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Early Arrival is not Advantageous for Rufous Bush-Robins Parasitized by Common Cuckoos

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In migratory insectivorous birds, early arrival on the breeding grounds can enhance the reproductive success of males. For example, early arrival may lead to priority of access to territories (von Haartman 1968, Ketterson and Nolan 1976, Myers 1981), which, in turn, may facilitate acquistion of the best territories (Brooke 1979, Bensch and Hasselquist 1991, Lundberg and Alatalo 1992, Aebischer et al. 1996). Early arriving males also can experience advantages in obtaining mates (Alatalo et al. 1984, Arvidsson and Neergaard 1991, Møller 1994, Lozano et al. 1996) and in increasing the subsequent recruitment probability of their offspring into the breeding population (Møller 1994).

Early arrival also has some costs, such as experiencing harsh weather conditions at the beginning of the breeding season that result directly in mortality (Anderson 1965, Whitmore et al. 1977, Møller 1994). Males that arrive early in the breeding season often are in better physiological condition (e.g. Arvidsson and Neergaard 1991) or have higher phenotypic quality (Møller 1994) than those arriving later, which may allow high-quality males to overcome these costs more effectively than can lower-quality males. Thus, phenotype-dependent costs and benefits of early arrival may explain individual variation in arrival dates (Møller 1994).

The costs and benefits of early arrival have been studied in migratory insectivorous bird species free from brood parasitism. Another cost of early arrival could come from brood parasitism if early arriving males experience a higher probability of being parasitized than later males. The main purpose of this paper is to test two hypotheses in the Rufous Bush-Robin (*Cercotrichas galactotes*). The first (hereafter, "Hypothesis I") is that early arriving male Rufous Bush-Robins exhibit the general patterns established in other migratory insectivorous birds of: (1) a positive correlation between fitness-related phenotypic traits and arrival date on breeding grounds; and (2) a significant negative correlation between arrival date and reproductive success, when the effects of brood parasitism and nest predation are removed. The second hypothesis (hereafter, "Hypothesis II") is that early arriving males experience higher rates of nest predation and parasitism by the Common Cuckoo (*Cuculus canorus*) than do late-arriving males.

Study species.—The Rufous Bush-Robin is a small (ca. 23 g) passerine that generally is very scarce throughout its breeding range in Europe. It is locally common only in man-made habitats around the Guadalquivir Valley in southern Spain and is strictly a summer visitor to its breeding range around the Mediterranean Sea (Cramp 1988). It breeds in Mediterranean zones with temperature above 25°C, mainly in dry lowlands, and winters in the northern Afrotropics, reaching southern Iberia in late April or early May (Cramp 1988). Rufous Bush-Robins commonly produce two broods (López-Iborra 1983, López and Gil-Delgado 1988) before they return to their winter quarters in mid-September (Cramp 1988, Alvarez 1994a). This species is a common host of the Common Cuckoo in Spain (Congreve 1927, López and Gil-Delgado 1988, Alvarez 1994a).

Study area and methods.—The study was conducted in 1993 and 1994 in the wine-growing region of Los Palacios, southern Spain (37°9′N, 2°14′W; elevation 12 m), an area with small agricultural crops and fruit trees scattered among the vineyards. The region is characterized by high temperatures (above 40°C) during summer. Rufous Bush-Robins show a marked preference for nesting in the vineyards, although we have found nests in fruit trees, groups of prickly pear (*Opuntia* spp.), and directly on the ground (covered by the vineyard canopy).

Male Rufous Bush-Robins were captured in net traps shortly after their presumed arrival. The day that an individual was first observed was considered its arrival date. All males were marked with numbered aluminum bands (Spanish Institute for Nature Conservation) and color bands, which allowed individual recognition during the breeding season and in successive years. We measured the keel length of males with a dial caliper. We used this trait as a biometric indicator of individual quality because: (1) it probably is correlated with flying ability because the keel supports the pectoralis and supracoracoideus muscles, and the strut-like arrangement of the pectoral girdle (Gill 1990); and (2) it also can be correlated with individual quality (Bryant and Westerterp 1982). Chicks were banded with aluminum bands and one color band (different each year) at the age of

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nine days and weighed with a spring balance (± 0.5 g).

We visited the study area every day during male arrival and searched for singing males in all possible territories. Male Rufous Bush-Robins are easy to detect because they use conspicuous song perches and sing frequently upon arrival at the breeding grounds. By closely following the breeding activities of pairs and looking for nests in the vineyards (and other possible locations), we recorded all clutches of each pair. Nests were checked twice a week during incubation and every two days during the nestling period. Laying date was defined as the day when the first egg was laid, and clutch size was defined as the total number of eggs laid. Predation and parasitism rates were calculated as the percentage of nests depredated and parasitized, respectively.

We recorded the number of cuckoos seen while checking bush-robin nests. We used the number of cuckoos seen per week as an estimate of cuckoo abundance. This method resembled a line transect, which is known to yield a relative estimate of bird abundance (Järvinen and Väisänen 1975).

Statistical procedures.—Arrival date of four males was recorded in both years, but only a randomly chosen observation of every individual was included in the analyses in order to avoid pseudoreplication. For variables such as arrival date and laying date, day 1 was considered to be the day when the first male appeared in the breeding area each year. The other variables were corrected for year effects by subtracting from each value the mean value of the year and thereby obtaining residuals. Because we were unable to obtain estimates of all variables for all individuals, sample sizes differed among analyses.

We used logistic regression and the maximum-likelihood method (Cox 1970) to study the relationship between the probability of being parasitized (dependent variable) and arrival date (independent variable). We used nonparametric statistics such as Spearman correlation due to small sample sizes and an absence of normality for several variables (Siegel and Castellan 1988). We calculated statistical power for Spearman correlations performed with small sample sizes. Because significance criteria for sample sizes fewer than eight are not reported in Cohen (1988), we fitted the significance criteria based on samples sizes reported in Cohen (1988) to an exponential function ($r = 0.999$) for a significance level of 0.05. Next, we calculated the expected values of significance criteria for sample sizes of seven and six. All tests were two-tailed; means are reported ± SD.

Results.—The mean arrival date was 20.2 May ± 11.9 days ($n = 10$) in 1993 and 16.6 May ± 11.7 days ($n = 9$) in 1994 (first-arrival dates of 1 May 1993 and 24 April 1994). Arrivals were highly

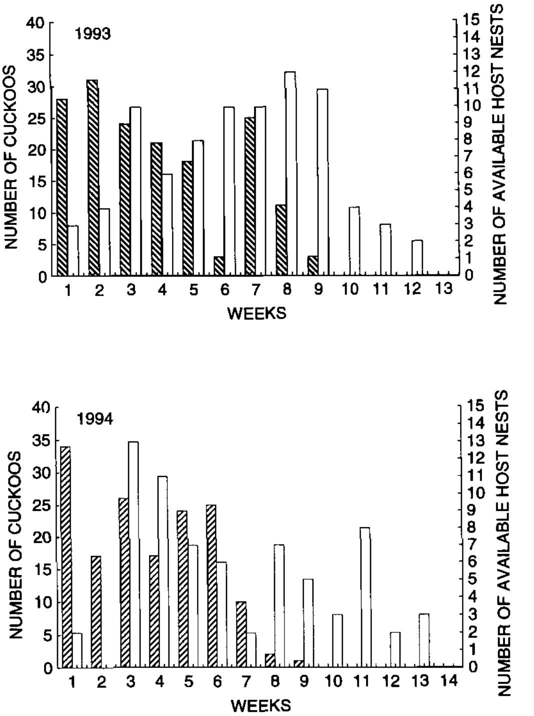

FIG. 1. Number of cuckoos seen per week (shaded columns) and number of available host nests per week (open columns) in the study area in 1993 and 1994. First week was 19 to 25 May in 1993 and 10 to 16 May in 1994, when the first available host nest was recorded. Available host nests were considered those in the laying stage.

asynchronous, spanning 40 days in 1993 (between 1 May and 10 June) and 37 days in 1994 (between 26 April and 2 June). Cuckoos were present in the study area at least two weeks earlier than Rufous Bush-Robins in both years, and they remained during the first nine weeks of the hosts' breeding period (Fig. 1). Cuckoos left the host breeding area in early to mid-July. The last cuckoo was seen on 14 July in 1993 and 6 July in 1994.

In order to avoid the effects of confounding factors such as nest predation and brood parasitism, we considered only the first clutch of every bush-robin pair. Females mated with early arriving males laid earlier than females paired with later-arriving ones (Table 1). Excluding the first clutches that suffered parasitism or predation, the first clutch was larger for early arriving males (Table 1). Moreover, male arrival date was negatively correlated with the number of young fledged from the first clutch and with mean body mass of the nestlings (Table 1). Although sample sizes were small, all Spearman correlation coefficients exceeded the significance criteria for these sample sizes. Thus, if the effects of parasitism and predation are removed,

TABLE 1. Spearman rank correlations (r_s) for laying date, clutch size, number of fledged young, and mass of young versus male arrival date. Significant criteria of statistical power for correlation coefficients at $P = 0.05$ also are reported (r_c).

Variable	Male arrival date			
	r_s	n	P	r_c
Laying date	0.84	15	0.001	0.514
Clutch size	−0.78	7	0.04	0.731
No. of fledged young	−0.76	7	0.05	0.731
Body mass of young	−0.93	6	0.008	0.770

males arriving early had higher breeding success than those arriving late, in accordance with the second part of Hypothesis I.

Arrival date was not significantly correlated with male keel length ($r_s = -0.03$, $n = 17$, $P = 0.91$), which is inconsistent with the first part of Hypothesis I. However, keel length was positively related to breeding success measured as the total number of young fledged during the breeding season ($r_s = 0.51$, $n = 17$, $P = 0.04$).

Cuckoos were present in the area during the first nine weeks of host breeding in both years. The breeding season of the host began on 19 May 1993 and 10 May 1994. Dividing the host breeding season into two parts (i.e. cuckoos present vs. absent), the proportion of nests depredated was significantly higher in 1993 when cuckoos were present (64%, 29 of 45) than when they were absent (28%, 6 of 21; Fisher exact test, $P = 0.009$) and nearly significantly higher in 1994 when cuckoos were present (41%, 13 of 32) than when they were absent (19%, 7 of 36; Fisher exact test, $P = 0.067$). The rate of nest predation was higher among early arriving males ($r_s = -0.49$, $n = 19$, $P = 0.03$; Fig. 2). Therefore, fledging date of the first successful brood was not significantly correlated with male arrival date ($r_s = -0.04$, $n = 15$, $P = 0.9$).

Although we did not find a significant negative correlation between parasitism rate and male arrival date ($r_s = -0.07$, $n = 19$, $P = 0.8$), first clutches of early arriving males were parasitized more than those of late-arriving males (maximum likelihood $\chi^2 = 8.77$, df = 1, $P = 0.003$). Thus, like nest predation, parasitism reduced the number of fledglings produced by early arriving males relative to late-arriving ones.

Considering all clutches, and including parasitized and depredated nests, females laid earlier (Table 1) and laid more eggs ($r_s = -0.51$, $n = 18$, $P = 0.03$; Fig. 3A) when paired with an early arriving male. However, females paired with early arriving males produced fewer successful broods ($r_s = 0.46$, $n = 18$, $P = 0.05$; Fig. 3B). Moreover, male arrival date was not correlated with the total number of fledglings produced ($r_s = 0.17$, $n = 19$, $P = 0.48$; Fig. 3C) or with

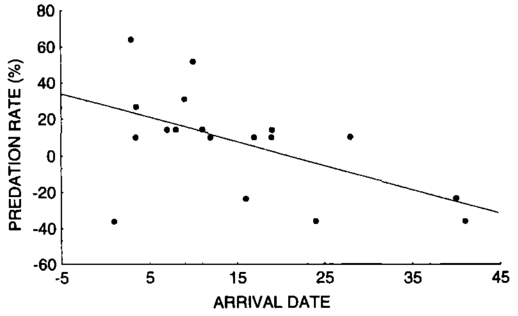

FIG. 2. Relationship between male arrival date (independent variable) and percentage of nest predation (regression equation: $x = 27.35 - 1.32\ y$). Fledging and arrival dates are days since 1 May 1993 and 24 April 1994.

fledgling mass ($r_s = -0.4$, $n = 17$, $P = 0.1$; Fig. 3D). Therefore, in accordance with Hypothesis II, early arriving males were more affected by cuckoos through nest parasitism and predation and were not more successful than later-arriving males.

Discussion.—Male Rufous Bush-Robins that arrived in the breeding area early had higher breeding success if their nests were not parasitized or depredated because their females reproduced earlier in the breeding season, laid larger first clutches, and produced more fledglings than females paired with later-arriving males (Table 1). Furthermore, early arriving males produced heavier young than late-arriving ones (Table 1), which would improve the probability of recruitment into the breeding population (Magrath 1991). Thus, when the effects of brood parasitism and predation are excluded, early arrival conveys a reproductive advantage to male Rufous Bush-Robins.

Common Cuckoos left our study area when host nests were still available (Fig. 1), as also reported for cuckoos parasitizing Eurasian Reed-Warblers (*Acrocephalus scirpaceus*; Wyllie 1981). Cuckoos were considered to be the main nest predators of bush-robins because: (1) predation rates were higher when cuckoos were present than when they were absent; (2) other nest predators in our study area, namely ocellated lizards (*Lacerta lepida*) and snakes, should maintain constant predation rates (because their metabolic rates remain nearly constant and they do not provide parental care to their offspring); and (3) Common Cuckoos are the main predators of unparasitized host nests of several other host species (Wyllie 1981, Bibby and Thomas 1985, Davies and Brooke 1988) and in one other study of Rufous Bush-Robins (Alvarez 1994b).

Early arriving males were affected at a higher rate by cuckoos because these males suffered higher rates of nest predation and had a higher probability of being parasitized than late-arriving

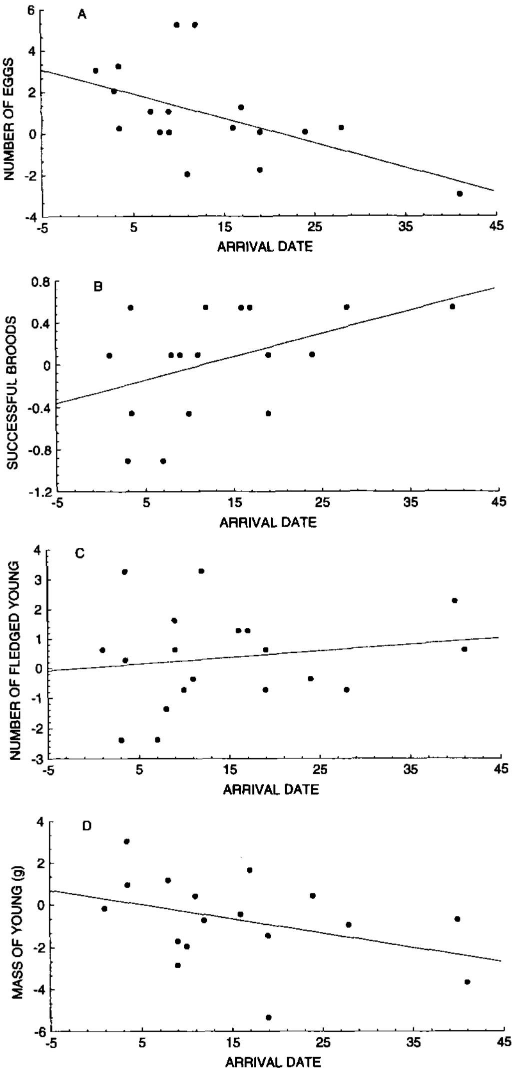

FIG. 3. Relationship between male arrival date (independent variable) and (A) total number of eggs in the season (regression equation: $x = 2.48 - 0.12\ y$); (B) number of successful broods ($x = -0.25 + 0.02\ y$); (C) total number of fledglings in the season ($x = 0.02 + 0.02\ y$); and (D) mean body mass of young ($x = 0.34 - 0.07\ y$). Arrival dates are days since 1 May 1993 and 24 April 1994.

males (Fig. 2). Thus, when nest predation and parasitism were included, early arriving males did not obtain higher reproductive success (measured as the total number of fledglings produced in the breeding season) than late-arriving males (Fig. 3C). Furthermore, young of early arriving males were not heavier than those of late-arriving ones (Fig. 3D). Therefore, cuckoo parasitism and nest predation decrease the reproductive success of early arriving males and counteract what otherwise would be an advantage of early arrival.

Cuckoos reduce the possibility of early arriving males producing more fledglings from first clutches than from later ones. Although females mated with early arriving males laid earlier than females mated with later males, fledging dates of young from early arriving and late-arriving males were not significantly different. Therefore, early arrival did not convey an advantage to males, even though the number of young from first broods tends to be higher than from late broods among birds in general (Martin 1987). Moreover, compared with parents that raise only their own chicks, parents parasitized by cuckoos raise fewer young per season because they have a longer nesting period and therefore a longer time between first and second clutches.

Several studies have reported that nest predation decreases as the breeding season progresses (e.g. Nice 1957, Thompson and Nolan 1973, Byrkjedal 1980), although this is not always the case (see Lack 1954, Bibby 1978). To our knowledge, however, no study has suggested that parasitism and predation can be influenced by male arrival dates. In Rufous Bush-Robins, the risk of nest parasitism and predation appear to increase with the early arrival of males.

We suggest that prior to parasitism by cuckoos, arrival dates of male Rufous Bush-Robins were correlated with phenotypic quality, as recorded for other migratory bird species (e.g. Arvidsson and Neergaard 1991, Møller 1994). Parasitism and predation by Common Cuckoos counteracted the selective pressures that favored early arrival in bush-robins. This would explain the current lack of a relationship between male arrival date and phenotypic quality or condition.

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