Yearly and Seasonal Variation of Breeding Parameters in a Declining Multi-Brooded Passerine, the Tree Sparrow

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Yearly and seasonal variation of breeding parameters in a declining multi-brooded passerine, the Tree Sparrow

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Over a five-year period we monitored breeding parameters in a colony of Tree Sparrows *Passer montanus* in central Spain. This multi-brooded species can raise one to three broods per season. In this study, we analyzed inter-brood variation in reproductive success to infer the existence of seasonal patterns. We also explored inter-annual variation of life-history traits, which is of particular interest in a declining species like the Tree Sparrow. In agreement with our expectation of a multi-brooded species, clutch size showed a quadratic relationship with laying date. We found that the inter-brood interval varied significantly depending on the number of breeding attempts, which suggests that the species may engage in time-saving behaviours as reported for other multi-brooded passerines. Nestlings from second broods fledged in better condition than nestlings from first and third broods. Fewer fledglings were produced in third broods than in preceding breeding attempts. The reproductive output of third broods varied to a large extent among years, whereas inter-annual variation was much less marked in first and second broods. Over the years, we also detected a decrease in nestling size (tarsus and wing length), which was consistent among breeding attempts. Finally, the productivity of the colony remained fairly stable over the study period. This pattern contrasts with negative population trends detected by national monitoring programmes. The proximity of wetland habitats in the surroundings of our colony – essential for adequate invertebrates for the chicks – is suggested as a main reason for this difference.

Key words: breeding success, life-histories, multiple breeding, *Passer montanus*, seasonal and inter-annual trends

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A correct timing of breeding is crucial to any bird species. Single-brooded species are adapted to time breeding so that their nestlings are in the nest when food is most plentiful (Lack 1954). In contrast, species that breed more than once per season seem to opt for a different tactic, by maximizing the number of annual broods. In this regard, Lack (1954) suggested that multi-brooded species should lay *as soon as conditions permit*. This notion was refined by Crick *et al.* (1993) who argued that multi-brooded species should start laying before the optimal clutch size is largest. Following this reasoning, there should be an increase followed by a decrease in clutch size through the season (Crick *et al.* 1993). Thus, multi-brooded species

seem to opt for a 'quantity over quality' strategy. That is, seasonal productivity of multi-brooded species not only depends on the productivity of each breeding attempt, but also on the number of broods that parents can raise (Crick *et al.* 1993, Soler *et al.* 1995, Weggler 2006). It is clear, therefore, that single and multiple breeders differ in their strategies for maximizing fitness (Stearns 1992).

Concerning multiple breeders, they must decide how to allocate their reproductive investment between successive breeding attempts (e.g. Robinson *et al.* 2010). This aspect is interesting because it allows us to obtain valuable information for discerning general (annual) trends on the basis of the outcome of each of

the breeding attempts, or to quantify the repeatability of a particular behaviour to assess its susceptibility to environmental factors (e.g. parental care, Nakagawa *et al.* 2007). In this sense, multi-brooded species constitute a good model to analyze yearly changes in breeding parameters because they offer more than a single 'observation' (trait measure) per breeding pair. Recent studies have reported negative shifts in the number of nesting attempts per year for some double or multi-brooded species, which have been attributed to decreases in the availability of nestling food (e.g. Donald *et al.* 2002) and adjustments to changing climatic conditions (Husby *et al.* 2009). However, in general, most life-history studies are focussed on species that normally breed no more than once per season while multiple breeders have received very little attention.

The Tree Sparrow *Passer montanus* is a hole-nesting passerine, and is found in rural and suburban areas. Tree Sparrows are multi-brooded, with an extended breeding season, and the chicks are fed by both parents with a wide range of invertebrate species including caterpillars, beetles and spiders (e.g. Field *et al.* 2008). One characteristic of Tree Sparrows is their fickle nature; this species is known to suddenly appear at a site, form large colonies and then, suddenly dissapear again quickly (Summer-Smith 1995). In recent decades, this species has suffered a widespread decline in much of Europe. For instance, the UK Tree Sparrow population was reduced by 97% between 1970 and 2002 (Gregory *et al.* 2002). In Spain, the Tree Sparrow also shows a negative trend (–49%, Carrascal & Palomino 2008, Sociedad Española de Ornitología 2011). Consequently, this previously secure species is now evaluated as "Declining" (BirdLife International 2004).

In this five-year study, we assess inter-brood and inter-annual variation in reproductive parameters of Tree Sparrows from a colony in central Spain. First, we explore intra-seasonal variation to test whether Tree Sparrows show characteristics typical of multi-brooded species. Specifically, we explore whether clutch size shows a seasonal decline or whether instead it shows a mid-season peak, as is common in multi-brooded species (Klomp 1970, Crick *et al.* 1993). We also test the consequences of multiple-brooding in terms of productivity and time-saving mechanisms (length of the inter-brood interval). In addition, we explore the existence of consistent inter-brood patterns among years (e.g. are second clutches always the most productive?). That is, whether the inter-annual variability observed for certain breeding parameters (nestling condition, fledgling success) show a general trend that is consistent among breeding attempts. In a second step, we assess the annual variation in reproductive parameters observed during the study period. We pay special attention to the variation in the productivity of the colony over the years because recent studies have provided evidence for the existence of negative population trends for sparrows *Passer* sp. in Western and Central Europe (Crick & Siriwardena 2002, Vincent 2005, Brichetti *et al.* 2008, Murgui & Macías 2010).

METHODS

The study was conducted over five consecutive years (2006–2010) on the campus of the University of Castilla-La Mancha, in the city of Toledo (central Spain, 39°51'N, 4°01'W). The area comprises gardens, suburban areas and undisturbed fragments of riverside forest close to the Tagus River. Fifty pairs of nestboxes, composed of a woodcrete nestbox (type 1B, Schwegler) and wooden nestbox, were erected at the end of 2001 (see García-Navas *et al.* 2008a). In 2008, wooden nestboxes were removed due to low occupation (mean occupancy rate: 33%). After this change, the occupancy rates of woodcrete nestboxes did not increase; they remained similar to that reported in previous years ('before removal' period 2003–2007: 76%; 'after removal' period 2008–2010: 77%). Data from wooden nestboxes (2006 and 2007) were not included in subsequent analyses. Thus, all results presented here correspond to breeding attempts made in woodcrete nestboxes. Replacement clutches and deserted or predated nests were excluded from our data set; we only considered true first, second and third clutches.

In Spain, Tree Sparrows raise one to three broods per season (1st broods: April–May: 2nd broods: mid-May–June, 3rd broods: July–early August; Sánchez-Aguado 1984, Cordero 1986, García-Navas *et al.* 2010). The length of the incubation period is 10–11 days and nestlings fledge after 13–17 days (Summer-Smith 1995, Cramp 1998).

Nestboxes were checked frequently from early April to the end of July to obtain basic reproductive parameters [date of the fist egg, clutch size, length of the incubation period, hatching success (proportion of eggs hatched), number of fledged young and fledgling success (proportion of eggs that resulted in fledglings)] for each breeding attempt. Nestlings were measured on day 13 post-hatching. Nestlings were weighed with an electronic balance (accuracy: 0.1 g), their tarsus length was measured with a digital calliper to the nearest

0.01 mm and the wing length was measured to the nearest 1 mm with a top ruler using the 'maximum cord' method (Svensson 1992). Tree Sparrows use only one nest during the breeding season (Seel 1968; V. García-Navas, pers. obs.). We calculated the overall reproductive output of each nestbox (breeding pair) as the total number of successfully raised chicks (i.e. fledged young) over the entire breeding season. In this way, we obtained the annual mean productivity of the colony.

Inter-annual and within-season variability of reproductive variables was analysed using generalized linear mixed models (GLMMs) implemented with the PROC MIXED macro of SAS (SAS Institute 2004) and assuming a normal distribution of errors (Gaussian error structure). Study year (2006–2010) and clutch type (first, second, third breeding attempt) and its interaction were fitted as fixed factors. As Tree Sparrows reuse the same nestbox for their second and third brood, we included nest identity as random effect to avoid pseudoreplication. Laying date and brood (or clutch) size were incorporated in all models as covariates because these traits are important to the reproductive ecology of most passerine species. We included mean tarsus length as a covariate in the model assessing nestling body mass to correct for structural size differences between individuals. So, we used size-corrected mass as indicator of body condition. Initially, each GLMM was constructed with all explanatory terms fitted. Final models were selected following a backward procedure, by progressively eliminating non-significant terms. The result is the minimal most adequate model for explaining the variability in the response variable, where only the significant explanatory terms are retained. Denominator degrees of freedom were computed using Satterthwaite' method. In relation to the effect of timing on female productivity, we also explored the relationship between both variables (laying date and clutch size) by means of Pearson' correlations and considering each one of the three periods (first, second and third breeding attempts) separately. We then constructed a new model including the quadratic term of laying date to account for potential non-linear relationships. We also checked whether the effects of laying date and laying date^2 on clutch size are due to within-subject or between-subject effects using within-group centring (van de Pol & Wright 2009). Finally, we compare the reproductive output of single-, double- and triple-brooded females by means of t-tests to assess how multiple breeding affected productivity and fledgling success of pairs. Reproductive parameters were checked for statistical normality according to Zuur *et al.* (2010). Hatching and fledgling

successes were arcsine square root transformed prior to analyses. Post-hoc pairwise comparisons were conducted using Fisher's test. All P-values refer to two tailed tests. Values reported are means ± SE.

RESULTS

Mean annual number of breeding attempts was 1.74 ± 0.75 (median 2). The proportion of females initiating only a single clutch per season varied between 5 and 26% (overall mean: 17%). Mean laying date differed significantly among years (Table 1A). The 2007 and 2010 breeding seasons began later in comparison to the remaining years (2006: 43.98 ± 1.32, 2007: 49.63 ± 1.41, 2008: 46.34 ± 1.15, 2009: 42.95 ± 1.12, 2010: 55.53 ± 1.12). The date of the first egg differed significantly among single-brooded, double-brooded and triple-brooded females (Table 1A). Single-brooded females postponed the start of the egg-laying period in comparison with those females that bred more than once (median date of first clutch initiation, single-brooded: 19.54 ± 1.72, double-brooded: 10.35 ± 1.15, triple-brooded: 8.65 ± 1.16). The number of days elapsed between one breeding attempt and the subsequent one remained almost constant (interval 1st–2nd clutches $F_{4,149} = 1.06$, $P = 0.37$; 2006: 38.71 ± 1.57, 2007: 40.19 ± 1.57, 2008: 43.00 ± 1.48, 2009: 40.64 ± 1.57, 2010: 41.45 ± 1.89 days, interval 2nd–3rd clutches $F_{4,72} = 0.35$, $P = 0.84$; 2006: 35.06 ± 1.64, 2007: 35.18 ± 1.97, 2008: 36.85 ± 1.46, 2009: 34.53 ± 1.69, 2010: 36.20 ± 1.69 days). Inter-brood interval between first and second clutches was greater in comparison with that of second and third clutches (interval 1st–2nd clutches 40.67 ± 4.20, interval 2nd–3rd clutches 35.66 ± 6.42, $n = 74$, $Z = 4.75$, $P < 0.001$) The number of days elapsed between first and second clutches varied significantly depending on the degree of multi-brooding, i.e. the number of breeding attempts ($F_{2,154} = 4.78$, $P = 0.03$; double-brooded 42.17 ± 0.98, triple-brooded: 39.06 ± 1.02 days).

Mean clutch size varied among years (Table 1B). The general trend was consistent among the three breeding attempts even when controlling for timing of laying (see Table 1B). That is, the observed annual variation in mean clutch size showed a similar pattern for all clutch types (Figure 1A). Clutch size differed significantly among breeding attempts with third breeding attempts having significantly smaller clutches than both first and second attempts (Table 1B; Figure 1A; Fisher's test: both P-values <0.001). A seasonal trend was found for this parameter in the middle and late

part of the season; clutch size decreased with laying date for second ($r = -0.16$, $n = 164$, $P = 0.04$) and third clutches ($r = -0.38$, $n = 79$, $P < 0.001$) but no significant trend was recorded for first clutches ($r = -0.08$, $n = 200$, $P = 0.26$). When all clutches were pooled, we found a significant quadratic relationship of clutch size with laying date, which showed a mid-season peak (Figure 1B, laying date: $F_{1,440} = 5.55$, $P = 0.02$, laying date$^2 = F_{1,440} = 13.51$, $P < 0.001$). This relationship is due to both within- and among-subject effects. The contribution of the within-subject variation to this relationship was larger ($F_{1,508} = 12.22$, $P < 0.001$) in comparison with that of the among-subject variation ($F_{1,508} = 6.03$, $P = 0.01$).

The incubation period differed significantly among years (Table 1C). This result was mainly due to the extremely short incubation period registered for the first clutches in 2006 (Figure 2). Clutch type had no effect on the length of the incubation period (Table

1C). There was a year × clutch type interaction which indicates that the yearly variation observed for this parameter was not consistent among breeding attempts (Table 1C).

Hatching success did not vary significantly among years (Table 1D). There was a seasonal trend in this parameter: hatching success for third clutches tended to be lower in comparison with the preceding breeding attempts (Table 1D; Figure 3A). However this pattern was not consistent among breeding tempts as revealed by the interaction year × clutch type, which was marginally significant (Table 1D). Fledgling success did not differ significantly among years (Table 1E). Clutch type influenced this parameter; the proportion of fledged young in the third clutches was lower with respect to the other two breeding attempts (Table 1E; Figure 3B; Fisher's test: both P-values <0.001). There was no significant interaction between study year and clutch type (Table 1E).

Table 1. GLMMs for basic reproductive parameters (A–C), breeding success (D–E, I) and nestling measurements (F–H) of tree sparrows in relation to study year (5 years, 2006–2010) and clutch type (clutch; 1st, 2nd, 3rd breeding attempt). Laying date and clutch/brood size were included as covariates. Nest identity was fitted as random factor. The overall productivity of the colony (per year) was 290 (2006), 253 (2007), 282 (2008), 256 (2009) and 221 (2010) fledglings.

| Parameter	Test	P	Parameter	Test	P	Parameter	Test	P
A. Laying date			**B. Clutch size**			**C. Incubation**		
Year	$F_{4,512} = 11.92$	<0.01	Laying date	$F_{1,511} = 31.49$	<0.001	Laying date	$F_{1,466} = 8.42$	<0.01
Clutch	$F_{2,512} = 1373.58$	<0.001	Year	$F_{4,511} = 4.67$	<0.01	Clutch size	$F_{1,466} = 20.72$	<0.001
Year × Clutch	$F_{8,503} = 0.55$	0.81	Clutch	$F_{2,511} = 14.37$	<0.001	Year	$F_{4,466} = 3.07$	0.02
Nest ID	$Z = 0.44$	0.32	Year × Clutch	$F_{8,503} = 0.49$	0.86	Clutch	$F_{2,465} = 1.26$	0.28
			Nest ID	-	-	Year × Clutch	$F_{10,466} = 4.99$	<0.001
						Nest ID	-	-
D. Hatching success			**E. Fledgling success**			**F. Tarsus length**		
Laying date	$F_{1,502} = 0.30$	0.58	Laying date	$F_{1,514} = 7.51$	<0.01	Laying date	$F_{1,417} = 6.26$	0.01
Clutch size	$F_{1,466} = 0.14$	0.30	Brood size	$F_{1,514} = 5.44$	0.02	Brood size	$F_{1,417} = <0.01$	0.96
Year	$F_{4,502} = 1.13$	0.34	Year	$F_{4,502} = 1.29$	0.57	Year	$F_{4,22} = 3.55$	<0.001
Clutch	$F_{2,465} = 2.97$	0.049	Clutch	$F_{2,514} = 22.25$	<0.001	Clutch	$F_{2,422} = 3.55$	0.03
Year × Clutch	$F_{12,513} = 1.75$	0.05	Year × Clutch	$F_{8,501} = 1.02$	0.42	Year × Clutch	$F_{8,422} = 2.55$	0.01
Nest ID	-	-	Nest ID	-	-	Nest ID	$Z = 0.21$	0.42
G. Body condition			**H. Wing length**			**I. Productivity (fledgling production)**		
Laying date	$F_{1,425} = 6.56$	0.01	Laying date	$F_{1,417} = 1.80$	0.18	Laying date	$F_{1,515} = 11.57$	<0.001
Brood size	$F_{2,425} = 5.86$	<0.01	Brood size	$F_{1,417} = 0.31$	0.57	Year	$F_{4,503} = 0.56$	0.68
Tarsus length	$F_{1,425} = 422.91$	<0.001	Year	$F_{4,417} = 3.13$	0.40	Clutch	$F_{2,515} = 26.99$	<0.001
Year	$F_{4,425} = 8.96$	<0.001	Clutch	$F_{2,421} = 8.42$	<0.001	Year × Clutch	$F_{8,503} = 0.91$	0.51
Clutch	$F_{2,425} = 5.86$	<0.01	Year × Clutch	$F_{12,421} = 3.00$	0.42	Nest ID	-	-
Year × Clutch	$F_{8,415} = 1.94$	0.06	Nest ID	$Z = 0.18$	0.42			
Nest ID	$Z = 0.50$	0.31						
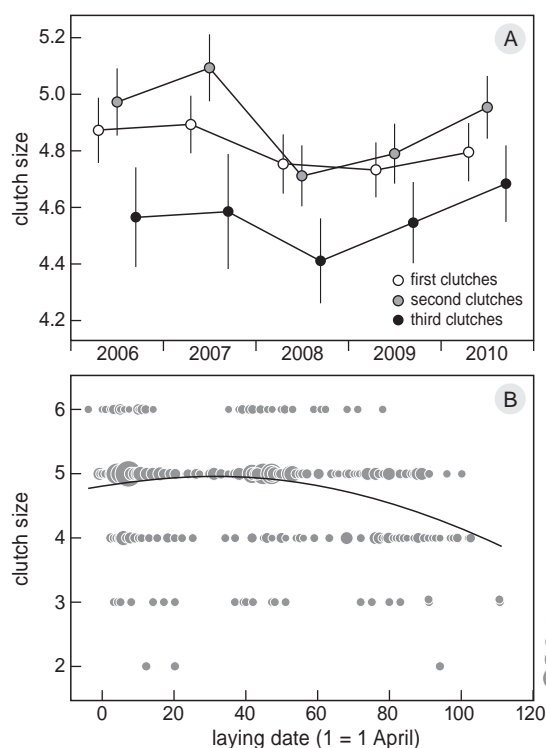
Figure 1. (A) Mean clutch size of Tree Sparrows in relation to study year (2006–2010) and clutch type and (B), seasonal variation of clutch size by laying date (quadratic regression: y = 4.78 + 0.0101×x − 0.0002×x²).

Figure 2. Mean length of the incubation period of Tree Sparrows in relation to study year and clutch type. Means ± SD are given.

Figure 3. Yearly and seasonal variation of (A) hatching success and (B) fledgling success from a Tree Sparrow colony in central Spain. Means ± SD are given.

Regarding nestling condition, we found a yearly negative trend for nestling tarsus length (Table 1F; Figure 4A). Nestling size also varied among breeding attempts; chicks from the third clutches had shorter tarsi in comparison with those of first and second clutches (Table 1F; Figure 4A; Fisher's test: both *P*-values <0.001). The interaction year × clutch type was non-significant. That is, the temporal decline observed for this parameter was consistent among breeding attempts (Table 1F; Figure 4A). On the other hand, nestling body condition (body mass corrected for tarsus length) tended to increase in the last breeding seasons (Table 1G; Figure 4B). Nestling body condition also differed significantly among breeding attempts; chicks from the first and third clutches were lighter in comparison to those of the second breeding attempts (Table 1G; Figure 4B; Fisher's test: both *P*-values <0.01). The interaction between study years and clutch type was marginally significant (Table 1G). This means that the relative body condition of nestlings from first, second and third clutches varied by year. Mean wing length varied significantly among breeding attempts but not
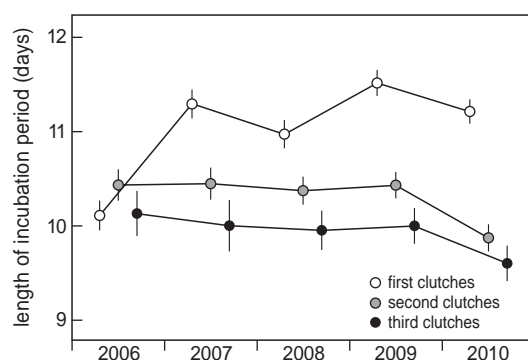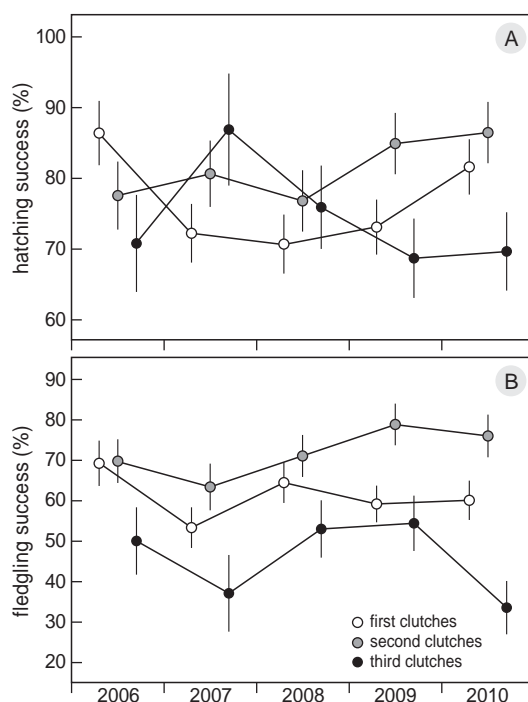
among years (Table 1H; Figure 4C). There was no significant year × clutch type interaction (Table 1H).

The mean productivity (number of fledged young per breeding attempt) did not differ significantly among years (Table 1I). The reproductive output of Tree Sparrows was lower at the end of the season (Table 1I) whereas the interaction study year × clutch type was non-significant (Table 1I). The total number
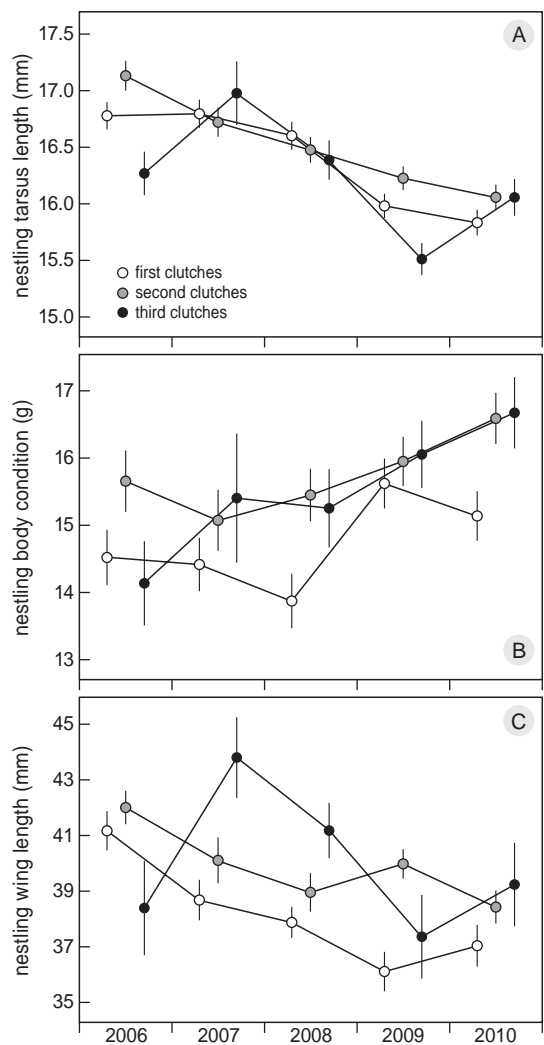
Figure 4. Yearly and seasonal variation of nestling measurements (A: mean tarsus length, B: mean body condition, C: mean wing length) from a Tree Sparrow colony in central Spain. Means ± SD are given.

of successfully fledged young per pair per season ranged from 1 to 14. There was no significant inter-annual variation in productivity (2006: 8.05 ± 3.35, 2007: 5.76 ± 2.36, 2008: 6.24 ± 3.09, 2009: 6.81 ± 2.82, 2010: 5.48 ± 3.04; χ^2: 8.28, $P = 0.08$). Single-brooded females had a similar fledging success and a similar productivity in their first breeding attempt in comparison with those that laid two or three clutches (Table 2, all P-values > 0.1) However, the reproductive output (in terms of both fledgling success and fledgling productivity) corresponding to the second breeding attempt was higher for triple-brooded females than for those that laid twice (Table 2, fledgling success: $t = -4.11$, $P < 0.001$, fledgling productivity: $t = -4.27$, $P < 0.001$).

DISCUSSION

Our results are in agreement with the notion advocated by Crick *et al.* (1993) according to which multi-brooded species should be selected to start laying before the date on which the clutch size is highest. We found that the clutch size of Tree Sparrows initially increased with a mid-season peak and then declined. A similar parabolic relationship between clutch size and time of year has been described for a few multi-brooded passerines breeding in the Iberian Peninsula (Greenfinch *Carduelis chloris* and Goldfinch *C. carduelis*: Gil-Delgado *et al.* 2002, Black Wheatear *Oenanthe leucura*: Soler *et al.* 1995, but see Rufous Bush Robin *Cercotrichas galactotes*: Palomino *et al.* 1998). The time interval between the first breeding attempt and the subsequent one varied significantly depending on the number of breeding attempts; triple-brooded females had shorter intervals between breeding attempts than those that bred twice. This suggests that Tree Sparrows, as well as other multi-brooded species, must resort to time-saving behaviours (brood overlap, nest reuse) in order to enhance the number of annual broods that can be produced (Westmoreland *et al.* 1986, Weggler 2006).

Table 2. Fledgling success and fledgling production of tree sparrows in relation to the number of clutches produced. Means ± SD are shown.

Number of clutches	*n*	Fledgling success			Fledgling productivity		
		First brood	Second brood	Third brood	First brood	Second brood	Third brood
Single-brooded	41	53.33 ± 40.35			2.33 ± 1.82		
Double-brooded	83	61.10 ± 33.94	61.80 ± 34.80		2.88 ± 1.64	2.97 ± 1.72	
Triple-brooded	101	62.49 ± 34.82	80.39 ± 26.48	43.55 ± 33.39	3.49 ± 1.69	3.93 ± 1.32	2.00 ± 1.55

Thus, it is likely that time constraints (and, to a lesser extent, the lack of availability of empty nestboxes) deter the birds from moving in search of a new nest-site despite the accumulation of debris and the presence of ectoparasites (see more below), which can have detrimental effects on nestling condition (Richner *et al.* 1993, Rendell & Verbeek 1996a,b; Mazgajski 2007). The costs of nest-site switching may offset costs associated with the reuse of soiled cavities as has been shown experimentally in other multi-brooded passerines (Stanback & Rockwell 2003). On the other hand, we found a seasonal decline in clutch size for second and third broods, which indicates that Tree Sparrows try to avoid extending their long breeding period beyond the time-window in which conditions (mainly food abundance) are sufficient for successful reproduction. For instance, breeding success for the third broods was lower in comparison with that of the preceding breeding attempts, which may reflect worsening conditions at the end of the season. In this regard, previous studies on diet composition of nestling Tree Sparrows noted that Lepidoptera larvae constitute their main food source during April and May whereas diverse invertebrates (aphids, coleopterans, orthopterans and dipterans) and vegetable material compose the bulk of the diet during the summer period (Veiga 1990, Anderson *et al.* 2002, Field *et al.* 2008). Thus, for half of the season Tree Sparrows would benefit from the caterpillar peak, which usually occurs in May. This would explain the longer tarsi and the highest values of body condition for nestlings from second clutches. The possible positive influence of the caterpillar peak on the breeding performance of Tree Sparrows in terms of enhanced feeding conditions is supported by the findings of Sasvari & Hegyi (1994) who found that young from second broods were fed more frequently than those of the first and third broods. Meanwhile, chicks from the third clutches fledged in poorer condition (smaller size and lower body condition) in comparison with those of the first two breeding attempts. In addition, the reproductive output of third broods largely varied among years (see Table 1A). Such inter-annual variability was much less marked in the case of both first and second broods. The low prospects of third broods may be indicative of the exhaustion of body reserves of Tree Sparrows during the first and second broods (McGillivray 1983, Sasvári & Hegyi 1994). However, we found that the second broods of triple-brooded females were more productive in comparison with that of those females for which it supposed the last breeding attempt of the season (double-brooded females).

In our Tree Sparrow colony, some reproductive parameters showed inter-annual variation, such as the timing of egg-laying or nestling condition. In some cases, the temporal pattern of breeding parameters showed a negative tendency, a gradual decline over the course of the years. This was especially obvious for nestling size; we observed that both tarsus and wing length decreased over the last 5 years and that such an effect was quite consistent among breeding attempts. As a result of such reduction in tarsus length over the years, nestling body condition increased in the last breeding seasons. So, it seems that in the first half of the study period there was a strong selection for maximizing the growth rate. However, in most conditions the allocation of resources to growth entails certain costs, such as a reduction in fat stores (Ricklefs 1984, Ardia 2006). Why priorities for resource allocation changed among years, with chicks showing rapid growth in the beginning of the study period is unknown. One of the factors suggested as a driving force shaping nestling growth strategies is the risk of predation (Bosque & Bosque 1995). In this colony, predation rates are low (<5%) and thus other factors should be responsible for the observed changes in the allocation of resources among seasons. One possibility is that the existence of inter-annual variation in ectoparasite prevalence (mites *Dermanyssus* sp.) is playing a role. High infection rates would encourage the chicks to divert resources to components of growth (structural size: tarsus and wing length) that allow an earlier emancipation date (i.e. shortening the length of the nestling period, see Puchala 2004, García-Navas *et al.* 2008b). However, this possibility is purely speculative given that we did not quantify ectoparasite abundance systematically, and should be confirmed through an experimental approach. In this vein, Stanback & Dervan (2003) suggested that multi-brooded cavity nesters should take steps to minimize parasitism costs associated with being multi-brooded. We found that in most of the nests adult Tree Sparrows deposited green material (fresh leaves and fennel *Foeniculum vulgare*) on the cup lining of the nest once the chicks fledged, a behaviour which is thought to have evolved as a mechanism to control nest-dwelling ectoparasites (Sengupta 1981, Clark & Mason 1988).

On the other hand, the reproductive success of Tree Sparrows varied among years but no general pattern was evident. The causes of annual variation in the reproductive performance of Tree Sparrows have not been analysed although several authors have pointed out that the abundance of food resources constitutes one of the limiting factors of the reproductive success of

this and other passerine birds (Martin 1987, Summers-Smith 1995, Newton 1998). The reproductive output did not vary significantly among years; the productivity of the colony remained fairly stable over the study period. These results contrast with data supplied by national monitoring programmes in which a marked population decline for this species has been reported during the last decade (Carrascal & Palomino 2008, Sociedad Española de Ornitología 2011). In our colony, close to the Tagus River, Tree Sparrows seem to have no problem in obtaining a key food resource, wetland invertebrates (mainly aphids). Seasonal shortages of this prey type have been pointed out as one of the main causes of nesting failure late in the season (Seel 1970, see also Vincent 2005). Furthermore, it has been shown that Tree Sparrows show a marked preference for breeding sites adjacent to aquatic habitats (Gregory 1999, Field & Anderson 2004). For instance, Field & Anderson (2004) noted that persisting and productive colonies of Tree Sparrows in lowland England are now associated with wetland habitats. This suggests that the productivity and fate of Tree Sparrows settled in open dry farmland habitats may be rather different to that of our colony, and similar to that of many farmland species in Spain (Gil-Delgado *et al.* 2002, De Juana 2004) and the rest of Europe (Donald *et al.* 2001), which have suffered a marked decline during recent decades due to agricultural intensification.

In sum, on basis of the intra-seasonal patterns reported here we can conclude that Tree Sparrows present characteristics typical of multi-brooded species; there was a maximum in clutch size in the half of the season (a mid-season peak), single-brooded females delayed the start of the egg-laying period in comparison with those that laid more than once, and the inter-brood interval varied significantly depending on the number of breeding attempts. Regarding the annual variation of basic breeding parameters of this species we found that some parameters (tarsus and wing length) tended to decrease over the years, but we failed to find a negative tendency in terms of productivity in this colony.

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SAMENVATTING

In het onderhavige onderzoek werd gedurende vijf jaar in het midden van Spanje de broedbiologie van de Ringmus *Passer montanus* onderzocht. Deze soort kan een tot drie broedsels per seizoen grootbrengen. Zoals te verwachten is voor een soort met een erg lang broedseizoen nam de legselgrootte toe met de datum van het eerste ei om vervolgens af te nemen. Het interval tussen opeenvolgende broedpogingen was korter voor vrouwtjes die driemaal broedden dan wanneer ze tweemaal een nest maakten. Jongen uit tweede legsels vlogen met een betere lichaamsconditie uit dan jongen uit eerste of derde broedsels. Derde broedsels produceerden minder uitgevlogen jongen dan eerdere broedsels. Het aantal uitgevlogen jongen uit derde

broedsels varieerde tussen de jaren veel meer dan die uit de eerste en tweede broedsels. Gedurende het onderzoek bleken de jongen – ongeacht uit welk broedsel ze afkomstig waren – minder groot te worden (afgaande op de lengte van tarsus en vleugel). De onderzochte kolonie bleef door de jaren heen een constant aantal jongen produceren. Dit is in schril contrast met de dalende trend in productie die elders zichtbaar is. De auteurs veronderstellen dat de nabijheid van moerasgebieden – belangrijk als bron van voedsel voor de jongen – essentieel is voor Ringmussen om meerdere broedsels groot te kunnen brengen.

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