

Clutch and egg size variation, and productivity of the House Sparrow (*Passer domesticus*): effects of temperature, rainfall, and humidity

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Abstract: This study was conducted on the campus of the regional department of the forestry service, encompassing 2.25 ha in Antalya city center. The area has gardens and is surrounded by trees, providing nesting and feeding opportunities for many songbird species. The study aimed to determine clutch and egg size variation, breeding success, and productivity of the House Sparrow (*Passer domesticus*), in terms of clutch size and breeding attempts, and to evaluate variation in temperature, rainfall, and humidity in terms of breeding attempts and years, and their possible effects on given parameters of the species. In total, 2016 eggs were laid in 393 clutches and clutch size varied from 1 to 11 eggs; the clutches most commonly contained 4-6 egg in the 3 consecutive years. Mean egg length, width, weight, volume, and sphericity index were 21.16 ± 0.03 mm, 14.99 ± 0.01 mm, 2.02 ± 0.01 g, 2.38 ± 0.01 cm³, and 71.01 ± 0.09 , respectively. Breeding attempts were affected by temperature ($r = 0.97$ $P < 0.0001$) and rainfall ($r = -0.84$ $P < 0.001$). Egg length was affected by rainfall ($r = 0.60$ $P < 0.041$), humidity ($r = 0.59$ $P < 0.044$), and temperature ($r = -0.81$ $P < 0.002$), and egg volume was affected by temperature ($r = -0.68$ $P < 0.015$). This study shows that the House Sparrow population in the study area exhibited important variation in clutch and egg size, which was affected by changes in temperature, rainfall, and humidity.

Key words: House Sparrow, *Passer domesticus*, breeding success, clutch size

Ev Serçesi (*Passer domesticus*)'nin yumurta küme büyüklüğü, yumurta boyutları ve verimliliği: sıcaklık, yağış ve nemin etkisi

Özet: Çalışma, Antalya'nın şehir merkezinde 2.25 hektarlık araziye sahip olan Orman Bölge Müdürlüğü'nün bahçesinde yürütülmüştür. Çalışma alanında bulunan ve ağaçlarla çevrili olan küçük bahçeler, birçok ötücü kuş türüne yuvalanma ve beslenme olanağı sağlar. Çalışmanın amacı, Ev Serçesi (*Passer domesticus*)'nin yumurta küme büyüklüğü ve yumurta boyutlarındaki farklılıkları, üreme başarısını ve verimliliğini, yumurta küme büyüklüğü ve kuluçka dönemlerine bağlı olarak tespit edilmesi ve ayrıca kuluçka dönemleri ve yıllar baz alınarak sıcaklık, yağış ve nem oranlarındaki değişimlerin ve bu değişimlerin ilgili parametrelere olası etkilerinin değerlendirilmesidir. Üç yıllık çalışma sonucunda, Ev Serçesinin 393 kuluçkaya 2016 yumurta bıraktığı, yumurta küme büyüklüğünün 1-11 adet yumurta arasında değiştiği ve yaygın olarak 4-6 yumurtalı kümelerin yapıldığı tespit edilmiştir. Yumurtaların ortalama boy, en, ağırlık, hacim ve küresel indeksi sırasıyla $21,16 \pm 0,03$ mm, $14,99 \pm 0,01$ mm, $2,02 \pm 0,01$ g, $2,38 \pm 0,01$ cm³ ve $71,01 \pm 0,09$ olarak hesaplanmıştır. Kuluçka

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dönemlerinin sıcaklık ($r = 0,97$ $P < 0,0001$) ve yağış ($r = -0,84$ $P < 0,001$); yumurta boyunun yağış ($r = 0,60$ $P < 0,041$), nem ($r = 0,59$ $P < 0,044$) ve sıcaklık ($r = -0,81$ $P < 0,002$); ve yumurta hacminin sıcaklık ($r = -0,68$ $P < 0,015$) değişimlerinden etkilendiği belirlenmiştir. Bu çalışma ile incelenen Ev Serçesi popülasyonunun yumurta küme büyüklüğünün ve yumurta boyutlarının önemli farklılıklar gösterdiği ve bu parametrelerin sıcaklık, yağış ve nemdeki değişimlerden etkilendiği ortaya konulmuştur.

Anahtar sözcükler: Ev Serçesi, *Passer domesticus*, üreme başarısı, yumurta küme büyüklüğü

Introduction

Egg size varies greatly among avian populations, but little within individuals (Christians, 2002). Egg size varies with laying order, date of laying, and clutch size (Slagsvold et al., 1984; Järvinen, 1991), and genetic, ontogenetic, and environmental factors (Potti, 1993). Variation in the size and quality of eggs can have important long-term consequences for the survival of offspring (Williams, 1994). Hatchability of eggs may also be affected by their size (Pinowska et al., 2002), especially under severe weather conditions (Järvinen and Väisänen, 1983; Nilsson and Svensson, 1993). For example, larger eggs tend to have higher hatching success rates (Perrins, 1996), and lead to larger hatchlings, faster nestling growth (Hipfner and Gaston, 1999; Pinowska et al., 2004), and more male offspring (Mead et al., 1987). Experimental studies have shown that, even though egg size co-varies with parental quality and age, egg size alone can have important effects on the quality of nestlings (Bolton, 1991; Smith and Bruun, 1998; Strycky et al., 1999).

Ecological factors, such as food availability, predator pressure, and weather, are well known to influence the life history and reproductive success of a species (Lack, 1968). In the last decade much effort was expended to investigate the effects of climatic factors on reproduction, survival, and population dynamics (Yom-Tov, 2001; Lindström and Kokko, 2002; Laaksonen et al., 2006). Many researchers have analyzed the effect of ambient temperature on egg size and reproductive performance in birds (Järvinen and Ylimaunu, 1986; Järvinen, 1994; Perrins, 1996; Stevenson and Bryant, 2000; Barkowska et al., 2003; Saino et al., 2004). The relationship between rainfall and reproductive performance is thought to be due to the positive effect of rainfall on food availability for adults and/or chicks (Boag and Grant, 1984; Zann et al., 1996). Recently, several studies that tested the effects of rainfall-related factors on bird breeding

performance were based on testing specific hypotheses rather than on looking for correlations (Morrison and Bolger, 2002; Coe and Rotenberry, 2003; Bolger et al., 2005). For example, rainfall could act as a proximate factor triggering the beginning of specific physiological processes, such as sex hormone production or gonad growth (Leitner et al., 2003; Hau et al., 2004; Fulgione et al., 2005). In comparison to temperature and rainfall, the influences of humidity on clutch size, egg size, and other breeding parameters are less known.

The aims of the present study were to determine (1) the variation in clutch and egg size, breeding success, and productivity, (2) the correlations between egg dimensions, breeding attempts, and clutch size, as well as between breeding attempts and productivity, (3) the variation in temperature, rainfall, and humidity between years and breeding seasons, and (4) the effects of climatic factors on clutch size, egg size, breeding success, and productivity of the House Sparrow for 3 consecutive years.

Materials and methods

This study was conducted from 2001 to 2003 on the campus of the regional department of the forestry service covering an area of 2.25 ha located in the city center (36°53'00"N, 30°42'00"E) of Antalya, Turkey (Figure 1). Sixty-two 14 × 20 × 22-cm wooden nest-boxes with 1.5-cm thick walls and a 3.5-cm entrance hole were placed in trees and monitored for 3 breeding seasons. In order to determine the number of breeding attempts by individual sparrows, 24 adult females were tagged with a unique combination of 2- or 3-colored plastic spiral rings in 2003. Nineteen of the tagged females (79.1%) used the nest-boxes and the number of breeding attempts did not differ between tagged and non-tagged females during the 3 years (Aslan et al., 2005). The nest-boxes were

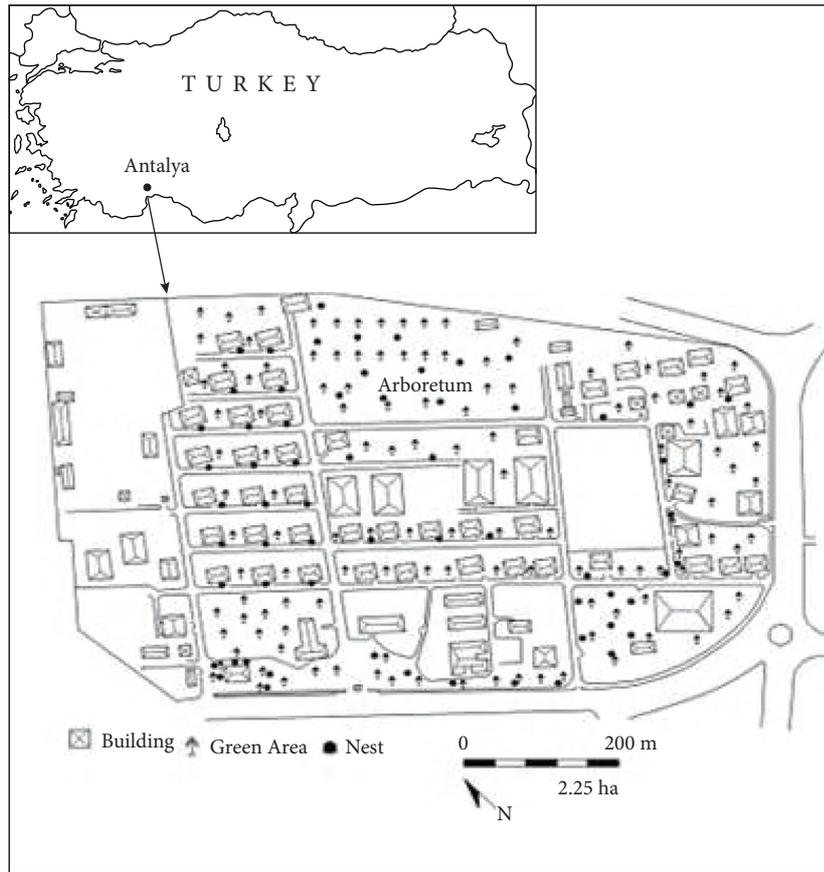


Figure 1. Geographic location of the study area.

checked twice daily (0800-1000 and 1600-1800) to determine clutch initiation date, the number of breeding attempts, egg size (length, width, weight, volume, and sphericity index), clutch size (number of eggs in the clutch), and breeding parameters (unhatched and hatched eggs, dead nestlings, and fledglings). The exact dates of the onset and termination of breeding seasons were previously evaluated in Aslan et al. (2005) and, therefore, the timing of breeding is not discussed in this report.

Eggs were measured only in completed clutches and were weighed to the nearest 0.5 g in a plastic bag with a 5-g Pesola spring scale (accuracy ± 0.01 g) in a plastic tube that kept out wind. Length and width of each egg were recorded with digital calipers to the nearest 0.05 mm. We calculated egg volume using Hoyt's (1979) equation ($V = 0.5 \times L \times B^2$), where V is egg volume (cm^3), L is egg length, and B is egg width (both in mm). The sphericity index was calculated as

$100 \times B/L$ (Winkel, 1970). Mean egg size was calculated by clutch size and by successive breeding attempts. Values of breeding parameters by breeding attempt and clutch size allowed us to estimate breeding success and productivity (Appendix). Breeding success was estimated for each clutch size and breeding attempt was estimated with 2 different methods. With the first method, breeding success was defined as the number of all successful clutches with at least 1 fledgling per specific clutch size ($BS_1 = 100 \times FL/CS$, where FL is the total number of fledglings in each clutch size and CS is the total number of eggs per clutch with at least 1 fledgling). With the second method, breeding success was defined as the number of clutches with at least 1 fledgling ($BS_2 = 100 \times FL/H$, where H is the total number of eggs hatched with at least 1 fledgling (Bairlein, 1996; Kiziroğlu, 2008, 2009)). Productivity was calculated for BS_1 as $100 \times H/H_{\text{total}}$ and for BS_2 as $100 \times FL/FL_{\text{total}}$ for each clutch

size and breeding attempt. Values of climatic factors (temperature, precipitation, and humidity) were obtained from the Antalya Meteorological Station, which is about 5 km from study area, and are presented in Table 1.

Statistical analysis

Data were analyzed using SPSS v.11.0 for Windows. Variation in climatic factors between breeding seasons (from the beginning of April to the end of July) was determined with ANOVA. Variations in egg dimensions and breeding parameters for each clutch size and breeding attempts were determined using ANOVA, and differences and similarities between egg dimensions and breeding parameters for each clutch size and breeding attempts were compared using Duncan's multiple comparison analysis. Groups represented by the same letter are significantly similar and the others are significantly different. Those represented by more than 1 letter are similar to groups represented by the same letter. Furthermore, breeding success was compared between clutch sizes and breeding attempts using ANOVA. Correlations between egg parameters and climatic factors were determined with Pearson's correlation test. Significance was set at $P < 0.05$ for all statistical tests. For each test, degrees of freedom (df) and significance levels are reported. All results are presented as mean \pm standard error (SE).

Results

Clutch and egg size

Clutch size varied from 1 to 11 eggs; however, only 2-8 eggs per clutch were found in all years. One-egg clutches ($n = 3$ eggs) were abandoned by females and none of them hatched; therefore, these clutches were included in the statistical analyses to determine differences between breeding parameters, but were excluded from calculations on breeding success and productivity due to hatching failure. Clutches of 9-11 eggs ($n = 60$ eggs) were laid by more than 1 female and were added to the statistical analysis because of hatching. In total, 153 (38.9%), 121 (30.8%), 91 (23.2%), and 28 (7.1%) clutches were laid in the 1st, 2nd, 3rd, and 4th attempts, respectively (Figure 2).

Most clutches contained 4-6 eggs and the most common was 5 eggs. Three-year mean clutch size was 5.17 ± 0.07 eggs and differences in mean clutch size between each breeding attempt were statistically significant ($F_{3,389} = 20.082$, $P < 0.0001$). Mean clutch size and numbers decreased from the first 2 to the last 2 attempts (Figure 3).

In all, 1941 (75 eggs could not be measured) eggs from 378 clutches were measured, and egg length, width, weight, volume, and sphericity index were determined as 21.16 ± 0.03 mm, 14.99 ± 0.01 mm, 2.02 ± 0.01 g, 2.38 ± 0.01 cm³, and 71.01 ± 0.09 ,

Table 1. Mean monthly temperature, rainfall, and humidity in the study area.

Climatic factors	Year	Months											
		J	F	M	A	M	J	J	A	S	O	N	D
Temperature (°C)	2001	11.4	11.5	15.9	16.8	21.7	25.6	28.5	28.7	25.6	21.0	14.2	11.1
	2002	9.1	12.5	14.3	15.9	21.0	26.6	29.3	28.7	24.3	20.6	15.6	10.0
	2003	12.7	8.9	11.7	15.8	23.1	26.5	29.7	29.6	24.5	20.8	15.5	11.5
Rain (mm)	2001	217.7	96.2	9.5	97.3	62.0	-	0.4	-	2.0	16.3	907.2	483.2
	2002	52.0	22.3	48.8	118.0	9.9	0.1	20.4	1.3	5.5	40.8	68.1	584.4
	2003	368.0	122.7	398.8	128.5	84.1	10.5	-	-	8.0	21.6	53.8	577.6
Humidity (%)	2001	67.5	59.8	66.6	67.8	61.0	63.4	69.1	68.6	67.7	55.5	67.9	71.6
	2002	56.0	63.2	71.3	78.8	73.5	62.7	63.8	63.1	69.9	58.2	65.1	64.3
	2003	73.1	51.5	60.3	66.5	57.7	57.3	50.2	54.3	58.1	62.7	61.4	64.9

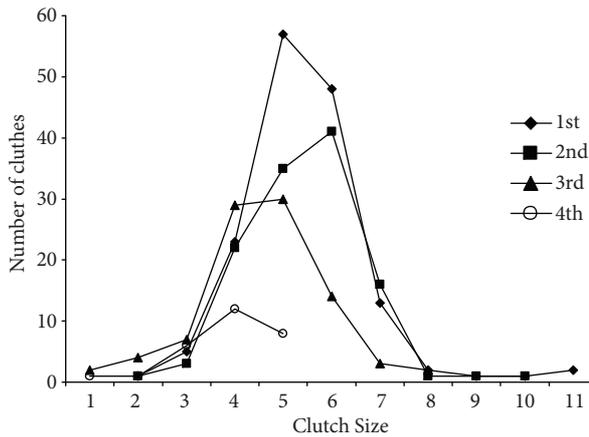


Figure 2. Frequency distribution of clutch size based on breeding attempts.

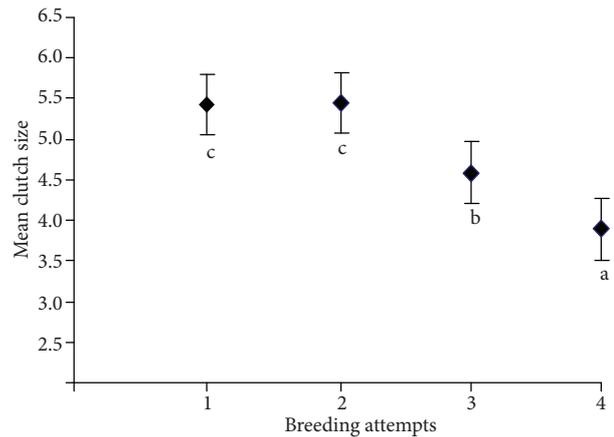


Figure 3. Mean clutch size of breeding attempts (letters denoting differences are given below the error bars).

respectively. The size of eggs differed between breeding attempts (Table 2); egg length, width, weight, and volume values for the first 2 attempts were higher and clearly decreased in the last 2 attempts; in contrast, sphericity index values increased from the first to last breeding attempt. Egg dimensions also differed between clutch sizes (Table 3). Clutch size ($r = -0.30, P < 0.0001$), and egg length ($r = -0.20, P < 0.0001$), width ($r = -0.12, P < 0.0001$), weight ($r = -0.08, P < 0.0001$), and volume ($r = -0.20, P < 0.0001$) were negatively correlated with breeding attempt, while the sphericity index was positively correlated with breeding attempt ($r = 0.12, P < 0.0001$). Moreover, egg length ($r = 0.07, P < 0.003$), width ($r = 0.09, P < 0.0001$), and volume ($r = 0.10, P < 0.0001$) were positively correlated with clutch size.

Differences in temperature and rainfall between years were not statistically significant ($P > 0.05$), whereas differences in humidity were significant ($F_{3,12} = 4.517, P < 0.024$). Differences in temperature and rainfall between breeding attempts were statistically significant (temperature: $F_{3,12} = 159.121, P < 0.0001$; rainfall: $F_{3,12} = 14.338, P < 0.0001$), while no differences in humidity were observed ($P > 0.05$). The number of breeding attempts was positively correlated with temperature ($r = 0.97, P < 0.0001$), but negatively correlated with rainfall ($r = -0.84, P < 0.001$). Egg length was positively correlated with rainfall ($r = 0.60, P < 0.041$) and humidity ($r = 0.59, P < 0.044$), while it was negatively correlated with temperature ($r = -0.81, P < 0.002$). Furthermore, there was a negative correlation ($r = -0.68, P < 0.015$) between temperature and egg volume.

Table 2. Differences and similarities in egg size between breeding attempts.

Egg sizes	Breeding Attempts				ANOVA
	1st	2nd	3rd	4th	
Length	21.33 ± 0.04 c	21.24 ± 0.04 c	20.85 ± 0.06 b	20.48 ± 0.11 a	$F_{3,1937} = 30.58, P < 0.0001$
Width	15.00 ± 0.02 c	15.08 ± 0.02 c	14.87 ± 0.03 b	14.73 ± 0.05 a	$F_{3,1937} = 20.15, P < 0.0001$
Weight	2.03 ± 0.01 bc	2.04 ± 0.01 c	1.99 ± 0.02 b	1.92 ± 0.03 a	$F_{3,1937} = 8.04, P < 0.0001$
Volume	2.41 ± 0.01 c	2.42 ± 0.01 c	2.31 ± 0.01 b	2.23 ± 0.02 a	$F_{3,1937} = 37.79, P < 0.0001$
Sph. Index	70.48 ± 0.13 a	71.15 ± 0.17 ab	71.53 ± 0.21 bc	72.11 ± 0.45 c	$F_{3,1937} = 9.37, P < 0.0001$
n	788	634	423	96	

n: Total number of eggs measured.

Table 3. Egg size according to clutch size.

Clutch size	n	Length (mm)	Width (mm)	Weight (g)	Sphericity index	Volume (cm ³)
1	3	20.74 ± 0.27 ab	14.87 ± 0.10 ab	2.09 ± 0.08 b	71.72 ± 0.81 ab	2.30 ± 0.05 a
2	14	20.65 ± 0.30 ab	14.82 ± 0.18 a	2.02 ± 0.05 b	71.95 ± 1.38 ab	2.27 ± 0.06 a
3	63	20.98 ± 0.16 ab	14.86 ± 0.09 ab	1.98 ± 0.05 b	71.01 ± 0.55 ab	2.33 ± 0.04 ab
4	324	20.85 ± 0.07 ab	14.90 ± 0.03 ab	2.00 ± 0.01 b	71.67 ± 0.23 ab	2.32 ± 0.01 ab
5	625	21.29 ± 0.05 bc	14.99 ± 0.02 ab	2.01 ± 0.01 b	70.58 ± 0.16 ab	2.39 ± 0.01 ab
6	588	21.22 ± 0.04 abc	15.03 ± 0.02 ab	2.06 ± 0.01 b	70.97 ± 0.16 ab	2.40 ± 0.01 ab
7	224	21.11 ± 0.07 abc	14.97 ± 0.04 ab	2.01 ± 0.02 b	71.11 ± 0.30 ab	2.37 ± 0.01 ab
8	40	21.24 ± 0.18 bc	15.20 ± 0.08 bc	1.95 ± 0.02 b	71.73 ± 0.49 ab	2.46 ± 0.04 bc
9	18	21.30 ± 0.17 bc	14.78 ± 0.12 a	1.98 ± 0.02 b	69.51 ± 0.96 a	2.33 ± 0.03 ab
10	20	20.52 ± 0.24 a	14.92 ± 0.09 ab	1.59 ± 0.08 a	72.97 ± 1.19 b	2.28 ± 0.02 a
11	22	21.77 ± 0.19 c	15.36 ± 0.07 c	2.32 ± 0.07 c	70.63 ± 0.44 ab	2.57 ± 0.04 c
Total	1941	21.16 ± 0.03	14.99 ± 0.01	2.02 ± 0.01	71.01 ± 0.09	2.38 ± 0.01
ANOVA		F ₁₀₋₁₉₃₀ =27.38, P < 0.0001	F ₁₀₋₁₉₃₀ =3.83, P < 0.0001	F ₁₀₋₁₉₃₀ =10.74, P < 0.0001	F ₁₀₋₁₉₃₀ =2.52, P < 0.005	F ₁₀₋₁₉₃₀ =6.41, P < 0.0001

n: Total number of eggs measured for each clutch size.

Breeding success and productivity

When data for the 3-year period were pooled, the mean number of unhatched, hatched, dead nestlings, and fledglings per clutch was 2.28 ± 0.09, 2.85 ± 0.09,

1.05 ± 0.06, and 1.80 ± 0.07, respectively, and differed between clutch sizes (Table 4). Analysis showed that 5-egg clutches and the first breeding attempt were the most productive.

Table 4. Breeding parameters according to clutch size.

Clutch size	n	Unhatched eggs	Hatched eggs	Dead nestlings	Fledglings
1	3	1.00 ± 0.00 a	0.00 a	0.00 a	0.00 a
2	7	1.43 ± 0.20 ab	0.57 ± 0.20 ab	0.00 ± 0.00 a	0.57 ± 0.20 ab
3	21	1.45 ± 0.26 ab	1.55 ± 0.26 abc	0.41 ± 0.17 ab	1.14 ± 0.22 ab
4	86	1.66 ± 0.15 ab	2.34 ± 0.15 abcd	0.86 ± 0.12 abc	1.48 ± 0.13 abc
5	130	2.24 ± 0.14 ab	2.76 ± 0.14 bcde	0.95 ± 0.11 abc	1.81 ± 0.12 abc
6	103	2.67 ± 0.19 ab	3.33 ± 0.19 cdef	1.30 ± 0.14 abc	2.03 ± 0.16 abc
7	32	2.72 ± 0.35 ab	4.28 ± 0.35 def	1.69 ± 0.24 abc	2.59 ± 0.27 bc
8	5	3.00 ± 0.00 ab	5.00 ± 0.00 ef	2.60 ± 0.51 c	2.40 ± 0.51 bc
9	2	3.50 ± 0.50 b	5.50 ± 0.50 f	2.00 ± 1.00 bc	3.50 ± 0.50 c
10	2	8.00 ± 2.00 c	2.00 ± 2.00 abcd	0.50 ± 0.50 ab	1.50 ± 1.50 abc
11	2	8.50 ± 2.50 c	2.50 ± 2.50 bcd	0.00 ± 0.00 a	2.50 ± 2.50 bc
Total	393	2.28 ± 0.09	2.85 ± 0.09	1.05 ± 0.06	1.80 ± 0.07
ANOVA		F ₁₀₋₃₈₂ = 8.96, P < 0.0001	F ₁₀₋₃₈₂ = 8.20, P < 0.0001	F ₁₀₋₃₈₂ = 4.08, P < 0.0001	F ₁₀₋₃₈₂ = 3.72, P < 0.0001

n: Total number of each clutch size.

There were no significant differences between the breeding success of clutch sizes and breeding attempts, according to ANOVA (BS_1 : $F_{7-378} = 1.99$, $P > 0.436$ and BS_2 : $F_{7-306} = 1.42$, $P > 0.198$) (Figure 4A-D).

In contrast, BS_2 (Figure 4 B) for clutch size, and BS_1 and BS_2 for breeding attempts differed according to Duncan's test (Figure 4C-D). In addition, clutch size correlated with BS_1 ($r = -0.17$, $P < 0.005$) and BS_2 ($r =$

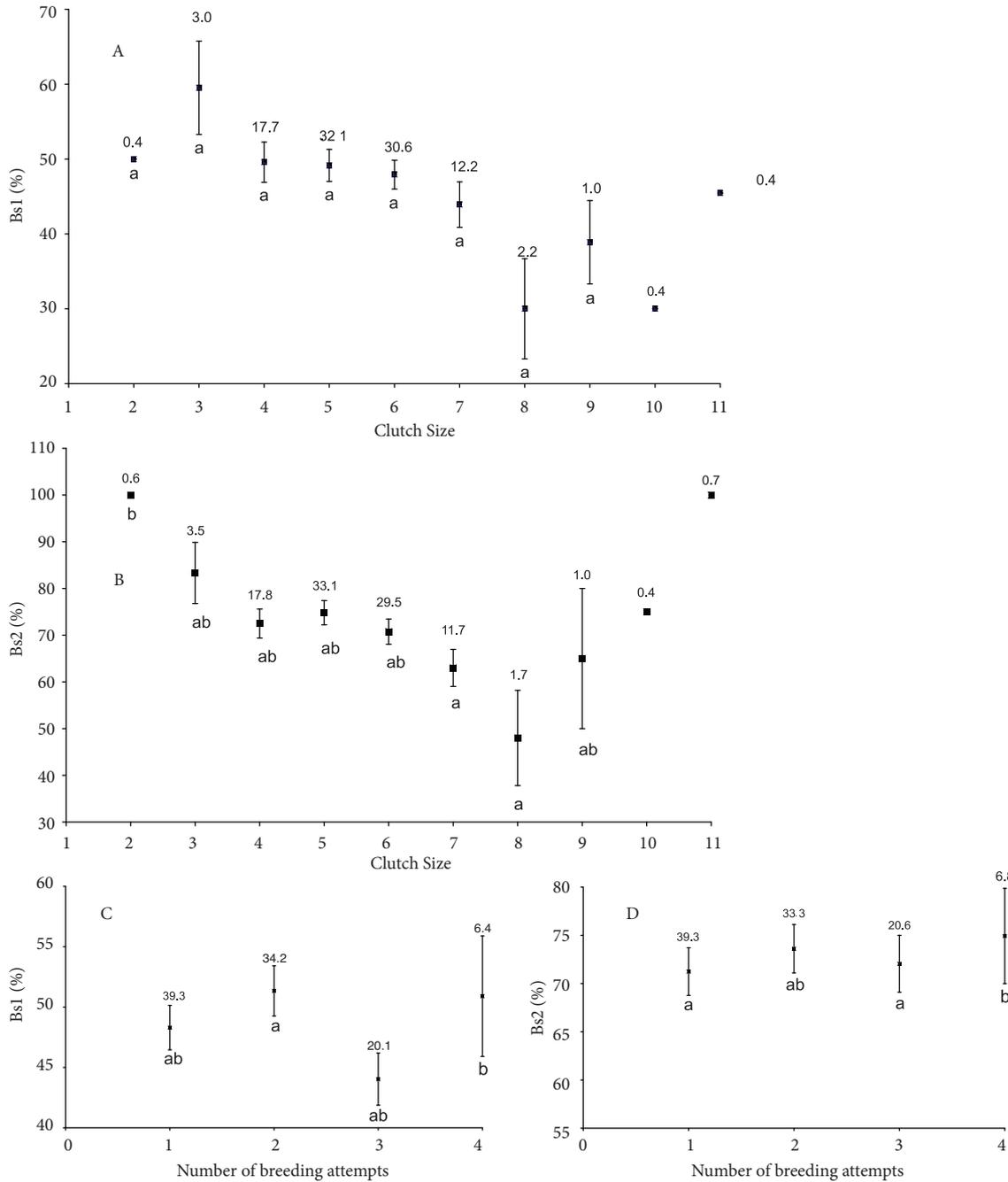


Figure 4. Breeding success and productivity according to clutch size (A and B) and breeding attempts (C and D) (productivity of each clutch size and breeding attempt as a percentage, and letters denoting differences in breeding success are given above and below the error bars).

-0.18, $P < 0.003$), but no relationships were observed between breeding success and breeding attempts. Productivity of breeding attempts clearly decreased from the 1st to 4th attempts ($r = -0.988$, $P < 0.0001$ for BS_1 and $r = -0.981$, $P < 0.0001$ for BS_2).

Discussion

In the House Sparrow, clutch size usually ranges from 2 to 7 eggs (Haartmann, 1969; Balat, 1974). In Iraq and Israel, clutch size varies from 2 to 7 and from 3 to 7 eggs, and the modal clutch size and most successful clutch size is 5 and 6 eggs per clutch, respectively (Al-Dabbagh and Jiad, 1988; Singer and Yom-Tov, 1988). In contrast, Seel (1968) reported that clutches of 4 eggs are the most common and the most successful in England. According to Erdoğan and Kızıroğlu (1995), and Sıki (1992), clutch size in Turkey ranges from 3-6 and 3-7 eggs, respectively, and the most common and most successful clutch size was 5 eggs per clutch. In the present study, clutch size ranged from 1 to 11 eggs and clutches of 4-6 eggs were common. The most common and most successful clutch size was 5 eggs. These results support Murphy's claim (1978) that females lay fewer eggs than their maximum reproductive capacity allows. Jones and Ward (1976) also suggested that females inherit the ability to vary clutch size within a certain range and that the upper limit of clutch size is firmly fixed. Nonetheless, as reported by Charnov and Krebs (1974), there might be a trade-off between a female's longevity and her level of reproduction in a particular time. Seasonal variation in clutch size has been reported by Seel (1968) and Murphy (1978), as clutch size is variable between breeding attempts. The differences in seasonal clutch size observed in the present study seem to support this variation. We observed that mean clutch size was the highest in the first 2 breeding attempts, and decreased slightly with the 3rd and 4th breeding attempts. Lack (1966) reported that seasonal changes in clutch size can be adaptive; larger clutches should be laid when conditions for raising young are most suitable. Our results support this hypothesis, as the first 2 clutches, which were larger, occurred when conditions in the study area were suitable. A decrease in food supplies and variation in climatic conditions result in a decrease in breeding performance (Lack, 1968). The

seasonal variation in food supplies during the breeding period in the study area is also thought to be the reason for clutch and egg size differences between breeding attempts.

For several bird species temperature close to the upper critical level could have a negative effect on egg size (Lorenz and Almquist, 1936; Kendeigh, 1941; Mueller, 1961; Clark and Amin, 1965). In the present study, 1st and 2nd breeding attempts with larger corresponding clutches were recorded in April and May, whereas the 3rd and 4th breeding attempts with smaller clutches were recorded in June and July (Aslan et al., 2005). Mean temperature during these months ranged from 16.2 °C in May to 29.2 °C July (Table 1). This suggests that the more suitable temperatures ranged from 16 to 22 °C, and that higher temperatures had negative effects on both clutch size and egg size. Productivity of the studied population also declined as temperature increased. It was observed that an increase in temperature resulted in an increase in the number of breeding attempts; however, temperature had a negative effect on clutch size and, consequently, clutch size and egg size decreased from the first to last 2 breeding attempts. In contrast, rainfall had a positive effect on the number of breeding attempts. In addition, egg length was positively affected, not only by rainfall, but also by an increase in humidity. Rainfall rates, as opposed to humidity, during the breeding period were significantly different and clearly decreased from April to August.

It was reported that the production of eggs by passerines is energetically expensive (Ricklefs, 1974; Murphy, 1978; Pinowska, 1979; Järvinen and Väisänen, 1984), but others reported that it is not (Krementz and Ankney, 1986; Ward, 1996). There was a positive correlation between clutch size and egg size in the present study, suggesting that larger clutches contain larger eggs, which must require much more energy and should be expensive for the females.

Lack's hypothesis (1954, 1966) implies that the modal clutch size is more productive than other clutch sizes, whereas Klomp (1970), and Jones and Ward (1976) argued that birds are capable of laying clutches that vary in size and a modal clutch size can be smaller than the most productive one. The negative correlation between clutch size and breeding success observed in the present study supports Lack's

hypothesis (1954, 1966) that larger clutch sizes are not necessarily associated with improved breeding success and that modal clutch size is more important for breeding success. Clutch size, the number of unhatched eggs, hatched eggs, dead nestlings, and fledglings are the most important patterns for determining breeding success and productivity in birds (Deckert, 1969; Kiziroğlu, 1981). In the present study, means of breeding parameters based on clutch size were significantly different, whereas no differences were observed between breeding successes using ANOVA. Nonetheless, Duncan's test results did show significant differences between BS_2 . Despite differences in breeding patterns, the effect of climatic conditions, decreases in food supplies, and reduced breeding desire of females during the breeding period, no differences were observed between the breeding successes of breeding attempts by ANOVA, but according to Duncan's test results, the differences were significant. Clutches of 4-6 eggs were the most productive and productivity of the breeding attempts decreased from the first to the last breeding attempt during the breeding season. These results show that the House Sparrow had consistent breeding success

and productivity during the breeding season in the study area.

In conclusion, the results obtained in the present study and our previous work (Aslan et al., 2005) show that nesting House Sparrows have a flexible response to changes in environmental conditions. Overall, temperature and rainfall had a greater effect on clutch size, egg size, and reproductive performance than did humidity. It is thought that data from this study and our previous study could provide a basis for monitoring future changes and to test specific hypotheses concerning the breeding ecology of the House Sparrow in the study area.

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Clutch and egg size variation, and productivity of the House Sparrow (*Passer domesticus*):
effects of temperature, rainfall, and humidity

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Clutch and egg size variation, and productivity of the House Sparrow (*Passer domesticus*):
effects of temperature, rainfall, and humidity

Appendix. Breeding parameter values according to breeding attempt, clutch size, and year.

Breeding attempts	Clutch size	n	*n	Unhatched eggs	Hatched eggs	Dead nestlings	Fledglings
I	2	1	2	2	-	-	-
	3	5	15	7	8	1	7
	4	23	92	37	55	25	30
	5	57	285	140	145	56	89
	6	48	288	142	146	49	97
	7	13	91	28	63	24	39
	8	2	16	6	10	5	5
	9	1	9	4	5	1	4
	10	1	10	6	4	1	3
	11	2	22	17	5	-	5
	Total		153	830	389	441	162
II	2	1	2	1	1	-	1
	3	3	9	6	3	2	1
	4	22	88	43	45	17	28
	5	35	175	65	110	31	79
	6	41	246	99	147	64	83
	7	16	112	45	67	27	40
	8	1	8	3	5	4	1
	9	1	9	3	6	3	3
	10	1	10	10	-	-	-
	Total		121	659	275	384	148
III	1	2	2	2	-	-	-
	2	4	8	6	2	-	2
	3	7	21	14	7	1	6
	4	29	116	47	69	22	47
	5	30	150	70	80	28	52
	6	14	84	34	50	21	29
	7	3	21	14	7	3	4
	8	2	16	6	10	4	6
Total		91	418	193	225	79	146
IV	1	1	1	1	-	-	-
	2	1	2	1	1	-	1
	3	6	18	5	13	2	11
	4	12	48	18	30	9	21
	5	8	40	12	28	13	15
Total		28	109	37	72	24	48
Total	1	3	3	3	-	-	-
	2	7	14	10	4	-	4
	3	21	63	29	34	9	25
	4	86	344	145	199	73	126
	5	130	650	290	360	125	235
	6	103	618	275	343	134	209
	7	32	224	87	137	54	83
	8	5	40	15	25	13	12
	9	2	18	7	11	4	7
	10	2	20	16	4	1	3
	11	2	22	17	5	-	5
Total		393	2016	894	1122	413	709

n: Total number of each clutch size; *n: total number of eggs for each clutch size.