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*Regular research paper*

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## THE EFFECT OF ENVIRONMENTAL FACTORS AND NESTING CONDITIONS ON CLUTCH OVERLAP IN THE FERAL PIGEON *COLUMBA LIVIA* F. URBANA (GM.)

**ABSTRACT:** Clutch overlap is a reproductive strategy of the Feral Pigeon, which results in an increase in the number of clutches produced by a pair and, as follows, an increase in the number of young raised. It is dependent on the length of time the clutch is cared for and the length of the interval between clutches. Both these component elements of clutch overlap are directly affected by environmental conditions, such as the length of day and ambient temperature. The duration of clutch care and the clutch interval were distinctly shorter in the warmer part of the year with a longer day than during the fall and winter. We believe that ambient temperature has a significant effect on the length of the clutch interval, as it is a decisive factor in the achievement of thermoregulation ability in the nestlings. Earlier achievement of this ability by nestlings in higher ambient temperatures (at  $T_a = 21.5^\circ\text{C}$ , normothermy appeared in the 6<sup>th</sup> to 7<sup>th</sup> post-embryonic day in the life of nestlings, while at  $T_a = 19.5^\circ\text{C}$  – in 8–9 days) allows both parents to forage for longer periods of time and to start a new breeding cycle earlier. We confirmed that nesting conditions (the number of nests in a breeding pair's territory, brood size and location of the nest in the colony) also influenced the duration of clutch care and the length of clutch interval, and therefore, the degree of clutch overlap. The clutch interval was shorter when parents only cared for one young, than when two young were in the nest. Breeding pairs with large territories that included two

nests had shorter clutch intervals than those pairs with only one nest. Young raised in nests located close to egresses left the colony more quickly than young in nests farther away.

**KEY WORDS:** Feral Pigeon, *Columba livia*, clutch interval, clutch overlap, normothermy, breeding strategy

### 1. INTRODUCTION

Pigeons have the best developed strategy among birds for producing many clutches in a season, developed as a result of both physiological and behavioural characteristics. Depending on the species, females lay small clutches of small eggs, from 1 to 2 eggs (Goodwin 1983, Robertson 1988), and if a clutch is lost, the birds are able to lay again within a short period of time. Pigeons build simple nests, and the nesting cycle is short (Burley 1980, Westmoreland *et al.* 1986). Both parents incubate the eggs and feed the nestlings. In the first days after hatching, nestlings are fed a nutritious crop milk (Bharathi *et al.* 1997), a factor promoting their fast development. Pigeons and doves have an extended breeding season (Górski and Górka 1995, Górski *et al.* 1998, Hetmański 2004).

The Feral Pigeon is the only representative of Columbidae from a moderate and cool climate that breeds throughout the entire year (Lees 1946, Goodwin 1960, Dunmore and Davis 1963, Häkkinen *et al.* 1973, Murton *et al.* 1974, Johnston 1984, Dabert 1987, Johnston and Janiga 1995, Hetmański 2004). An additional biological characteristic of this species that increases the reproductive effectiveness of breeding pairs is their ability to care for two clutches simultaneously (Burley 1980, Johnson and Johnston 1989). This enables the clutch interval to be shortened, thereby increasing the number of clutches in a season. Partial overlapping of successive clutches has been described in several other pigeon species (Westmoreland *et al.* 1986, Westmoreland and Best 1987, Ten Cate and Hilbers 1991, Ten Cate and Tabor-sky 1992). It is rarely used by other birds and when it occurs, it is most often an optional strategy (Hays 1984, Wiggins *et al.* 1984, Hill 1986, Blockstein 1989, Smith *et al.* 1989, Verhulst and Hut 1996, Dowding *et al.* 1999).

Burley (1980) demonstrated that clutch overlap in the Feral Pigeon occurs when the young require the least amount of care, that is, towards the end of their stay in the nest. At this time, the breeding pair lays a new clutch. This strategy is directly tied to the outlay of the parents' energy resources. Except for the time when the young are fed crop milk, requiring a high level of resource outlay, the parents are able to raise two broods.

Burley (1980) also showed that the degree of clutch overlap varies among breeding pairs and depends on the breeding experience of pigeons. Johnson and Johnston (1989) reported that the interval between successive clutches varies with the time of year, and is dependent on the female's plumage pattern, body mass and tarsus length. There is little information about the effect of environmental conditions on the duration of caring for the brood, clutch interval and clutch overlap of the Feral Pigeon (Burley 1980, Johnson and Johnston 1989). Evidence for such an influence should emerge, as the Feral Pigeon breeds in all seasons of the year with distinctly different weather conditions. The goal of this study was to determine whether there is

an association between the duration of clutch care, clutch interval and clutch overlap with the length of day and ambient temperature. We also analysed the effect of nesting conditions (the number of nests in the nesting territory, brood size and location of the nest in the colony) on pairs' breeding intensity, as shown by the length of clutch interval and degree of clutch overlap.

## 2. STUDY AREA AND METHODS

The research was conducted in Słupsk (NW Poland, 54°28'N, 17°10'E), a city of 100,000 residents. Breeding cycles of the Feral Pigeon were observed in five colonies between 1997–2000, and in three colonies in 2001, located in towers or attics in the centre of the city. All the pigeons in the breeding colonies studied were individually ringed before the study began. The birds were captured at night in the buildings after closing off their means of egress. Successive captures of all the pigeons in the study colonies took place three times during the year to ring any immigrant pigeons.

Observations conducted over many hours from blinds set up in the breeding colonies allowed us to determine the number of breeding pairs, the beginning and ending dates of the breeding season, the number of clutches raised by pairs, changes in pair composition, as well as nest locations and territorial boundaries. These observations were conducted in each breeding colony every 2–3 weeks from January to August, and once per month during the rest of the year. A total of 54 pairs bred in the first breeding season, with 90, 113 and 97 pairs in successive seasons. Because some pigeons began breeding directly after moulting, that is, between October and December, and the remaining pairs began in the next calendar year, their breeding season lasted over a two-year period. In effect, defining a season as 1997/1998 means that the breeding period began in the fall/winter of 1997 and ended in 1998. For the time of commencement, termination and length of breeding season for the studied breeding pairs of the Słupsk population, see Hetmański (2004).

Additional observations were conducted twice per week from January to August, and

once weekly during the remainder of the year to determine nest contents, date of egg laying, hatching dates, size of eggs and nestlings and reasons for their loss. The young were ringed while still in the nest as we conducted the nest checks.

The day the first egg was laid was considered the starting date of the clutch. In cases when only one egg was found, the previous day was deemed as the laying date because observations were conducted early in the morning. If two eggs were found it was assumed that the first egg appeared three days earlier as the second egg is laid about 40 hours after the first (Johnston and Janiga 1995). To minimise error in defining the start date of a clutch, we used the hatch date of the nestlings (the incubation period is 18 days – Burley 1980, Johnston and Janiga 1995, Vatnick and Foertsch 1998) and measured their body mass in the first days after hatching.

The completion of a clutch was set at the date the last young of the clutch left the nest colony. It was difficult to determine the exact date the last young fledged, so we designated it as the middle day of the period between the nest check where the nestling was confirmed to be present in the colony and the next check where it was no longer observed in the building.

The duration of clutch care by the breeding pair was considered as the number of days from the appearance of the first egg to the fledging of the last nestling. The time the

parents cared for the young after fledging was not included in the duration of clutch care, as this was very difficult to determine.

The interval between successive clutches was defined as the number of days from the date the first egg was laid to the date the first egg of the next clutch was laid (Burley 1980) (Fig. 1). Clutch intervals were also calculated in cases where the second clutch ended in the loss of eggs or nestlings.

Clutch overlap of the studied breeding pairs was based on the number of days two clutches were cared for simultaneously (Burley 1980) (Fig. 1). The degree of clutch overlap was calculated as follows:  $O_1/D$ , when a given clutch overlapped only with an earlier clutch ( $O_1$  – the number of days a given clutch overlapped with an earlier one,  $D$  – the duration of clutch care),  $O_2/D$  when a given clutch overlapped with only a successive clutch ( $O_2$  – the number of days a given clutch overlapped with a successive one) or  $(O_1 + O_2)/D$ , when a given clutch overlapped with both an earlier clutch and a successive one. Clutch overlap is represented by a fraction or percent value.

In May and June of 2003–2004, we conducted studies to determine the effect of ambient temperature [ $T_a$ ] on the length of clutch interval. We wanted to learn if the time it took the nestlings to achieve the thermoregulation ability was associated with ambient temperature  $T_a$ . We hypothesized that earlier physiological development of thermoregulation in nestlings in higher ambient

A – onset of parental investment in clutch  
B – end of investment of brood  
 $D_1, D_2, D_3$  – duration of successive clutches (days)  
 $O_1$  – overlap with the preceding clutch  
 $O_2$  – overlap with following clutch

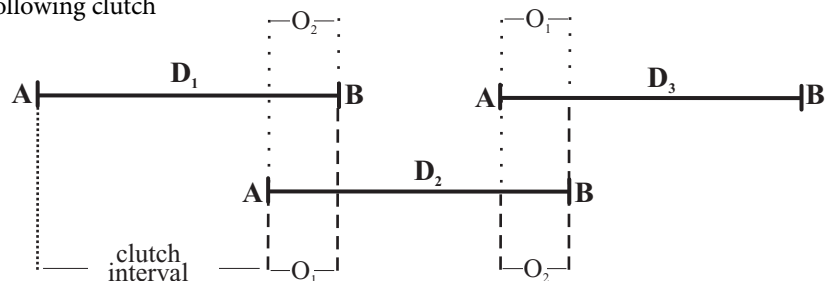


Fig. 1. Scheme presenting method of designating the length of the clutch interval and clutch overlap in the Feral Pigeon city population.

temperatures would allow their parents to start a new nesting cycle more quickly. The achievement of temperature regulation ability (euthermy) was determined by measuring the body temperature of nestlings [ $T_b$ ] from day 3 to 11 of their lives.  $T_b$  was measured with an electronic thermometer THERM 2244-1 (made in Germany) to within 0.01°C. The thermometer's probe was placed in the cloaca of an earlier ringed nestling, always at the same depth of 15 millimetres. The body temperature of each nestling was taken three times – directly upon removal from the nest, at 5 minutes and then 10 minutes after individual removal from the nest. We accepted the ability of nestlings to regulate their body temperature as the time when their  $T_b$  once outside of the nest did not decrease more than 0.5°C within 10 minutes. The difference between nestlings'  $T_b$  directly upon removal of the nest and  $T_b$  after an interval of 10 minutes outside of the nest was used to calculate the decrease of  $T_b$ .

A total of 882  $T_b$  measurements were taken of 294 individuals. These were multiple measurements of the same nestlings. The ambient temperature [ $T_a$ ] of the quarters inhabited by the colony was taken at the same time measurements were made of the cloacal temperature and body mass [ $M_b$ ] of the nestlings. The Mann-Whitney U-test or Kruskal-Wallis H-test was used to compare the average values of two or more samples, and association was tested by either the Pearson correlation coefficient ( $r$ ) or the Spearman rank-order ( $r_s$ ).

### 3. RESULTS

#### 3.1. The number of clutches and duration of care

Breeding pairs of the Feral Pigeon produced from 1 to 9 clutches in a season, averaging from  $4.0 \pm 1.54$  ( $n = 97$ ) in the 2000/2001 breeding season to  $4.6 \pm 2.00$  ( $n = 113$ ) in the 1998/1999 season. If considering only those clutches which resulted in one or two successfully fledged young, 1 – 7 such clutches were cared for by pairs, averaging from  $2.5 \pm 1.36$  ( $n = 81$ ) in the 2000/2001 season to  $2.8 \pm 1.34$  ( $n = 95$ ) in the 1999/2000 season. Clutches were observed in all months of the year, but the fall season (September-October) yielded the least number, as this was the time pigeons moulted (Hetmański 2004). Most clutches were laid between March-July, comprising from 70% of all broods in the second study season ( $n = 414$ ) to 79% in the first, that is, the 1997/98 season ( $n = 241$ ). The appearance of clutches peaked in April, May or June. The number of clutches established in particular months of the breeding season was positively correlated with the length of day ( $r_s = 0.783$ ,  $P < 0.01$ ) and ambient temperature ( $r_s = 0.452$ ,  $P < 0.01$ ).

Breeding pairs cared for their clutches for an average  $60.4 \pm 4.96$  days over the entire study period ( $n = 606$ ). The longest duration of care occurred in autumn, with the shortest occurring from July to August (Table 1). These data are taken from the entire study period as the distribution of the length of time

Table 1. Changes in the duration of clutch care and clutch intervals for particular periods of the breeding season of the Feral Pigeon (*Columba livia f. urbana*) in Słupsk city.

	Periods of breeding					Comparison of mean values
	Oct.-Dec.	Jan.-Feb.	March-Apr.	May-June	July-Aug.	
Duration of clutch in days $\pm$ SD	$65.2 \pm 4.34$ n = 20	$62.9 \pm 5.76$ n = 85	$60.5 \pm 5.31$ n = 174	$59.4 \pm 4.26$ n = 208	$59.2 \pm 3.84$ n = 119	H = 51.41 $P < 0.001$
Length of interval in days $\pm$ SD	$63.5 \pm 7.28$ n = 17	$51.0 \pm 9.12$ n = 103	$45.6 \pm 7.33$ n = 210	$44.7 \pm 6.71$ n = 220	$47.5 \pm 9.48$ n = 29	H = 91.04 $P < 0.001$

clutches were cared for was very similar in each year of the study ( $\chi^2 = 0.696$ ,  $P > 0.05$ ). Duration of care of the clutches depended on the length of day ( $r_s = -0.830$ ,  $P < 0.001$ ), and, to a lesser degree, on the ambient temperature ( $r_s = -0.549$ ,  $P < 0.01$ ). The number of young in a clutch was also a factor influencing the duration of care by the parents (Fig. 2). Clutches with only one hatched and cared for nestling ( $n = 137$ ) lasted on average  $59.7 \pm 4.69$  days and were shorter than clutches resulting in the fledging of two young  $60.7 \pm 4.74$  ( $n = 388$ ) (Mann-Whitney U-test,  $U = 2.64$ ,  $P < 0.01$ ). These data include clutches from the entire study period. Similar findings result when comparing these types of clutches from a narrower time period, that is, from March to July –  $59.1 \pm 4.24$  days ( $n = 107$ ) and  $60.1 \pm 4.36$  days ( $n = 300$ ) respectively (Mann-Whitney U-test,  $U = 2.36$ ,  $P < 0.05$ ). The difference in duration of care between clutches with one or two young was similar throughout the year ( $\chi^2 = 0.166$ ,  $P > 0.05$ ) (Fig. 2).

The duration of clutch care by the breeding pair also depended on the location of the nest in the quarters occupied by the breeding colony. We observed that young in nests closer to egresses left the building more quickly than those young in nests farther away. In one of the study colonies located in a high tower, young raised on the floor left the building about 7 days later (average duration of clutch care between March and July was  $63.3 \pm 4.55$  days,  $n = 55$ ) than young raised in nests close to the egresses (clutches lasted during this same time  $55.7 \pm 3.25$  days,  $n = 36$ ) (Mann-Whitney U-test,  $U = 6.89$ ,  $P < 0.001$ ). Young from the lower regions of the tower most likely needed more time to achieve better physical condition to overcome the almost 3 meter height to the egresses.

### 3.2. Interval between successive clutches and factors influencing its length

Breeding pairs laid successive clutches while still caring for young from an earlier

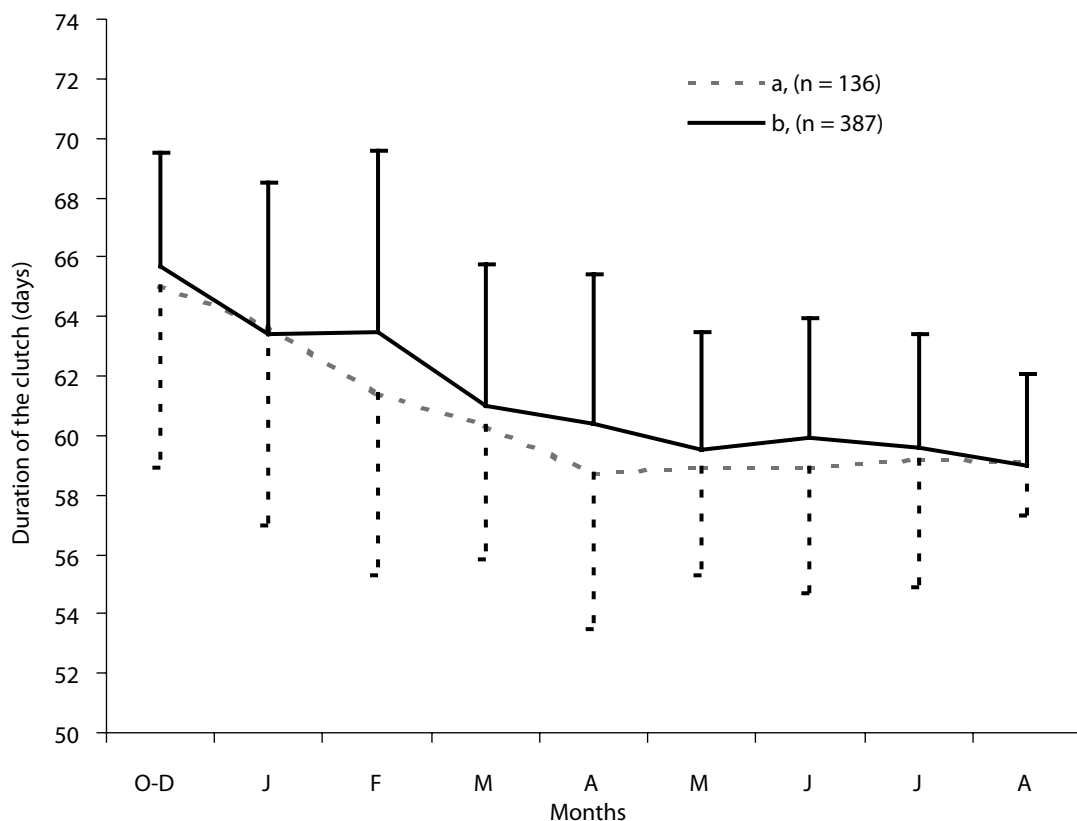


Fig. 2. Mean values ( $\bar{x} \pm SD$ ) of the duration of clutch care for nests with one (a) and two young (b) in particular periods of the breeding season in the Feral Pigeon population.

clutch. Based on data from four breeding seasons, we determined that the clutch interval lasted on average  $46.9 \pm 8.56$  days ( $n = 579$ ). In particular seasons, this interval lasted from  $45.7 \pm 7.21$  days ( $n = 96$ ) in the first breeding season to  $47.6 \pm 7.89$  days ( $n = 174$ ) in the third season (Kruskal-Wallis test,  $H = 9.49$ ,  $P < 0.05$ ). The distribution of the monthly clutch interval values were similar for each study year ( $\chi^2 = 3.25$ ,  $P > 0.05$ ).

The shortest clutch interval of the Feral Pigeon was 32 days. In this case, the new clutch appeared when the young of the previous clutch was 14 days old, as incubation of the eggs lasts 18 days (Burley 1980, Vatinick and Foertsch 1998).

Clutch interval changed in successive months of the year and was dependent on the length of day ( $r_s = -0.6711$ ,  $P < 0.05$ ). The longest clutch intervals occurred in autumn, and starting with winter it continually decreased until achieving its lowest value in May and June (Table 1).

The clutch interval also depended on the ambient temperature  $T_a$  ( $r_s = -0.549$ ,  $P < 0.01$ ). The average value of  $T_a$  between

May 27 and June 28, 2003 was  $21.5 \pm 3.11^\circ\text{C}$  ( $n = 33$ ), higher than the average noted for the period of May 17 – June 21, 2004 ( $19.5 \pm 3.15^\circ\text{C}$ ,  $n = 36$ ) (Mann-Whitney U-test,  $U = 2.30$ ,  $P < 0.05$ ). In 2003 with its higher  $T_a$ , 37.5% of the first nestlings ( $n = 24$ ) achieved thermoregulation ability at 6 days of age, weighing an average of  $112.7 \pm 24.89$  g. Most of the nestlings studied (71%,  $n = 24$ ) achieved euthermy in the 6<sup>th</sup> and 7<sup>th</sup> day of age (their average body mass was  $125.0 \pm 26.11$  g,  $n = 17$ ). In the 8<sup>th</sup> day of their lives, almost all the young (92%,  $n = 24$ ) achieved this state (Fig. 3). However, in 2004, the first nestlings achieved thermoregulation ability only in their 8<sup>th</sup> day of life (21%,  $n = 14$ , with a body mass of  $128.7 \pm 2.31$  g), while most of the studied nestlings (79%,  $n = 14$ ) attained this ability in the 9<sup>th</sup> and 10<sup>th</sup> day of life when they weighed on average of  $138.7 \pm 17.96$  g. In 2003, 8 day old nestlings weighed  $148.2 \pm 27.17$  g ( $n = 24$ ) and were distinctly heavier than nestlings of the same age in 2004 –  $111.1 \pm 19.86$  g ( $n = 14$ ) (Mann-Whitney U-test,  $U = 3.46$ ,  $P < 0.001$ ). The earlier achievement of normothermy by nestlings in 2003

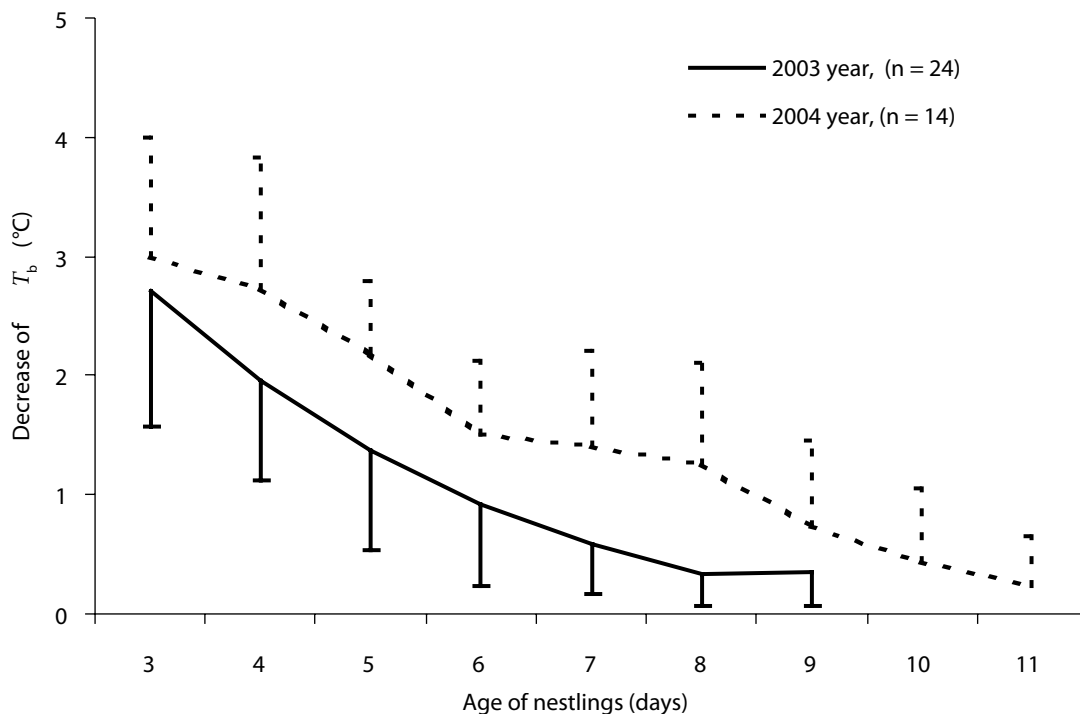


Fig. 3. Mean values ( $x \pm \text{SD}$ ) of the decrease in nestling body temperature (difference between  $T_b$  upon removal from the nest and 10 minutes after removal from the nest) in successive days of life in 2003 (ambient temperature  $T_a = 21.5^\circ\text{C}$ ) and in 2004 ( $T_a = 19.5^\circ\text{C}$ ).

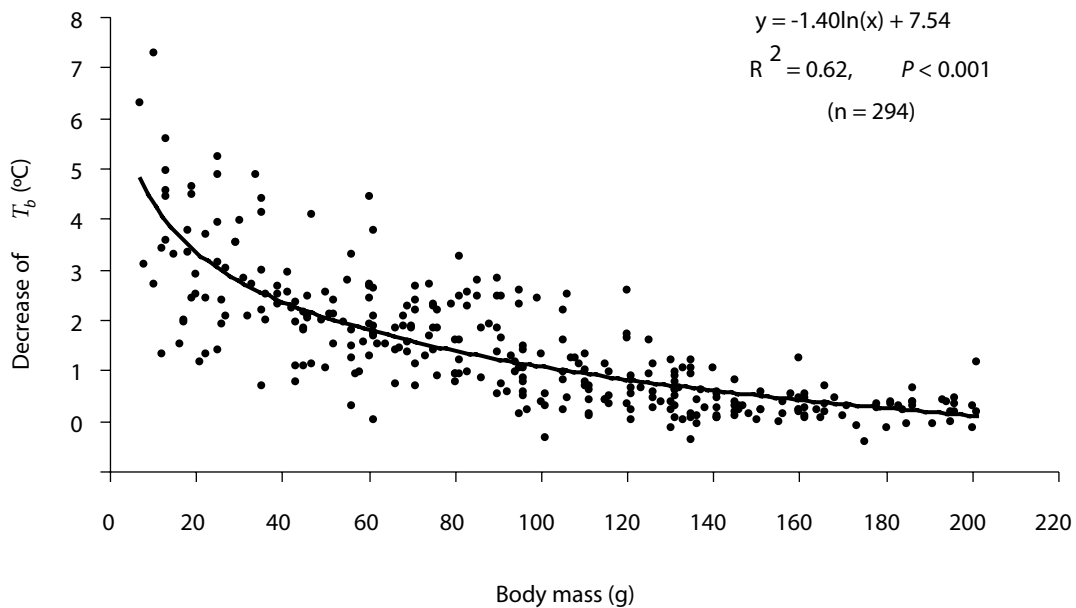


Fig. 4. The effect of body mass on the decrease in nestling body temperature  $T_b$ . Combined data from 2003 and 2004. For an explanation of  $T_b$  decrease, see, Fig. 3.

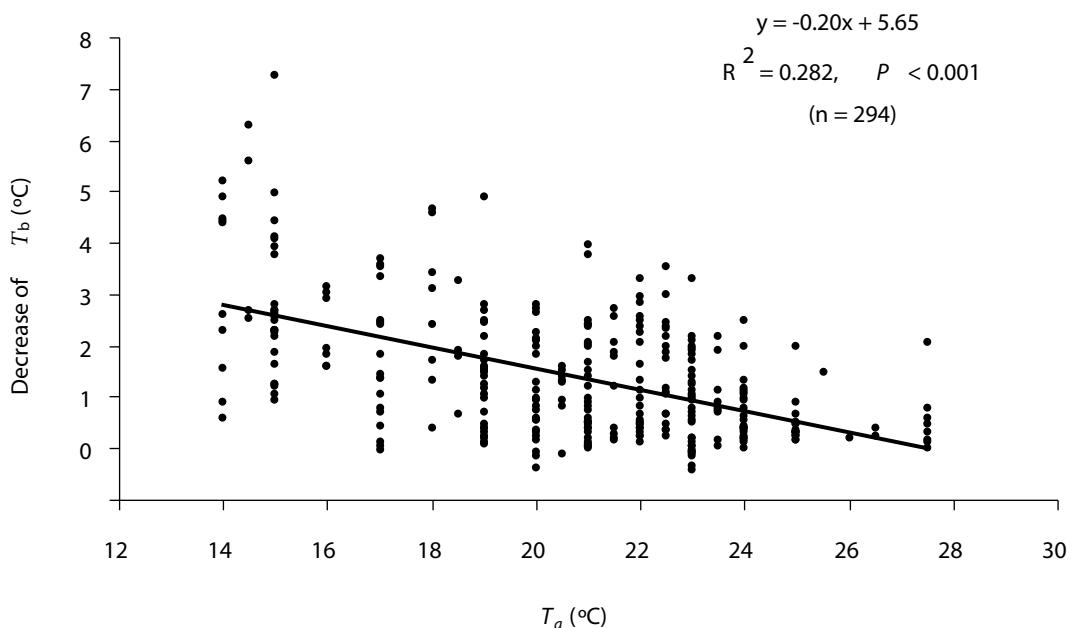


Fig. 5. The effect of ambient temperature  $T_a$  on the decrease in nestling body temperature  $T_b$ . Combined data from 2003 and 2004.

was related to a higher ambient temperature  $T_a$  and a faster growth of body mass  $M_b$ . Both factors ( $T_a$  and  $M_b$ ) influenced the speed of attaining thermoregulation by the nestlings. It is indicated by the correlation coefficients  $r_s = -0.846, P < 0.001$  for the relationship  $T_b$  versus nestlings  $M_b$  and  $r_s = -0.484, P < 0.001$  for the relationship  $T_b$  versus  $T_a$  (Figs. 4, 5).

The size of the nesting territory of breeding pairs varied, and their size was directly dependent on the density of breeding pairs in the colony and the character of the colony's location. Pairs in towers frequently nested on narrow construction beams and roof supports, where only one nest could be built. However, the density of pairs nesting in attics

was lower and quite often these pairs had two nests, usually placed at some distance from each other. The average clutch interval of pairs with a small nesting territory and only one nest was  $47.4 \pm 7.23$  days ( $n = 119$ ). This was longer than the clutch interval of pairs with two nests in their territory –  $46.1 \pm 9.13$  days ( $n = 460$ ). This barely one-day difference in the average values was statistically significant (Mann-Whitney U-test,  $U = 2.68$ ,  $P < 0.01$ ). Using these same comparative criteria for the intervals occurring between March to July, when the breeding activity of the pigeons was at its peak, the effect of the number of nests became even more apparent. For pairs with only one nest the average interval was  $47.0 \pm 6.76$  days ( $n = 98$ ), while the average for pairs with two nests was  $44.8 \pm 7.39$  days ( $n = 356$ ) (Mann-Whitney U-test,  $U = 3.44$ ,  $P < 0.001$ ).

Despite the fact that 3 or more eggs, and even 3 nestlings in the early stages of development were observed in some nests, only 1–2 young were fledged from the clutch. We confirmed that the clutch interval was

shorter when only 1 nestling hatched and was raised. The average clutch interval for the entire period of the study was  $42.8 \pm 7.54$  days ( $n = 139$ ), while for pairs raising a clutch of 2 nestlings, the average was  $48.6 \pm 8.34$  days ( $n = 309$ ) (Mann-Whitney U-test,  $U = 7.50$ ,  $P < 0.001$ ). In both cases, the distribution of the average monthly interval values between clutches in the season was similar ( $\chi^2 = 0.674$ ,  $P > 0.05$ ) (Fig. 6). In the case of the remaining clutches, where two nestlings hatched but only one left the nest (the second one died), the next clutch appeared on average after  $47.2 \pm 8.60$  days ( $n = 131$ ). Thus, the number of young raised influenced the length of clutch interval.

### 3.3. Clutch overlap

The degree of a pair's clutch overlap depended on the duration of care of the clutch ( $D$ ) and the length of clutch interval. A given clutch could overlap with one or two clutches at both ends of the breeding cycle (Fig. 1). The first and last clutches of the season of

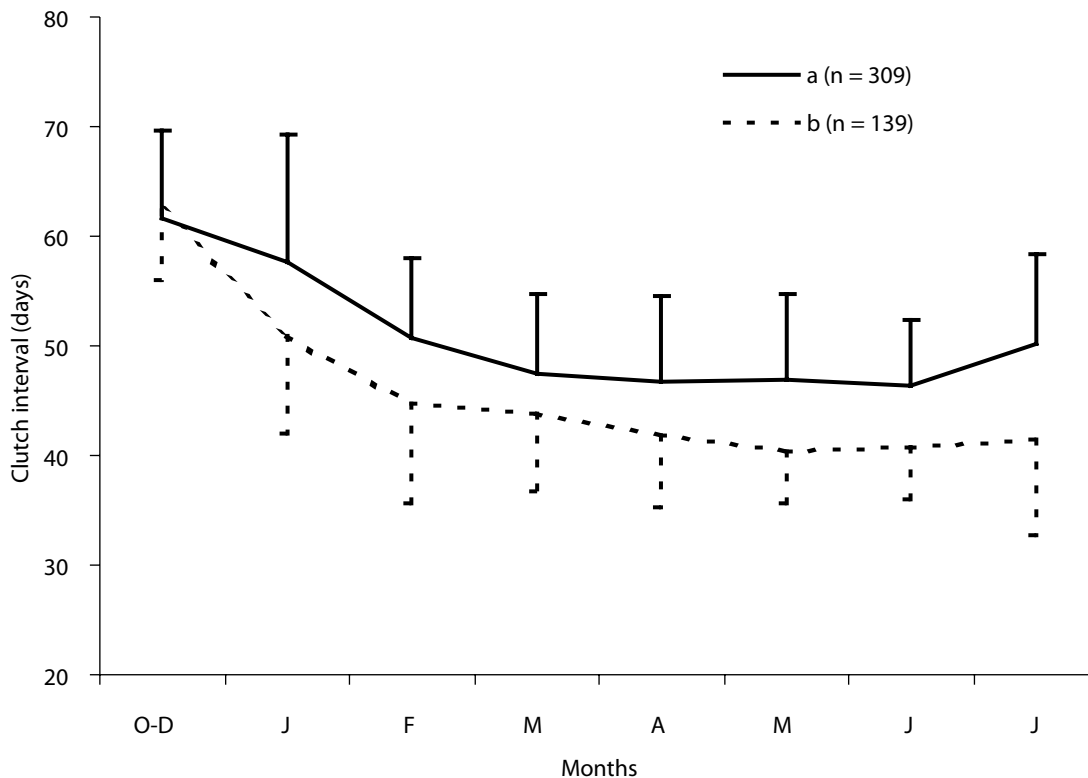


Fig. 6. The mean values ( $\bar{x} \pm SD$ ) of the clutch interval for successive months of the season (a – clutches with two young, b – clutches with one young).

a studied breeding pair overlapped with only one other clutch, that is, either the next one or the earlier one respectively. A higher degree of clutch overlap occurred from the second to the second-to-last clutches in the season, as they overlapped with two clutches, except in the situation where an earlier or later clutch was lost. The degree of clutch overlap with only one clutch was on average  $0.20 \pm 0.11$  ( $n = 282$ ). It was lowest from October to December, and achieved a constant level of about 0.23 (Fig. 7) from March to August. This means that during 23% of the time a clutch was being raised, the breeding pair was also caring for an additional clutch.

Clutches which overlapped with others at both ends of the breeding cycle showed the highest degree of overlap, resulting in an average of  $0.41 \pm 0.14$  ( $n = 12$ ) in February to  $0.52 \pm 0.15$  ( $n = 41$ ) in June (Fig. 7). The highest rate a clutch overlapped (0.86) was observed in May, but such high rates ( $> 0.80$ )

were related to the nestlings remaining in the breeding colony's quarters for an extended period of time.

Caring for two clutches simultaneously is directly tied to an additional expenditure of energy by the breeding pair. Examining the degree a clutch overlap for all the clutches in a season shows that the Feral Pigeon population allocates the most reproductive energy during the period of most intense breeding, that is, from March to July (Fig. 7).

#### 4. DISCUSSION

The Feral Pigeon breeds during the entire year, thus it is influenced by favourable and unfavourable weather conditions associated with the various seasons of the year. This urbanised form of the Rock Dove surmounts all hardships caused by the weather, and the deciding factor determining the end of the breeding season is the start of the

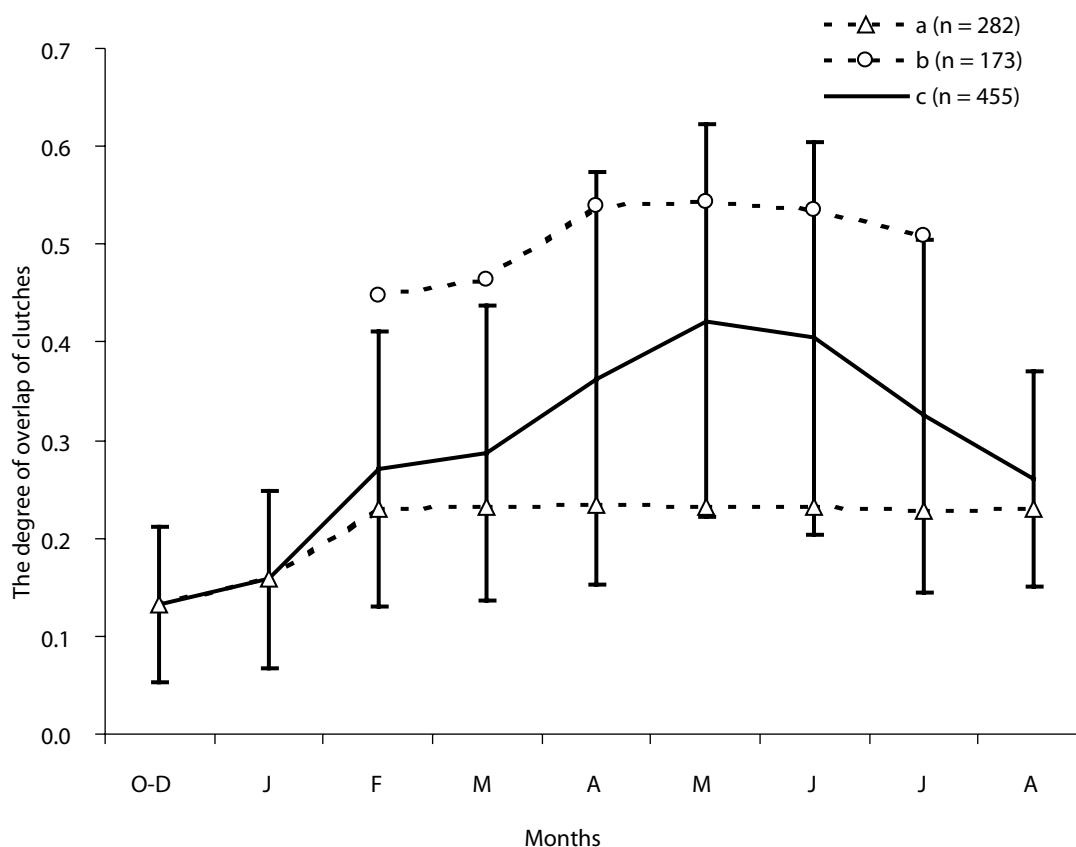


Fig. 7. Clutch overlap with one other clutch (a), with two clutches (b) and total for all clutches in the season with standard deviation (c).

bird's moult in autumn (Hetmański 2004). Moult, a high energy physiological process, is the first brake in reproducing Feral Pigeons and occurs asynchronously from August to October, and sometimes even to November, with the peak in September. Successive months bring worsening weather conditions and, primarily, a markedly shorter day. Late autumn and early winter follow with their unfavourable conditions for breeding, and yet about 5% of pairs begin reproducing, starting a new breeding season in the period of October to December (Hetmański 2004). Such pairs laid clutches throughout the entire winter, spring and summer, ending their breeding season at the onset of moult. It is hard to explain why these same pairs began breeding in autumn, given that pigeons often lack enough food during this time of the year (Kasprzak and Hetmański 2004). The answer is most likely a high level of experience in breeding as well as in foraging among such pairs. A majority of pairs begin the breeding season in January, February or March with improving weather conditions (Hetmański 2004). The reaction of the Słupsk city population of Feral Pigeon to weather conditions is reflected not only in the start of the breeding season and the number of clutches raised in particular months, but also in the length of time young are cared for, the length of the clutch interval and the degree of clutch overlap. Johnson and Johnston (1989) demonstrated that clutch intervals are significantly longer in the autumn and early spring during periods of bad weather than in the summer. Burley (1980) states that the strategy of clutch overlap used by pigeons allows breeding pairs to react more quickly to changing environmental conditions than other bird species caring for only one clutch per season consisting of many eggs. How do the two main environmental factors (length of day and ambient temperature) affect clutch intervals, which also differed significantly during different seasons of the year in the population? It seems that an explanation lies in the influence of ambient temperature on the development of nestlings' ability to regulate their body temperature. Earlier attainment of this ability enables parents to shorten the duration of incubation of the nestlings, thereby enabling them to start the next reproductive

cycle earlier. The studies in Słupsk city demonstrate that most nestlings achieved thermoregulation ability already in their 6<sup>th</sup> or 7<sup>th</sup> day of life in conditions of higher ambient temperatures (average  $T_a$  21.5°C in 2003), while in lower temperatures (average  $T_a$  19.5°C in 2004), this ability was attained only in the 9<sup>th</sup> and 10<sup>th</sup> day of post-embryonic life. Correspondingly, a longer clutch interval in autumn and winter compared to the warmer seasons of the year can be explained by the longer duration of clutch care: 64 days in the winter vs. 59 days in the summer. Nestling development was slower when days were shorter and ambient temperatures lower, because one parent incubated while the other foraged. The effect was a slower growth in the pigeon nestlings' body mass, and the association between the development of the ability to regulate body temperature and increase in body mass is very clear (Fig. 4). Similarly, one parent of the White Pelican (*Pelecanus erythrorhynchos* Gm.) always stays in the nest with the nestlings until they reach full endothermy (Abraham and Evans 1999), and Northern Flicker (*Colaptes auratus* L.) parents were observed more often in the nest with the nestlings in lower ambient temperatures than in higher temperatures (Wiebe and Elchuk 2003). We believe that postponing energy-costly thermogenesis in the nestlings during unfavourable environmental conditions could be advantageous from a physiological and evolutionary point of view.

In addition to ambient temperature and length of day, nesting conditions – such as the number of nests in a territory and number of young in a nest – also played an important role in determining clutch intervals. The existence of two nests in a territory allowed parents to care for two clutches independently and prevented the young of an earlier clutch from interfering in the start of a new nesting cycle. From March to July, when environmental conditions were conducive to the occurrence of short clutch intervals, breeding pairs could start a new cycle in a second nest when the young in the first nest were still poorly developed. Breeding pairs with two nests used this strategy very often. However, the existence of only one nest in a territory impeded the appearance of a suc-

ceeding clutch because the young still occupying the nest hampered the start of a new nesting cycle, thereby increasing the clutch interval. The number of nests in a territory did not play a significant role during the fall and winter, as unfavourable weather conditions did not allow for short intervals. New clutches appeared late in these circumstances, only when the young were able to move about their parents' entire territory, allowing them to start a new breeding cycle in the vacated nest. The number of nests in a territory is a function of the breeding colony's density. It turns out that a high density, which increases losses of eggs and nestlings (Haag 1988, 1991), and the existence of small nest territories, hampers the tempo of the appearance of successive clutches. This, then, is a second negative effect on the production of young during a season in breeding colonies that are too dense.

The clutch interval also depends on the number of nestlings being raised in the nest. Our studies confirm the conclusions of Burley (1980), Johnson and Johnston (1989), Ten Cate and Hilbers (1991) and Ten Cate and Taborsky (1992), that the clutch interval is clearly shorter when only one nestling hatched in the clutch than when two hatched and were raised. This is due to the smaller energy outlay of the parents in the care of only one young, which was confirmed in *Streptopelia risoria* L. (Ring Dove) by Brisbin (1969). In such cases, males initiate courtship more quickly, which stimulates earlier ovulation in females (Ten Cate and Hilbers 1991).

The degree of clutch overlap depended above all on whether a given clutch overlapped with one clutch or with two at both ends of the nesting cycle. Overlapping with two clutches occurred primarily from March to July, when environmental conditions were most favourable, and resulted in an increase of energy expenditure by the parents. The degree of overlap was significantly lower in the fall and winter when the season's first clutches appeared, and again at the end of the breeding season (August) (Fig. 7), thus reducing the required energy outlay of the parents during poorer weather conditions (fall and winter) and directly before moulting (August). We believe that the degree of clutch overlap

is not the best indicator of pigeons' breeding intensity, because this depends not only on the length of the clutch interval but also on how long the young are cared for. Care for the young can be extensively lengthened if they are raised in nests located at a significant distance away from the colony's egresses. The extended stay of young in the nest increases the degree of clutch overlap, but in such cases this is not the result of a short clutch interval. Clutch overlap is an excellent way to study the distribution of energy outlays of each parent as they care for two separate clutches. We do not know, for example, how a pair invests its energy in the care of young who are forced to spend more time in their parents' nest territory.

A better indicator of pigeons' breeding intensity is the length of the clutch interval. It serves as a good reflection of a breeding pair's reaction to external factors. Day length and ambient temperature play a leading role in determining the clutch interval, while other factors, such as age and experience of the birds (Burley 1980), condition of the females (Johnson and Johnston 1989) and nesting conditions play a secondary role.

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