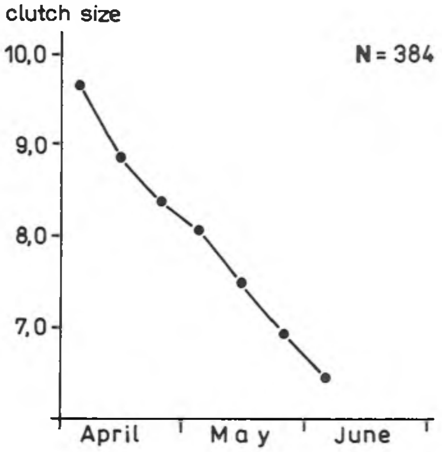


Figure 8. Clutch size in relation to the date of laying.

Table 4. Nesting losses

	Early nests*			Late nests**			Total		
	1978	1979	1980	1978	1979	1980	1978	1979	1980
Natural nests:									
Proportion of unsuccessful nests	71%	86%	71%	88%	100%	82%	79%	92%	76%
Number of nests	63	7	48	49	5	38	112	12	86
Nest baskets:									
Proportion of unsuccessful nests	45%	44%	74%	83%	64%	63%	60%	51%	69%
Number of nests	129	55	80	83	33	57	212	88	137

* initiated 1 April – 10 May
** initiated 11 May – 10 June

Predators were the chief cause of nest loss, accounting for 80–91% of all losses (Table 5). Desertion of nests accounted for 0–15% of failures. This figure, however, may be underestimated because some deserted nests may have been destroyed by predators between two successive visits. Nest loss caused directly by changes in water level (included in "others" in Table 5) were strikingly low.

Nest losses also include dead eggs and eggs disappearing during incubation. The former were rare and, among clutches that hatched, they varied from 0 to 1.8% in natural nests and from 0.4 to 1.7% in nest baskets. Partial nest losses during incubation happened rather frequently, accounting for 8.3–10.7% of eggs in natural nests and 2.2–6.8% in baskets, on the average (Table 6).

Table 5. Causes of nesting losses

	1978		1979		1980	
Causes of losses	Natural nests	Nest baskets	Natural nests	Nest baskets	Natural nests	Nest baskets
Predated	88%	80%	82%	86%	88%	91%
Deserted	3%	15%	3%	7%	–	9%
Others	9%	5%	9%	7%	12%	5%
Number of unsuccessful nests	88	127	11	45	65	95

Table 6. Partial nest losses

	1978		1979		1980	
	Natural nests	Nest baskets	Natural nests	Nest baskets	Natural nests	Nest baskets
Number of nests observed	27	77	–	44	15	35
Proportion of clutches with partial losses	30%	30%	–	11%	33%	26%
Proportion of clutches with eggs containing dead embryo	–	12%	–	5%	13%	3%
Number of eggs in nests observed	218	662	–	358	112	258
Eggs lost	8.3%	6.8%	–	2.2%	10.7%	5.4%
Dead eggs	–	1.7%	–	0.8%	1.8%	0.4%
Total losses of eggs	8.3%	8.5%	–	3.0%	12.5%	5.8%

Late nests suffered greater losses than early nests (Fig. 9). A great majority of losses occurred during egg laying. Among natural nests, 80% of all losses took place in this phase. For nests in baskets, this proportion was 66% (Table 7).

Thirteen females were found preyed upon in the sample plots. Dead females accounted for 2% of the nests in 1978, 1% in 1979 and 2% in 1980. These estimates should be fairly accurate because in nest cases large amounts of water surrounding islands should have prevented predators from removing carcasses.

Predators occurring in the study area were highly efficient at destroying nests of birds. Hooded Crows, the chief predator, were regularly seen preying on Mallard nests as well as nests of Coot, diving ducks *Aythya* and Black-headed Gulls *Larus ridibundus*. Magpies and Marsh Harriers were of minor importance because of their low numbers. Of 527 shells found on sample plots out of nests, 76% belonged to Mallard, 21% to Coot and 3% to diving ducks. It should be noted, however, that the study plots were selected with regard to high Mallard densities. Crows and Magpies also destroyed nests in baskets.

Mammalian predators occurred in the study area in the breeding season only in 1978. In later years, this area was flooded almost over the entire season; thus, nests were not available to them. Because of technical difficulties, mammalian predations were not distinguished from avian ones.

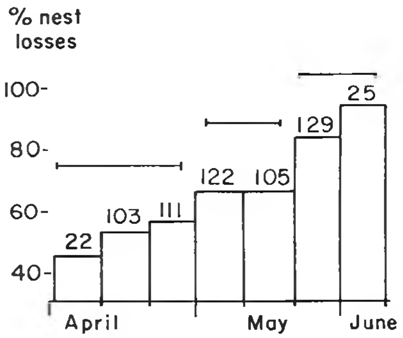


Figure 9. Nest losses and the timing of egg laying (1978–1980). Differences between groups joined by bars significant ($p<0.01$). Numbers above histogram columns are sample sizes.

Table 7. Proportion of nests predated in different stages of incubation.

	Nests predated	
Incubation stage	Natural nests	Nest baskets
Incomplete clutches or first days of incubation	80%	66%
First or second 10 days of incubation	16%	27%
Second ten or last days of incubation	4%	7%
Number of nests	111	207

Difference between proportion of losses for incomplete clutches in natural nests and nest baskets significant ($p<0.01$).

Mortality of young

Duckling mortality estimated from the size of broods was 24%, 35%, and 3% in successive years (Table 8). This method of mortality estimation does not include broods that completely disappeared. However, the proportion of broods composed of one or two ducklings, which may be an indirect indication of the number of females that lost all young, was as low as 4%.

Table 8. Mortality of young as determined from changes in the brood size (sample size in parenthesis)

	1978	1979	1980
Mean clutch size	8.3	7.6	7.5
Mean number of young hatched*	7.9	7.7**	6.9
Mean brood size at age 1–4 weeks	6.6 (39)	5.0 (11)	6.8 (50)
Mean brood size at age 5–8 weeks	6.0 (11)	5.0 (9)	6.7 (52)
Mortality of young	24%	35%	3%

* Mean weighed on the proportion of young from early and late nests (significant difference in clutch size) for natural nests and nest baskets separately and then weighed on the proportion of broods from natural nests and nest baskets for the whole population (significant difference in egg losses during incubation).

** Mean based on nests in baskets only because of small sample size for natural nests.

Production from the population

Productivity calculated from mean values for successive developmental stages in natural nests was 2.2 flying young per breeding female in 1978, and 2.7 in 1980 (sample size was small in 1979, so it is excluded from these calculations (Table 9)).

As nesting losses in baskets were lower, the reproductive output of this group was higher, and amounted to 3.7 young/female in 1978, 3.6 in 1979, and 3.7 in 1980.

The losses of first nests (early nests) were lower; thus, these nests contributed more to population production: 1.8 juveniles in 1978 and 1.9 in 1980 from natural nests; and 3.4 in 1978, 3.0 in 1979 and 1.9 in 1980 from nest baskets. Renests (late nests) had lower productivity: 0.6 in 1978 and 1.2 in 1980 from natural nests and 0.8 in 1978, 1.5 in 1979 and 2.5 in 1980 from nest baskets.

Extrapolation of the productivity estimates obtained for the sampling plots to the whole breeding population under study shows that approximately 4200 young Mallard reached flight stage in 1978, versus

Table 9. Population productivity calculated per 100 females

	1978		1980	
	First nests*	Renests*	First nests	Renests
Breeding pairs	100	70	100	70
Nesting losses	71%	88%	71%	82%
Female mortality	1%	1%	1%	1%
Successful females	29	8	29	13
Clutch size	8.8	7.1	7.8	7.4
Eggs laid by successful females	255	57	226	96
Partial egg losses in successful nests**	8.3%	8.3%	12.5%	12.5%
Young hatched	234	52	198	84
Mortality of young**	24%	24%	3%	3%
Young at flight age	178	40	192	81
Productivity per nesting attempt	1.8	0.6	1.9	1.2
Average productivity per female including renesting attempt	2.2		2.7	

* first nests according to early nests (1 April – 10 May), renests according to late nests (11 May – 10 June).

** due to small sample sizes, data for early and late nests were pooled.

1670 young in 1980. Per unit area, the reproductive output was 85 young/100 ha in 1978, and 33 young/100 ha in 1980.

The effect of nest baskets on the increase in the number of young, resulting from a higher breeding success, appeared to be small on the scale of the whole population, and the proportion of extra young from nest baskets was 5.9% in 1978 and 6.8% in 1980.

Discussion

Breeding population

According to Nowysz and Wesolowski (1978), the breeding population of Mallard in this area in 1969–1972 comprised 1800–2000 pairs. Thus, numbers in 1978 were not exceptionally high. Most studies have not recorded such abrupt changes in the number of ducks as those at Slonsk (Boyd & King, 1960; Michelson *et al.* 1968a and b; Dzubin 1969; Fiala 1972; Bengtson 1972). However, a similar situation was noted by Balser *et al.* (1968). During his 6-year study, two crashes in Mallard numbers occurred, both related to heavy flooding. A similar situation took place in Slonsk in 1979. Flood waters heavily limited the number of nest sites and, until the beginning of May, 2–3 m water levels precluded foraging by Mallard (Fig. 1).

The observations show that Mallard from the breeding population moved to adjacent areas covered with shallow water, thus providing suitable nesting and feeding conditions.

The flood of 1979 created conditions for a natural experiment on the effects of drastic habitat changes on the breeding population of Mallard. What factors would be most important in such situations: a strong attachment to the place of earlier nesting found for this population from ringing data; availability of nesting sites; or food resources? A mass emigration to an adjacent habitat shows that Mallard are characterised by a high adaptability in their selection of nesting sites. Under extreme conditions, this adaptability can outweigh a strong site tenacity. It seems that the available food resources were most responsible for the moving out. This is implied by the fact that the emergence of traditional nest sites during the mid-nest initiation period did not lead to a return of the ducks.

The severe winter before the spring of 1979 could also contribute to a reduction in Mallard numbers through poor wintering conditions and increased hunting pressure on wintering grounds. The literature available on the effects of winter losses on duck survival in Europe is not consistent. Haartman (1971) has shown that the number of Tufted Ducks *Aythya fuligula* in Finland heavily declined after severe winters. According to Grenquist (1965), the number of Mallard in Finland dropped by two-fifths of the normal stock after heavy winter. British data, however, does not suggest that Mallard are sensitive to hard winters, nor was the breeding population reduced after such winters (Boyd 1964; Boyd & King 1964). It can be suggested that the severe winter of 1978–9 could contribute to a decline in the size of breeding Mallard population in the study area, but not to the extent revealed by census data. This decline cannot be explained by reproductive output in the preceding season as it was similar in the successive study years (Table 9). The fact that the population increased only slightly in 1980 may have been due to low production of young in the entire population in 1979.

Large changes in numbers were coupled with small changes in the population structure in successive years. Sex ratio was similar from one year to another. It was also similar to that recorded in other, even geographically very distant populations (Eygenraam 1957; Bezzel 1959; Bellrose *et al.* 1961). The maintenance of a similar sex ratio when the density of Mallard population varied is interesting, taking into account that unpaired males could readily emigrate when habitat conditions were not favourable in 1979. Habitat-related changes in sex ratio recorded by Johnsgard and Buss (1956) did not occur in the study area.

Another population feature which showed little variation was the composition of groups and their proportion in the breeding population. Large annual variations in the density of breeding pairs had no effect on group structure. The proportion of pairs was high almost over the entire nesting period. This was probably an outcome of high nesting losses and frequent formation of new pair bonds. Such an interpretation seems to be reasonable in view of the fact that, in Mallard populations with a high nesting success in Canada, the proportion of pairs rapidly declined (Dzubin 1969; Dzubin & Gollop 1972). This comparison suggests that the proportion of pairs in the middle of the breeding season could be used as a simplified measure of nesting success. This would be a rough, relative measure, but simple and easy to use over large areas, impossible when nesting success has to be estimated by visiting nests.

Absence of lone females in groups in the pre-nesting period and their low proportion in the middle of the breeding season may indicate that, in this population, females were not limited by availability of males, following nest failure.

Nests

Tree nesting was characteristic of this population. Such nesting habits are known in Mallard but, in the literature, no such mass utilisation of both trees and nest baskets has been described (Cowardin *et al.* 1967; Fruzinski 1967; Bishop & Barratt 1970; Bjarvall 1970). In other species nesting in this area, such as Greylag Geese, Coot, and diving ducks, losses caused by changes in water level were much higher in comparison with Mallard, being the major determinant of breeding success. Mallard commonly nested on trees; thus, changes in water level could not directly affect their nesting success. Some of our observations suggest that selection of such nesting sites was not related only to the shortage of other suitable sites. In some periods of 1978 and 1980, nesting on the ground was possible, but most nests were placed on trees. It is known from ringing data that many females utilise the same nest basket or the same tree year after year. This is particularly the case in females that had been successful the previous year. Nests located on the ground were more likely to be flooded than those on trees and in nest baskets (Figs. 1 & 4). It is possible that the nest site tenacity resulting from nesting success also has bearing on the selection of nesting site.

Clutch size was quite consistent among years, and similar to that known from other populations (Linkola 1962; Kux 1963; Bezzel 1966; Balat 1967; Dzubin & Gollop 1972; Melde 1973). Therefore, when compared with the variability of other components of population productivity such as nesting success and survival of young, clutch size variation had little effect on reproductive output. However, a decline in the clutch size with time reduced the importance of late (replacement) clutches to population productivity.

In some species of ducks, the proportion of mixed clutches increases with the density of breeding pairs and, as a result, breeding success is reduced. Some authors (Jones & Leopold 1967; Bengtson 1972; Patterson 1976) suggested that this operates against overcrowding. A low proportion of mixed clutches in the population under study when the density was high does not support this interpretation.

Losses and productivity

Nesting success was the bottleneck of the population reproduction. Partial nest loss, mortality of young and of adult females, played a subordinate role. It follows, from the review of Canadian studies presented by Dzubin and Gollop (1972), that nesting success is the most diversified and variable component of reproduction. In most cases, this stage of the reproductive cycle is subject to heaviest losses, rarely less than 50% (Dzubin and Gollop 1972). In some populations, high nesting success was coupled with low survival of young and this second source of losses became important. This was related, however, to specific habitat conditions (Hildén 1964; Dzubin & Gollop 1972; Newton & Campbell 1975).

Partial losses of eggs from clutches hatched in natural nests, which reached 9.3–12.5% in the study population, are characteristic of Mallard populations in other areas as well. A review by Hildén (1964) shows that they range from 4.2 to 12.7% and, as shown by Dzubin and Gollop (1972), found the mean value to be 8%. According to Bengtson (1972), mean partial egg losses in Iceland are 9.3%.

Small differences in nesting losses in different years, when there were significant differences in the density of the breeding population, show that the total density of breeding population was not a factor.

Early nests contributed substantially more to reproductive output than late nests. This is due to a combination of higher success rates and larger clutch sizes of the former group.

An increase in nesting losses with time through the season, has been observed by many authors (Keith 1961; Bengtson 1972; Dzubin & Gollop 1972; Newton & Campbell 1975). Some authors found an opposite relationship (Coulter & Miller 1968). As the present study and the literature quoted above show that predators accounted most for nesting failure of Mallard, it may be expected that the amount of losses depends primarily on the kind and density of predators and the general concealment of nests.

Nest predators appeared to be the key factor limiting nesting success of the population under study. They accounted for 80–91% of all nest failures. The main predator in the study area was the Hooded Crow. A specific feature of the study habitat was almost complete lack of plant nest cover. This facilitated their detection by avian predators, and nests were particularly vulnerable during egg laying, when the female was frequently off the nest. A particular role of plant cover with respect to avian predators was emphasized by many authors (Miller 1971; Dwernychuk & Boag 1972; Schranck 1972; Duebbert & Kantrud 1974). High losses of incomplete nests were recorded by Bengtson (1972) in Iceland, where Ravens *Corvus corax* were the main predators. Keith (1961) found no relationship between the stage of incubation and nest losses but, in his study area, avian predators were rare; instead, mammalian predators were important.

Although nests in baskets suffered significantly lower losses than natural ones, losses were still fairly high. The artificial nests were introduced in this area to enhance production of young. In the early years, losses in baskets were low and sporadic (B. Fruzinski, pers. comm.). However, establishment of baskets in high density over 10 years inadvertently created the opportunity for predators to capitalise on them. Higher success in baskets may result primarily from better nest concealment than in natural nests. Because a small number of baskets was used, relative to the total population size, their overall impact on population production was low. The influence of nest baskets on the number of breeding pairs the region can support has yet to be determined.

Mortality of young was the most important factor (after nesting losses) determining productivity. The mean size of broods 5–8 weeks old was 5.9 ducklings in the study area. This figure is similar to those reported for other populations, e.g., 5.8–6.9 (Eygenraam 1957); 5.1 (Smith 1971); and 6.0 (Stoudt 1971). The mortality, estimated as 24%, 35%, and 3% in the study population was rather low as compared with that found for other populations (Dzubin & Gollop 1972). Small sample sizes, however, prevented conclusions.

Factors accounting for mortality of young were not analysed directly. It seems, however, that the study area provided good conditions for rearing young. Dense vegetation offered much concealment; low water level at that period ensured the emergence of vast islands and shoals. Also, food conditions were rather favourable because of a great abundance of invertebrates. In this situation, the most probable mortality agents were weather and predation.

Productivity of the population estimated as 2.2 and 2.7 juveniles per female seems to be consistent with other populations. There is very little comparable data in the literature on this subject. Dzubin and Gollop (1972) provide data based on calculations for successive stages of the reproductive cycle. European data based on the proportion of young in the hunting bag contains much uncertainty and does not provide a clear picture of productivity (Havlin & Havlinova 1969; Boyd *et al.* 1975). Studies conducted in Canada in two habitats showed that productivity ranged from 0.5 to 3.3 young per female (Dzubin & Gollop 1972). Bellrose *et al.* (1961) analysed the hunting bag in the U.S.A., using correction factors. Their data revealed that productivity varied from 1.33 to 4.67 young per female, with an average of 2.2, over a 17-year study period.

Conclusions

The population under study occupies a specific habitat that differs in many respects from the habitats most frequently occupied by Mallard in Poland. The most important differences include variable water, the large extent of the area, high density of breeding pairs, heavy pressure of avian predators and low human disturbance.

In this situation, Mallard show a high adaptability, commonly using trees as nesting sites, and moving to adjacent habitats during flood.

Despite specific features of the habitat and large changes in the density of breeding

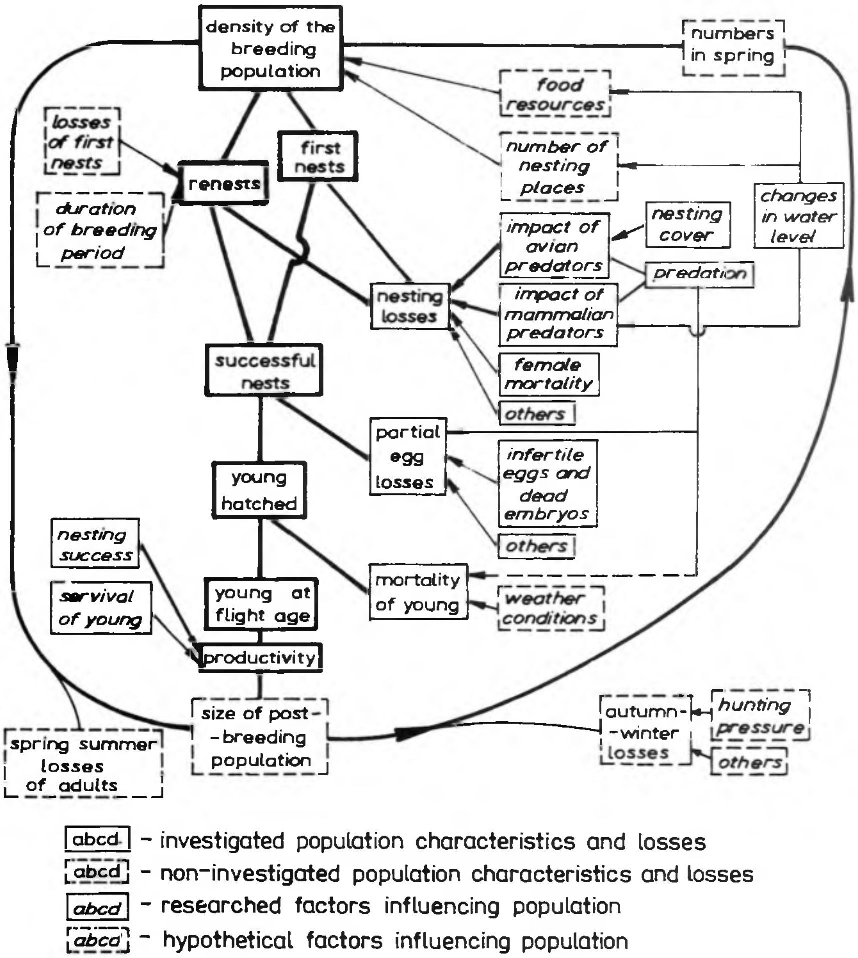


Figure 10. A model for functioning of the studied population.

population, most population characteristics did not vary much from year to year, and they were similar to those observed in other populations, living in different habitats. This is particularly the case for sex ratio, group structure, clutch size, partial nest loss during incubation, and productivity. A low nesting success resulting from the specific habitat structure (no plant cover at nests) was compensated in part by a high survival of young.

This study analyses only one aspect of population dynamics in the annual cycle, which is reproduction. This is, however, a very important aspect; thus, an attempt was made to show it in a scheme for population functioning throughout the year (Fig. 10).

Predation was the main factor limiting reproduction of the study population, but annual changes in the size of breeding population also depended on changes in habitat conditions, such as available food supply and number of nesting sites.

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Summary

Mallard *Anas platyrhynchos* showed a high adaptability in flooded areas at the confluence of the Warta and Oder Rivers, Western Poland, using trees as nesting sites and moving to adjacent habitats during extreme flooding. Nesting losses, which ranged from 76–79% in natural nests and from 51–69% in nest baskets, had the greatest effect on population productivity. Duckling mortality (3–35%), partial egg loss (8.3–12.5%), and changes in clutch size were of less importance. Predation was the main factor limiting Mallard reproduction, but size of breeding population depended also on changes in habitat conditions. The calculated productivity was 2.2–2.7 flying young per breeding female for natural nests and 3.6–3.7 for nest baskets.

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