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Breeding parameter changes in two syntopic urban Sparrow species with contrasting population trends

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The number of House Sparrows (*Passer domesticus*) in urban populations has decreased considerably in recent decades in many parts of Europe, particularly in its western part. In Warsaw (Poland), between the 1970s/1980s and the 2000s a decline of almost 50% was recorded. During the same period, Tree Sparrows (*Passer montanus*), a species also known to have decreased in western Europe, increased significantly in Warsaw. This paper addresses the changes in breeding parameters of both species between the 1980s and the 2000s, i.e., in the period when their numbers changed significantly. Both species have advanced their breeding periods. Despite that the advancement was more significant in the House Sparrow, it did not appear to influence the number of breeding attempts per year, which increased in the Tree Sparrow. In addition, clutch size increased in the Tree Sparrow but not in the House Sparrow. In both species, the level of egg losses did not change, while the nestlings losses decreased, resulting in higher average brood productivity. The annual breeding productivity increased in both species due to fewer breeding losses, and in the Tree Sparrow due to a higher number of broods per season. The results suggest that food availability for sparrow nestlings (likely arthropod resources) in the urban habitats of Warsaw are sufficient to ensure both sparrow species a high level of breeding success. This contrasts with the conclusions of studies of urban House Sparrow populations in western Europe. The strong improvement in Tree Sparrow breeding productivity may be a factor that has determined the growth of its population in recent times.

1. Introduction

The House Sparrow (*Passer domesticus*) and the Tree Sparrow (*Passer montanus*) are closely related, ecologically similar species. In areas where their ranges overlap, they may occur in the same or in different habitats (Dyer *et al*. 1977, Summers-Smith 1995). The general ecological similarities are pronounced in, for example, the breeding strategy, i.e., the phenology and number of broods, clutch size, productivity and often also in the choice of nest-sites (Seel 1968a, 1968b, 1970, Anderson 1978, Summers-Smith 1995). The nestlings of sparrows are fed with arthropods, but the species composition of the food items delivered may differ quite significantly between the two species, even though the average size of prey items is similar (Anderson 1984). The food of adult sparrows differs considerably, at least in non-urban habitats (Hammer 1948, Grün 1975). The significant differences in the ecologies of the House and Tree Sparrow are the result of divergence in body size (Grün 1975, Sánchez-Aguado 1986, Veiga 1990), as well as a different degree of dependence on humans (Cordero 1993). These differences may also be induced by competition between the two species, typically for nest-sites or nestling food (Anderson 1978, Veiga 1990, Cordero 1993).

In recent decades, populations of House and Tree Sparrows have decreased in many parts of Europe. In Great Britain, where the status of both species is well known, the pattern of changes in their numbers in agricultural landscapes is similar: a clear decline, beginning in the 1970s and lasting up to the 1990s, which was followed by a stabilization of numbers at a lower level or, locally, even with a slight increase in numbers (Gregory *et al.* 2002, Baillie *et al.* 2010). However, in the cities of Great Britain and other countries in western Europe, House Sparrow numbers have continued to decline (Robinson *et al.* 2005, De Laet & Summers-Smith 2007). The overall data show that the pattern of changes in Tree Sparrow numbers in central and central–eastern Europe is similar to that found in the western part of the continent. However, the House Sparrow populations in the central and central–eastern Europe are probably still decreasing not only in cities, but also in farming areas (Sudfeldt *et al.* 2008, Reif *et al.* 2009, Kuczyński & Chylarecki 2012, Węgrzynowicz 2013a).

The demographic factors responsible for the decrease in numbers of the European population of the Tree Sparrow are not clear (Siriwardena *et al.* 2000). On the other hand, it seems that the demographic mechanism of the House Sparrow population decline in the farming regions has been identified. It is highly probable that the decline was caused by a reduction in winter survival, without negative changes in breeding productivity (Crick *et al.* 2002, Hole *et al.* 2002). It is rather unlikely that the decline in the House Sparrow in urban habitats was connected with the decrease in farmland area, so the populations of this species inhabiting both habitats should be considered separately (De Laet & Summers-Smith 2007). An earlier study of urban populations suggested that the decline of House Sparrow populations in this habitat may have been caused by a reduction in brood productivity due to a shortage of food for nestlings (Mitschke *et al.* 1999, Peach *et al.* 2008). The lack of arthropods, which are the main component of sparrow nestlings diet, may have been the result of such factors as the intensification of gardening in urban greenery, improvement in street hygiene and increased concentrations of toxic substances in urban habitats (Bower 1999, Summers-Smith 2003, Crick *et al.* 2002, Peach *et al.* 2008, Shaw *et al.* 2008).

The information on the causes of the House Sparrow's decline in urban habitats derive mostly from western Europe. The population breakdown seems to have come later in the eastern part of the continent. For example, the pronounced decrease in House Sparrow populations in Polish towns and cities took place at the turn of the last century, i.e., ten years later than in western Europe (Węgrzynowicz 2013a). This suggests that the causes of decline started to operate later in central–eastern Europe. However, it is also possible that the causes of population change are different in various parts of the continent. Tree Sparrow population trends in cities as well as the causes of changes in its habitat are poorly known because it tends to avoid urban habitats in western Europe (and particularly in the Great Britain; Ivanov & Summers-Smith 1997).

In Warsaw, populations of both sparrow species are abundant. Although they have different habitat preferences (breeding densities of the House Sparrow grow along the urbanization gradient, unlike the Tree Sparrow), they co-occur in many areas (Węgrzynowicz 2012). The number of House Sparrows in Warsaw decreased between the 1970s/1980s and the 2000s, while the Tree Sparrow population grew in this period (Węgrzynowicz 2012). The causes of the contrasting trends of these closely-related, syntopic species, may lie in the different changes in their breeding parameters, which, in turn, may reflect ecological differences between the two sparrows. The aim of this study was to: 1) examine whether the breeding parameters of the House and Tree Sparrow populations in Warsaw changed between 1980s and the 2000s, following considerable population changes in both species, and 2) to compare breeding parameters of the House and Tree Sparrow.

Table 1. Description of study plots. OS – Ogród Saski Park, OK – Ogród Krasińskich Park, ZOO – zoological garden, PPa – two parks studied in 1980s, PPb – 7 parks studied in 2000s, RW – riparian woodlands (2 plots), HE – housing estates. Location within the city: C – center of downtown, P – periphery of downtown, O – outside downtown. The mean density of appropriate nest-boxes (see chapter 2.2) on particular plots in the periods of study is given.

Plot	Characteristics				Number of broods studied			
	Location	Area (ha)	Nest-boxes/10 ha		Pdom		Pmon	
			1986–89	2005–09	1986–89	2005–09	1986–89	2005–09
OS	C	15.0	20.3	20.0	175	47	4	41
OK	C	10.0		14.0		13		22
ZOO	P	40.0	19.0	10.0	128	15	43	35
PPa	P,O	avg. 51.5	16.2		41		158	
PPb	C,P,O	avg. 12.0		24.0				140
RW	P,O	9.0-14.0		ca 10.0				33
HE	O	18.0		5.0		7		2

2. Material and methods

2.1. Study area

The study was carried out in Warsaw, Poland (52°23’N, 21°01’E), in two periods: 1986–1989 and 2005–2009. Most (88%) data on House Sparrow broods in the former period were obtained from the park situated in the city centre (OS), and from the zoological garden (ZOO) (Table 1; Fig. 1). In the 2000s data on House Sparrow broods were gathered mostly (76%) in the two areas studied in the previous period (OS and ZOO). Most (77%) data on Tree Sparrow broods in the 1980s were from a park situated beyond the city centre, while in the 2000s its broods were studied on 13 plots: in 10 parks (including OS, OK and ZOO), on a housing estate and on two plots in riparian woodlands (Table 1; Fig. 1). In total, 28% of the Tree Sparrow broods studied in the 2000s were located in the same areas as in the 1980s, and 36% from plots OS, ZOO and OK, where House Sparrow broods were also investigated in the 2000s. In both period the densities of nest-boxes on study plots ranged usually from 10 boxes / 10 ha to 62 boxes / 10 ha (Table 1).

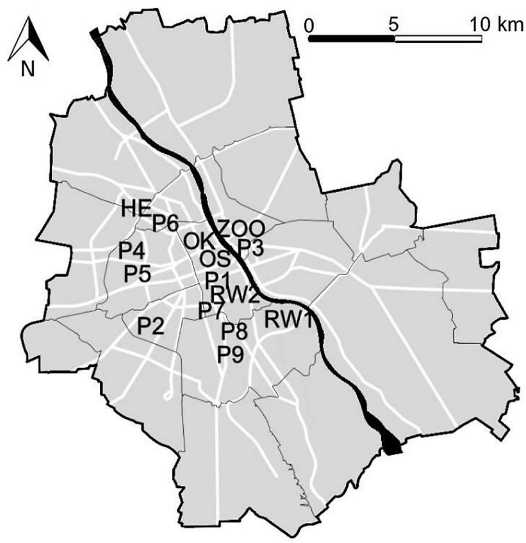

Fig. 1. Study plots. HE – housing estate, OK – Ogród Krasińskich Park, OS – Ogród Saski Park, P1–P9 – other parks, RW1, RW2 – riparian woodlands, ZOO – zoological garden.

2.2. Nest-boxes

In both periods all of the nest-boxes were installed on trees at heights of ca 4 metres, except for three boxes affixed to the walls of buildings on the 7th and 8th floors – these provided data on a few broods in the 2000s. The large majority of the nest-boxes in both periods were similar: they were made of wood, with approximate inner dimensions 11–13 × 11–13 × 25 cm, and had an entrance hole diameter of 33 mm. The impact of any differences in nest-box design on the breeding results (Møller *et al*. 2014) can thus be excluded.

Table 2. Changes in breeding parameters of the House Sparrow from the 1980s to the 2000s. For medians an interquartile range is given, for means – standard deviations. Differences were examined with two-way Mann-Whitney U-test or chi-square test (when marked with asterisk). Parameters: FED_E – earliest FED; FED_1, FED_2, FED_3 – median FED in successive broods; N_B – mean number of breeding attempts made by a pair in particular years; P_2, P_3 – proportions of pairs which made 2nd and 3rd brood; C_S – clutch size; L_E – losses of eggs; L_N – losses of nestlings; P_B – mean productivity of all broods; P_S – productivity of broods with success; P_Y – year productivity.

Param.	1986–1989	*N*	2005–2009	*N*	Statistics	*P*
FED_E	11 Apr ± 6 days	4 y.	6 Apr ± 2 d.	3 y.	3.0	0.38; ns
FED_1	24 Apr (20–28 Apr)	161	9 Apr (7–15 Apr)	37	377.5	< 0.001
FED_2	30 May (25 May–7 Jun)	125	16 May (13–22 May)	33	514.0	< 0.001
FED_3	2 Jul (25 Jun–8 Jul)	58	18 Jun (16–22 Jun)	12	98.5	0.001
N_B	2.14 ± 0.75	161	2.22 ± 0.63	37	3601.0	0.64; ns
P_2	0.78 ± 0.42	125	0.89 ± 0.31	33	–1.463*	0.144; ns
P_3	0.36 ± 0.48	58	0.32 ± 0.47	12	0.223*	0.824; ns
C_S	4.55 ± 1.02	344	4.55 ± 0.87	82	12178.5	0.978; ns
L_E	1.38 ± 1.60 (30.3%)	344	1.05 ± 1.55 (23.1%)	82	12835.0	0.183; ns
L_N	1.12 ± 1.47 (29.0%)	282	0.83 ± 1.05 (19.9%)	69	11342.5	0.019
P_B	2.25 ± 1.82	344	2.80 ± 1.69	82	16157.0	0.013
P_S	3.16 ± 1.15	245	3.48 ± 1.08	66	8888.5	0.028
P_Y	4.82 ± 2.88	161	6.22 ± 2.91	37	3739.0	0.015

2.3. Fieldwork methods

In 1986–1989 the data were gathered by J. Pinowski and his team for a study of the mortality of eggs and nestlings of House and Tree Sparrows (Luniak 1990, Pinowski *et al.* 1991, 1995). The individual data for each brood from this period were used in the present analysis. In the 1980s nest-boxes were checked twice a week during the laying and incubation period, i.e., during these stages each brood was inspected at least four times. After hatching, the broods were visited every 1–2 days. Unhatched eggs and some nestlings were taken away for laboratory analysis (Pinowski *et al.* 1991, 1995). The data from these broods are excluded from the present analysis. In 2005–2009 each brood was checked 4–5 times: at least twice at the egg stage and at least twice when nestlings were present. The inspection dates were determined on the assumption that incubation (from the laying of the last egg to hatching) lasts for an average of 12 days in both species and that nestlings leave the nest no earlier than 13 days after hatching (Summers-Smith 1995, Anderson 2006). Following the basic study period, encompassing three successive broods of sparrows, an additional inspection of nest-boxes was carried out in order to check for possible fourth broods. In the 1980s such inspections were performed on all study plots and in the 2000s on every plot where House Sparrows used nest-boxes and on some plots (ca 60% of all plots studied) where only Tree Sparrows broods were found in nest-boxes.

2.4. Data analysis

Differences in the following breeding parameters were tested between the House and the Tree Sparrow separately for 1980s and 2000s, and within species between the 1980s and the 2000s.

- First egg-date (FED): the date at which a pair laid its first egg; the analyses include the date for the earliest pair in the year (FED_E) and median date for all pairs in successive broods (FED_1, FED_2, FED_3). The FED was determined on the assumption that both sparrow species lay one egg per day (Seel 1968a). If this was not possible, the first-egg date was estimated on the basis of the hatching date or the state of development of the nestlings (Seel 1968a, Balát 1971). Possible error should not have exceeded two days.
- Number of broods (N_B): mean number of breeding attempts made by a pair in particular

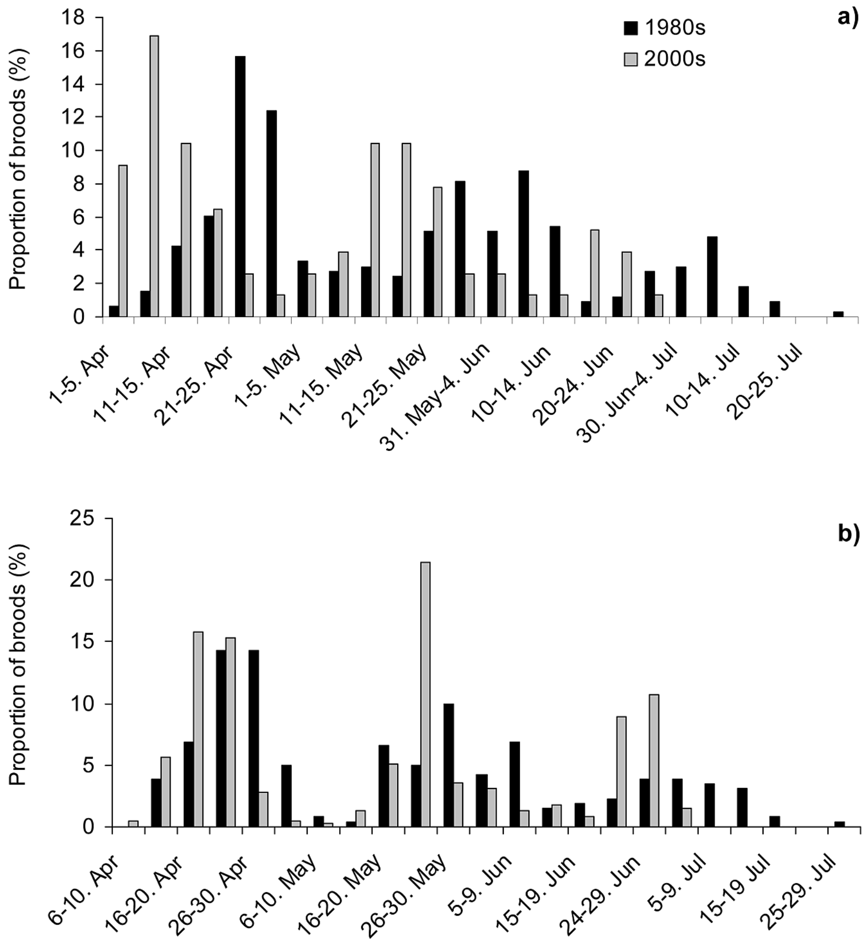

Fig. 2. Changes in the laying pattern between 1986–1989 and 2005–2009 in the House Sparrow (a) and the Tree Sparrow (b).

years. In the temperate zone House and Tree Sparrows usually have three quite well defined broods in a season (e.g., Seel 1968a, Pinowski & Wieloch 1972). In both species, the particular pairs usually use the same nest sites during successive broods (Summers-Smith 1963, 1995). In this paper, the particular clutches are treated as 1^{st}, 2^{nd} and 3^{rd} broods on the basis of the number of breeding attempts in a given nest-box (Seel 1968a). The analyses include also the proportions of pairs which made 2^{nd} and 3^{rd} brood (P_2 and P_3, respectively).

– Clutch size (C_S): mean number of eggs laid.
– Losses of eggs (L_E): number of eggs lost per clutch.
– Losses of nestlings (L_N): number of nestlings lost per hatched brood.
– Productivity of broods (P_B): number of fledglings (nestlings that reach the age of 11–12 days) per brood initiated.
– Productivity of broods with success (P_S): number of fledglings per brood in which at least one nestling fledged.
– Year productivity (P_Y): a sum of productivities of successive broods in a given season per a breeding pair.

Temporal changes were tested by comparing species-specific values from the 1980s and 2000s. Differences in the breeding parameters of House and Tree Sparrow were tested by comparing values for both species in particular period. The Mann-Whitney U-test was used for comparing two variables, and the chi-square test for differences in proportions. The calculations were performed using Statgraphics Plus 5.1 software.

Table 3. Changes in breeding parameters of the Tree Sparrow from the 1980s to the 2000s. For medians an interquartile range is given, for means – standard deviations. Differences were examined with two-way Mann-Whitney U-test or chi-square test (when marked with asterisk). Parameters: FED_E – earliest FED; FED_1, FED_2, FED_3 – median FED in successive broods; N_B – mean number of breeding attempts made by a pair in particular years; P_2, P_3 – proportions of pairs which made 2nd and 3rd brood; C_S – clutch size; L_E – losses of eggs; L_N – losses of nestlings; P_B – mean productivity of all broods; P_S – productivity of broods with success; P_Y – year productivity.

Param.	1986–1989	*N*	2005–2009	*N*	Statistics	*P*
FED_E	16 Apr ± 4 days	4 y.	11 Apr ± 3 d.	5 y.	0.0	0.019
FED_1	25 Apr (21–29 Apr)	96	20 Apr (17–23 Apr)	111	7377.0	< 0.001
FED_2	29 May (25 May–6 Jun)	76	23 May (21–25 May)	97	3211.5	< 0.001
FED_3	4 Jul (27 Jun–11 Jul)	33	25 Jun (23–28 Jun)	65	236.5	< 0.001
N_B	2.14 ± 0.79	96	2.46 ± 0.75	111	4613.5	0.011
P_2	0.79 ± 0.41	76	0.87 ± 0.33	97	–1.492*	0.137; ns
P_3	0.34 ± 0.48	33	0.59 ± 0.49	65	–4.201*	< 0.001
C_S	4.81 ± 1.16	205	5.18 ± 0.81	273	44333.5	< 0.001
L_E	1.40 ± 1.68 (29.1%)	205	1.29 ± 1.67 (24.9%)	273	23528.5	0.509; ns
L_N	0.90 ± 1.30 (22.9%)	178	0.55 ± 0.69 (13.4%)	258	13516.0	0.001
P_B	2.63 ± 1.92	205	3.37 ± 1.70	273	42965.5	< 0.001
P_S	3.46 ± 1.33	156	3.74 ± 1.41	246	26163.5	0.063; ns
P_Y	5.63 ± 4.54	96	8.29 ± 4.60	111	6969.5	< 0.001

3. Results

3.1. Changes in breeding parameters in the 1980s–2000s

In the 1980s, the first egg of the earliest clutch in a year (FED) appeared in the House Sparrow between 3 and 18 April. In the 2000s, they appeared between 4 and 7 April, but the difference is not significant (Table 2). In the Tree Sparrow, these dates were significantly earlier in the 2000s (7–13 April) than in the 1980s (14–24 April; Table 3). The median first-egg dates in successive House Sparrow broods were 14–15 days earlier in the 2000s than in the 1980s (Table 2), and in the case of the Tree Sparrow by 5–9 days (Table 3; Fig 2).

The average number of broods per breeding pair did not change significantly in the House Sparrow but did so in the Tree Sparrow mainly due to an increased the proportion of pairs that made a third breeding attempt (Tables 2 and 3). Moreover, whereas the average clutch size did not change in the House Sparrow, it increased in the Tree Sparrow. In the House Sparrow the proportions of clutches with different numbers of eggs did not differ significantly between two periods (χ^2 = 2.800; *df* = 5; *P* = 0.732; Fig. 3a). In the Tree Sparrow the proportion of clutches with 5 and more eggs increased, while the proportion of clutches with 4 and fewer eggs decreased (Fig. 3b), and the difference in this patterns was significant (χ^2 = 17.311; *df* = 5; *P* = 0.002).

The number of egg losses did not change in either species, while the number of nestling losses decreased significantly in both species (Tables 2 and 3). The average breeding productivity of both species was higher in the 2000s than in the 1980s (Tables 2 and 3). The number of fledglings per successful nest increased slightly in the House Sparrow, while in the Tree Sparrow this parameter did not change (Tables 2 and 3). Finally, annual productivity increased by 29% in the House Sparrow and by 47% in the Tree Sparrow (Tables 2 and 3).

3.2. Comparison of the breeding parameters of the House and Tree Sparrow

In the 1980s, the median first-egg dates in successive broods were similar for both species, whereas in the 2000s the House Sparrow initiated all three consecutive broods significantly earlier than the Tree Sparrow (Table 4). The proportion of breeding pairs that made a second attempt did not differ between the two species in either period. The number of broods per breeding pair, as well as the pro-

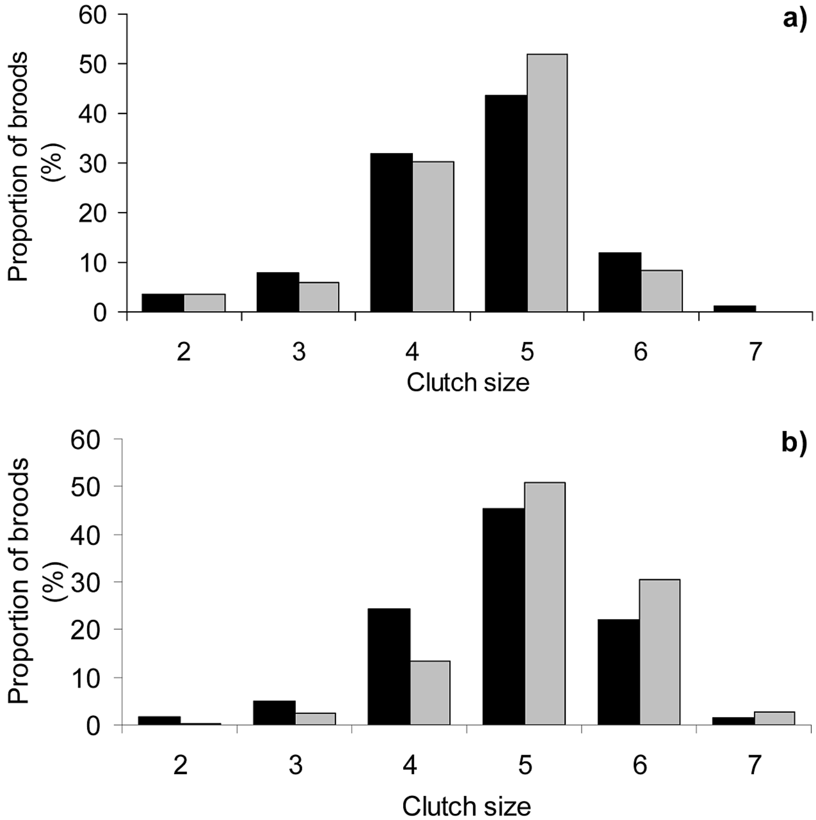

Fig. 3. Changes in the clutch size between 1986–1989 (black; N=344) and 2005–2009 (grey; N=82) in the House Sparrow (a) and the Tree Sparrow (b).

portion of pairs that made a third attempt, differed significantly between both species only in the 2000s, being higher in the Tree Sparrow than in the House Sparrow (Table 4). In both periods, the average clutch size of the House Sparrow was smaller than in the Tree Sparrow, this difference being more significant in the 2000s than in the 1980s (Table 4). In both periods, the mean number of eggs and nestlings lost did not differ significantly between both species (Table 4). Breeding productivity was lower in the House Sparrow than in the Tree Sparrow: the difference was significant for all broods in both periods (in the 2000s it was greater than in the 1980s), for successful broods only in the former period, and for annual productivity only in the latter (Table 4).

4. Discussion

In recent decades, the House and Tree Sparrow have displayed contrasting trends in their numbers in the urban habitats of Warsaw. From the 1970s/1980s to the 2000s, numbers of the former decreased by 48%, while those of the latter increased by 68% (Węgrzynowicz 2012). However, the current study shows that only the Tree Sparrow population trends could be explained by changes in breeding productivity, as this has increased considerably during population growth. Also the House Sparrow's annual breeding productivity has increased, which suggests that the decline of this species in Warsaw was probably triggered by other factors.

Between the 1980s and the 2000s, the nestling losses fell in both species. Both sparrow species feed their chicks mostly with arthropods (Summers-Smith 1995, Anderson 2006). In the case of sparrow broods in nest-boxes, most losses of nestlings are due to death from starvation, although a certain proportion of chicks die from diseases and other factors (Mackowicz *et al*. 1970, Seel 1970). The improvement in nestling survival in both species suggests that the amount of invertebrates in

Table 4. Differences in breeding parameters of the House and Tree Sparrow in the 1980s and in the 2000s. The values are the mathematical differences between particular parameters of the House and Tree Sparrow reported in Tables 2 and 3. For medians an interquartile range is given, for means – standard deviations. Differences were examined with two-way Mann-Whitney U-test or chi-square test (when marked with asterisk). Parameters: FED_E – earliest FED; FED_1, FED_2, FED_3 – median FED in successive broods; N_B – mean number of breeding attempts made by a pair in particular years; P_2, P_3 – proportions of pairs which made 2nd and 3rd brood; C_S – clutch size; L_E – losses of eggs; L_N – losses of nestlings; P_B – mean productivity of all broods; P_S – productivity of broods with success; P_Y – year productivity.

Param.	1986–1989	Statistics	P	2005–2009	Statistics	P
FED_E	–5 days	14.0	0.112; ns	–5 d.	14.0	0.065; ns
FED_1	–1	10328.5	0.365; ns	–11	5693.0	< 0.001
FED_2	1	5478.5	0.778; ns	–7	3356.5	< 0.001
FED_3	–2	1252.5	0.447; ns	–7	233.5	0.004
N_B	0.00	7591.0	0.939; ns	–0.24	2061.5	0.049
P_2	–0.01	–0.167*	0.867; ns	0.02	0.319*	0.750; ns
P_3	0.02	0.300*	0.764; ns	–0.27	–2.848*	0.004
C_S	–0.26	39389.0	0.001	–0.63	19223.0	< 0.001
L_E	–0.02	31090.0	0.594; ns	–0.24	10188.5	0.08; ns
L_N	0.22	20294.0	0.235; ns	0.28	5755.5	0.058; ns
P_B	–0.38	39299.0	0.014	–0.57	16730.0	0.005
P_S	–0.30	20494.0	0.015	–0.26	11421.5	0.07; ns
P_Y	–0.81	7239.5	0.474; ns	–2.07	1498.5	0.016

Warsaw parks is sufficient to successfully rear young. On the other hand, the shortage of adequate food may lead to a reduction in the mass of nestlings that are fed with invertebrates; the weight of fledglings is a determinant of subsequent survival (Tinbergen & Boerlijst 1990, Naef-Daenzer & Keller 1999). In this study, nestlings were not weighed. In other studies, however, the weight reduction in House Sparrow nestlings due to a shortage of appropriate food was accompanied by high nestling mortality (Peach *et al*. 2008, Seress *et al*. 2012), an observation not made in Warsaw. Similar relationships have been found in other passerine species. Tiainen *et al*. (1989) found that in broods of Starling (*Sturnus vulgaris*) reduced due to starvation, nestlings weights were smaller than in the bigger broods.

The high productivity of House Sparrow broods in Warsaw contrasts the results of studies in western Europe. For example, in Hamburg, Germany, of several broods initiated in April none produced a fledgling (Bower 1999). In studies in Leicester, England, Peach *et al*. (2008) found that in two years of a three-year study the reproductive output of House Sparrows was insufficient to maintain their population level. There are indications that the amount of insects, particularly aphids, has decreased considerably in western European cities and the insufficient availability of invertebrates is thought to be the most important cause of the decline in urban House Sparrow populations in western Europe (Mitschke *et al*. 1999, Summers-Smith 2003, Peach *et al*. 2008). The causes underlying the differences in breeding productivity between Warsaw and cities in Western Europe are not clear, however, it is possible that they are related to different arthropod abundances. It is worth mentioning that in Berlin, a city situated relatively close to Warsaw, the level of nestling mortality in House Sparrow broods studied in 2000s was low and that the body mass of nestlings was not reduced (Grasnick & Böhner 2008).

Studies comparing the broods of two sparrow species in the same area usually indicate a higher productivity in the Tree Sparrow than in the House Sparrow: this is a result of the larger clutch size and smaller breeding losses (especially at the chick stage) in the former. On the other hand, the House Sparrow usually makes more breeding attempts per season (Seel 1968a, 1968b, 1970, Mackowicz *et al*. 1970, Pinowski & Wieloch 1972, Strawiński & Wieloch 1972, Anderson 1975, 1978, Wieloch & Fryska 1975). In Warsaw, most of the differences in the breeding parameters between House and Tree Sparrows in both seasons were consistent with this scheme: the exception was the number of nesting attempts per pair during the season. It did not differ between the species in the 1980s, but in the 2000s it was higher in the Tree Sparrow. In general, the number of breeding attempts in a sparrow population depends on the onset of the breeding season – the earlier it begins, the larger the number of pairs that lay a third clutch, and hence, the larger the total number of broods per pair in a given year (Seel 1968a, Mackowicz *et al*. 1970). Both sparrow species advanced their breeding season in Warsaw between the 1980s and the 2000s; however, only the Tree Sparrow may have benefited from this advancement by increasing the average number of breeding attempts, a reaction also recorded in other multi-brooded species (e.g., Jenni & Kéry 2003). In the House Sparrow, which in fact advanced its breeding season to a greater extent than the Tree Sparrow, the average number of broods per year did not change significantly.

It is symptomatic that the differences in breeding parameters between the two sparrow species were more pronounced in the 2000s than in the 1980s (which is confirmed by usually higher statistical significance for the differences in the 2000s). This was due not to a decrease in the House Sparrow's breeding parameters but to a significant improvement in those of the Tree Sparrow. The annual productivity of Tree Sparrows in Warsaw (8.29 fledglings/nest/year) was also high with comparison to populations from non-urban areas in the same region of Europe (an average of 5.25 fledglings/nest/year, treating values from all 10 study areas as an independent sample; Mackowicz *et al*. 1970, Scherner 1972, Strawiński and Wieloch 1972, Wieloch and Fryska 1975, Gauhl 1984, Zang 1993). Such high productivity of the Tree Sparrow population in Warsaw may be associated with its ongoing synurbization. This was suggested by Węgrzynowicz (2013c) who showed that there were relatively small differences in the breeding results of Tree Sparrows in an urbanisation gradient. They used anthropogenic food to a high degree, and exhibited a gradual shift from areas with less human pressure to more urbanized areas. The superior reproductive success in the Tree Sparrow compared with the House Sparrow in Warsaw, demonstrated in this paper, may result in a preponderance of the former over the latter. The consequence is an increase in competitive pressure from the Tree Sparrow on the House Sparrow, which may lead to such effects as a considerable advancement of the onset of the breeding season in the latter, since in places where both sparrow species compete for nest sites, it is advantageous for each to start breeding earlier than its competitor (Anderson 1978, Veiga 1990).

To sum up, both sparrow species improved their reproductive effects between 1980s and 2000s, which was pronounced in higher annual breeding productivity. However, in the Tree Sparrow this improvement was more significant, due to increase in such parameters as clutch size and number of broods per year which did not change in the House Sparrow. Despite the generally great similarity between these two sparrow species (both are hole-nesters, feed their nestlings with invertebrates etc.), more subtle differences, such as preferences for particular types of nest sites, breeding season phenology etc., may have a significant effect on the trends of their breeding parameters, and consequently, in population trends. The differences in population trends of the House and Tree Sparrow may also be associated with different reactions to habitat changes, which take place particularly rapidly in urban landscapes. Some authors (e.g., Vepsäläinen *et al*. 2005) emphasize the fact that the Tree Sparrow is more adaptable to habitat changes and is more mobile and effective in searching for basic resources such as nest sites and food than the House Sparrow.

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Ajalliset muutokset vähenevän varpusen ja lisääntyvän pikkuvarpusen pesimäparametreissa Varsovan urbaanissa ympäristössä

Varpusen (*Passer domesticus*) urbaaneissa ympäristöissä esiintyvät populaatiot ovat vähentyneet viime vuosikymmeninä eri puolilla Eurooppaa.

Puolan Varsovassa varpuspopulaatio lähes puoliintui 1980-luvun ja 2000-lukujen välillä. Samaan aikaan pikkuvarpunen (*Passer montanus*) lisääntyi merkittävästi niin Varsovassa kuin muuallakin Euroopassa.

Tässä työssä tutkitaan onko näiden lajien pesintää kuvaavissa parametreissa tapahtunut sellaisia muutoksia 1980- ja 2000-lukujen välillä, jotka voisivat selittää kyseisten lajien populaaatiokoossa havaittuja erisuuntaisia muutoksia. Molempien lajien pesintä aikaistui. Sen seurauksena pesintäyritysten lukumäärä lisääntyi pikkuvarpusella. Varpusella pesintäyritysten määrä ei kuitenkaan lisääntynyt vaikka sen pesintä aikaistui pikkuvarpusta voimakkaammin. Pesyekoko kasvoi vain pikkuvarpusella. Haudonnan aikana menetettyjen munien määrä ei muuttunut kummallakaan lajilla, mutta pesäpoikasten kuolemat vähenivät. Tämä lisäsi lentoon lähteneiden poikasten määrää ja vuosittaista poikastuottoa molemmilla lajeilla. Pikkuvarpusen poikastuotto kasvoi myös useampien pesintäyritysten kautta.

Tulosten perusteella Varsovan urbaaneissa ympäristöissä ruuan saatavuus on riittävä poikasten kasvattamiseen molemmilla varpuslajeilla. Tämä poikkeaa Länsi-Euroopan urbaaneista varpusen populaatioista joissa poikastuotto on heikkoa. Voimakkaasti parantunut pikkuvarpusen poikastuotto saattaa hyvinkin osaltaan selittää viimeaikaista voimakasta populaation kasvua.

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