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Author: Hetmański, Tomasz

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Dispersion asymmetry within a Feral Pigeon *Columba livia* population

Tomasz HETMAŃSKI

Department of Zoology, Pomeranian University, Arciszewskiego 22b, 76–200 Słupsk, POLAND, e-mail: t.hetmansk@onet.eu

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Abstract. The aim of the study was to determine the pattern of dispersion in Feral Pigeons, as well as the factors influencing the degree of dispersion. Aside from studying variation in dispersion among the bird colonies, the direction and distance of dispersion were also analysed. The results of the study point unequivocally to strong dispersion asymmetry in the population, which is mainly age-biased. There were great differences in dispersion between adult (reproducing) individuals and young individuals that had not yet joined the breeding population. Each year, young individuals which had permanently left their natal colonies accounted for 20–30% of the young birds that ultimately joined the breeding population. The insignificant degree of dispersion among adult birds (from 0 to 0.8% per year) was due to their strong philopatry towards their breeding sites. A lack of reproductive success did not have any effect on dispersion in the case of the breeding pairs studied. A factor conducive to a bird's departure from the natal colony was the high density of breeding pairs present in the colony. It was found that the direction of dispersion was from a colony with a higher density to a colony with a lower density of pigeons. The Feral Pigeons did not emigrate to join colonies of domestic pigeons kept on the outskirts of the city, nor did they emigrate to other towns in the neighbourhood of the study area (Słupsk, NW Poland). The time when young birds left the natal colony did not influence the degree of their dispersion. Young birds that left their natal colony experienced significantly higher breeding success in their new colony, compared to those young birds that remained in the natal colony, where the density of breeding pairs was high. Young females dispersed more often than young males, although this difference was not statistically significant. This article also discusses the dispersion mechanism in the case of young pigeons.

Key words: Feral Pigeon, *Columba livia*, animal movement, dispersal pattern

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INTRODUCTION

Philopatry is understood as fidelity towards a site or a natal group (e.g. family, colony, population). On the other hand, when an animal leaves its familial, and often also social group to join another one or to claim new territory, this is referred to as dispersion (Greenwood & Harvey 1982). The dispersion pattern varies widely across the animal kingdom. The mechanism of dispersion is not very well known, due to the many difficulties involved in studying it. Various animal species exhibit dispersion asymmetry within their populations, which means that dispersion varies significantly with respect to sex (Pärt & Gustafsson 1989, Double et al. 2005, Chernetsov et al. 2006) and/or between individuals from different age groups (Holenweg 2001). According to Dittman et al. (2005), less territorial individuals are more inclined to disperse. Among those mammals that live in groups, it is generally the males that migrate (Greenwood & Harvey 1982, Lefebvre et al. 2003, Jack & Fedigan 2004), while in the case of birds, it is most often the females (Greenwood 1980, Greenwood & Harvey 1982, Plissner & Gowaty 1996, Green & Cockburn 2001). The mechanism of dispersion remains little known because the contributing factors that determine whether or not an animal is forced to leave its familial group are complex and manifold, and include: increased population density (Aars & Ims 2000), competition for territory (Kokko & Lundberg 2001), avoidance of inbreeding (Pusey & Wolf 1996, Gandon 1999, Perrin & Mazalov 1999,

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Aars & Ims 2000), and a lack of reproductive success (Haas 1998, Grosbois et al. 2003, Winkler et al. 2004, Fowler 2005). Sensitivity and/or unresponsiveness to these variables may vary according to age and sex, which leads to dispersion asymmetry within a given population. Dispersion inevitably involves certain costs (Greenwood & Harvey 1982, Plissner & Gowaty 1996). For example, individuals that migrate earlier may face a greater risk of mortality (Green & Cockburn 2001). But birds that disperse also get a chance of finding conditions better than those present in their familial group, which may then result in future increased breeding success. On the other hand, remaining in the group may lead to a different type of cost, related to increased population density and inbreeding (Greenwood & Harvey 1982, Pusey & Wolf 1996). Studies on as many animal species as possible examining the influence of environmental factors, as well as the costs and benefits of dispersion versus remaining in the familial group (population), will lead to a better understanding of the evolution of dispersion within the animal kingdom. Other issues currently being studied concern defining the stages of dispersion with regard to individuals and examining various dispersal search tactics among individuals (Doerr & Doerr 2005).

The Feral Pigeon is a sedentary bird that nests in breeding colonies (Johnston & Janiga 1995). Sedentary birds exhibit mainly natal dispersion, understood as movement between the places of birth and first breeding, with adult birds dispersing to a much lesser degree (de Bruijn 1994). Studies of the pattern of dispersal among sedentary birds are especially significant because dispersal is a primary mechanism to prevent inbreeding. The Feral Pigeon is a species very commonly found in a majority of large cities throughout the world. This bird is strongly tied to the urban environment, with populations predominantly clustered in city centres (Steiner & Zahner 1994, Sacchi et al. 2002). What makes studying this urban variety of the Rock Pigeon interesting is that the domesticated variety is known for its strong philopatry towards breeding sites. There is still little scientific literature published that compares these two varieties of the Rock Pigeon, especially with regard to behaviour. The selective breeding of domesticated pigeons and the natural selection of Feral Pigeons may result not only in anatomical and morphological differences between the two varieties, but also in significant differences in behaviour. Currently, the Domestic Pigeon is selectively bred for long-distance flight and increased philopatry. Scientific studies have been mainly focused on determining which navigation strategies Domestic Pigeons use to return to their lofts (Wiltschko 1996, Hagstrum 2000, Holland et al. 2000). Because Homing Pigeons seldom join Feral Pigeon populations, they contribute little to the formation of the Feral Pigeon gene pool (Haag 1998b).

Research data on the pattern of dispersal in the Feral Pigeon are fragmentary and largely inadequate. Johnston & Janiga (1995) conducted a literature search, which found that only some aspects of natal dispersion had been studied. A complete picture of the Feral Pigeon's pattern of dispersal has yet to be achieved. Such information could be interesting not only to ornithologists, but to breeders of Domestic Pigeons as well.

The aim of the study was to describe the dispersion pattern for the Feral Pigeon, assess the influence of population density within the breeding colony, and of breeding success upon dispersion, as well as to determine the periods during which the young fly out of the nests and disperse. The examination of the direction and distance of dispersal, as well as of the benefits (and costs) that may be obtained by the birds that disperse, were additional aims of this study.

MATERIALS AND METHODS

Research was conducted between 1997 and 2001 in the city of Słupsk (NW Poland 54°28′N, 17°10′E) in five of over 35 Feral Pigeon breeding colonies. The study period spanned four breeding seasons, with the limitation that only three of the colonies were studied during the last year. The building administrators where the remaining two colonies were located did not grant permission for the last year of the study.

All of the colonies studied were situated in the city centre of Słupsk. Four of the colonies were located in close proximity to each other (50 to 200 m), while the fifth colony was approximately 700–800 m from the others. The colonies differed with respect to breeding pair density, which was equal to, respectively, 0.03 to 0.09 pairs/m^2 (City Hospital, attic), 0.1 to 0.3 (Agricultural Social Insurance Fund (KRUS) Office, attic), 1.1 to 2.1 (St. Jack's Church, tower), 2.1 to 3.6 (Municipal Building, tower) and 3.7 to 4.3 (Museum of Central Pomerania, tower).

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Prior to the beginning of the study, all of the birds from the colonies under consideration were ringed. In the course of the study, new individuals (fledglings and immigrants) were ringed as part of nest inspection, or when trapped during the night. Each pigeon was ringed with three coloured bands. The work carried out in the colonies consisted of observing the pigeons from blinds set up inside the buildings. This enabled to determine the number of breeding pairs as well as the size of their nesting territories, to identify the sex of each paired individual and to note the presence of any unpaired individuals. Observation from the blinds was carried out in all the colonies once every 2 to 3 weeks during the birds' peak reproductive season (from January until August) and once a month during the remaining months of the year. Within the colonies, the nests of breeding pairs were also periodically checked for the appearance of new clutches, to monitor the hatching of nestlings and departure of fledglings from the nest, as well as to ring the fledglings. The date of departure was designated as the date halfway between nest inspections, when the fledgling was still found in the nest, and when its absence was detected in the colony.

Throughout the entire study period, all the Feral Pigeon foraging sites located within the city limits were being visited several times a week and the incidence of ringed birds at these locations was noted. Such observations allowed to directly monitor the presence of these birds within the population, even if they were no longer seen in any of the colonies. Prior to the start of the study, I also visited all the breeders of Domestic Pigeons within the administrative boundaries of the city of Słupsk. The breeders were informed about the study and asked to contact me if they happened to notice the arrival of pigeons fitted with characteristic plastic rings noticeably different from those commonly used by breeders. The study area also encompassed adjacent cities, including Koszalin (ca. 60 km from Słupsk), where a Feral Pigeon population was present; as well as Ustka (18 km away), Bytów (50 km away), and Lębork (50 km away), where no resident populations of this species existed during the course of this study. The study was conducted by the author as well as students permanently residing in the above mentioned cities. Our goal was to register the presence of any ringed pigeons from Słupsk at these locations.

The sex of adult pigeons was determined based on the behaviours they exhibited inside the nesting territory and at foraging sites (Haag 1991a). The pigeons were divided into two age groups: young and adult. The birds that were considered to be young were those that had left their parents' nests and had not yet started breeding. We were able to determine when fledglings joined the breeding populations because they all were ringed. There were several reasons why I did not analyze the dispersion of young birds that had gone missing or died before becoming part of the breeding population. First of all, it was difficult to ascertain whether or not these young, immature birds were returning to their natal colony for the night. Also, it was not possible to fully ascertain whether the absence of a young bird from the colony was permanent or only temporary. And so, dispersion analysis was carried out on those young individuals that ultimately survived and joined the breeding population. The reproductive activities of these young birds was easy to observe from behind the blinds since, as they form, the breeding pairs spend a lot of time within their respective nesting territory. From observations carried out at the foraging sites on the other hand, it was possible to ascertain at which point in time individuals that had emigrated from their natal colony, joined the breeding population. The characteristic behaviour of a male guarding the female in the period before she lays eggs (Lovell-Mansbridge & Birkhead 1998) is easy to observe at locations where the pigeons feed, and it serves as sufficient proof that a breeding pair exists. Pigeons that were reproducing were treated as adult individuals, and their actual age was not taken into account.

To qualify as dispersing individuals, the birds in question had to have left their natal colony permanently and had to have moved into another breeding colony, or to a section of a building not previously occupied by pigeons.

More data about breeding of studied population have been presented in Hetmański (2004) and Hetmański & Barkowska (2007).

I used a χ^2 analysis, with Yates correction, to test for differences between adult and young birds, as well as males and females in the frequency of dispersal. For correlation analyses Spearman rank correlations were used. The analysis of variance (ANOVA) was used to compare mean values. Significance was set at $p \leq 0.05$ for all statistical analyses.

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RESULTS

Age and sex dependent dispersal

The survival rates of young in the period between fledging and recruiting to the breeding population was 34.0% (n = 194), 26.8% (n = 302) and 17.6% (n = 394) of young produced in successive breeding seasons of the study. I established that the dispersion of pigeons affects mainly young individuals. Looking at the young, who were eventually recruited to the breeding population, 27.9% of them first left their natal colony (n = 215). All of these birds left the natal colony before they started to reproduce, so they were not yet part of the breeding population at the time of their departure. It was difficult to ascertain the age at which the young birds were leaving the natal colony. Some observations pointed to the fact that the dispersing young birds varied widely in age. Emigration involved very young fledglings, as well as young but already sexually mature birds. During the study period, I observed several dozen foreign fledglings originating from other colonies. I also observed three cases where foreign males introduced non-paired, ringed females to their colonies. For adult (reproducing) individuals, dispersion was be very low (Table 1). In the course of the entire study period, there was only one pair of birds which (being at least in their third year) left the breeding colony. This pair failed to produce even one nestling, partly because their territory was un-suitable for the construction of a stable nest, but mainly because a pair of Jackdaws *Corvus monedula* nested in close proximity. Jackdaws often attacked adult pigeons that were close to their nest, especially during breeding season. Other breeding pairs who were unsuccessful in reproduction did not leave their natal colonies. They constituted from 11% (n = 54) to 18.7% (n = 91) of all breeding pairs during the breeding seasons studied. And still, a lack of reproductive success did not cause them to leave their respective breeding colonies during the following season.

During each breeding season, I found that young females tended to leave their natal colony more frequently than young males, but this difference was statistically insignificant for each year of the study (Table 1).

Effect of breeding pair density and timing of fledging on dispersal

Whether young pigeons left their natal colonies or not was dependent upon breeding pair density. Young birds from colonies crowded with breeding pairs emigrated more often than those originating from colonies where the population density of pairs was lower (1997/1998: $r = 0.827$, $p < 0.05$; 1998/1999: $r = 0.909$ $p < 0.05$, $n = 5$, Fig. 1).

Furthermore, it was determined that the emigrating young were moving from colonies with high breeding pair density to colonies where this density was low. Out of the total of 60 birds that emigrated from all the colonies studied, 11 of them moved to another colony included in the study. Of these 11 individuals, 10 settled in new colonies with a lower pair density than in their natal colony. Only one individual moved from a colony with a lower density to a colony with a higher density of reproducing pigeons. All these birds paired with pigeons from the new colonies.

No evidence was found that would point to the migration of Feral Pigeons to other cities or to colonies of Domestic Pigeons within the city boundaries of Słupsk. No sightings of any pigeons that had been ringed in Słupsk were reported in the other neighbouring cities of Central Pomerania.

The time of fledging had no effect on the level of dispersion among the surviving young joining

Table 1. The difference in dispersion between the adult (reproducing) individuals and the young individuals produced during each breeding season; as well as between young females and males in the Feral Pigeon population in Słupsk. * — $p < 0.001$. Sample size in parentheses.

Seasons	Dispersion % (N)					
	Adults	Young	χ^2 test	Young males	Young females	χ^2 test
1997/98	0 (114)	19.7 (66)	21.35*	18.9 (37)	20.7 (29)	0.0
1998/99	0 (186)	33.3 (81)	65.36*	28.3 (46)	40 (35)	0.76
1999/2000	0.8 (242)	29.4 (68)	61.53*	24.3 (37)	35.5 (31)	0.55
2000/2001	0 (205)	-	-	-	-	-
Total	0.3 (747)	27.9 (215)	206.96*	24.2 (120)	32.6 (95)	1.49

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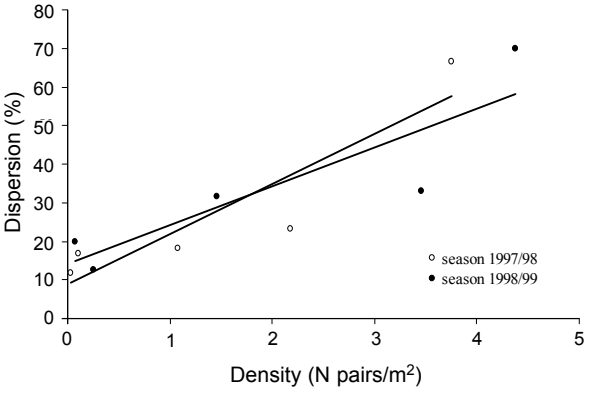


Fig. 1. The dependence between dispersal of young Feral Pigeons and breeding pair density in colonies they fledged.

the breeding population. Birds leaving their natal colonies fledged in nearly every month of the year (Fig. 2) and their number was directly proportional to the number of young leaving the nest (χ^2 = 3.37, $p > 0.05$, df =5).

Number of fledglings produced by dispersing birds and birds remaining in their natal colonies

In searching for an answer as to whether it was advantageous for young birds to leave the natal colony and move to a new site, I compared the number of fledglings produced during each season by the migrating birds, to the number of fledglings produced by birds remaining in the natal colonies. I was able to determine the breeding success of 11 birds (18.3 %) among the 60 individuals that permanently left their natal colonies

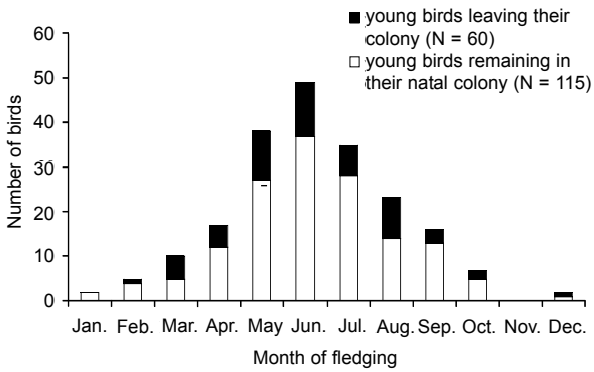


Fig. 2. Proportion of birds remaining and emigrating among the young of the study colonies that joined a breeding population and month of fledging.

during the study period and subsequently joined a breeding population. These individuals moved from one to another of the 5 study colonies. It turned out that during the first breeding season, they produced more fledglings than birds remaining in their natal colonies (Table 2). This difference was especially pronounced in relation to birds that remained in natal colonies with high breeding pair density. The difference in fledgling production between the dispersing birds and birds remaining in natal colonies crowded with breeding pairs was statistically significant (Table 2). The breeding success of dispersed birds was even higher than that of the native birds of the colonies they joined, where the density was low. This difference in the numbers of reared young was not statistically significant however (ANOVA, between emigrating pairs and native pairs from Hospital and KRUS, $p > 0.05$, according to Tukey's T test). This may indicate that the young birds moving into a new colony ended up staying permanently, having found particularly favourable conditions there for breeding. The young that emigrated had high nesting success during the second breeding season also. These birds were still producing significantly more fledglings than birds remaining in natal colonies where nesting conditions were unfavourable due to the high density of breeding pairs (Table 2). The greater number of reared young resulted not only from higher brood safety, but also from the opportunity to begin breeding earlier in a colony with low density.

DISCUSSION

This study shows that there is dispersal asymmetry in the Feral Pigeon population. Dispersal was dependent on the age, but was independent of sex of the pigeons. The difference was pronounced between young individuals that were not yet reproducing, and adult, reproducing individuals. Dispersion among young birds was relatively high and remained at a stable level of 20 to 33% a year. In birds older than seven weeks, Edrich & Keeton (1977) found that 50% of their sample flew from the home loft and never returned, but these data may also include birds that died. At the same time, hardly any adult birds left their breeding colonies. Strong philopatry predominantly among adult individuals was evident; they did not leave a colony, even if nesting conditions there were unfavourable due to high breeding pair density. The study colonies

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Table 2. A comparison of young migrating birds and young birds remaining during successive reproductive seasons in the breeding colonies studied with regard to fledgling production in successive breeding seasons. N — sample size.

Pigeons	Mean density (N pair/m^2)	Number of fledglings produced by birds in:					
		1st breeding season		2nd breeding season		3rd breeding season	
		mean ± SD	N	mean ± SD	N	mean ± SD	N
Emigrating		4.7 ± 2.87	11	5.8 ± 3.34	11	5.3 ± 0.58	3
Remaining at:							
Hospital	0.1	3.8 ± 2.08	24	6.3 ± 2.05	11	-	-
KRUS	0.03	3.2 ± 2.36	24	7.0 ± 2.83	6	5.0 ± 2.0	3
Municipal Building	3.3	1.1 ± 1.73	55	2.0 ± 1.53	34	3.1 ± 1.41	20
St. Jack's Church	1.8	0.9 ± 1.33	38	2.1 ± 1.83	21	3.0 ± 1.26	6
ANOVA		F = 18.89, df = 150, p = 0.00		F = 19.01, df = 80, p = 0.00		—	

differed significantly in the number of fledglings produced in a season, resulting from the considerable differences in breeding pair densities (Table 2, Hetmański & Barkowska 2007). Some adult pairs did not have any breeding success in the overly dense colonies, and yet this had almost no effect on dispersion. Jackdaw predation, which destroyed eggs and killed pigeon nestlings in the Municipal Building colony (Hetmański 2005, Hetmański & Barkowska 2007) resulted in the emigration of only one adult pair, and did not affect other pairs. A similar situation was shown in the case of the Eastern Kingbird *Tyrannus tyrranus*. Site fidelity of this species males was not reduced significantly by poor nest success in a previous year (Murphy 1996). In the case of other animal species however, a lack of reproductive success may increase the dispersion of individuals within a population (Haas 1998, Grosbois et al. 2003, Winkler et al. 2004, Fowler 2005). Fowler (2005) showed that breeding success and extent of kinship with the nearest neighbour had a positive effect on breeding philopatry, and consequently on fine-scale spatial and genetic structuring. There is a lack of data in the literature pertaining to dispersion in the case of the Rock Pigeon, but strong site attachment seen in the Feral and Homing Pigeons is most likely a trait inherited from the Rock Pigeon (Johnston & Janiga 1995). The evolution of coloniality in birds was the result of increased foraging efficiency and decreased predation risk (Rolland et al. 1998, Beauchamp 1999). Most likely, these same factors also led to the evolution of coloniality in the case of the Rock Pigeon, which exhibits high fidelity for its breeding sites. Is the strong philopatry of adult Feral Pigeons an advantage? It does not seem advantageous from the perspective of breeding effectiveness, since observations show that the breeding success of pairs living in highly dense colonies is low each year (Hetmański & Barkowska 2007). Strong competition for nesting territory makes it impossible for many pairs to improve their nesting conditions. Therefore, it would be more advantageous for these birds to leave their natal colony and find a new colony where their breeding success could be significantly higher. The costs of dispersion would be low in this case. Diurnal predators are practically absent in the urban environment, so birds are not endangered by them, while potential new breeding/nesting sites are often available in close proximity within the city. Furthermore, dispersing birds could continue using their old foraging sites, to which they are strongly tied. Additionally, the benefits of dispersal could be significant in the form of increased breeding success. From an evolutionary point of view, weakening philopatry and increasing dispersion among adult pigeons would be advantageous in an urban environment, where predator pressure is insignificant and foraging sites are in close proximity. However, not moving from a native colony probably results from the genetic conditioning of philopatry among adult individuals. Strong philopatry among adult pigeons turned out to be disadvantageous because the birds have little chance to increase their breeding success in overly dense colonies. In its functioning, the Feral Pigeon colony resembles those of seabirds. In the case of *Uria aalge*, fidelity towards breeding sites is also very high (Harris et al. 1996). Breeding pairs return to the same location year after year, although, due to competition, some pairs are forced to take up worse sites than before, nevertheless in close proximity to the nesting site of the previous year.

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It is a well-known phenomenon in the animal kingdom that dispersing individuals mainly move to where they can find better conditions (Ims 1989, Negro et al. 1997, Pasinelli & Walters 2002). Searching for better environmental conditions is one of many decisive mechanisms for the evolution of dispersion. The research conducted in Słupsk shows that young pigeons migrated from colonies with high breeding pair density to colonies with low breeding pair density. This type of dispersion was beneficial to them, since they attained much higher reproductive success in the new colonies than those individuals remaining in their natal colonies. The overcrowded colonies do not offer good nesting conditions due to strong competition between pigeons for nest sites. Competition, manifested by frequent fights among pigeons, increases the number of lost clutches and broods (Haag 1988, 1991b). Furthermore, higher numbers of ectoparasites in overcrowded colonies may also increase natal dispersion (Brown & Brown 1992). For many pigeons, the time between when they are able to leave the natal colony and when they join a breeding population seems to be highly critical, because it is during this period that, through dispersion, they are able to influence their future reproductive success. Later in life, after they have joined a reproducing population, they will be unable to significantly alter their reproductive success because of strong philopatry and attachment to their partner. The importance of this decision is further increased by the fact that pigeons have a short lifespan. Haag (1990) has shown that on the average they live 2.4–2.9 years. And so, the decision to remain in a natal colony characterised by unfavourable nesting conditions may be detrimental for many young pigeons, since they will not be able to produce even one fledgling in their short life.

The Feral Pigeons living in Słupsk tended to stay within the city boundaries. We did not witness any Feral Pigeons joining the colonies of Homing Pigeons, most of which were located on the outskirts of the city. Neither were the Feral Pigeons shown to migrate to other cities. In this sense, the Słupsk Feral Pigeon population behaved much like the population in Basel, Switzerland. Haag-Wackernagel (1998), who studied Feral Pigeons there, said that the birds' migration out of the city takes place very sporadically or rarely. Successive studies using modern research methods carried out on pigeons in that city confirmed earlier observations (Rose et al. 2006a, b) that pigeons are very attached to the urban environment. By contrast, in another city (Bratislava), pigeons exhibited a different behaviour and would travel to foraging sites located outside of the city (Janiga 1987, own obs).

Young females tended to emigrate more often than young males, but the differences were not great and statistically insignificant. Higher dispersal among females is typical for most bird species, in contrast to mammal species (Greenwood 1980). This is because the individuals of the more territorial sex are more closely tied to a site and do not readily disperse (Dittman et al. 2005). The Feral Pigeon male is more aggressive than the female (Castoro & Guhl 1958). He sets the boundaries of the territory and defends them, although the female also actively defends the nesting territory. However, it is the male's losing battle that determines the loss of territory. A male's territory is an important asset for attracting females, because a partner is chosen on the basis of territorial quality, which also affects how long the breeding pair will endure.

Feral Pigeons are able to reproduce all year round (Johnston & Janiga 1995, Hetmański 2004), and their fledglings may leave the nest at any time of the year as well. It was determined that the time of departure of the fledglings from the nest had no effect on their dispersion (Fig. 2). In some bird species, the time of departure from the nest may have an effect on dispersion. Nilsson (1989) found that in the Marsh Tit *Parus palustris*, early-hatched females dispersed farther than those hatched in the middle of the season. Although I have examined the pattern of dispersion for the Feral Pigeon, we still do not know the age when young disperse most readily, the factors underlying dispersion, and how long it takes the birds to settle into a new colony. Prior to taking up residence in a new colony, the birds most likely test it out with respect to competition for nesting space, and, even more important, whether the nesting territory will be safe enough for their developing progeny. That some individuals may find a partner from another colony probably plays a role in the dispersion of young pigeons. There are, however, some individuals that end up in a new colony by pure accident. Namely, fledglings had been observed in colonies other than their natal colonies. It would seem unlikely that the birds would intentionally move from one breeding colony to another at such a early age. This is why I suspect that they appeared in the new colony after getting lost somewhere in the city,

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and then simply followed other birds to a different breeding colony.

In summary, the research presented here fills a gap in knowledge about the pattern of dispersion in the urban variety of Rock Pigeon. My research results show that the Feral Pigeon does not deviate from the Homing Pigeon with regard to dispersion behaviour, although the two live in different environments. Strong philopatry exhibited by adult pigeons of both varieties is most likely inherited from the Rock Pigeon. The element of safety in the urban environment has not, however, influenced the behaviour of the Feral Pigeon. Such a change could be more beneficial in terms of potentially increased reproductive success for many birds. Moving to a new breeding colony could significantly increase breeding effectiveness, especially if the pigeons were moving from an overcrowded colony, with unfavourable nesting conditions, to a colony where the density of breeding pairs was lower. But pigeons are highly conservative in this respect. Even though the costs of dispersion would not be high (no predators, no need to look for new foraging sites), adult individuals do not migrate. Only the young individuals disperse, as they are less attached to their natal colony and its location. This was also observed by Edrich & Keeton (1977) in 7-week old young. This is not only a chance to increase their reproductive index, but also a way of decreasing inbreeding within the colonies.

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REFERENCES

Aars J., Ims R. A. 2000. Population dynamic and genetic consequences of spatial density-dependent dispersal in patchy populations. Am. Nat. 155: 252–265.

Beauchamp G. 1999. A comparative study of breeding traits in colonial birds. Evol. Ecol. Research 1: 251–260.

Brown C. R., Brown M. B. 1992. Ectoparasitism as a cause of natal dispersal in cliff swallows. Ecology 73: 1718–1723.

Castoro P. L., Guhl A. M. 1958. Pairing behavior of pigeons related to aggressiveness and territory. Wilson Bull. 70: 57–69.

Chernetsov N., Chromik W., Dolata P. T., Profus P., Tryjanowski P. 2006. Sex-related natal dispersal of White Storks (*Ciconia ciconia*) in Poland: how far and where to? Auk 123: 1103–1109.

de Bruijn O. 1994. Population ecology and conservation of the Barn Owl *Tyto alba* in farmland habitats in Liemers and Achterhoek (The Netherlands). Ardea 82: 1–109.

Dittman T., Zinsmeister D., Becker P. H. 2005. Dispersal decisions: common terns, *Sterna hirundo*, choose between colonies during prospecting. Anim. Behav. 70: 13–20.

Doerr E. D., Doerr V. A. J. 2005. Dispersal range analysis: quantifying individual variation in dispersal behaviour. Oecologia 142: 1–10.

Double M. C., Peakall R., Beck N. R., Cockburn A. 2005. Dispersal, philopatry, and infidelity: Dissecting local genetic structure in superb fairy-wrens (*Malurus cyaneus*). Evolution 59: 625–635.

Edrich W., Keeton W. T. 1977. A comparison of homing behavior in feral and homing pigeons. Z. Tierpsychol. 44: 389–401.

Fowler A. C. 2005. Fine-scale spatial structuring in cackling Canada geese related to reproductive performance and breeding philopatry. Anim. Behav. 69: 973–981.

Gandon S. 1999. Kin competition, the cost of inbreeding and the evolution of dispersal. J. Theor. Biol. 200: 345–364.

Green D. J., Cockburn A. 2001. Post-fledging care, philopatry and recruitment in brown thornbills. J. Anim. Ecol. 70: 505–514.

Greenwood P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. 28: 1140–1162.

Greenwood P. J., Harvey P. H. 1982. The natal and breeding dispersal of birds. Ann. Rev. Ecol. Syst. 13: 1–21.

Grosbois V., Reboulet A. M., Prévot-Julliard A. C., Bottin L., Lebreton J. D. 2003. Dispersal and recruitment in the Black-Headed Gull *Larus ridibundus*. Alauda 71: 139–144.

Haag D. 1988. Die dichteabhängige Regulation im Brutschwarm der Strassentaube *Columba livia forma domestica*. Ornithol. Beob. 85: 209–224.

Haag D. 1990. Lebenserwartung und Altersstruktur der Strassentaube *Columba livia forma domestica*. Ornithol. Beob. 87: 147–151.

Haag D. 1991a. Ethogramm der Taube. Veröffentlichung in der Reihe "ORN-Projekt" 13.

Haag D. 1991b. Population density as a regulator of mortality among eggs and nestlings of feral pigeons (*Columba livia domestica*) in Basel, Switzerland. In: Pinowski J., Kavanagh B. P., Górski W. (eds). Nestling mortality of granivorous birds due to microorganisms and toxic substances. PWN, Warsaw. pp. 21–31.

Haag-Wackernagel D. 1998. Ecology of Feral Pigeons in Basel, Switzerland. In: Farina A., Kennedy J., Bossŭ V. (eds)., Proc. VIIth Intern. Congr. Ecol., Florence, pp: 1–4.

Haas C. A. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: An experimental approach. Auk 115: 929–936.

Hagstrum J. T. 2000. Infrasound and the avian navigational map. J. Exp. Biol. 203: 1103–1111.

Harris M. P., Wanless S., Barton T. R. 1996. Site use and fidelity in the Common Guillemot *Uria aalge*. Ibis 138: 399–404.

Hetmański T. 2004. Timing of breeding in the Feral Pigeon *Columba livia f. domestica* in Słupsk (NW Poland). Acta Ornithol. 39: 105–110.

Hetmański T. 2005. Observations of a Jackdaws attempting to feed a pigeon fledgling. Berkut 14: 231–233.

Hetmański T., Barkowska M. 2007. Density and age of breeding pairs influence feral pigeon *Columba livia* reproduction. Folia Zool. 56: 71–83.

Holenweg P. A. 2001. Dispersal rates and distances in adult water frogs, *Rana lessonae*, *R. ridibunda*, and their hybridogenetic associate *R. esculenta*. Herpetologica 57: 449–460.

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Holland R., Bonadonna F., Dall'antonia L., Benvenuti S., Burt de Perera T., Guilford T. 2000. Short distance phase shifts revisited: tracking clock-shifted homing pigeons (Rock Dove *Columba livia*) close to the loft. Ibis 142: 111–118.
Ims R. A. 1989. Kinship and origin effects on dispersal and space sharing in *Clethrionomys rufocanus*. Ecology 70: 607–616.
Jack K. M., Fedigan L. 2004. Male dispersal patterns in white-faced capuchins, *Cebus capucinus* Part 2: patterns and causes of secondary dispersal. Anim. Behav. 67: 771–782.
Janiga M. 1987. Seasonal aspect of intensity and course of daily translocations of pigeons (*Columba livia* f. *domestica*) for food from Bratislava to its surroundings. Acta F. R. N. Univ. Comen. Zoologia 32: 47–59.
Johnston R., Janiga M. 1995. Feral pigeon. Oxford University Press.
Kokko H., Lundberg P. 2001. Dispersal, migration, and offspring retention in saturated habitats. Am. Nat. 157: 188–202.
Lefebvre D., Ménard N., Pierre J. S. 2003. Modelling the influence of demographic parameters on group structure in social species with dispersal asymmetry and group fission. Behav. Ecol. Sociobiol. 53: 402–410.
Lovell-Mansbridge C., Birkhead T. R. 1998. Do female pigeons trade pair copulations for protection? Anim. Behav. 56: 235–241.
Murphy M. T. 1996. Survivorship, breeding dispersal and mate fidelity in Eastern Kingbirds. Condor 98: 82–92.
Negro J. J., Hiraldo F., Donazar F. A. 1997. Causes of natal dispersal in the lesser kestrel: inbreeding avoidance or resource competition? J. Anim. Ecol. 66: 640–648.
Nilsson J. 1989. Causes and consequences of natal dispersal in the Marsh Tit, *Parus palustris*. J. Anim. Ecol. 58: 619–636.
Pasinelli G., Walters J. R. 2002. Social and environmental factors affect natal dispersal and philopatry of male red-cockaded woodpeckers. Ecology 83: 2229–2239.
Pärt T., Gustafsson L. 1989. Breeding dispersal in the Collared Flycatcher (*Ficedula albicollis*): possible causes and reproductive consequences. J. Anim. Ecol. 58: 305–320.
Perrin N., Mazalov V. 1999. Dispersal and inbreeding avoidance. Am. Nat. 154: 282–292.
Plissner J. H., Gowaty P. A. 1996. Patterns of natal dispersal, turnover and dispersal costs in eastern bluebirds. Anim. Behav. 51: 1307–1322.
Pusey A., Wolf M. 1996. Inbreeding avoidance in animals. TREE 11: 201–206.
Rolland C., Danchin E., de Fraipont M. 1998. The evolution of coloniality in birds in relation to food, habitat, predation, and life-history traits: a comparative analysis. Am. Nat. 151: 514–529.
Rose E., Haag-Wackernagel D., Nagel P. 2006a. Practical use of GPS-localization of Feral Pigeons *Columba livia* in the urban environment. Ibis 148: 231–239.
Rose E., Nagel P., Haag-Wackernagel D. 2006b. Spatio-temporal use of the urban habitat by feral pigeons (*Columba livia*). Behav. Ecol. Sociobiol. 60: 242–254.
Sacchi R., Gentilli A., Razzetti E., Barbieri F. 2002. Effects of building features on density and flock distribution of feral pigeons *Columba livia* var. *domestica* in an urban environment. Can. J. Zool. 80: 48–54.
Steiner R., Zahner A. 1994. Untersuchungen zu Siedlungsdichte und Aktionsradius der Straßentauben (*Columba livia f. domestica*) in Wien mit einer Bestandsschätzung für das gesamte Stadtgebiet. Egretta 37: 78–93.
Winkler D. W., Wrege P. H., Allen P. E., Kast T. L., Senesac P., Wasson M. F., Liambias P. E., Ferretti V., Sullivan P. J. 2004. Breeding dispersal and philopatry in tree swallow. Condor 106: 768–776.
Wiltschko R. 1996. The function of olfactory input in pigeon orientation: does it provide navigational information or play another role? J. Exp. Biol. 199: 113–119.

STRESZCZENIE

[Asymetria dyspersji w populacji gołębia miejskiego]

Badania nad dyspersją gołębia miejskiego prowadzono w latach 1997–2001. Kolonie lęgowe zlokalizowane były w śródmieściu Słupska i różniły się przede wszystkim zagęszczeniem par lęgowych wynoszącym od 0.03 do 4.3 pary/m^2. Wszystkie gołębie z badanych kolonii zostały indywidualnie oznakowane kolorowymi obrączkami jeszcze przed rozpoczęciem badań. W trakcie trwania badań obrączkowano w gniazdach podloty oraz imigrantów przybywających do kolonii. Celem badań było określenie wzorca dyspersji gołębia miejskiego oraz jakie czynniki mogą wpływać na rozpraszanie się ptaków. Analizowano również kierunek oraz dystans dyspersji. Wyniki badań wskazują jednoznacznie, że dyspersja gołębia miejskiego jest zróżnicowana w koloniach lęgowych, i że zależy od wieku oraz w mniejszym stopniu od płci ptaków. Gołębie opuszczające rodzime kolonie należały do ptaków młodych, nierozmnażających się. Spośród 215 młodych, które opuściły gniazda w badanych koloniach, 27.9% na stałe wyemigrowało do innych kolonii na terenie miasta. Pozostałe młode pozostały w swoich koloniach. Dyspersja zależała od zagęszczenia par lęgowych w koloniach. Młode z kolonii o wyższym zagęszczeniu częściej opuszczały rodzime kolonie niż młode ptaki z kolonii z niższym zagęszczeniem par lęgowych. Ptaki dorosłe, rozmnażające się, nie wykazywały tendencji do rozpraszania się i charakteryzowały się bardzo wysoką filopatrią do miejsc lęgowych. Niepowodzenie w rozrodzie nie miało wpływu na dyspersję osobników rozmnażających się. Nie stwierdzono, żeby gołębie emigrowały do kolonii gołębi domowych w granicach administracyjnych miasta Słupska, ani do sąsiadujących miast. Młode samice częściej od samców opuszczały rodzime kolonie lęgowe, jednakże różnica nie była statystycznie istotna. Ptaki przenosiły się z kolonii o wyższym do kolonii z niższym zagęszczeniu gołębi, w których osiągały wyższy sukces lęgowy niż ich rówieśnicy pozostający w koloniach.

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