

Density and age of breeding pairs influence feral pigeon, *Columba livia* reproduction

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A b s t r a c t. Breeding success and several breeding parameters were studied at 5 feral pigeon colonies. We found that density and the age of breeding pairs affect reproduction, with also the age of the nest significantly influencing reproductive indicators and success. Hatching, fledging and breeding success were higher in colonies with lower breeding pair densities. These indicators were also higher for experienced pairs compared to first time breeders. The number of nests in a pair's territory had little effect on breeding performance. Among all the breeding parameters studied (timing of breeding, length of the breeding season, number of broods per year) only the latter was positively correlated with the density of birds. Breeding pairs had significantly more broods during a year in highly dense colonies compared with those of low density. The remaining factors studied were similar in all breeding colonies regardless of their density. Breeding parameters were primarily dependent on breeding pair age – experienced pairs began breeding earlier, ended later, conducted a longer breeding season and, as a result, produced more broods per year. The age of a nest also influenced the breeding season. Many factors were found to cause egg and nestling loss. Mechanical damage to eggs, eggs and nestlings falling out of nests, embryo death, jackdaw predation, competition among fledglings, and nestling disease were dependent on the level of pigeons' reproductive activity, especially in overly dense colonies.

Key words: egg and nestling mortality, density dependence, intraspecific competition

Introduction

Density and site dependent population regulation has been confirmed in many animal populations. For example, reproductive success drops as breeding density increases in some mammals (K o s k e l a et al. 1999, R ö d e l et al. 2004) and birds (B i r k h e a d 1977, H a r r i s et al. 1996, 1997, W i l k e n s & E x o 1998, M u l l e r 2000, K o k k o et al. 2004, A r m s t r o n g et al. 2005). Studies of birds have shown that density can influence both clutch size (H u n t et al. 1986, D h o n d t et al. 1992, B o t h 1998) and survival rates of young after the breeding season (H u n t et al. 1986, B o t h & V i s s e r 2000, M c C a l l u m et al. 2000, P a r a d i s et al. 2002). The ways density influences breeding performance depends on the type of territory used by the animals. In species whose territory provides all the resources required for life, an increase in breeding pair density decreases access to those resources and unfavourably impacts on the quality and quantity of offspring (A r c e s e & S m i t h 1988, D h o n d t et al. 1992, K o s k e l a et al. 1999, B o t h & V i s s e r 2000, R ö d e l et al. 2004). Additionally, greater breeding pair density among species that reproduce in colonies (for example, seabirds) increases competition for nest sites (H u n t et al. 1986). Weaker pairs are forced to occupy sites of lesser quality, where breeding success is low or where birds simply do not reproduce (H a r r i s et al. 1996, 1997, K o k k o

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et al. 2004). In bird colonies, the physical characteristics of a nest site may play a large role in limiting reproductive success. When nest sites within a colony are of diverse quality, site dependent population regulation results (R o d e n h o u s e et al. 1997, K o k k o et al. 2004). The negative influence of high population density on breeding success has been proven in many animal species, but the actual mechanisms of how this factor impacts a population can differ among species, as well as within species because of variable environmental conditions. As a result, the mechanisms remain unclear. Another factor influencing reproductive performance is the age of the breeders (C u r i o 1983, M a r t i n 1991, 1995). The general model of age-dependent reproduction shows that an individual's reproductive success increases with advancing age and decreases when it becomes old.

In this study, we attempt to verify the above-mentioned mechanisms regulating the reproductive success of many species in the feral pigeon population. We took advantage of the diverse densities of breeding pairs in the colonies, and studied nesting conditions with respect to the number and quality of nests in the territories of pairs.

Feral pigeon breeding colonies are mainly concentrated in city centers (S a c c h i et al. 2002), where they breed in buildings, often in high densities. Breeding pairs occupy a defined nesting territory for many years and forage away from the colonial site (M u r t o n et al. 1972). This is similar to the functioning of seabird breeding colonies (H a r r i s et al. 1997). However, feral pigeon breeding strategy differs, as it is based on laying several clutches in a season (B u r l e y 1980, J o h n s t o n & J a n i g a 1995, H e t m a ń s k i & W o ł k 2005). Additionally, the breeding cycle of seabirds is synchronised, whereas in pigeons it is strongly asynchronous. Pigeons have an extended breeding season and can breed in unfavourable weather conditions (H ä k k i n e n et al. 1973, M u r t o n et al. 1974, J o h n s t o n 1984, D a b e r t 1987, H e t m a ń s k i 2004). The peak of the breeding season, when most pairs nest, occurs during the spring and summer months (March–August). Only a few pairs breed during other times of the year (H e t m a ń s k i 2004). This strongly extended breeding season may make it easier to distinguish density dependent from density independent factors that lower breeding success. Changes in weather conditions and food resources during the breeding season may play as important a role in limiting breeding success for this species as density independent factors. We hypothesised that density dependent factors will not only have a stronger influence in overly dense colonies, but will also increase during the peak breeding period of the colony, when negative interactions among breeders intensify.

Material and Methods

Studies were conducted in 1998–2000 at five feral pigeon breeding colonies located in buildings in the centre of Słupsk (NW Poland, 54°28'N, 17°10'E). The study colonies differed in breeding pair density between each other and between study years (Table 1). The highest pigeon densities were found in colonies located in towers: Museum of Central Pomerania, Regional Office and St. Hyacinth's Church. In two of these buildings, pigeons nested only in the upper reaches of the towers, placing their nests mainly on beams, shelves, wall nooks and ledges, while in the third building (Regional Office) nests were also located on the floor. The height of the towers ranged from 6 to several dozen meters. In the remaining two colonies (KRUS and Hospital), pairs nested almost exclusively on the floor.

All the pigeons in the study colonies were individually marked with colour bands before beginning the research. We then conducted two types of observations. The first type consisted of observing birds from a blind built in the colony itself. These observations

Table 1. Breeding pair density in the feral pigeon breeding colonies studied in 1998–2000.

Colonies	Density (n pairs/m ²)		
	1998	1999	2000
Church	1.08	1.46	2.08
KRUS	0.11	0.25	0.30
Museum	3.75	4.38	4.38
Hospital	0.03	0.07	0.09
Reg. Office	2.18	3.46	3.59

were conducted every 2–3 weeks from January to August, and once per month during the remaining months of the year. The purpose of conducting observations from blinds was to determine the number of pairs actually breeding and the location of their nests. We identified 54 breeding pairs in the first year of the study, 90 pairs in the second year and 113 pairs in the third. The second type of observation consisted of checking the nest contents of individual breeding pairs. Nest checks were conducted twice weekly from January to August and once per week in the remaining months of the year. During each check, we determined the number of eggs and nestlings in the nests and the reasons for their loss. These observations allowed us to distinguish six causes of egg loss.

Mechanically damaged eggs included eggs whose shells were cracked or dented, while eggs found beyond the nests were categorised as those having fallen out. Both these causes were put into one category, as many of the eggs found outside of the nests also had damaged shells.

Abandoned eggs were those that remained untended directly after laying or during the period of up to the 18th day of incubation (complete incubation lasts 18 days – V a t n i c k & F o e r t s c h 1998). Only eggs with intact shells were included in this category, as damaged shells could have influenced early abandonment of the eggs by the parents.

Embryo death was determined when an incubated egg did not hatch after having earlier confirmed that it contained a developing embryo. This was done by illuminating the egg with a flashlight to examine its contents. This category only included eggs with intact shells.

By conducting observations from a blind, we were able to determine that another reason for egg loss was predation by the jackdaw *Corvus monedula*. These birds preyed on pigeon nests only in one of the studied breeding colonies, and only on those nests found in the upper area of the tower near egresses. For this reason, all the eggs that disappeared from this part of the tower were considered losses resulting from predation.

Unfertilized eggs were those that had no sign of a developing embryo during the entire incubation period after having been checked by illumination with a flashlight.

Five main reasons for nestling loss were also identified. Small nestlings found dead next to the nest were categorised as having fallen out of the nest. Fledglings that had not yet gained the ability to fly and had fallen from a nest situated high in the structure of the colony were similarly categorised. They most often lacked parental care and died of hunger.

Jackdaw predation was another cause of nestling loss, and this occurred in only one of the studied breeding colonies. Nestlings with evident death-causing wounds as well as the disappearance from a nest of small nestlings in the area of the colony penetrated by jackdaws were included in this category.

Losses due to disease included those nestlings that had exhibited clear symptoms of illness, such as difficulty breathing, diarrhoea, thickening of the neck, secretion of mucus from the bill, deformed extremities.

Nestlings were also lost as a result of fledgling competition for food from adult birds. This occurred in places where the fledglings gathered, most often in a dark area of the colony, where parental pairs were unable to identify their own young from those of other pairs. As a result, their young often went hungry and died of starvation. This category also included young nestlings that died as a result of being trampled by their older siblings or unrelated fledglings.

Stunted development of nestlings effectively resulted in their deaths because the parents did not provide them with sufficient food. We did not observe the presence of unrelated young who could have stolen the food of the breeding pair in such cases. Development of the young was most often stunted when one parent was lost, but it also occurred when both parents were present, especially among inexperienced pairs.

In order to determine which of the above described reasons for egg and nestling loss was dependent on the breeding colonies' reproductive activity, we conducted the Spearman's rank correlation (r_s) test for these two variables. The independent variable was the breeding colonies' reproductive activity expressed as the number of nests occupied by breeding pairs in specific months of the year, and the dependent variable was the degree of egg or nestling loss caused by a defined reason.

Hatching success was defined as the number of hatched nestlings in proportion to the number of laid eggs. Fledging success was defined as the number of young that successfully left the nest in proportion to the number of hatched nestlings, and breeding success (total success) was defined as the number of young that had left the nest in proportion to the number of laid eggs.

The density of pigeons in the colonies was determined based on the maximum number of breeding pairs reproducing in a given year. Non-breeding birds were not considered, as their numbers are difficult to determine and fluctuate to a greater degree than those of pairs. To determine a particular pair's nesting conditions, we used the number of nests in their territory, which the female used to lay eggs, as well as the age of the nest. Due to the number of nests occurring in pairs' territories, we categorized them as territories with two nests or one. Parents in territories with two nests could care for the eggs and nestlings of two different broods at once. In the case of small territories, the breeding pair had only one nest, where frequently eggs were being incubated at the same time that nestlings were being reared from an earlier brood. Pigeon pairs' nests were also divided between old and new ones. The old nests were determined as those with a bowl-like shape at the beginning of the breeding season, formed thus as a result of their having been used to rear young in the previous season. New nests were those that had just been built.

The age of breeding pairs was not determined until after the first year of the studies, in 1999 and 2000. Young pairs were those where both partners were first-time breeders. Older (experienced) pairs were those where both partners had participated in at least one previous breeding season. The remaining pairs, where one partner was a first-time breeder and the other was experienced or whose previous experience was unknown (immigrants to the colony) were qualified as "other."

We established two categories of young birds: the first included young nestlings from the day of hatching to 14 days old. During this period, nestlings are especially cared for by their parents, as they are incubated until they achieve the ability to regulate their body temperature (normothermy). This period may even extend a few days more. H e t m a n s k i & W o ł k (2005) showed that nestlings achieve normothermy from the 6–7 to 9–10 day of life and that this is influenced by ambient temperature. However, these studies were conducted during

summer, and so one could assume that the period of incubation would be longer in the cooler months of the year by several days. Therefore, we assumed the first 14 days of a nestling's life as the period they were under the constant care of parents. The second age group (older) were those young 15 days or older to the time of fledging that were left alone in the nests for longer periods during the day.

Tests were conducted with the SAS 9.1 program for Windows. General linearized modeling (GLM) was used to study the influence of density, characteristics of nest sites and age of pairs on breeding success for specific pairs. Population density was treated as the covariant, while the study years, number of nests in a specific pair's territory, age of pair and age of nest were class factors. The age of a pair (young, old, other) was an additional factor for data from 1999 and 2000. ANOVA variance analysis test was used to compare mean values.

Results

Hatching, fledging and breeding success

Nestlings hatched from 68.5 % of eggs laid during the study period (n = 2160). Hatching success was not dependent on year of study (GLM: influence of year $F = 0.23$; $P > 0.05$), and was 69.5 % (n = 488) in the first year, 68.3 % (n = 770) in the second year and 68.2 % (n = 902) in the third year. However, hatching success differed among breeding colonies and

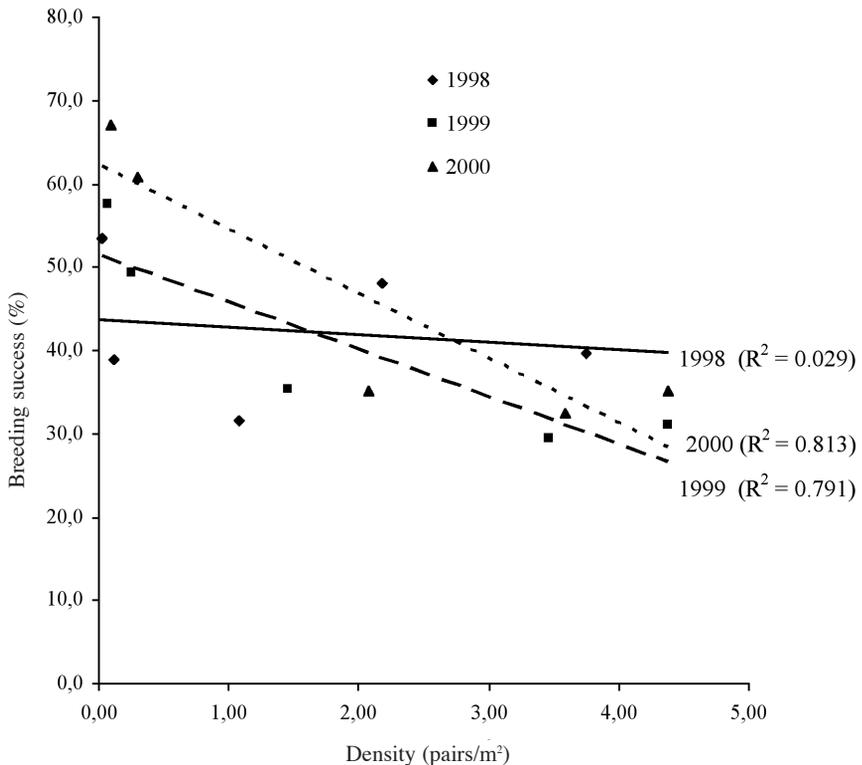


Fig. 1. The dependence of breeding success on the density of breeding pairs in the studied feral pigeons colonies for 1998, 1999 and 2000.

was lower in overly dense colonies (GLM: influence of density $F = 3.85$; $P < 0.05$). Fledging success changed significantly among study years, from 55.1 % ($n = 526$, 1999) to 64.1 % ($n = 615$, 2000) of hatched nestlings (GLM: influence of year, $F = 4.17$; $P < 0.05$), and was also dependent on the density of breeding pairs (GLM: influence of density, $F = 16.22$; $P < 0.001$). Overall breeding success was similarly dependent on the year (GLM: influence of year, $F = 5.00$; $P < 0.01$) and pair density, except for the first year of study where no such dependence was confirmed (Fig. 1).

The territories of breeding pairs differed by the number and quality of their nests. The number of nests had no influence on hatching success (GLM: $F = 0.97$; $P > 0.05$), fledging success (GLM: $F = 0.01$; $P > 0.05$) or breeding success (GLM: $F = 0.01$; $P > 0.05$) (Table 2). We found, however, that older, well formed nests were significantly safer than newly built ones, which resulted in significantly higher hatching success of pairs nesting in old rather than new nests (GLM: $F = 36.24$; $P < 0.001$). A similar dependence was confirmed for fledging success (GLM: $F = 6.89$; $P < 0.01$) and breeding success (GLM: $F = 24.68$; $P < 0.001$) (Table 3). Also, a breeding pair's age had a significant influence on: hatching success (GLM: $F = 20.00$; $P < 0.01$), fledging success (GLM: $F = 4.65$; $P < 0.05$) and overall breeding success (GLM: $F = 7.85$, $p < 0.001$). More nestlings hatched and more young left the nest of experienced pairs than young pairs (Table 4).

Table 2. Hatching, fledging and breeding success (%) of feral pigeon colonies for pairs with one or two nests in their territory in 1998–2000.

Success	1998		1999		2000	
	1 nest ($n = 20$)	2 nests ($n = 32$)	1 nest ($n = 38$)	2 nests ($n = 52$)	1 nest ($n = 57$)	2 nests ($n = 55$)
Hatching	61.6	73.2	64.7	69.1	59.0	77.4
Fledging	57.9	64.4	47.6	59.3	50.0	70.9
Breeding	37.9	44.1	32.0	41.4	30.5	54.1

Table 3. Hatching, fledging and breeding success (%) of feral pigeon colonies among breeding pairs nesting in old and new nests in 1998–2000.

Success	1998		1999		2000	
	new ($n = 10$)	old ($n = 42$)	new ($n = 10$)	old ($n = 80$)	new ($n = 19$)	old ($n = 93$)
Hatching	49.8	73.3	37.0	71.0	44.7	72.8
Fledging	53.7	64.2	30.4	56.9	40.5	64.0
Breeding	25.0	45.7	11.3	40.7	16.6	47.3

Table 4. Hatching, fledging and breeding success (%) of feral pigeon colonies among young, old and other pairs in 1999–2000.

Success	1999			2000		
	young ($n = 22$)	old ($n = 40$)	other ($n = 28$)	young ($n = 21$)	old ($n = 59$)	other ($n = 33$)
Hatching	51.1	74.6	69.4	51.1	74.8	66.6
Fledging	43.3	58.1	57.9	44.0	64.3	62.3
Breeding	24.6	43.2	39.3	25.0	47.7	43.1

Causes of egg loss

About 1/3 of the eggs laid did not hatch in each year of the study. Egg loss ranged from 30.5 % (n = 488) in the first year of the study to 31.7 % of eggs laid (n = 770) in the second year.

The most frequent causes of egg loss were shell damage or eggs falling out of nests (11.9 %, n = 2160 laid eggs), followed by abandonment (8.7 %), embryo death (5.4 %), predation (2.5 %) and lack of fertilization (2.3 %). Predation occurred in only one of the study colonies, in the Regional Office, where losses due to this cause were 6.3 % of eggs laid (n = 858).

Damaged eggshells and eggs found beyond the nests were more frequently found in colonies with higher densities (GLM: $F = 20.25$; $P < 0.01$). For the overly dense colony in the Museum of Central Pomerania, they represented 23.3 %, while the colony with the lowest pair density in the Hospital, they represented only 5.2 % of laid eggs. They were decidedly more frequently found in new nests rather than old ones (GLM: $F=59.76$; $P < 0.001$), as well as in nests of young pairs rather than older ones (GLM: $F=3.95$; $P < 0.05$).

Egg abandonment was negatively related to the density of breeding colonies (GLM: $F = 15.41$; $P < 0.001$) and positively dependent on the age of the breeding pair (GLM: $F = 7.20$; $P < 0.001$). We found no dependence between the occurrence of unfertilized eggs or embryo death and density, nest conditions, or age of breeding pairs.

Certain causes of egg loss intensified as the pigeons' reproductive activity increased, represented by the number of active nests during a year. These included damaged eggshells and eggs fallen out of nests, as well as jackdaw predation, and in one colony, embryo death (Table 5). Egg abandonment occurred more frequently outside the period of high reproductive activity, shown by the negative values of the correlation coefficients. This negative dependence was statistically significant in only one colony. This may be a strong factor outside the pigeons' peak reproductive period, that is, in the fall and winter, when unfavourable environmental conditions dominate. The highest number of eggs were abandoned in December – 27.0 % of eggs laid (n = 37). Eggs were also abandoned during peak reproductive periods, though less frequently. They were abandoned at that time for different reasons, that is, by single females (a total of 1.8 % eggs laid, n = 2160) who laid eggs between March and August, as well as by breeding pairs that did not have appropriate territories for nest building, where such pairs laid their eggs in foreign territories.

Table 5. Correlation values whose calculations are based on the dependence of specific causes of egg loss by pigeons' reproductive activity, expressed as the number of active nests based on monthly values. Causes of egg loss: a – damaged egg shells and eggs fallen from nests, b – abandoned eggs, c – embryo death, d – predation, e – unfertilized eggs.

Colonies	Spearman correlation coefficients				
	a	b	c	d	e
Church	0.794***	-0.253	0.294	-	0.150
KRUS	0.275	-0.264	0.335	-	0.138
Hospital	0.450***	-0.414*	0.261	-	0.030
Reg. Office	0.360*	-0.267	0.419*	0.532**	0.130
Museum	0.478*	-0.136	0.242	-	0.021

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Causes of nestling loss

Nestling loss was higher than the loss of eggs. Nestling loss was 37.5 % of hatched young (n = 339) in the first study year, 45.1 % (n = 526) and 35.8 % (n = 617) respectively in successive years.

Nestlings were lost predominantly because they fell out of nests, a fate affecting 14.8 % of young (n = 1482). Remaining causes occurred much more rarely and included: predation (7.1 %), disease (6.5 %), competition among nestlings (5.1 %), stunted development (2.7 %) and other, unidentified causes (3.2 %).

We found that small nestlings up to 14 days old under the continuous care of parents fell out of nests significantly less frequently than older young (GLM: $F = 34.56$; $P < 0.001$). This cause of mortality among young occurred significantly more often in overly dense colonies (GLM: $F = 22.10$; $P < 0.001$), to pairs with only one nest (n = 115) than those with two nests (n = 139) (GLM: $F = 8.58$, $P < 0.01$), as well as to pairs (n = 39) rearing young in new nests than those using old nests (n = 215) (GLM: $F = 22.18$; $P < 0.001$).

The jackdaw preyed on pigeon nestlings with various intensity in successive years of the study (GLM: influence of year $F = 6.42$; $P < 0.01$). It mainly attacked small nestlings (94.3 %, n = 105) up to 14 days old than older ones (5.7 %, n = 105) (GLM: $F = 31.50$; $P < 0.001$). But older nestlings (4.1 % of hatched young, n = 1482) died significantly more often because of illness than younger ones (2.4 %, n = 1482) (GLM: $F = 6.38$; $P < 0.05$).

We also confirmed a significant positive dependence between nestling mortality due to cohort competition and the density of pigeon pairs in the colonies (GLM: $F = 21.36$; $P < 0.001$), the number of nests on a pair's territory (GLM: $F = 10.19$; $P < 0.01$) and the age of the breeding pair (GLM: $F = 6.21$; $P < 0.01$). Young pairs lost 9.9 % of hatched nestlings due to competition (n = 131), old pairs lost 4.9 % (n = 689), and other pairs lost 2.8 % (n = 323).

Additionally, stunted development of nestlings significantly depended on a colony's density (GLM: $F = 5.51$; $P < 0.05$), but this relationship was reversed. Most such young were observed in colonies with lower densities. Other significant dependencies were not confirmed.

Some causes of nestling loss intensified with the increase of a colony's reproductive activity, expressed as the number of active nests in the year. The results of this research are presented in Table 6.

The complexity and simultaneous impact of many factors causing nestling loss makes it difficult to interpret the results. There was a strong correlation of nestling loss due their

Table 6. Correlation values whose calculations are based on the dependence of specific causes of nestling loss (%) on pigeon's reproductive activity, expressed by the number of active nests based on monthly values. Causes of nestling loss: a – nestlings falling out of nests, b – Jackdaw predation, c – nestling disease, d – competition among nestlings, e – stunted development of nestlings.

Colonies	Spearman correlation coefficients				
	a	b	c	d	e
Church	0.743***	0	0.101	0.362*	-0.216
KRUS	0.088	0	0.416*	0.040	0.157
Hospital	0.375*	0	0.428*	0.148	0.388*
Reg. Office	0.345	0.570**	0.335	0.518**	-0.094
Museum	0.416*	0	0.382*	0.172	0.303*

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

falling out of nests in the church, because all the fallen nestlings died of hunger at the bottom of the tower. However, no statistically significant correlation emerged for this factor with the level of pigeons' reproductive activity in the Regional Office because most of the young in nests located in the upper reaches of the tower were killed by jackdaws. Those young that fell from nests in this colony often survived by competing effectively for food with young being reared at the bottom of the tower. In the museum, on the other hand, where there was a very high pair density, losses due to disease and poor nestling development intensified with an increase in the colony's reproductive activity (Table 6). Dependence between nestling loss due to disease and poor development with a breeding colony's level of reproductive activity also emerged in colonies with lower densities of breeding pairs, that is, in KRUS and the hospital, where the impact of other nestling loss causes was small.

The influence of density, nesting conditions and age of breeding pairs on feral pigeon breeding parameters

Breeding pairs cared for an average of 4.4 ± 1.71 broods annually, with no variance in mean values among specific years of the study (ANOVA: $F = 1.73$; $P > 0.05$). The number of successful broods averaged 2.3 ± 1.58 and also was similar in successive years (ANOVA: $F = 0.92$; $P > 0.05$). The length of the breeding season lasted for an average of 183.2 ± 74.8 days, and no significant differences were found among study years (ANOVA: $F = 0.042$ $P > 0.05$). The influence of breeding pairs' density in the colonies on basic reproductive parameters of pigeons is presented in Table 7. We found that breeding pairs in colonies with higher densities had significantly more broods annually than those in less dense colonies. However, we did not confirm such an influence on the remaining parameters (Table 7). Reproductive experience had a much greater impact on the breeding season. Older pairs with at least one season's experience had significantly higher levels of reproductive parameters (Table 7). Experienced pairs ($n = 99$) on average produced 4.9 ± 1.6 broods, others ($n = 61$) 4.1 ± 1.5 , with young pairs ($n = 43$) producing 3.4 ± 1.4 broods annually. In the analysis of successful broods, these results were an average of 2.8 ± 1.5 , 2.2 ± 1.4 and 1.2 ± 1.3 respectively for old pairs, other, and young pairs. Experienced pairs also conducted a longer breeding season (average of 203.0 ± 73 days) than other pairs (173.9 ± 71) and young ones (125.0 ± 62 days).

Table 7. Dependence of reproductive parameters of the feral pigeon population on nesting conditions (density of breeding pairs and number of nests in a pair's territory) and age of breeding pair estimated using the GLM test.

	Breeding parameters				
	N broods	N successful broods	Length of season	Starting date	Ending date
Density of pairs	$F = 7.85$ $P < 0.001$	$F = 1.11$ $P > 0.05$	$F = 0.49$ $P > 0.05$	$F = 0.20$ $P > 0.05$	$F = 0.15$ $P > 0.05$
Number of nests in a territory	$F = 0.87$ $P > 0.05$	$F = 3.43$ $P > 0.05$	$F = 2.25$ $P > 0.05$	$F = 3.84$ $P = 0.05$	$F = 0.49$ $P > 0.05$
Age of breeding pair	$F = 5.41$ $P < 0.01$	$F = 5.59$ $P < 0.01$	$F = 12.18$ $P < 0.001$	$F = 20.51$ $P < 0.001$	$F = 5.25$ $P < 0.05$

Discussion

This three-year study shows that hatching success, fledging success and overall breeding success achieved lower values in colonies with higher densities of breeding pairs. Among breeding parameters, only the number of broods produced annually depended on density. This is because more frequent brood losses in overly dense colonies induced pairs to repeat breeding. The negative influence of high pigeon density on breeding success was also found in feral pigeon colonies by H a a g (1988, 1991). He pointed out that the main reason for the increase in brood loss in overly dense colonies is aggression and stress among pigeons. A similar situation is found in other bird species (H a r r i s et al. 1996, 1997, W i l k e n s & E x o 1998, L o & M ü l l e r 2000, K o k k o et al. 2004), but such a dependency was found lacking among some other populations (D e x h e i m e r & S o u t h e r n 1974, P ö y s ä & P e s o n e n 2003). H a a g (1991) shows that lower reproductive success in overly dense colonies is the direct result of increasing competition among breeders, greater stress among pigeons fighting for nest sites, intensified levels of disease and a high concentration of parasites. Our research shows that breeding pair density is an important reproductive regulator that unleashes an entire array of direct causes of egg and nestling losses. Mechanical egg destruction, eggs and young falling from nests and competition among nestlings were found to be dependent on density. These factors occurred significantly more frequently in colonies with higher densities of breeding pairs. It should be noted that the spatial structure of the buildings occupied by the pigeons played a large role in the level of specific causes of egg and nestling mortality. For example, the numerous egresses in the Regional Office tower enabled jackdaws to easily penetrate pigeons' nests. Pigeons breeding on the floor of this site saved many young that had fallen from nests located in the upper areas of the tower. However, there was also greater competition for food among fledglings there. The situation was different in colonies inhabiting the church and museum. The jackdaw was not present there, and all the young fallen from nests to the bottom of the towers died of hunger because no pairs bred on the floor. The differences in our results from H a a g ' s (1991) observations are based on the fact that unfertilized eggs and embryo death were not connected to density, while egg abandonment and stunted nestling development were negatively correlated with this factor. The role of these latter factors in overly dense colonies was weak due to the strong influence of density dependent factors, whereas in safe colonies with low densities, it became more meaningful.

Based on additional analyses of the causes of egg and nestling loss, we showed that some of these factors intensify with a colonies' increased reproductive activity (for example, eggs and nestlings falling from nests, predation, nestling disease, competition among nestlings). All pairs bred during the height of the breeding season, even those that did not have appropriate nesting sites. They made their nests in the most unsafe sites, where eggs easily rolled out and nestlings fell. A large production of nestlings, in turn, resulted in fledglings finding themselves mixed in among different breeding pairs, which increased competition for food from adult birds. Other causes of egg and nestling loss were not affected by the increase in pigeons' reproductive activity. These included unfertilized eggs, embryo death, and in the case of egg abandonment, this was found to have a negative correlation, which means that eggs were more frequently abandoned outside of the height of pigeons' breeding period.

A high density of breeding pairs results in many unfavorable interactions among breeders (H a a g 1991). It also leads to significantly worse nesting conditions for breeding pairs. This is because pigeons nest in confined spaces, so that an increase in breeding pairs must

lead to a decrease in their territory size and/or the occupation of new sites that are unsafe for eggs and nestlings. Small territories most often included only one nest. The most favorable situation for pairs and the safety of their progeny is when two nests exist, a result of pigeons' reproductive strategy of overlapping broods (B u r l e y 1980, H e t m a ń s k i & W o ł k 2005). However, the number of nests in a territory did not have much influence on hatching, fledging or breeding success. It only influenced the start of the breeding season. The quality of the nest had much more importance for reproduction. Old, well-formed nests shaped as bowls were significantly safer than new nests. For this reason, breeding success in old nests was significantly higher. We observed new pairs occupying narrow areas in the buildings (construction beams in the towers, slanted ledges, and even bells) where it was difficult to build a stable nest safe for incubating eggs and rearing nestlings. A well-formed and stable nest protects the brood from falling out (C o o n et al. 1981). The significance of nest site quality has been confirmed for colony nesting sea birds. Such physical characteristics of nest sites as site type (on a ledge or in a niche), the number of surrounding walls, and slope influenced the breeding success of the common guillemot *Uria aalge* (H a r r i s et al. 1997, K o k k o et al. 2004). Diversity in the quality of nest sites within a colony causes site dependent population regulation. This hypothesis states that a population's breeding success decreases because of the low success found in nests placed in the worst quality sites, while the breeding success of the best sites remains at a consistently high level, even when the population increases.

We also showed the existence of age dependent reproduction in the feral pigeon population. We found this to be a strong factor for population regulation, encompassing all aspects of pigeon reproduction. The age of a pair influenced each stage of breeding success and all indicators of reproduction. Experienced individuals had decidedly better reproductive results than first-time breeders, as was similarly confirmed for other avian (C u r i o 1983, D e s r o c h e r s 1992, M a r t i n 1995) and mammal populations (R ö d e l et al. 2004).

One important mechanism regulating feral pigeon reproduction is male-biased operational sex ratio (OSR). M a r c h e s a n (2002) proved experimentally that an increase in the number of males resulted in strong competition for females. As a consequence, egg loss increased and breeding success decreased. Free males were observed periodically in the study colonies, but they were never numerous. Thus, they most likely did not play a significant role in the loss of broods among breeding pairs.

The results of the research in Słupsk showed the existence of primarily density, age and, to a lesser degree, site dependent reproduction in the feral pigeon population. These regulators are known in many avian populations, but they do not always exist together in a given species. The ability of feral pigeons to reproduce in high densities and in the confined spaces of buildings causes all these mechanisms to play a role in limiting breeding success, above all in overly dense colonies. The internal structure of buildings occupied by a colony and the distribution of breeding pairs in them can, however, influence differences in the intensity with which specific causes of egg and nestling loss occur among colonies.

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