Bird Study (1999) **46,** 217–223

Breeding biology of the Roller *Coracias garrulus* in farming areas of the southwest Iberian Peninsula

JESUS M. AVILÉS*[1], JUAN M. SÁNCHEZ[1], ANGEL SÁNCHEZ[2] *and* DESEADA PAREJO[1] [1]*Grupo de Investigación en Conservación. Biología Animal, Universidad de Extremadura, Avda de Elvas s/n, E-06071 Badajoz, Spain and* [2]*Dirección General de Medio-Ambiente, Junta de Extremadura, Merida, Spain*

We studied the breeding biology of Rollers nesting in nestboxes installed in farming areas of Extremadura (southwest Spain). Laying dates of Rollers in Extremadura are the earliest in the Palearctic region. Clutch size was larger than in northern populations. In the studied population, yearly variation in clutch size could be explained by yearly variation in the timing of reproduction. Reproductive rates were higher than in more northerly populations. A seasonal decrease in breeding success of Rollers in Extremadura was caused by a reduction in clutch size and the percentage of hatched eggs, and a seasonal increase in mortality rate. The most successful clutches were those with six eggs although clutches with four and five eggs were the most frequent in Extremadura.

Roller *Coracias garrulus* populations are decreasing across its distribution area in the Palearctic region.[1–4] Since the second half of the eighteenth century, its extinction as a breeding bird has been reported in Denmark, Finland, Sweden, and in eastern Germany.[5–7] This general decrease has occurred in the Iberian population too, estimated in 1994 at between 4000 and 10 000 pairs[7] distributed in central and southern Iberia.[8,9] However, in the studied area of Extremadura, a yearly increase in breeding density has occurred as a result of the installation of nestboxes between 1986 and 1994.[10]

Information on the breeding biology of the Roller in Europe is very scarce, and gives only a general picture.[2,5] Durango[11] gave information on clutch size in a Swedish population which is now extinct, and recently Sosnowski & Chmielewski[12] studied the breeding behaviour of the species in a Polish population. In Iberia, Bernis[8] pointed out the preferences of the species for open areas, and recently the ecological factors implicated in territory choice during the breeding season have been studied.[13]

The aim of this study was to investigate the breeding biology of the Roller in dry agricultural areas of Spain, and in particular the annual and seasonal variation in breeding performance. Reproductive success is also analysed in relation to clutch size.

STUDY AREA AND METHODS

We studied the breeding population of Rollers in farming areas of Extremadura. These areas are characterized by the predominance of dry pastures (64.2%) and cereal crops, mainly wheat, barley and oats (28.4%). There are also small areas of scrub, mainly *Retama sphaerocarpa* (3.1%), and areas with holm-oaks *Quercus rotundifolia* (1.1%) as well as fruit trees (mainly Almond *Prunus dulcis*) and irrigated cultivation included in these crops.[14] The study area is in the mesomediterranean climate area.[15] During May and June the mean temperature is 17.7°C and the mean rainfall is 11.6 mm.

In 1986 the Forestry Agency of Extremadura began a conservation project involving the placement of wooden nestboxes in these steppe

*Correspondence author.
Email: javiles@unex.es

areas. The nestboxes were placed on the supports of electric power lines (for further details about the type and location of nestboxes see ref. 14). The use of nestboxes by Kestrels and Rollers has been described elsewhere.[14]

Roller nests in the boxes were monitored weekly from the first stages of breeding; visits were increased (every 3–4 days) during the nestling period to determine accurately the factors influencing the final breeding success. We measured (i) *hatching success* – the percentage of eggs within each clutch that hatched; (ii) *chick mortality rate* – the percentage of chicks hatched that died in the nest; (iii) the number of *fledglings per successful nest*; (iv) *breeding success* – the number of fledglings per pair that laid eggs; and (v) *egg productivity* – the number of fledglings as a proportion of the total number of eggs laid.

Parametric methods were used for statistical analysis when data met their assumptions, otherwise the respective non-parametric test was used. Normality of the variables was checked with Kolmogorov–Smirnov tests. Data expressed as a percentage were arcsine transformed following Sokal & Rohlf.[16] Sample sizes used for each calculation are listed in parentheses in the tables. When clutch size was used as a factor, extreme clutch sizes (one and seven eggs) were removed to avoid small sample sizes.

RESULTS

Laying date

The date of onset of egg laying in the Roller in the four seasons ranged from 1 May to 14 May (all years pooled, Table 1). The majority of pairs started laying during the second (32.1%) and

Table 1. Reproductive performance of Rollers in Extremadura.

	1988	*1989*	*1990*	*1991*	ANOVA *test* P	*All data pooled*
Onset of egg laying	14 May	7 May	3 May	1 May		
Mean laying date	39.00 ± 16.40 (15)	31.27 ± 11.83 (132)	24.67 ± 8.54 (296)	19.39 ± 10.89 (274)	$F_{3,706}$ = 50.824 <0.01	24.15 ± 11.38 (717)
Laying period (days)	48	49	53	53		
Mean clutch size	3.65 ± 1.34 (29)	3.65 ± 1.15 (149)	4.35 ± 1.20 (286)	4.41 ± 1.15 (353)	$F_{3,808}$ = 17.8 <0.01	4.23 ± 1.21 (817)
Hatching success	85.11 ± 26.91 (29)	64.68 ± 39.92 (144)	64.45 ± 40.41 (290)	70.86 ± 38.61 (349)	$F_{3,808}$ = 3.60 0.013	68.20 ± 39.29 (812)
Chick mortality (%)	4.01 ± 12.09 (27)	5.04 ± 17.10 (112)	4.77 ± 14.35 (219)	4.82 ± 14.98 (283)	$F_{3,637}$ = 0.87 0.990	4.82 ± 15.02 (641)
Fledglings per successful nest	3.33 ± 1.27 (27)	3.20 ± 1.26 (111)	3.81 ± 1.32 (220)	3.93 ± 1.33 (280)	$F_{3,631}$ = 9.17 <0.001	3.74 ± 1.34 (638)
Fledglings per breeding pair	3.10 ± 1.49 (29)	2.44 ± 1.75 (144)	2.86 ± 2.01 (290)	3.15 ± 1.97 (349)	$F_{3,808}$ = 4.76 0.003	2.93 ± 1.94 (812)
Egg productivity (%)	81.83 ± 28.48 (29)	61.40 ± 40.10 (144)	61.74 ± 40.02 (290)	74.48 ± 55.75 (349)	$F_{3,808}$ = 3.51 0.015	65.25 ± 39.26 (812)
Seasonal decline in clutch size	CS = 14.20–0.066 LD P = 0.007	CS = 10.58–0.046 LD P < 0.001	CS = 16.42–0.083 LD P < 0.001	CS = 11.37–0.046 LD P < 0.001		

Values are mean ± sd unless otherwise stated. Sample size n is given in parentheses. CS = clutch size; LD = laying date.

Table 2. Number of pairs laying in relation to laying date of Rollers in Extremadura.

Year	*1–10 May*	*11–20 May*	*21–30 May*	*31 May–9 June*	*10–19 June*	*20–29 June*
1988		1	8		1	5
1989	1	30	33	38	20	10
1990	9	87	122	65	10	3
1991	55	112	65	26	15	1
All years pooled	65	230	228	129	46	19
	(9.1%)	(32.1%)	(31.8%)	(17.9%)	(6.4%)	(2.6%)

the third (31.8%) ten days of May (Table 2).

There were significant differences between breeding seasons in the proportion of pairs that started laying in each ten-day period (Table 2; *G*-test: $G = 145.13$, $P < 0.01$, df = 10). The overall mean first-egg laying date was 24 May (Table 1).

Clutch size

The mean clutch size of the Roller in the studied population was 4.23 ± 1.21 ($n = 817$), and ranged from one to seven eggs. There were significant differences in clutch size between years (Table 1). The most common clutch sizes were four (28.5%) and five eggs (32.9%) (Table 3). We observed differences in the distribution of clutch sizes between years (Table 3; *G*-test: $G = 64.96$; $P < 0.01$; df = 12).

There were annual differences in the seasonal trends in clutch size (analysis of covariance: interaction year × laying date: $F_{3,702} = 7.50$, $P < 0.001$). However, a clear seasonal decline was registered in clutch size in all years (see Table 1). When laying date was controlled, annual differences in clutch size were significant too (analysis of covariance: $F_{3,705} = 3.57$, $P = 0.014$).

Reproductive rates

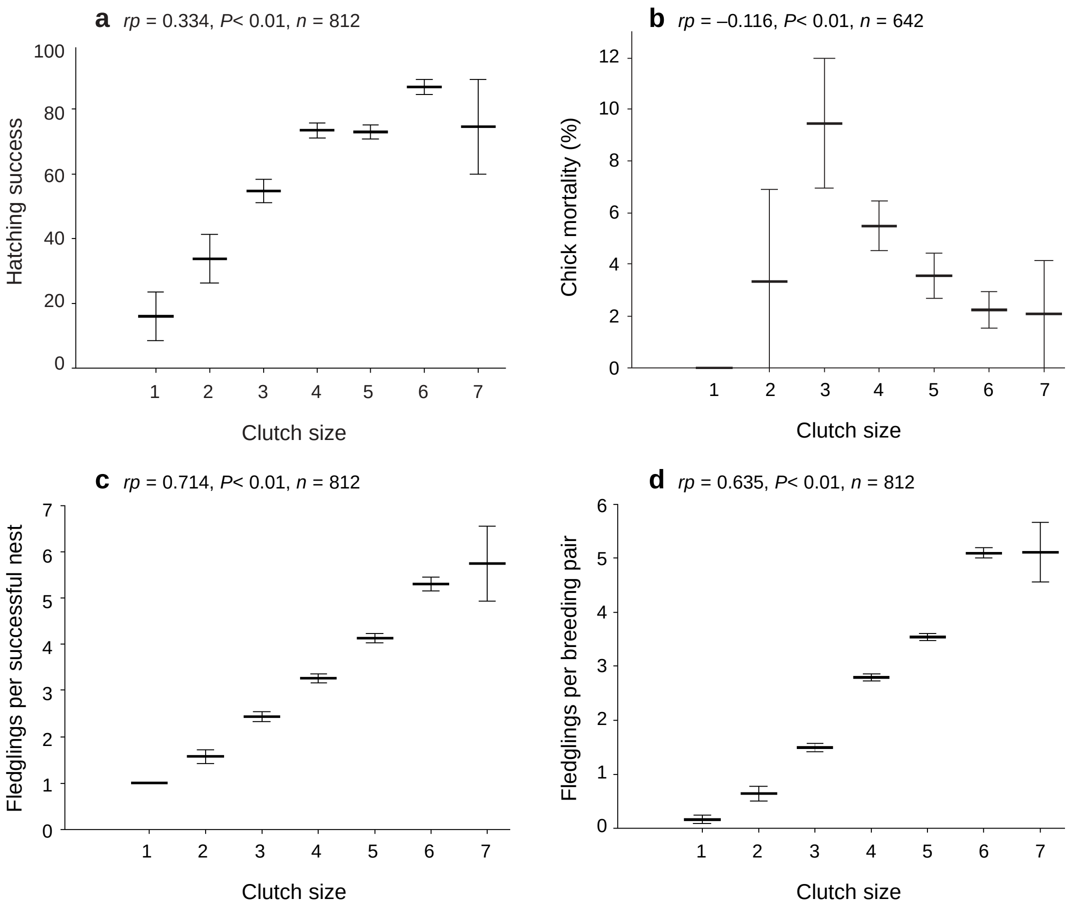
The hatching success ranged between 64% (1990) and 85% (1988), showing a significant yearly variation (Table 1). The number of fledglings per successful nest, the number of fledglings per pair that laid eggs, and the productivity all varied in relation to years (Table 1). However, mortality rate was very low in all four years, and showed no yearly variation (Table 1).

There were annual differences in seasonal trends in hatching success (analysis of covariance: interaction year × laying date: $F_{3,702} = 7.30$, $P < 0.001$), in the number of fledglings per pair that laid eggs (analysis of covariance: interaction year × laying date: $F_{3,702} = 5.35$, $P < 0.001$) and in productivity (analysis of covariance: interaction year × laying date: $F_{3,702} = 7.17$, $P < 0.001$). However, all of them decreased seasonally (Fig. 1). The number of fledglings per successful nest decreased seasonally ($b = -0.059$, $P < 0.001$; all data pooled); annual differences in the seasonal trends were not detected (analysis of covariance: interaction year × laying date: $F_{3,583} = 1.25$, $P = 0.287$). Chick mortality rate increased seasonally ($b = 0.171$, $P < 0.001$; all data pooled); again, no annual differences in the seasonal trends were detected (analysis of covariance: interaction year × laying date: $F_{3,587} = 1.09$, $P = 0.350$).

When laying date was controlled as a covariate of hatching success (analysis of covariance: $F_{3,705} = 8.99$, $P < 0.001$), fledglings per successful

Table 3. Number of pairs of Rollers laying in relation to clutch size in Extremadura.

Years	*1*	*2*	*3*	*4*	*5*	*6*	*7*
1988	1	6	5	10	4	3	
1989	12	5	37	62	28	5	
1990	6	10	54	70	106	33	7
1991	6	13	55	91	131	55	2
All years pooled	25	34	151	233	269	96	9
	(3.0%)	(4.2%)	(18.5%)	(28.5%)	(32.9%)	(11.7%)	(1.1%)



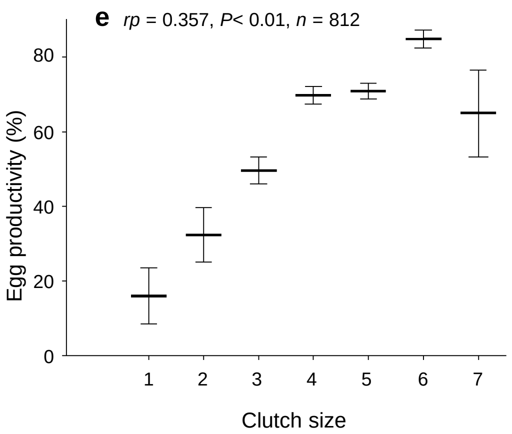


Figure 1. Relation between clutch size and reproductive performance in Rollers of Extremadura. (a) Hatching success; (b) chick mortality; (c) number of fledglings per successful nest; (d) number of fledglings per breeding pair; (e) egg productivity. Results of Pearson correlation (*rp*) between clutch size and reproductive variables considered in this study are given.

egg (analysis of covariance: $F_{3,705} = 5.79$, $P < 0.001$), productivity (analysis of covariance: $F_{3,705} = 8.05$, $P < 0.001$) and fledglings per successful nest (analysis of covariance: $F_{3,586} = 2.56$, $P < 0.054$) varied annually. However, chick mortality did not vary between years when laying date was controlled (analysis of covariance: $F_{3,590} = 0.067$, $P = 0.977$).

No effects of the interaction year × laying date × clutch size were detected on the reproductive performance of Roller in Extremadura (analysis of covariance: $P > 0.05$ in all cases). When laying date and year of study were controlled, all breeding parameters varied in relation to clutch size (Table 4, Fig. 1).

DISCUSSION

Table 4. Reproduction success of Roller in relation to clutch size (one to seven eggs).

	1	*2*	*3*	*4*	*5*	*6*	*7*	ANCOVA *P*
Hatching success	16.00 ± 37.41 (25)	33.82 ± 43.90 (34)	54.74 ± 45.10 (151)	73.49 ± 35.59 (233)	72.95 ± 34.62 (264)	86.80 ± 23.68 (96)	74.60 ± 34.83 (9)	$F_{4,1,804}$ = 23.1 <0.01
Chick mortality (%)	0.00 ± 0.00 (4)	3.33 ± 12.91 (15)	9.45 ± 24.63 (97)	5.49 ± 13.65 (197)	3.56 ± 13.21 (228)	2.24 ± 6.81 (92)	2.08 ± 5.89 (8)	$F_{4,1,633}$ = 2.6 0.018
Fledglings per successful nest	1.00 ± 0.00 (4)	1.57 ± 0.51 (14)	2.44 ± 0.74 (92)	3.27 ± 0.93 (199)	4.14 ± 1.00 (226)	5.31 ± 0.98 (92)	5.75 ± 1.58 (8)	$F_{4,1,627}$ = 103.8 <0.01
Fledglings per breeding pair	0.16 ± 0.37 (25)	0.64 ± 0.84 (34)	1.49 ± 1.33 (151)	2.79 ± 1.44 (233)	3.54 ± 1.72 (264)	5.09 ± 1.43 (96)	5.11 ± 2.42 (9)	$F_{4,1,804}$ = 93.0 <0.01
Egg productivity (%)	16.00 ± 37.42 (25)	32.35 ± 42.43 (34)	49.67 ± 44.37 (151)	69.85 ± 36.04 (233)	70.98 ± 34.56 (264)	84.90 ± 23.95 (96)	65.05 ± 39.31 (9)	$F_{4,1,804}$ = 23.7 < 0.01

Values are mean ± sd unless otherwise stated. Sample size *n* is given in parentheses.

Laying date

In the study area, the laying dates of Rollers are the earliest ever reported for this species.[2–12] Sosnowski & Chmielewski[12] place the majority of clutches in Poland between the first and second ten days of June, in contrast with the final two-thirds of May in Extremadura. Earlier reproduction in southern areas has been shown for other bird species, and has been interpreted as being due to the earlier onset of spring and production of food that occurs in those latitudes.[17–20] This fact has not been documented in Rollers,[2] largely because most studies have taken place in a narrow latitudinal range that has not included the southern extreme of the Roller distribution.

Although not conclusive, in Extremadura Roller breeding phenology appeared not to be influenced by weather conditions during the prebreeding period.[21] Similarly, in Poland[12] there was no relation between the start of reproduction in June and the mean temperature in May, but the species arrived earlier at breeding sites in those years with higher temperatures during this period. This argues against the hypothesis that variation in arrival dates at breeding sites is the cause of annual variations in the start of breeding.[22] Other ecological factors (e.g. food availability) may influence the physical condition of females during the prelaying period and so modify the start of reproduction.[23–26]

Clutch size

We found the largest clutches yet reported for the Roller,[11,12] although the mean clutch sizes in 1988 and 1989 (Table 3) were very similar to those obtained in Sweden (3.8 eggs)[11] and in Poland (3.59 eggs).[12] The most frequent clutch sizes were four or five eggs in Extremadura, but three or four eggs respectively in Sweden and Poland. This reverses the normal pattern of an increase in clutch size with latitude[27–31] and agrees with the Soler & Soler hypothesis[32] for hole-nesting birds with one brood. These authors propose that if egg size diminishes, large clutches can be advantageous in the south because egg size is under weaker selection pressure in the south.[33] However, although Roller egg dimensions in Extremadura are clearly smaller than in Sweden,[10] and the largest clutches in Extremadura are the most productive (this work), it would be necessary to study this at intermediate latitudes to confirm this hypothesis.

Reproductive rates

The reproductive success of Rollers in Extremadura during the four years of the study was higher than the 1.8 fledglings per nest recorded in Poland[12] and the 1.5 fledglings per nest in Germany,[34] although 3.2 fledglings per nest has been recorded in a good year in Germany.[34] These differences could have been caused by the status of the studied populations, because while Polish[12] and German[4,34] populations of Rollers are in decline, the studied population increased during the study period due to the provision of nestboxes.[10]

Seasonal decline in clutch size and reproductive rates

Roller clutch size seems to be constrained by laying date. Thus, if we ignore data from 1988 in which clutches were very late as a consequence of nestbox installation, we observe that clutch size was smaller in the year with the latest mean laying dates (1989).

Both clutch size and reproductive rates of Rollers showed a clear seasonal decline. The decrease in breeding success of Roller in Extremadura was caused by a reduction of clutch size and a reduction in the percentage of hatched eggs, as well as by a seasonal increase in chick mortality rate. It could be that the seasonal deterioration in food availability for the species was brought about by the intensive pesticide treatments that are used in the region during late May and June in order to control grasshoppers, which are the main prey of Roller chicks in the region.[35] Each bird would then lay as early as it could, resulting in laying dates being determined by individual quality, which would enable some birds to exploit the available food supply more rapidly than others.[25,26,36,37]

Reproductive success in relation to clutch size

The breeding success of Rollers in the study area varied in relation to clutch size. In general, the most successful clutches were those with six eggs because they had a low mortality rate (removing extreme one-egg and seven-egg clutches), and a higher hatching rate. Although clutches with four or five eggs, the most frequent size of clutch, had lower hatching rates than six-egg clutches, it was not possible to prove any limitation on the incubation capacity of females because we did not know the proportion of unhatched eggs that had been fertilized.[38]

It has been documented in other bird species that the most productive clutches are larger than the most frequent clutches[39–42] and this is common in hole-nesting birds in the south of their distribution area where clutch size is not constrained by egg dimensions.[32,33]

ACKNOWLEDGEMENTS

We are grateful to E. Costillo, C. Sendín, M. Flores and the Guard Service of Dirección General de Medio Ambiente de la Junta de Extremadura for their assistance with the fieldwork. A. Muñoz and C. Corbacho made several corrections on previous drafts. The final comments from K. Lessells, A. Gosler and an anonymous referee improved the text.

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(MS received 12 February 1998; revised MS accepted 6 August 1998)

