

A higher incidence of moult–breeding overlap in great tits across time is linked to an increased frequency of second clutches: a possible effect of global warming?

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Abstract

A higher incidence of moult–breeding overlap in great tits across time is linked to an increased frequency of second clutches: a possible effect of global warming? The rise of temperatures due to global warming is related to a lengthening of the breeding season in many bird species. This allows more pairs to attempt two clutches within the breeding season, thus finishing their breeding activity later in the season and therefore potentially overlapping these with post–breeding moult. We tested whether this occurred in two Spanish great tit *Parus major* populations. The proportion of pairs laying second clutches increased from 1% to 32% over the study period in one of the populations (Sagunto, 1995–2019), while it did not change in the other (Quintos, 2006–2019; mean 5%). We did not find any temporal trend for moult start date of late–breeding birds in any population. The proportion of individuals of both sexes that overlapped moult and breeding increased in Sagunto. For this latter population, sex and age, but not clutch type, contributed to the variability in the probability of overlapping in late–breeding individuals, this being higher for first–year males and lower for older females.

Key words: Post–breeding moult, Phenological changes, Climate change, *Parus major*, Great tit, Spain

Resumen

El incremento del solapamiento entre la muda y la reproducción en el carbonero común está ligado a un aumento en la frecuencia de segundas puestas: ¿Un posible efecto del calentamiento global? El ascenso de las temperaturas debido al cambio climático está relacionado con un aumento de la duración de la temporada reproductiva de muchas especies de aves. Esto permite que más parejas intenten poner dos puestas durante la temporada reproductiva y conlleva que terminen sus actividades reproductivas más tarde; por tanto, estas actividades se podrían solapar con la muda postnupcial. Hemos comprobado si esto ocurre en dos poblaciones de carbonero común (*Parus major*) de España. La proporción de parejas con segundas puestas se ha incrementado del 1% al 32% durante el periodo de estudio en una de las poblaciones (Sagunto, 1995–2019), mientras que en la otra no ha cambiado (Quintos, 2006–2019; media 5%). No hemos encontrado ninguna tendencia temporal en cuanto a la fecha de inicio de muda de los individuos que están criando en fechas tardías en ninguna de las dos poblaciones. La proporción de individuos de ambos sexos cuya muda y actividad reproductiva se solaparon se ha incrementado en Sagunto. En esta última población, el sexo y la edad, pero no el tipo de puesta, contribuyeron a explicar la variabilidad en la probabilidad de solapamiento entre los reproductores tardíos, ya que esta es mayor en los machos de primer año y menor en hembras adultas.

Palabras clave: Muda post–nupcial, Cambios fenológicos, Cambio climático, *Parus major*, Carbonero común, España

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Introduction

The rise in temperatures due to global warming has affected ecosystems in various ways in recent decades (Walther et al., 2002), and is predicted to have dramatic effects in the near future (Trisos et al., 2020). One of the most evident effects is the alteration of phenological events of plants and animals (Menzel and Fabian, 1999; Parmesan and Yohe, 2003). In birds, for example, the timing of reproduction (Both et al., 2004; Källander et al., 2017), moult (Morrison et al., 2015) and, for migratory species, migration (Charmanier and Gienapp, 2014; Tomotani et al., 2017) are all being affected by global warming.

Reproduction and moult both require the investment of substantial amounts of energy (Wilkinson, 1983). For reproduction, birds need to look for a mate, defend their territory, construct a suitable nest, form the eggs, incubate them and, lastly, take care of the chicks. As an example, the field metabolic rate of a sample of birds during incubation was 2.93 times higher than the basic metabolic rate (BMR), while that during the chick-rearing period was 3.38 times higher (Nord and Williams, 2015). On the other hand, for moult, birds must replace (partially or completely) their feathers to adequately maintain the main functions of the plumage, such as thermal insulation, flight, and appearance (Payne, 1972; Jenni and Winkler, 2020). Small birds, such as passerines, have the highest cost of moult per body mass (Hoye and Butcher, 2011), and BMR could be up to 2.11 times higher than that during the moulting period (Lindström et al., 1993).

In small passerines, moult and breeding compete for time, energy, and performance, so birds usually avoid overlapping these activities (Payne, 1972; Wilkinson, 1983; Hemborg and Lundberg, 1998; Jenni and Winkler, 2020). Most European passerines have annual cycles with regular, distinct, and relatively short periods for breeding and moult (Jenni and Winkler, 2020). Small passerines undergo a sequential moult at least once a year, and this usually occurs just after breeding (usually known as post-breeding moult), when food resources are still abundant (Hemborg et al., 2001; Moreno, 2004; Morrison et al., 2015; Tomotani et al., 2017; Jenni and Winkler, 2020). Notwithstanding the, some overlap between the end of breeding (while feeding the young or even during incubation) and the onset of moult has been repeatedly documented, both in migratory (pied flycatchers *Ficedula hypoleuca*; Morales et al., 2007) and resident species (great tits *Parus major*; Svensson, 1995), so a physiological trade-off could be expected in these overlapping birds (Svensson and Nilsson, 1997; Sanz et al., 2004). The consequences of this overlap include a reduction in breeding success, survival rate, and/or the quality of the feathers (Hemborg and Lundberg, 1998; Morales et al., 2007; Tomotani et al., 2017). However, some positive effects have been also reported, for example in body condition and stress levels, that might result in better survival probabilities for these birds (Morales et al., 2007).

Local environmental conditions might affect the degree of overlapping of breeding and moult in particular populations within a species. However, direct

comparisons of moult-breeding overlap between populations are scarce (Hemborg et al., 1998, 2001). Explanations for the between-population differences rely on latitudinal variation in the length of the breeding season. Thus, moult-breeding overlap is more common in northern populations, where the breeding season is short and many birds have to start moulting while still breeding, but it is also significant in southern Europe, probably because birds are time constrained by the hot, dry summer (Sanz, 1999; Hemborg et al., 2001). Similar situations might be expected when comparing populations living at different altitudes, as may occur in countries like Spain where altitudinal gradients are large.

Halupka and Halupka (2017) have shown that an average bird population in the northern hemisphere has increased its breeding season by 1.4 days per decade in the last 45 years, and this lengthening is independent from changes in mean laying dates. More specifically, the breeding season in multi-brooded species has increased by 4 days per decade, while it has decreased by two days per decade in single-brooded species. The lengthening of the breeding season in potentially multi-brooding species allows more individuals to lay two clutches within the same breeding season (Monroe et al., 2008; Townsend et al., 2013). This, in turn, increases the number of pairs involved in breeding activities late in the season. Overlapping is more frequent in late-breeding birds (Svensson and Nilsson, 1997; Hemborg et al., 2001), even though birds breeding late in the season start moulting later than those finishing their breeding activities earlier (Dhondt, 1973; Orell and Ojanen, 1980; Jenni and Winkler, 2020). Therefore, if more individuals are breeding late in the season and moulting dates do not change, the number of individuals overlapping moult and reproduction would increase (Moreno, 2004; Tomotani et al., 2017).

At the within-population level, not all birds have the same probability of overlapping. Males, for example, usually start moulting earlier than females (Orell and Ojanen, 1980; Tiainen, 1981; Ojanen and Orell, 1982) and have consequently been found to overlap breeding and moult more frequently (Orell and Ojanen, 1980; Hemborg, 1999; Moreno et al., 2001; Jenni and Winkler, 2020). On the other hand, the two activities often overlap more frequently in first-year birds than in older birds, maybe because the poorer condition of the primaries in younger birds inducing earlier moult or because younger birds start breeding later than older birds (Siikamäki et al., 1994; Hemborg et al., 2001). Finally, in potentially double-brooding populations, replacement clutches (those laid after a failed first one) are generally laid earlier than true second clutches (i.e. those laid after a successful one), so overlapping would probably occur more frequently among those individuals involved in second clutches.

In their analysis, Halupka and Halupka (2017) considered great tits as multi-brooded species. However, the variability in the proportion of pairs laying second clutches (those laid after a successful first one) is high between populations, and between years within populations. For example, means from several studies

compiled by Cramp and Perrins (1993) ranged from 2.6% in England to 54% in Ukraine, and reported a range of 2–93% of second clutches in different years in the Netherlands. Senécal et al. (2021) even showed significant variation in the proportion of second clutches between nearby plots within a general study area (from less than 5% in densely populated plots to about 30% in low-density plots). Therefore, depending on their propensity to lay second clutches, different populations might respond differently to lengthening of the breeding season.

We selected two Spanish great tit populations located in areas with different climate conditions and a different incidence of second clutches. The first population was in Sagunto, on the Mediterranean coast, just above sea level, and 36% of the pairs laid two clutches (see Results). The second population was in Quintos, in Central Spain, at about 900 m a.s.l., and only 7% of the pairs laid two clutches (see Results).

Our main objectives were (1) to check whether the proportion of individuals with overlapping post-breeding moult and reproduction has increased over the last 25 years, and (2) to identify individual traits related to the probability of this increase. We aimed to answer the following specific questions for each population: (1) is there a temporal trend in the proportion of pairs attempting replacement or second clutches? (2) is there a temporal trend in the date of moulting of late-breeding pairs? (3) what proportion of the breeding population shows overlaps in breeding and moult? (4) is there a temporal trend in the proportion of individuals showing overlapping of breeding and moult? (5) which individual traits (sex, age) are related to the probability of overlapping? (6) does the probability of overlapping differ between birds attempting replacement clutches and those involved in second clutchew?

To classify species as single- or multi-brooded, Halupka and Halupka (2017) considered multi-brooded as those species where, at least in some populations, more than 30% of the individuals laid more than one clutch. If we apply this criterium to the population level, our population of Sagunto would fit within the multi-brooded category, while that from Quintos would fit the single-brooded category. Following the results of Halupka and Halupka (2017), the breeding season would be expected to increase in Sagunto, with more pairs being able to lay two clutches. Milder climate conditions by the coast might allow birds to delay moulting to avoid overlap. In contrast, the breeding season in Quintos would be expected to contract, causing a decrease (or at least not promoting an increase) of second clutches (as occurs in central European populations; Visser et al., 2003; Husby et al., 2009). If the favourable season were shorter reduced, moult may tend to occur earlier, potentially increasing the incidence of a moult-breeding overlap. Concerning individual traits, our predictions were that (1) males would start moulting before females, and the overlap would thus be more frequent; and (2) first-year individuals would overlap more frequently. Finally, we would expect that (3) birds involved in second clutches would overlap more frequently than those raising replacement clutches.

Methods

The study was conducted in two wild great tit populations breeding in nestboxes in Spain. One was located within an extensive orange *Citrus aurantium* monoculture near Sagunto (Valencia, eastern Spain; 39° 42' N, 0° 15' W, 30 m a.s.l.), and data relevant for the present study are available between 1995 and 2019 (Álvarez and Barba, 2014; Rodríguez et al., 2016). The study area in Sagunto has changed over the years, from about 150 ha in the first years to about 450 ha in recent years, but the density of nestboxes has remained almost constant at about 1 nestbox per ha. The other population was located in deciduous forest patches at the Reserve of Quintos de Mora (Toledo, central Spain; 39° 32' 44" N, 4° 19' 41" W, 800–1235 m a.s.l.), where relevant data are available from 2006 to 2019 (Bueno-Enciso et al., 2017). The study area in Quintos is about 50 ha, and the density of nestboxes was about 4 nestboxes per ha.

Mean surface temperatures in Spain have increased at a rate of 0.3°C per decade since 1960 (Vicente-Serrano and Rodríguez, 2017; see also Pérez et al., 2015 for a more detailed study of the eastern part of the country). Six of the ten hottest years from 1965 to 2019 are characterised by a Mediterranean climate, though the weather in Sagunto, on the Mediterranean coast, is milder than that in Quintos (Chazarra et al., 2018).

Each nestbox was inspected at least weekly, and daily in some periods, from mid-March until the end of the breeding season in mid-July, and basic breeding parameters (date of laying of the first egg, clutch size, number of hatchlings and fledglings) were recorded. Dates are presented as 'April date' (1 April = day 1).

Adults were captured with door-traps at the nestboxes when feeding 10–12 day-old nestlings and fitted with individually numbered metal rings. The sex and age (first-year or older) of each individual was noted (Svensson, 1992). We also recorded whether the bird was moulting its primary feathers when trapped (Tomotani et al., 2017). Adult great tits have a complete post-breeding moult and, while breeding, rarely moult feathers other than their primaries (Orell and Ojanen, 1980). In our case, the most advanced birds were moulting their fourth primary.

For each year, we considered that moult started the first day we caught the first adult moulting at least one of its primary wing feathers. All birds found to be moulting in Sagunto, and most in Quintos, were caught when raising their replacement or second brood. As the occurrence of moult was assessed when capturing the birds while feeding nestlings, we were unable to determine the date of start of moulting of birds laying only one clutch (with the exception of 9 individuals that had late first clutches in Quintos). Since birds laying only one clutch could have started moulting earlier (Dhondt, 1973; Orell and Ojanen, 1980), the date of start of moult should be virtually valid for the subset of the population laying two clutches within the season.

Each year, the breeding population at each study area was estimated as the number of first clutches laid. We considered as first clutches those started

within the first 30 days after the start of the first clutch of that year (Van Noordwijk et al., 1995; Álvarez and Barba, 2014). The rest of the clutches of the season were allocated into three types: (1) replacement clutches (laid after failure of a first clutch); (2) second clutches (laid after successful fledging of a first clutch); and (3) unknown clutches. Replacement and second clutches were identified either because at least one of the parents was ringed, or by spatial proximity and phenological concordance (Borgman and Wolf, 2016). From data on ringed birds, we know that pair bond is virtually stable in great tits in both study populations throughout the season. We therefore know that most birds did not change their partners between the first and second clutches if both were alive, and that second or replacement clutches are laid in nearby nestboxes, or, on many occasions, in the same nestbox (pers. obs.). As an example of within season mate and site fidelity, in 2019, from 18 pairs where both adults were identified in two consecutive breeding attempts, 16 pairs (89%) maintained their composition (same male and female), while in the other two pairs the female bred with a different male. The two missing males were not observed to be breeding again with other females this season, or in subsequent seasons (2020 and 2021). Concerning site fidelity, 11 of these pairs laid their second clutch in the same nestbox, 6 did so in a contiguous nestbox (about 50 m distance), and 1 about 200 m away from the first box. This within-season mate and site fidelity is well-known in great tits, and has been quantified even between seasons in one of the study populations (Andreu and Barba, 2006). We were as careful as possible with these criteria, so some breeding attempts each year could not be clearly attributed to a specific pair. Thus, 'unknown' clutches are those which were laid late in the season (after the temporal limit to be considered true first clutches) but could not be clearly classified as replacement or second clutches of any particular pair. Although we did not check for temporal trends in these unknown clutches, the individuals involved were used for analyses when appropriate (see below). We are aware that despite taking maximum care in identifying clutch types, we may have misclassified some. However, we believe such possibilities would be relatively few, and would not bias the results.

To study the proportion of individuals in each population for whom breeding and moulting stages overlapped, we identified the laying date of the clutch of the first individual we caught moulting each year. We considered that all the pairs that started laying (replacement, second or unknown clutches, or even first clutches in the case of Quintos) after this date could potentially overlap breeding and moult that year. From these potentially overlapping pairs, we caught only a fraction of individuals, mostly because nests failed before the date of trapping, but also because on some occasions parents avoided the traps. There may also have been logistic reasons. Thus, to estimate the number of individuals probably overlapping each year, we extrapolated the proportion of individuals which were actually moulting from those trapped,

to the number of individuals which could potentially overlap. Thus, for each year, we computed: (1) the total number of breeding pairs (i.e. the number of first clutches); (2) the total number of individuals that could potentially overlap breeding and moult (those belonging to pairs starting a clutch later than the first individual found moulting), and (3) the proportion of individuals, from the total breeding population, in which breeding and moulting probably overlapped.

We collected data from mean daily temperatures from March and April in each of the 34 study years in Sagunto and 14 in Quintos from the meteorological stations of 'Sagunto–Pontazgo', 4 km from the study area of Sagunto, and Ciudad Real (Instituto), 45 km from the study area of Quintos. From these, we calculated monthly temperatures.

To explore the temporal variation in the proportion of second and replacement clutches, we used Generalized Linear Mixed Models (GLMM) fitted with a binomial distribution and logit function (Zuur et al., 2009), in which the response variable was a data frame containing two columns: the annual number of pairs with and without second or replacement clutches. These models included the year as an explanatory variable. The study year as a categorical variable was also included as a random effect. As available years differed, we performed separate analyses for each population. The small number of birds overlapping breeding and moult in Quintos precluded the analyses relating individual characteristics and overlapping probability in this population. For the population of Sagunto, we performed exploratory analyses to determine the potential relationship between individual characteristics and clutch type and the occurrence of overlapping. As above, we used Generalized Linear Mixed Models (GLMM) fitted with a binomial distribution and logit function to test for the effect of sex (fixed factor) and year (covariate) on the proportion of individuals that overlapped moult and breeding each year. GLMM analyses fitted with a binomial distribution (moulting vs. no moulting) and logit function were also carried out to evaluate the relative contribution of the relevant variables (sex, age, and clutch type) as predictors of the probability of overlapping breeding and moult. In these GLMM, study year as categorical variable was also included as a random effect. The models were run in R (R Core Team, 2014) using the *lme4* packages (Bates et al., 2015) to calculate fixed term estimates and the *car* package (Fox and Weisberg, 2011) to calculate *p*-values from the analyses of deviance of the models on the basis of Wald χ^2 tests.

Results

Breeding attempts per pair per year

In Sagunto, breeding data were recorded for 2701 pairs between 1995 and 2019. Of these, 51% laid only one clutch, 16% made a replacement clutch after a failed first clutch, and 20% laid a second clutch after a successful first clutch. Thirteen percent of the

Table 1. Number of breeding pairs (NBP) and proportion of pairs laying only one clutch (POOC), a first and a replacement clutch (FRC), or a first and a second clutch (FSC), from 1995 to 2019 in Sagunto. Unknown clutches (UC) are those which could not be attributed to any of the previous groups (probably late first, or early replacement).

Tabla 1. Número de parejas reproductoras (NBP) y proporción de parejas que solo hacen una puesta POOC), parejas que hacen una primera puesta y una reposición (FRC) y parejas que hacen una primera puesta y una segunda puesta (FSC), entre 1995 y 2019 en la población de Sagunto. Las puestas desconocidas (UC) son aquellas que no pudieron atribuirse a ninguno de los grupos anteriores (probablemente primeras puestas tardías o reposiciones tempranas).

Year	NBP	POOC (%)	FRC (%)	FSC (%)	UC (%)
1995	91	67.03	14.29	6.59	12.09
1996	113	76.99	22.12	0.88	0.00
1997	106	67.92	21.70	6.60	3.77
1998	97	55.67	22.68	8.25	13.40
1999	115	66.96	19.13	0.87	13.04
2000	122	72.95	11.48	4.10	11.48
2001	98	50.00	28.57	11.22	10.20
2002	98	11.22	62.24	6.12	20.41
2003	113	53.98	6.19	20.35	19.47
2004	40	47.50	0.00	17.50	35.00
2005	25	68.00	0.00	16.00	16.00
2006	37	62.16	8.11	10.81	18.92
2007	49	30.61	34.69	18.37	16.33
2008	81	77.78	3.70	3.70	14.81
2009	75	36.00	5.33	24.00	34.67
2010	117	36.75	11.11	31.62	20.51
2011	134	61.19	8.21	20.90	9.70
2012	133	43.61	12.78	32.33	11.28
2013	134	35.82	29.10	27.61	7.46
2014	142	48.59	11.97	22.54	16.90
2015	146	58.22	15.07	21.23	5.48
2016	138	36.96	10.87	32.61	19.57
2017	163	35.58	15.95	38.65	9.82
2018	164	48.17	10.98	27.44	13.41
2019	170	50.59	4.71	35.29	9.41
Total	2701	51.24	15.85	19.77	13.14

breeding pairs laid a 'second' clutch, but we could not determine whether it was a replacement clutch or a second clutch, and they were classified as 'unknown' (table 1). In this study area, there was no temporal trend in the percentage of replacement clutches ($R^2 = 8.88\%$; Estimate = -0.035 ± 0.024 ; $Z = 1.48$; $P = 0.14$). In contrast, the proportion of pairs laying a second clutch increased across the study years ($R^2 = 76.9\%$; Estimate = 0.1108 ± 0.015 ; $Z = 7.55$; $P < 0.001$) from 1% to 32% (fig. 1).

Data for Quintos were recorded from 505 pairs from 2006 to 2019. From these, 92% laid only one clutch, 2% laid a replacement clutch, and 5% laid a second clutch, with the remaining 1% being unknown (table 2). Neither the percentage of replacement clutches ($R^2 = 12.16\%$; Estimate = 0.108 ± 0.894 ; $Z = 0.89$; $P = 0.37$) nor the percentage of second clutches ($R^2 = 1.28\%$; Estimate = 0.038 ± 0.102 ; $Z = 0.37$; $P = 0.70$; fig. 1) showed a significant temporal trend.

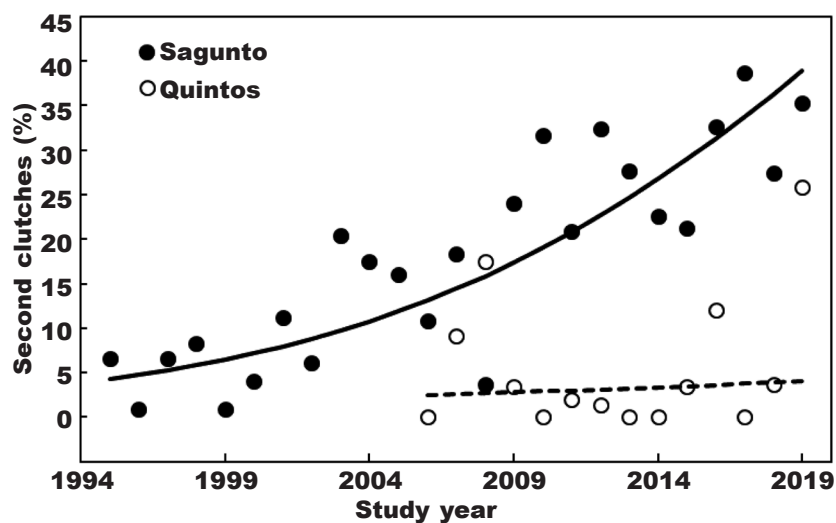


Fig. 1. Proportion of pairs that laid a second clutch after a successful first attempt between 1995 and 2019 in Sagunto (continuous line result from GLMM) and Quintos (dotted line result from GLMM).

Fig. 1. Proporción de parejas que hicieron una segunda puesta después de una primera puesta exitosa entre 1995 y 2019 en la población de Sagunto (línea continua como resultado del modelo lineal generalizado mixto del GLMM) y la de Quintos (línea discontinua como resultado del GLMM).

Temporal trends in moult–breeding overlap

The date at which we captured the first moulting bird varied between June 2 and June 28 in Sagunto, and between May 15 and June 24 in Quintos. We did not find a significant temporal trend over the years in either population (Sagunto: $R^2 = 10.7\%$; $F_{1,21} = 2.39$; $P = 0.14$; Quintos: $R^2 = 8.8\%$; $F_{1,6} = 1.482$; $P = 0.518$).

Considering the whole population each year, the proportion of birds estimated to overlap breeding and moulting activities in Sagunto varied between 0% (in 1996, 2000 and 2004) and 28% (in 2002), and increased over the years for both sexes (table 3, fig. 2). Globally, more males (18%) than females (7%) overlapped moult and reproduction, and this difference remained across the years. In Quintos, however, there were no differences between sexes in the proportion of individuals overlapping, and no significant temporal trend in the proportion of individuals overlapping (table 4). The interaction between sex and year was not significant in either study ($P > 0.05$).

Characteristics of birds overlapping breeding and moult

The number of birds found overlapping in Quintos was too small for meaningful statistical analyses, so only data from Sagunto were included in this section. Of the data included, we considered only those birds caught after the capture of the first moulting bird each year, and we refer to them here as 'late-breeding' birds. In most years, the first individual observed to be moulting was a male ($\chi^2_1 = 7.68$, $P = 0.01$). Consequently, many more late-breeding males (67%)

than females (27%) overlapped their moulting and breeding activities (table 5; fig. 3), with this occurring more frequently in first-year breeding birds than in older birds (table 5; fig. 3). However, the type of clutch (replacement vs. second clutch) did not affect the probability of overlapping moulting while still feeding young (table 5; fig. 3).

Discussion

Proportion of second clutches, timing of moulting and overlap

The general picture gives the impression that European passerines are generally advancing their breeding season in response to global warming, which would supposedly lengthen the breeding season, which would promote more pairs to attempt a second brood. However, this chain of events does not always occur. Visser et al. (2003), for example, examined the effect of raising ambient temperatures in 13 European great tit populations and found that only five of them had advanced their laying dates. Second, an advance of the onset of laying does not necessarily entail a longer breeding season (Møller et al., 2010; Gullett et al., 2013). Moreover, the breeding season could be lengthened independently of changes in mean laying dates (Halupka and Halupka, 2017). Finally, the three studies exploring temporal trends in the proportion of great tits presenting double brooding in several European populations showed a decline over the last years (Visser et al., 2003; Husby et al., 2009; Matthysen et al., 2011).

Table 2. Number of breeding pairs (NBP) and proportion of pairs laying only one clutch (POOC), a first and a replacement clutch (FRC), or a first and a second clutch (FSC), from 2006 to 2019 in Quintos. Unknown clutches (UC) are those which could not be attributed to any of the previous groups (probably late first, or early replacement clutches).

Tabla 2. Número de parejas reproductoras (NBP) y proporción de parejas que solo hacen una puesta (POOC), parejas que hacen una primera puesta y una reposición (FRC) y parejas que hacen una primera puesta y una segunda puesta (FSC), entre 2006 y 2019 en la población de Quintos. Las puestas desconocidas (UC) son aquellas que no pudieron atribuirse a ninguno de los grupos anteriores (probablemente primeras puestas tardías o reposiciones tempranas).

Year	NBP	POOC (%)	FRC (%)	FSC (%)	UC (%)
2006	7	100.00	0.00	0.00	0.00
2007	33	81.82	0.00	9.09	9.09
2008	40	82.50	0.00	17.50	0.00
2009	58	94.83	1.72	3.45	0.00
2010	32	96.88	3.13	0.00	0.00
2011	51	96.08	1.96	1.96	0.00
2012	72	95.83	2.78	1.39	0.00
2013	48	100.00	0.00	0.00	0.00
2014	27	96.30	3.70	0.00	0.00
2015	29	93.10	0.00	3.45	3.45
2016	25	84.00	4.00	12.00	0.00
2017	25	96.00	4.00	0.00	0.00
2018	27	96.30	0.00	3.70	0.00
2019	31	74.19	0.00	25.81	0.00
Total	505	92.28	1.58	5.35	0.79

In absolute contrast with the above studies on great tits, however, the proportion of pairs laying a second clutch in Sagunto increased from 1% to 32% over a 25-year period. Although an increase of second clutches has been reported for other species (Monroe et al., 2008; Townsend et al., 2013), this is, to our knowledge, the first time that it has been found for great tits. The Quintos population showed an intermediate behaviour, with no significant trend in the proportion of pairs laying second clutches over the years. The frequency of second clutches is generally low in great tits (Cramp and Perrins, 1993) and is likely to change with environmental conditions (Husby et al., 2009; Reed et al., 2013; Senécal et al., 2021). To explain the reduction of second clutches in several European populations, Visser et al. (2003) suggested that, as caterpillar development accelerates with increasing ambient temperatures, food for the nestlings is scarcer late in the season in warm years, so the reproductive value of second clutches decreases. At least some Mediterranean great tit populations do not depend as much on a single caterpillar peak to feed their

Table 3: Results of the GLMM fitted with a binomial distribution testing for a temporal trend in the proportion of males and females overlapping at Sagunto throughout the study years ($R^2 = 53.25\%$).

Tabla 3. Resultados del modelo lineal generalizado mixto (GLMM) con distribución binomial para comprobar si existe alguna tendencia temporal en la proporción de machos y hembras con solapamiento en la población de Sagunto durante los años de estudio ($R^2 = 53,25\%$).

Source	Estimate \pm SE	Z	P
Intercept	-4.57024 \pm 0.495	9.23	< 0.001
Sex	-0.569 \pm 0.046	12.31	< 0.001
Year	0.134 \pm 0.031	4.27	< 0.001

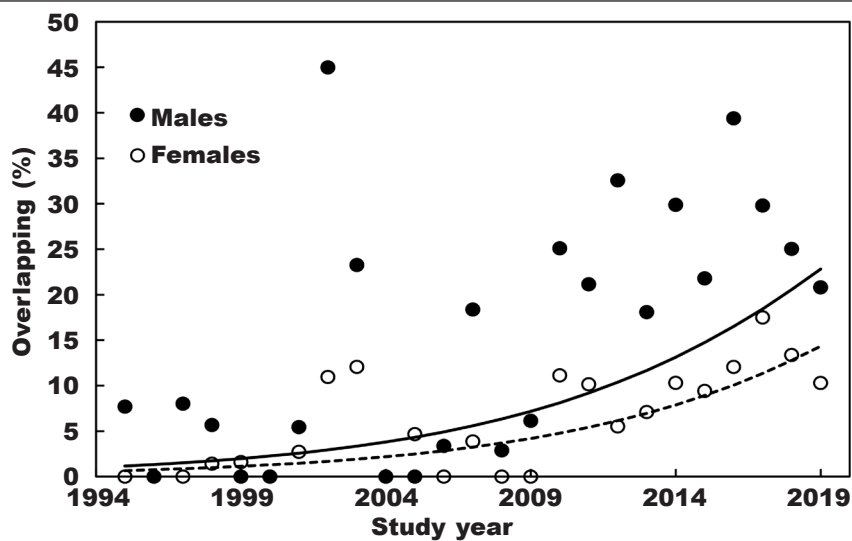


Fig. 2. Variation in the proportion of males (continuous line result from GLZ) and females (dotted line result from GLMM) overlapping moulting and breeding activities across the study years in Sagunto.

Fig. 2. Variación en la proporción de machos (línea continua como resultado del modelo lineal generalizado, GLZ) y hembras (línea discontinua como resultado del modelo lineal generalizado mixto, GLMM) cuya muda y actividad reproductiva se solaparon durante los años de estudio en la población de Sagunto.

nestlings (Barba and Gil-Delgado, 1990; Blondel et al., 1991; Pagani-Núñez et al., 2011), so the 'food' constraint late in the season might not be such a problem for late-breeding. Our population from Sagunto is known to feed its nestlings mainly with moths, using caterpillars only for the very early clutches (Barba and Gil-Delgado, 1990; Barba et al., 1996). Feeding on moth species avoids the dependence on a single food peak and probably provides acceptable breeding conditions late in the season (Barba et al., 1994, 2004). The scenario in Quintos is probably more similar to other populations in central and northern European, with parents depending more on a relatively short caterpillar peak to feed their nestlings (80% of the nestling diet; García-Navas et al., 2013). The role that food plays in the case of the population in Sagunto would be worth studying in detail, since available data are relatively old and caterpillar and moth phenology might well have changed.

Adult great tits perform a complete moult once a year, starting between early May and late June in different European populations (Flegg and Cox, 1969; Orell and Ojanen, 1980; Dhondt, 1981). Although it generally starts after the nestlings have fledged, some authors have reported moult initiation while rising second broods, or even when still feeding first-brood nestlings (especially in males) (Flegg and Cox, 1969; Orell and Ojanen, 1980; Dhondt, 1981). Dates found in Quintos and Sagunto seem to be at the end of this time window, but it should be noted that birds laying only one clutch were

not caught thereafter, so they might have started moulting before double-brooding birds (Orell and Ojanen, 1980; Dhondt, 1973) but gone undetected. In Sagunto, no individual was captured moulting while feeding first-brood nestlings, but some individuals were found moulting when raising their first brood in Quintos. Some studies have reported an advance of the timing of moult, related to global warming, in different species (Helm et al., 2019; Kiat et al., 2019; Nadal et al., 2021). To the best of our knowledge, this advancement has not been reported for European great tit populations. In our study areas, we did not find any consistent trend in the onset of moulting over the years, though we should keep in mind that we only have data on late-breeding birds.

Great tit populations in general, and the two populations studied here in particular, are resident, so migration pressure is not a potential factor governing moulting dates. A potential strategy for those pairs attempting two clutches would be to delay the moulting dates, thus avoiding or minimizing moult-breeding overlap. This should have been especially noted in our Sagunto population, where many more pairs are now laying second clutches. However, the dry, hot summers of the Mediterranean region could be an important limiting factor for developing energetically demanding activities by these dates (Dhondt, 1981; Hemborg et al., 2001). For example, heat stress might reduce the immune response and interfere with the moult-immunity trade-off by constraining seasonal delays in moulting (Moreno et al., 2001; Moreno, 2004). Thus, in Sagunto, the continuous

Table 4. Results of the GLMM fitted with a binomial distribution testing for a temporal trend in the proportion of males and females overlapping at Quintos throughout the study years ($R^2 = 86.13\%$).

Tabla 4. Resultados del modelo lineal generalizado mixto (GLMM) con distribución binomial para comprobar si existe alguna tendencia temporal en la proporción de machos y hembras con solapamiento en la población de Quintos durante los años de estudio ($R^2 = 86,13\%$).

Source	Estimate \pm SE	Z	P
Intercept	-4.051 \pm 0.882	4.60	< 0.001
Sex	-0.204 \pm 0.458	0.45	0.66
Year	-0.187 \pm 0.145	1.29	0.20

increase of the proportion of pairs laying two clutches, and then finishing their breeding activity later in the season, and the maintenance of the moulting dates, made the increase of individuals overlapping moult and reproduction over time inevitable. We have shown that the proportion of individuals that present breeding overlap and moult has increased over the years, from 1% to 23% for males and from 0% to 14% for females (fig. 2). The continuous increase of individuals following this strategy suggests that the benefits of raising two clutches per year override the potential costs of overlapping in the population of Sagunto.

Characteristics of bird which show overlapping

This section concerns only the great tit population of Sagunto, where sample size was sufficiently large to perform adequate statistical analyses. In agreement with previous studies on several passerine species (Flegg and Cox, 1969; Orell and Ojanen, 1980; Tiainen, 1981; Ojanen and Orell, 1982; Hemborg and Merilä, 1998; Hemborg and Lundberg, 1998; Hemborg, 1999; Hemborg et al., 2001; Jenni and Winkler, 2020), we observed that males started moulting earlier, and overlapping was more common in males than in females. Some authors have suggested that males 'need' to start moulting before females, either because they take longer time than females to complete the moult (e.g. Hemborg, 1999), or because they need to finish moulting earlier to be able to allocate energy to territory defence in autumn (Dhondt, 1973). The relative cost of overlap is another potential reason for sexual differences. For example, Hahn et al. (1992) stated that males invest less energy in reproduction than females (Westneat and Sherman, 1993; Queller, 1997), so they can afford

Table 5. Results of the GLMM fitted with overlap status (moulting vs. non-moulting) as the dependant variable (binomial distribution) and year, sex, age (first year vs. older birds), and clutch type (replacement or second clutch) from birds at Sagunto ($R^2 = 25.41\%$). Study year as categorical variable was also included as a random effect.

Tabla 5. Resultados del modelo lineal generalizado mixto (GLMM) con el solapamiento (muda o no muda) como variable dependiente (distribución binomial) y el año, el sexo, la edad (primer año o mayor) y el tipo de puesta (reposición o segunda) como variables independientes en las aves de la población de Sagunto ($R^2 = 25,41\%$). El año de estudio fue también incluido como un efecto aleatorio en forma de variable categórica.

Source	Estimate \pm SE	Z	P
Intercept	-1.760 \pm 0.500	3.52	< 0.001
Clutch type	-0.097 \pm 0.101	0.96	0.34
Sex	-0.968 \pm 0.083	11.62	< 0.001
Age	0.221 \pm 0.086	2.57	0.010
Year	0.086 \pm 0.028	3.10	0.002

to allocate energy in breeding and moulting activities simultaneously. Hemborg (1998) also suggested that females may have larger fitness costs than males from a moult-breeding overlap. Finally, females might be more constrained than males to overlap for physiological reasons. In this sense, Miller (1961) and King (1973) suggested that gonadal activity delays moult in females especially.

Siikamäki et al. (1994) and Hemborg et al. (2001) found that first-year pied flycatchers *Ficedula hypoleuca* from several European populations overlapped more often than adults. In agreement with these age differences in flycatchers, first-year males and females in Sagunto overlapped more frequently than older birds. Siikamäki et al. (1994) suggested that plumage condition might be inferior in first-year individuals, and they could thus need to start moulting earlier than older birds, and that as first-year individuals start breeding later, overlapping is more probable. Although Siikamäki et al. (1994) themselves considered these explanations unlikely, Morales et al. (2007) found that early moult increases survival chances, so perhaps young birds, with more survival prospects, could prioritize moulting over reproductive investment. As with the differences between sexes, asymmetries in the relative costs, hormonal differences, or even lack of experience, might be behind these 'age effects', and more research is

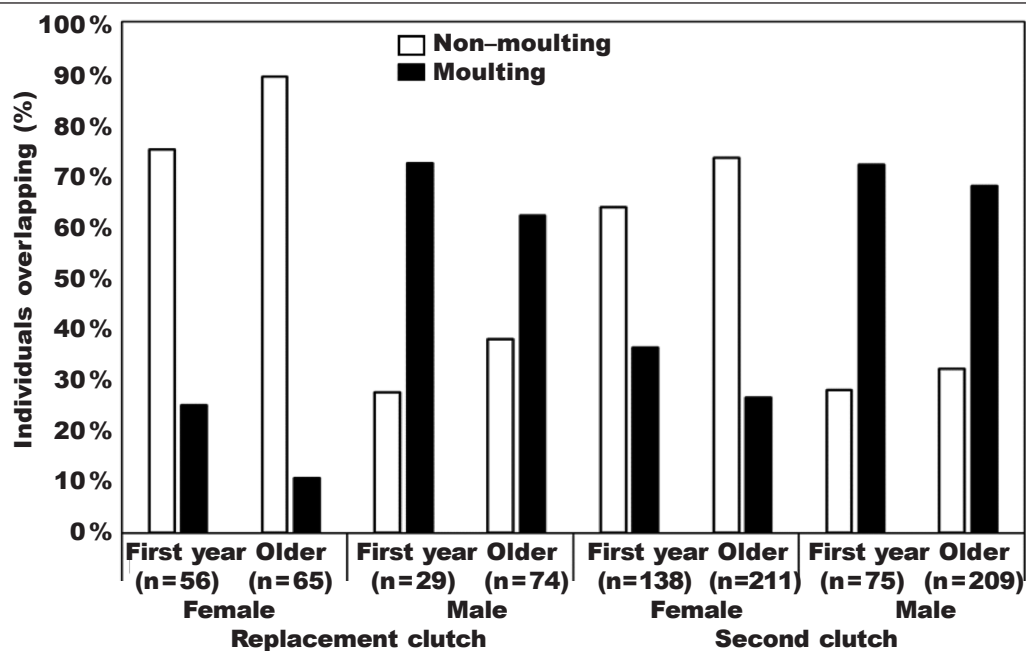


Fig. 3. Proportion of individuals overlapping moult and breeding caught during the breeding season depending on their sex (male vs. female), age (first year vs. older) and clutch type (replacement vs. second clutch) over the study years in Sagunto.

Fig. 3. Proporción de individuos cuya muda y actividad reproductiva se solaparon y que fueron capturados durante la temporada reproductiva dependiendo de su sexo (macho o hembra), edad (primer año o más de un año) y tipo de puesta (puesta de reposición o segunda puesta) durante los años de estudio en Sagunto.

clearly needed. It should also be noted that only two species, and a handful of populations, support this conclusion, and differences between age classes are not always found (Sanz, 1999; Morales et al., 2007).

Replacement clutches can be laid at any moment after the failure of a first clutch, while second clutches are laid after a first brood flies off. Second clutches therefore usually start later than replacement clutches. Moreover, birds laying second clutches have made a greater previous effort than those laying replacement clutches, since the former have raised their first brood up until independence, while the effort of the latter might have been ended at any moment between egg laying and fledging. Nevertheless, we found no differences between birds in their propensity to overlap moult and breeding according to the type of their second breeding attempt. Thus, other factors, such as date, the current physiological state of the birds, and/or their sex and age, might govern the propensity to overlap moult and breeding activities. We are not aware of any previous study dealing with this aspect of the moult–breeding overlap issue.

Summarizing, we observed that sex and age, but not clutch type, contributed to explain the variability in overlapping probability between individuals in our populations. This probability was higher for males and for first-year individuals. These results are consistent with

our initial hypotheses regarding sexual and age-related differences in overlapping breeding and moult. With the current global warming scenario, we can expect an increase in the proportion of pairs attempting second clutches, and therefore an increasing proportion of individuals (even females) overlapping moult and breeding in the near future in the population of Sagunto, contrasting sharply with other European populations, including those of Quintos studied here. The challenge now is to test whether this increase in the proportion of individuals overlapping two energetically demanding activities, such as breeding and moult, has consequences on the breeding performance and survival of adults and their nestlings.

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