Timing of breeding in the azure-winged magpie in Spain

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Abstract. Timing plays a central role in the success of breeding activities, particularly in variable and unpredictable climates. In this paper we investigate the proximate factors influencing the timing of breeding behaviour in the azure-winged magpie (*Cyanopica cyanus*) in a Mediterranean environment. The azure-winged magpie is a social corvid, colonial breeder, mostly single-brooded, which shows cooperative breeding in some populations. The study population was intensively monitored for a period of three years. The breeding season started in late March or early April and lasted around three months. The laying date varied significantly among the three years of intensive study (1995-1997). Data on the first laid egg in the whole population were related to the temperature and precipitation in the month preceding egg laying (March, data for 11 years). The timing of the first egg was significantly delayed after heavy rainfall in March. When corrected for the effect of precipitation, the timing of the first egg was no longer significantly related to the temperature in March. Comparing data from 10 populations of this species (8 from Spain, 2 from Japan) revealed that breeding dates were not related to latitude but to altitude, so that every 100 meter increase above sea level produced a delay of 4 days in the average timing of the first egg in the population.
Key words: *Cyanopica cyanus*, azure-winged magpie, timing of breeding, laying date, altitude.

Resumen. *El momento de la reproducción del rabilargo en España.* El momento de la reproducción juega un papel fundamental en el éxito de las actividades de cría, particularmente in climas variables e impredecibles. En este contexto, investigamos aquellos factores próximos que pueden influenciar el inicio del comportamiento de cría del rabilargo (*Cyanopica cyanus*) en un ambiente mediterráneo. El rabilargo es un córvido social, colonial, normalmente realiza una sola puesta, y en algunas poblaciones presenta cría cooperativa. La población de estudio fue seguida de modo intensivo durante tres años. El inicio de la época de cría se situó entre finales de marzo y primeros de abril y su duración media fue de aproximadamente tres meses. La fecha de puesta varió significativamente entre los tres años de estudio intensivo (1995-1997). Los datos acerca del primer huevo puesto en la población, estaban relacionados con la temperatura y la precipitación del mes anterior a la puesta (marzo, datos referidos a 11 años). El inicio de la puesta se retrasaba cuando la precipitación en Marzo era mayor. Cuando corregimos el efecto de la precipitación, el inicio de la puesta no resultó significativamente relacionado con la temperatura de marzo. Una revisión de 10 poblaciones de rabilargo (8 en España y 2 en Japón) reveló que la fecha de puesta no estaba relacionada con la latitud pero sí con la altitud, de modo que por cada incremento de 100 m sobre el nivel del mar se produce un retraso de 4 días en el inicio de las actividades de cría.

Introduction

Animals are selected to time their life history stages to the seasonality of environments in which they live. Lack (1950) argued that selection favours individuals that rear their offspring during the season when productivity is maximized or mortality is minimized. Both theoretical and empirical studies (Lack, 1954; Perrins, 1970; Drent & Daan, 1980; Daan et al., 1988; Price et al., 1988; Landa, 1992; Schulz, 1993; Meijer et al., 1999; Hau, 2001) indicate that timing of breeding is extremely important for reproductive success.

Although breeding phenology is primarily controlled by changes in the photoperiod, environmental variables such as temperature and rainfall have been reported to produce short term effects on the timing of breeding in birds (Immelman, 1971). Increases in temperature may directly promote egg formation and laying, thus favouring the occurrence of hatching close to the peak of food availability (Lack, 1950, 1968; Newton, 1964; McCleery & Perrins, 1998).Warm temperatures during early spring have been reported to correlate with advanced breeding in several bird species, such as tits *Parus* spp. (Perrins, 1965, 1973; Slagsvold, 1976; Murton & Westwood, 1977; O'Connor, 1978; Orell, 1983; Orell & Ojanen, 1983; Schmidt, 1984). However, higher spring temperatures promoting advancement in the phenology of vegetation and arthropods did not advance the breeding phenology in the great tit (Visser et al., 1998), so temperature may not be a direct proximate factor.

Rainfall may affect breeding phenology of birds in a different way. High precipitations during the first days of spring may delay the breeding season. This effect of precipitation might be due to rainfall itself or, as some authors have suggested, to the reduction of insulation and hence reduced temperature (Birkhead, 1991; Navarro & Bucher, 1992). On the other hand, previous rainfall may be a prerequisite for successful breeding, especially in semiarid environments, because productivity of most plants and invertebrates depend on it (e.g. Herrera, 1980; Pianka, 1988; Wingfield & Kengy, 1991). Thus, rainfall rather than ambient temperature may be the most important proximate factor determining the onset of breeding activities in semiarid ecosystems.

Geographic factors such as altitude or latitude have also been shown to affect timing of breeding. For instance, increases in latitude in the north hemisphere were associated to delays in laying phenology (Baker, 1938; Dors, 1971; Slagsvold, 1975). Similarly, an effect on delay in breeding was found to be related to increases in altitude for several passerine species (e.g. Sanz 1997; 1998), including the magpie (*Pica pica*, Birkhead, 1991).

The azure-winged magpie (*Cyanopica cyanus*) is a social corvid (Cramp & Perrins, 1994), occurring in eastern Palearctic Asia and the Iberian Peninsula (Goodwin, 1986). Its breeding system is colonial and the presence of helpers at the nest has been reported in the Japanese (Hosono, 1983, Komeda et al., 1987) and Iberian subspecies (*Cyanopica cyanus cooki*; Valencia et al., 2003). Azure-winged magpies, like most passerines in temperate areas, begin their breeding activities in spring (Cramp & Perrins, 1994). Available literature on this species indicates that breeding dates may vary between the two main areas of distribution, in Asia and Iberia, but also within the Iberian populations (rev. Cramp and Perrins, 1994). Thus, the earliest record for the beginning of the breeding season, in late March (Goodwin, 1986), as well as reports on first broods starting in early June (Araujo, 1975), show a range of variation greater than two months among Iberian populations. However, no work has so far investigated which factors could underlie these temporal patterns of variation between populations and years.

In this study we analyse some factors potentially affecting the timing of breeding in the azure-winged magpie, including meteorological and geographical variables. First, we explore the relationships between meteorological factors and breeding dates in one Spanish population in different years. Second, we look at the association between geographical factors and timing of breeding in different populations throughout their worldwide latitudinal and altitudinal distribution.

Methods

Study Area and Population

The study area is located 22 km north of the city of Badajoz (39º 03' N, 6º 48' W), in the middle of the species' Iberian distribution (Sacarrao, 1967). The predominant habitat is a dehesa (open holm oak *Quercus ilex* woodland) ecosystem. The climate is typically Mediterranean, with dry-hot summers and mild-wet winters. Total rainfall is usually between 300 and 600 mm. Most rains fall in spring and to a lesser extent in autumn. Rains are absent from late May to late September, so that the long summer is characterized by dryness and high temperatures.

During the study period, we monitored an azure-winged magpie colony consisting of an average of about 33 breeding pairs annually, nesting in holm oaks over an area of about 100 hectares. Since 1992, birds in this population have been captured and marked with metal and coloured plastic rings for individual identification.

Data collection

Most data were recorded during the period of intensive field work between 1995 and 1997, although for the analysis of reproductive phenology and meteorological variability we included data from 1995 to 2002 and from 1984 to1986 (data from Cruz, 1988), thus covering a total number of 11 years of study.

From late March or early April onwards the study area was searched for nests at least twice weekly. Trees with nest were marked, and nests were monitored until fledging at least once every two days. Observations on nests were done with a telescope from a hidden position during at least one hour every second day. Observations of individual nests were intensified during the days just after they were found (up to three hours of continuous observation), in order to identify the members of the pair. The sex of breeders was assigned according to their behaviour: only females are known to incubate the eggs and brood the young (Goodwin, 1986; Hosono, 1966; Komeda et al., 1987).

To estimate the duration of the breeding season, we used six years in total, three years of intensive study (1995-1997) together with data from Cruz (1988) for 1984, 1985 and 1986.

We considered laying date for an individual female as the date when she laid the first egg of the clutch. Likewise, laying date for the colony in one year was the laying date of the earliest female recorded in that year. The earliest laying date ever recorded in our colony was March 25th, so dates were expressed in number of days by assigning number 1 to the 1st of March. Mean laying date for a population when data from several years were available was the average laying date for those years.

Mean daily temperature and rainfall were obtained from the Valdesequera meteorological station placed within the study area until 1997. After 1997 the Valdesequera station ceased working and we used the data from the Villar del Rey station, 10 km northward. Data used in the analyses

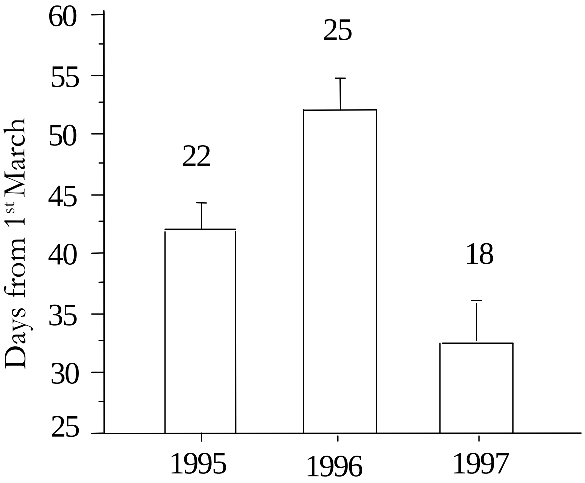

Figure 1. The laying date of azure-winged magpies in three breeding seasons (first clutches only). Bars show means and 95% confidence intervals. N indicates number of broods.

were mean daily temperature and total rainfall of March, which is approximately one month before the earliest recorded date for laying in the study species. Nevertheless, total rainfall from January to March was also used.

Data Analysis

For those analyses where breeding pairs were used as independent cases, we included only those pairs with at least one individually recognizable member, in order to avoid double counting due to replacement clutches within a season.

Normality of the dependent variable (laying date) was confirmed by the Kolmogorov-Smirnov test in the Stat View 4.5 statistic package (normality test for laying date: chi-square = 0.182; N = 11; p > 0.999). Relationships between variables were analysed by linear regressions. Variances were compared by the Snedecor F (Zar, 1984). All probabilities were two-tailed, and differences were considered significant when p<0.05.

Results

The laying date for first broods varied significantly for the three years of intensive study (ANOVA: $F_{2,62}$ = 54.64, p <0.0001; Fisher *a posteriori* tests p<0.0001 in all cases). In 1995 mean laying date occurred around April 9th, in 1996 at April 20th, in 1997 around March 31st (Figure 1). If we consider only the date when the first egg was laid in the entire colony, then we were able to include data from 11 years (from 1984 to 1986, and from 1995 to 2002). The starting of the laying period ranged from 25th of March to 11th of April, hence a total variation of 17 days.

The duration of the whole breeding season, from the first egg laid to the fledging of the last chicks, was 93 days in 1984 and in 1985, 88 days in 1986, 94 days in 1995, 88 days in 1996 and 102 days in 1997 (mean for the six years 93.00±5.14 SD). Thus the observed range of variation for these six years was 14 days.

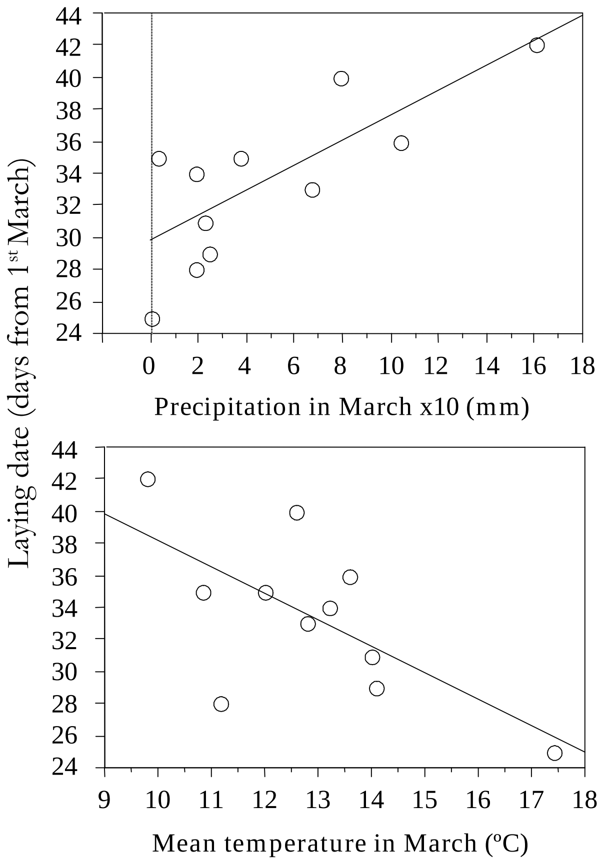

Figure 2. The relationship between the date when the first egg was laid in the colony (laying date) and total precipitation in March (above) and mean temperature in March (below) for 11 years of study.

Interannual variations in the beginning of laying did not explain the differences in the duration of the breeding season (data for six years: from 1984 to 1986 and from 1995 to 1997: r=0.45, N=6, p=0.34), and the beginning of laying was not significantly related to the end of the breeding season (r=0.68; N=6; p=0.14).

To investigate the relationship between environmental factors and the beginning of the breeding season, we were able to include the date when the first egg was laid in the colony for the sample of 11 years. Laying date was not significantly related to rainfall of the three months before the breeding season (January to March: r=0.48; N=11; p=0.13), but it was positively related to rainfall in March (r=0.77; N=11; p=0.005; r^2=0.60; y=29.60+0.08x) and negatively to mean temperature in March (r=-0.66; N=11; p=0.027; r^2=0.43; y=54.53-1.64x; Figure 2). Stepwise regression with total rainfall of March and mean temperature in March as independent variables, showed that precipitation in March was the only significant variable (F=13.42; df=1,9; p=0.005), and mean temperature in March lost significance when the effect of precipitation was removed (partial F=3.50; p>0.05).

By using available data from different azure-winged magpie populations (Table 1) we performed a

Table 1. Dates for the beginning of the laying period (laying date) and geographical data for several azure-winged magpie populations (latitude in North Hemisphere and altitude in metres above sea level).

Laying date	Latitude	Altitude	Location	Authors
10 April	40º06'	300	Candeleda (Spain)	Muñoz Pulido et al. (1990)
1 June	40º20'	1250	Avila (Spain)	Araujo (1975)
25 May	36º43'	1100	Nagano (Japan)	Komeda et al. (1987)
26 April	37º20'	15	Aljarafe (Spain)	Pacheco et al. (1975)
18 April	37º00'	10	Doñana (Spain)	Redondo (pers. comm.)#
15 May	36º18'	1000	Azumino (Japan)	Yamagishi & Fujioka (1986)
16 April	38º28'	560	Los Bermejos (Spain)	Hidalgo de Trucios (pers. comm.)♦
10.5* April	38º00'	250	Andújar (Spain)	Arias de Reyna & Redondo (pers. comm.)
3 April	38º01'	200	Montoro (Spain)	Arias de Reyna (pers. comm.)♣
2.5 April	39º03'	200	Valdesequera (Spain)	This study (11 years average)

*Average data from 1992 and 1993; #Data from 1998; ♦Data from 1984; ♣Data from 1993

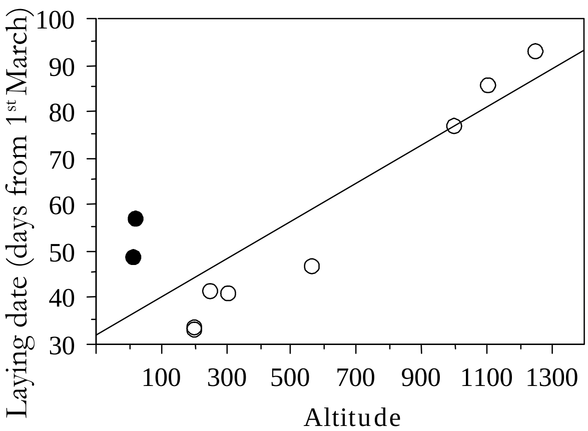

Figure 3. The relationship between the laying date of first egg in the population (ld) and altitude (alt) for ten azure-winged magpie populations (data of several years averaged per population). Two regression lines are shown: the continuous line for all ten populations (r^2=0.75, ld=36.03+0.04*alt) and the broken line excluding Doñana populations (filled symbols; r^2=0.98, ld=-23.21+0.06*alt).

stepwise regression with laying date as dependent variable, and latitude and altitude as independent variables. The range of latitude included (roughly 10 degrees) was not significant in explaining laying date (partial F=1.25; df=1,8; p>0.05), while altitude (from 10 to 1250 meters above sea level) explained an important proportion of the variance (75%) in the date of first laying across populations (F= 23.95; df=1,8; p=0.001). According to our data, the date of first laying was delayed by 4.1 days for every 100 metres increase in altitude (r=0.87; N=10; p=0.001; Figure 3). Two outlying points were the populations in the marsh area of Doñana (Doñana and Aljarafe). If we remove these two points the relationship is much stronger and altitude can explain as much as 98.1% of variance in laying date (r=0.99; N=8; p<0.0001; Figure 3). Alternatively, if we exclude the Japanese populations the relationship still holds, either with (r=0.78; N=8; p=0.023) or without Doñana (r=0.99; N=6; p=0.0003).

Discussion

The start of the breeding period for birds in temperate areas of the Northern Hemisphere is in general related to the increase in the photoperiod during the spring, the exact timing being fine-tuned by the prevailing weather conditions and food availability (Perrins, 1970; Immelman, 1971; Marzluff & Balda, 1992; Lamberchts et al., 1997). Our results show that azure-winged magpies in our study area started breeding by late March or early April, but that interannual variations in the timing of breeding can be predicted by weather conditions in the month before the start of egg laying. Although ambient temperature may have an effect, the overriding factor was high rainfall leading to delayed breeding.

In temperate ecosystems, warm spring temperatures may favour early breeding as they tend to advance the peak of food availability (e.g. Perrins, 1965, 1973; Slagsvold, 1976; Murton & Westwood, 1977; O'Connor, 1978; Orell, 1983; Orell & Ojanen, 1983; Schmidt, 1984; but see Visser et al., 1998). In Mediterranean jackdaws *Corvus monedula*, the laying date was also found to start earlier with higher March temperatures (e.g.: Soler & Soler, 1987).

In Mediterranean ecosystems, rainfall and temperature are the main limiting factors for productivity and as a consequence affect food availability for many avian species (Herrera, 1980; Olea et al., 1991). Temperature is important, especially during spring, regulating the growth of plants and hence the reproduction and population growth of many invertebrate species, but in semiarid environments the main limiting factor is usually rainfall, which triggers many growth and breeding processes (Herrera, 1980; Pianka, 1988; Olea et al., 1991; Wingfield & Kengy, 1991). For example in subtropical semiarid areas, where rainfall is unpredictable, the amount of precipitation, probably by its effects on food availability, has been reported as the main proximal factor in determining both the timing and the investment in reproduction (e.g. clutch size) for many species of birds (Marchant, 1960; Immelmann, 1973; Boag & Grant, 1984; Schoech, 1996). Nias & Ford (1992) found in the superb fairy-wren (*Malurus* *cyaneus*) that rainfall in the previous months favoured earlier breeding and longer duration of the breeding season. Experimental studies by Hau (2001) with small ground finches (*Geospiza spp.*) also showed that although the ultimate cause for the effect of rainfall on the starting of breeding is probably its effects on food availability (insect and grass seed abundance), birds may respond to rainfall cues directly by starting gonadal development and reproductive behaviour.

For our study animals rainfall was the main proximate factor affecting laying phenology, but in contrast to other studies its effect was to delay breeding. One possibility is that rainfall is itself associated with lower temperatures by means of reduced insulation (Navarro & Bucher, 1992). This explanation was proposed by Birkhead (1991) for the black-billed magpie. He indicated that when spring temperatures were low, breeding tended to be late, and that high rainfall levels during the pre-laying period appeared to delay the onset of breeding. In his study, the relationship between rainfall and laying date was no longer significant when controlling for temperature, while the correlation between laying date and temperature was still significant after the effect of rainfall was removed. It therefore appeared that cold springs rather than wet ones resulted in later breeding for the Magpie in the Sheffield area (Birkhead 1991).

However, contrary to the Magpie in Sheffield, our partial correlation shows that the statistical relationship was stronger with rainfall than with temperature. Rainfall might have other delaying effects besides its potential relationship with ambient temperature. One possible explanation is that feeding efficiency will be reduced in persistent rain. Another possibility is that rainfall could have negative effects on the survival of eggs, especially during the first days of laying, mostly caused by the open architecture of nests in this species. Further studies are needed to examine the relationship between spring rains and ultimate factors affecting breeding success.

Environmental factors affecting the onset of breeding do not seem to explain the end or the duration of the breeding period in our study birds. An earlier laying date does not determine a longer breeding period, and there is no significant relationship between the dates for starting and ending the breeding season. We would expect either of these relationships if birds used all the available period for breeding until the conditions became extreme in the summer (Valencia et al., 2000), or if the duration of the whole breeding period showed little yearly variation. However, our results seem to indicate that the end of the breeding period is highly unpredictable and is probably related to hazardous events. Predation, for example, is responsible for most (some 80%) brood losses in our study area and may favour replacement clutches which contribute to delaying the end of the breeding season (Cruz et al., 1990).

Our data for 11 years show that breeding in our study area is earlier than in other areas of the Iberian Peninsula (Goodwin, 1986; Cramp & Perrins, 1994). Geographic factors such as altitude or latitude have been reported to affect the timing of breeding. For instance, increases in latitude in the north hemisphere were associated to delays in laying phenology (Baker, 1938; Dors, 1971; Slagsvold, 1975). The same effect in delaying breeding was found related to increases in altitude (e.g. in the black-billed magpie: Birkhead, 1991). We did not find any significant relationship between laying date and latitude for the azure-winged magpie, possibly because the range in the distribution of the populations included was narrow (only 10 degrees). However, altitude appeared highly correlated with laying date, so that a difference of 100-metres was associated with 4-days delay in laying date. Birkhead (1991) found a similar relationship for the magpie (3-days delay for every 100 metres of altitude) and he attributed this to a decrease in temperature with altitude. In studying the relationship between altitude and laying date, we included two populations (Doñana and Aljarafe) with very different environmental conditions, mostly because they are both located in marsh areas. In these two populations some parts remain wet and productive during the summer (Roger & Myers, 1980), which is not the case for the dehesa system. This may produce a displacement or extension of the peak of food availability closer to the summer, and could explain the delayed breeding dates for these populations as compared to other drier areas.

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References

Araujo, J., 1975. Estudios sobre el rabilargo (*Cyanopica cyanea*) en una colonia de cría de Avila. *Ardeola*, 21: 469-485.

Baker, J. R., 1938. The evolution of breeding seasons. In: *Evolution: Essays on aspects of evolutionary biology:* 161-177; G.R. De Beer, Ed.). Clarendon Press, Oxford, UK.

Birkhead, T., 1991. *The magpies*. Poyser, London.

Boag, B. T. & Grant, P. R., 1984. Darwin's finches (*Geospiza*) on Isla Daphne Major Galapagos: Breeding and feeding ecology in a climatically variable environment. *Ecol. Monographs*, 54: 463-489.

Cramp, S. & Perrins, C. M., 1994. *Handbook of the birds of Europe the Middle East and North Africa. Vol VIII.* Oxford: Oxford University Press.

Cruz, C., 1988. Contribución al conocimiento de la biología del rabilargo *(Cyanopica cyanus* Pall., 1776) PhD. Thesis, University of Extremadura.

Cruz, C., de Lope, F. & da Silva, E., 1990. Éxito reproductor del Rabilargo (*Cyanopica cyanea* Pall) en Extremadura. *Ardeola*, 37 (2): 179-195.

Daan, S., Dijkstra, C., Drent, R. & Meijer, T., 1988. Food supply and the annual timing of avian reproduction. *Proc. int. ornithol. Congr., XIX*, 392-407.

Dors, J., 1971. *La vida de las aves* (tomo I) Destino. Barcelona.

Drent, R. & Daan, S., 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea*, 68: 225-252.

Goodwin, D. 1986. *Crows of the world.* London.

Hau, M., 2001. Timing of breeding in variable environments: tropical birds as model systems. *Horm. Behav.*, 40: 281-290.

Herrera, C. M., 1980. Composición y estructura de dos comunidades mediterráneas de passeriformes. *Doñana Acta Vert.*, 7(4): 1-340.

Hosono, T., 1966. A study of the life history of Blue Magpie (1). Breeding biology. *Misc. Rep. Yamashina Inst. Ornithol.*, 4: 327-347.

Hosono, T., 1983. [A study of the life history of the Blue Magpie. II. Breeding helpers and nest-parasitism by cuckoos]. *J. Yamashina Inst. Ornithol.*, 15: 63-71.

Immelman, K., 1971. Ecological aspects of periodic reproduction. In: *Avian Biology*, Vol. I. Ed. D.S. Farner, J.R. King & K.C. Parkes. pp. 341-389. New York: Academic Press.

Immelmann, K., 1973. Role of the environment in reproduction as source of "predictive" information. In: *Breed Biology of Birds* (ed. Farner, D.S.) pp. 121-147. National Academy of Sciences: Washington, DC.

Komeda, S., Yamagishi, S. & Fujioda, M., 1987. Cooperative breeding in Azure-Winged magpies, *Cyanopica cyana*, living in region of heavy snowfaall. *Condor*, 89: 835-841.

Lack, D., 1950. The breeding seasons of European birds. *Ibis*, 92: 288-316.

Lack, D., 1954. *The natural regulation of animal numbers*. Clarendon Press, Oxford.

Lack, D., 1968. *Ecological adaptations for breeding in birds*. London: Methuen.

Lambrechts, M. M., Blondel, J., Maistre, M. & Perret, P., 1997. A single response mechanism is responsible for evolutionary adaptive variation in a bird's laying date. *Proc. Nat. Acad. Sci. USA* 94: 5153-5155.

Landa, K., 1992. Seasonal declines in offspring fitness and selection for early reproduction in nymphoverwintering grasshoppers. *Evolution*, 46: 124-135.

Marchant, S., 1960. The breeding of some S.W. ecuadorian birds. *Ibis*, 102: 349-382, 584-589.

Marzluff, J. M. & Balda, R. P., 1992. *The Pinyon Jay.* San Diego: Academic Press.

McCleery, R. H. & Perrins, C. M., 1998….temperature and egg-laying trends. *Nature,* 391: 30-31.

Meijer, T., Nienaber, U., Langer, U. & Trillmich, F., 1999. Temperature and timing of egg-laying of European Starlings. *Condor*, 101: 124-132.

Muñoz-Pulido, R., Bautista, L. M., Alonso, J. C. & Alonso, J. A., 1990. Breeding success of Azure-winged Magpies *Cyanopica cyana* in Central Spain. *Bird Study*, 37: 111-114.

Murton, R. K. & Westwood, N. J., 1977. *Avian breeding cycles.* Oxford Univ. Press, London, England.

Navarro, J. L. & Bucher, E. H., 1992. Annual variation in the timing of breeding of the Monk Parakeet in relation to climatic factors. *Wilson Bull.,* 104 (3): 545-549.

Newton, I., 1964. The breeding biology of the Chaffinch. *Bird Study*, 11: 47-68.

Nias, R. C. & Ford, H. A., 1992. The influence of group size and habitat on reproductive success in the Superb Fairy-Wren *(Malurus cyaneus*). *Emu*, 92: 238-243.

O'Connor, R .J., 1978. Nest-box insulation and the timing of laying in the Wytham Woods population of Great Tits *Parus major*. *Ibis*, 120: 534-537.

Olea, L., Paredes, J. & Verdasco, M. P., 1991. Características y producción de los pastos de las dehesas del S.O. de la Península Ibérica. *Pastos*, 20-21: 131-156.

Orell, M. & Ojanen, M., 1983. Timing and length of the breeding season of the Great Tit, *Parus major*, and the Willow Tit *P. montanus* near Oulu, northern Finland. *Ardea*, 71: 183-198.

Orell, M., 1983. Breeding and mortality in the Great Tits *Parus major* and the Willow Tit *P. montanus* in Oulu, Northern Finland. *Acta Univ. Oul. A* 148. Biol, 19.

Pacheco, F., Alba, F. J., García, E. & Pérez Mellado, V., 1975. Estudio sobre la biología de reproducción del rabilargo *Cyanopica cyanus* (Pall.). *Ardeola*, 22: 55-73.

Perrins, C. M., 1965. Population fluctuations and clutch size in the Great Tit, Parus major. *J. Anim. Ecol.,* 34: 601-647.

Perrins, C. M., 1970. Timing of birds'breeding seasons. *Ibis*, 112: 241-255.

Perrins, C. M., 1973. Some effects of temperature on breeding in the Great Tit and Manx Shearwater. *The environment and reproduction in mammals and birds* (ed. J.S. Perry & I.W Rowlands), suppl. 19. Proc. of the Symposium of the Soc. for the studiy of fertility.

Pianka, E. R., 1988. *Evolutionary ecology.* Harper & Row. Nueva York.

Price, T., Kirkpatrick, M. & Arnold, S. J., 1988. Directional selection and the evolution of breeding date in birds. *Science*, 240: 798-799.

Rogers, P. M. & Myers, K., 1980. Animal distributions, landscape clasification and wildlife management. Coto Doñana, Spain. *J. Appl. Ecol.*, 17: 545-565.

Sacarrao, G. F., 1967. Remarques sur la variation geographique de la Pie-bleue, *Cyanopica cyanus* (Pall.) dans la Peninsula Iberique, specialment an Portugal. *Arq. Mus. Bocage,* I (12): 241-248.

Sanz, J. J., 1997. Geographic variation in breeding parameters of the Pied Flycatcher *Ficedula hypoleuca. Ibis*, 139: 107-114.

Sanz, J. J., 1998. Effects of geographic location and habitat on breeding parameters of Great Tits. , 115: 1034-1051.

Schmidt, K. H. 1984. Spring temperature and time of laying in tits. *J. Ornithol.*, 125: 321-332.

Schoech, J., 1996. The effect of supplemental food on body condition and timming of reproduction in a cooperative breeder, the Florida scrub-jay. *Condor*, 93: 234 -244.

Schulz, E.T., 1993. The effect of birth date on fitness of female dwarf perch, *Micrometrus minimus* (Perciformis: Embiotocidae). *Evolution*,47: 520-539.

Slagsvold, T., 1975. Breeding time of birds in relation to latitude. *Norw. J. Zool.*, 23: 213-218.

Slagvold, T., 1976. Annual and geographical variation in the time of breeding of the Great Tit *Parus major* and the Pied Flycatcher *Ficedula hypoleuca* in relation to environmental phenology and spring temperature. *Ornis Scand.*, 7:127-145.

Soler, M. & Soler, J. J., 1987. Fenología de puesta en *Corvus monedula.* Análisis de los factores que pueden afectarla. *Ardeola*, 34: 3-14.

Valencia, J., Cruz, C. & Carranza, J., 2000. Second broods in a Mediterranean cooperatively-breeding corvid: the Azure-winged Magpie. *Etología*, 8: 25-28.

Valencia, J., Cuz, C. & González, B., 2003. Flexible helping behaviour in the Azure-winged Magpie. *Ethology* (in press).

Visser, M. E., van Noordwijk, A. J., Tinbergen, J. M. & Lessells, C. M., 1998. Warmer springs lead to mistimed reproduction in great tits (*Parus major*). *Proc. R. Soc. Lond.* B 265: 1867-1870.

Wingfield, J. C. & Kenagy, G. J., 1991. Natural regulation of reproductive cycles. In: *Vertebrate endocrinology: fundamentals and biomedical implications* (ed. M. P. Schrubman and R. E. Jones). New York: Academic Press.

Yamagishi, S. & Fujioda, M., 1986. Heavy brood parasitism by the Common Cuckoo *Cuculus canorus* on the Azure-winged Magpie *Cyanopica cyana. Tori*, 34:91-96.

Zar, J. H., 1984. *Biostatistical analysis*. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 718 pp.