

Double-nesting behaviour and sexual differences in breeding success in wild Red-legged Partridges *Alectoris rufa*

FABIÁN CASAS,^{1*} FRANCOIS MOUGEOT^{1,2} & JAVIER VIÑUELA¹

¹*Instituto de Investigación en Recursos Cinegéticos, IREC (CSIC, UCLM, JCCM) Ronda de Toledo s/n., 13071, Ciudad Real, Spain*

²*Estación Experimental de Zonas Áridas (EEZA, CSIC), General Segura 1, 04001 Almería, Spain*

Double-nesting behaviour, a rare breeding system in which females lay in two nests, one incubated by herself and the other one by her mate, could be considered an intermediate stage in the evolutionary trend from biparental to uniparental care of single clutches. We examined the occurrence and success of double-nesting behaviour in Red-legged Partridges *Alectoris rufa* in Central Spain. Clutch size and hatching success were recorded, as well as the variation in these between years and between incubating sexes. Participation in incubation was higher for females (94.76%) than males (41.0%), and the proportion of incubating males varied markedly between years, with no incubating males in one dry year and approximately 50% of males incubating in other years. There was significant variation among years and between sexes in laying date, clutch size and hatching success. Clutch size decreased with later laying date in males and females. The probability of clutch loss to predation differed between sexes, being much higher for nests incubated by females. Our results suggest that both rainfall and predation influence the occurrence and success of double-nesting.

Keywords: breeding system, clutch size, gamebird, hunting management models, incubation, nesting success, parental care, predation, Spain.

The evolution and regulation of offspring number, parental care and breeding systems is important in behavioural ecology (Skutch 1982, Winkler & Walters 1983, Martin 1987, Clutton-Brock 1991, Ligon 1999). In most endotherms with internal fertilization, females invest more than males in rearing offspring, often without any help from mates (Clutton-Brock 1991). Birds are an exception because approximately 80% of species provide biparental care to offspring, although females usually invest more than males (Lack 1968, Cockburn 2006). An intriguing exception to the general rule of higher female investment is found in a small group of bird species (*c.* 1% of all species, mainly precocial species within the Ratites and Charadriiformes) in which males are the main providers of parental investment, taking charge of incubation and post-hatching chick care (Lack 1968,

Cockburn 2006). The evolutionary origin or functional basis of this unusual reversal in sexual roles has remained a puzzling question in evolutionary biology for decades (Lack 1968, Clutton-Brock 1991, Ligon 1999, Owens 2002, Cockburn 2006). Another small group of bird species exhibits double-nesting behaviour: two clutches are laid simultaneously and both male and female incubate and take care of chicks simultaneously or sequentially in the same breeding season (cases within Charadriiformes and Galliformes; Hildén 1975, Green 1984). This system may be an intermediate stage in the evolutionary trend from biparental to uniparental care (or *vice versa*, depending on the ancestral state), the most common evolutionary transition detected by phylogenetic analyses (Owens 2002, Reynolds *et al.* 2002, Cockburn 2006).

Contrary to Lack's (1947) predictions, birds can rear more young than the number of eggs they lay (Monaghan & Nager 1997), but a trade-off may exist between parental investment in reproduction

*Corresponding author.
Email: Fabian.Casas@uclm.es

and self-maintenance (Clutton-Brock 1991). Clutch size variation in northern temperate climates has long been attributed to food limitation rather than to nest predation (Roff 1992), although predation may explain clutch size variation within latitudes (Martin & Clobert 1996). Precocial birds have relatively minor reproductive costs as compared with altricial species, due to early feeding autonomy of chicks. Galliformes in general are able to lay a large number of eggs within a breeding season (Lack 1968), and it has been questioned why no more species exhibit double clutch behaviour (Green 1984). A basic functional link between double-nesting behaviour and clutch size is hatching success, as a main trait determining fitness and thus viability of double clutching behaviour or male uniparental care systems (Fernández & Reboresda 2007).

The Red-legged Partridge *Alectoris rufa* is a gamebird with high productivity, exhibiting a peculiar breeding system of double-nesting behaviour (Cramp & Simmons 1980, Green 1984). Male incubation behaviour varies among species of the genus *Alectoris*, but appears common only in the Red-legged Partridge (Cramp & Simmons 1980, Green 1984, Vavalekas *et al.* 1993). Females lay eggs in two different nests, and when both clutches are laid, females usually start incubation of the second clutch while males incubate the first one (Green 1984). This breeding system may be shaped by a complex set of trade-offs in male and female behaviour, such as pairing status, mate quality, body condition, laying date, population density and sex ratio (Green 1984, Clutton-Brock 1991, Blomqvist *et al.* 2001, Owens 2002, Cockburn 2006).

Because incubation may commonly involve a period of time and energy limitation in birds (Deeming 2002), and a period of high predation risk for adults (Potts 1980), paternal investment in incubation could affect future survival. Accordingly, it has been shown that the costs of breeding for incubating males in precocial species can be high (Holt *et al.* 2002, Fernández & Reboresda 2003). Ultimately, however, the opportunity for male incubation of a second clutch depends upon the physiological ability of females to lay two clutches. Laying eggs in two different nests is thus the female decision at the root of the double-nesting strategy. Females take the risk of losing their investment when leaving a clutch under the care of their mates (Owens 2002) and the probability of nest abandonment by males is considered a key trait in explaining variation in breeding

systems of birds (Owens & Bennett 1997, Varela *et al.* 1997, Owens 2002). In Red-legged Partridges, such nest abandonment may be relatively common (Green 1984, Rueda *et al.* 1993).

We studied the breeding ecology of Red-legged Partridges in Central Spain, with particular reference to differences between sexes in clutch size and hatching or nesting success. This is the first longitudinal study with contrasting environmental conditions to examine the factors affecting the occurrence and success of male incubation behaviour. The most important previous research was conducted on an introduced population in a sub-optimal area (Green 1984). We studied wild Partridges in the core area of their natural range and in their optimal habitat, the agrarian pseudosteppes of Iberia, where densities are highest (Blanco-Aguir *et al.* 2003, Vargas *et al.* 2006). We examined the factors affecting the occurrence of double clutching and the differences between sexes and years in clutch size and hatching success, in order to evaluate the advantages derived for each sex from incubating a clutch and assuming the parental duties.

METHODS

Study area

The study area covered 125 km² and was located in Campo de Calatrava (Central Spain, 38°50'N, 4°33'W, 610 m asl). This comprises undulating farmland dominated by a mosaic of crops, mainly cereals (particularly barley) interspersed with olive groves, vineyards, and a few patches of dry annual legume crops (mainly Vetch *Vicia sativa*) and Sugar Beet *Beta rubra*. Natural vegetation is very scarce, and includes small areas of short scrubland and pastureland limited mainly to the rocky tops of hills. Other crops, ploughed or abandoned farmland, and buildings (mainly country houses) cover < 10% of the area. The study area included four game estates, characterized by three different hunting management policies (hereafter sites; see Casas 2008 for more information).

Capture, radiotracking and nest monitoring

We conducted fieldwork from February to June in 2003–2005 and in 2007. Over the 4 years, we caught 159 adult Partridges in February–March (39 in 2003, 44 in 2004, 32 in 2005 and 44 in 2007)

and studied different individuals in different years. In 2003–2005, we used cage traps with live adult Partridges as a decoy. Traps were baited with wheat. In 2007, birds were caught at night, by spotlight and a hand-held net, and by locating roosting birds with a powerful head-torch or using an infra-red camera (Panatec; Madrid, Spain).

All birds were sexed from plumage, biometry and ornaments (Sáenz de Buruaga *et al.* 2001). We took a blood sample from the brachial vein (0.5–1 mL) to confirm the sex of birds using genetic analyses of blood samples (J. T. García & M. Calero unpubl. data). Each individual was fitted with a necklace radio-transmitter with a mortality sensor (10 g; Biotrack, Wareham, Dorset, UK) and released at the capture site. Most nests (98.6%) were found once incubation had begun. The first time nests were located, we recorded their exact position by GPS, date, type of habitat and clutch size. Nest fate was monitored by locating tagged birds every 1–5 days. Replacement clutches ($n = 5$) were excluded from analyses.

Determination of overall clutch size of female Red-legged Partridges is a difficult task due to double-nesting behaviour (Green 1981, 1984). The only way to determine the total number of eggs laid by a female is to monitor both members of the pair simultaneously. From 2003 to 2005, the capture method (cage traps) had a low success rate in catching both members of breeding pairs (16 pairs from 115 individuals caught). In 2007, the level of pair capture improved (16 pairs from 44 individuals caught). We checked pair breeding status by radiotracking and observations of tagged birds in social pairs. Because of mate changes between capture and incubation ($n = 4$), cases of predation ($n = 14$) or transmitter failures ($n = 2$), only 12 tagged pairs could be followed throughout the breeding season. Moreover, intraspecific nest parasitism or polygamy is relatively common in this species (Casas *et al.* 2006a, 2006b). For all these reasons, we only considered the clutch size of each individual nest, but acknowledge that this does not accurately reflect the real laying effort of each female. However, given that our main objective was to study inter-annual variation in clutch size, and that energy requirements during incubation increase with increasing clutch size (Ward 1996, Williams 1996), this should still be a reasonable estimate of incubation and parental effort.

The onset of incubation (± 2 days) was estimated for each nest. This was done using one of

three methods for an individual nest. First, daily radiotracking allowed us to determine the exact day when incubation began (in 2003–2005, and most nests in 2007). Secondly, we estimated the day incubation started based on egg density (some nests in 2007). Egg density was calculated as the egg weight divided by egg volume. Egg volume was calculated from egg measurements (volume = egg width² \times π \times egg length \times 0.000164). We established the daily egg density loss of incubated eggs, and estimated how many days eggs had been incubated, given their measured density during the nest visit, using the following formula: number of days incubated (± 2 days) = (egg density \times -139.5) + 145.9 (F. Mougeot & F. Casas unpubl. data). Thirdly, at nests where exact hatching date was known either because nests were visited during hatching or because the day the radiotagged bird left the nest with recently hatched chicks was known, we back-dated the onset of incubation assuming that incubation lasts 24 days and that it starts after laying of the last egg (Del Hoyo *et al.* 1994, Cabezas-Díaz & Virgos 2007).

Females lay eggs every 2 days on average (Cabezas-Díaz & Virgos 2007), so we estimated laying dates as the day incubation started, minus the final clutch size multiplied by 2 days. Laying dates were indexed relative to the 1st of March (day 1) for all years.

We determined hatching success (proportion of eggs hatched) by visiting nests soon after hatching was detected (1–2 days). Because we were interested in the natural variation in nesting success, we excluded from our analyses clutch losses due to agricultural practices ($n = 13$) or poaching ($n = 3$).

Statistical analysis

We used STATISTICA 6.0 (proportion of females and males incubating; StatSoft, Tulsa, OK, USA) and SAS 8.01 (all other analyses; SAS 2001). We considered nest incubation rate as the percentage of radiotagged individuals of each sex that began to incubate a nest, independently of final nest fate. Individuals that died before incubation ($n = 22$ females, $n = 18$ males) were excluded from these analyses. We tested for differences between sexes in nest incubation rate (0 = no incubation; 1 = incubation) using generalized linear models (GLM) with a binomial error distribution and logit link function. Initial models included sex, year, site and their interactions as explanatory variables. Laying

date and clutch size were fitted using a normal error distribution and an identity link function. We used all nests ($n = 65$) for which we knew final clutch size (excluding cases in which the clutch was lost during laying, $n = 1$; or in which the final clutch size was not recorded, $n = 4$). Initial models included laying date, site, sex, year and their two-way interactions as explanatory variables. After backward model selection (Crawley 1993) to remove effects not significant at $P = 0.05$, we used a Tukey *post-hoc* test to determine significant differences among sites or years. We analysed variation in the probability of a clutch being lost to predation of the incubating birds using GLMs with a binomial error distribution and a logit link function. Initial models included site, sex, year and their two-way interactions as explanatory variables. Variation in hatching success considering only successful nests ($n = 34$) was analysed using GLM, and excluded eggs losses due to partial (< 20% of eggs) predation of clutches. The dependent variable (number of young hatched) was fitted to models using a Poisson error distribution and log link function, with the log of clutch size included as an offset in the model. Explanatory variables included laying date, sex, year and their two-way interactions. Given that management differences between sites could influence predation pressure and breeding parameters, we include 'site' as a fixed effect in our models, to test for possible 'site' differences. All data are expressed as means \pm sd.

RESULTS

Proportion of females and males incubating

We found 47 nests incubated by females and 23 incubated by males. The probability of incubation differed significantly between sexes ($\chi^2 = 28.7$, $df = 1$, $P < 0.001$). Of radiotagged females, 94.7% ($n = 50$) incubated, compared with 41.0% of radiotagged males ($n = 49$). The proportion of females incubating did not differ significantly

Figure 1. Inter-annual variations in: (a) proportion (%) of birds incubating, (b) mean \pm se laying date (1 = 1st of March), (c) mean \pm se clutch size (number of eggs) and (d) mean \pm se hatching success (proportion of eggs hatched, excluding clutch losses due to predation) according to the sex of the incubating bird. Sample size above bars refers to the number of radiotagged males and females alive during breeding seasons (in a) or the number of clutches (in b–d).

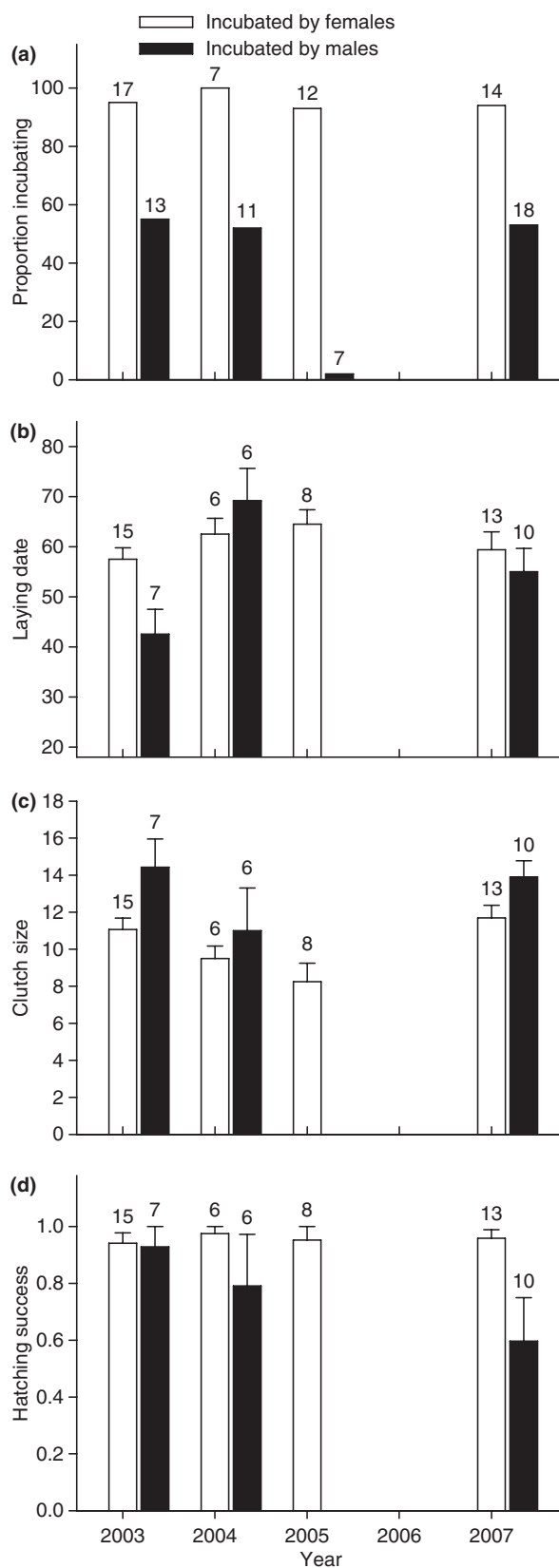


Table 1. Nesting parameters of males and females (year, nest separation distance, clutch size and incubation start date; 1 = 1st April) of complete radiotagged pairs of Red-legged Partridges with two nests simultaneously active.

Pair	Year	Nest separation (m)	Clutch size		Incubation start date	
			Male	Female	Male	Female
1	2004	76	12	10	53	43
2	2007	381	14	11	43	37
3	2007	314	17	12	47	41
4	2007	96	16	14	61	40

between years ($\chi^2 = 1.07$, $df = 3$, $P = 0.78$; Fig. 1a) or sites ($\chi^2 = 1.01$, $df = 2$, $P = 0.6$). In contrast, the proportion of males that incubated varied markedly between years ($\chi^2 = 10.46$, $df = 3$, $P = 0.005$; Fig. 1a), but not between sites ($\chi^2 = 2.78$, $df = 2$, $P = 0.24$). This effect was mainly due to the influence of data from 2005, when no males incubated at all, while the proportion of males incubating in the other three years was similar (Fig. 1a). Double-nesting behaviour was recorded for only four tagged pairs (Table 1), and thus 33% of tagged pairs monitored until late breeding season incubated two nests (double-nesting behaviour). Only females incubated in the remaining 67% of tagged pairs.

Laying date variation

Laying date did not vary significantly between sites ($F_{2,59} = 1.88$, $P = 0.161$), but did vary between years ($F_{3,59} = 5.14$, $P = 0.003$) and according to the sex of the incubating bird, depending on year (sex: $F_{1,59} = 1.60$, $P = 0.211$; sex \times year interaction: $F_{2,59} = 3.16$, $P = 0.049$). Laying occurred earlier in 2003 than in other years (Fig. 1b). Clutches incubated by males were laid earlier than those incubated by females in this year of early laying, but later in 2004, the year when laying was delayed (Fig. 1b). In the four tagged pairs (Table 1), Red-legged Partridge males normally started incubation later than females, but unfortunately no data were available for any tagged pair in 2003, when females began incubation later than males.

Clutch size variation

Clutch sizes did not differ between sites ($F_{2,59} = 0.40$, $P = 0.669$), but varied among years

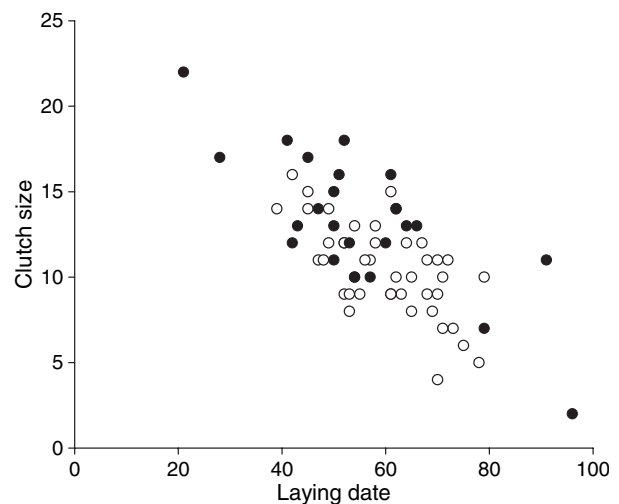


Figure 2. Relationship between laying date and clutch size [white dots (○), nests incubated by females; black dots (●), nests incubated by males].

($F_{3,59} = 4.99$, $P = 0.004$) and between incubating sexes ($F_{1,59} = 8.70$, $P = 0.005$). Average clutch sizes were largest in 2003 and 2007, and smallest in 2005 (Fig. 1c). Clutches incubated by males were larger than those incubated by females (12.7 ± 0.69 and 10.1 ± 0.47 , respectively; all years combined). Between-sex differences in clutch size were significant in 2003 ($F_{1,21} = 6.14$, $P = 0.022$), marginally significant in 2007 ($F_{1,21} = 4.08$, $P = 0.056$), but not significant in 2004 ($F_{1,10} = 0.39$, $P = 0.547$; Fig. 1c). Clutch size also decreased with advancing laying date, similarly for both sexes (model controlling for year and sex; laying date: $F_{1,59} = 54.29$, $P < 0.001$; sex \times laying date interaction: $F_{1,59} = 0.49$, $P = 0.485$; Fig. 2).

Variation in hatching success

Clutch losses due to predation

The probability of a clutch being lost to predators did not differ between sites ($\chi^2 = 0.78$, $df = 2$, $P = 0.676$) or years ($\chi^2 = 3.26$, $df = 3$, $P = 0.353$), but did differ between sexes ($\chi^2 = 7.99$, $df = 1$, $P = 0.005$). Total losses due to predation occurred in 40.0% of nests incubated by females ($n = 30$), but in only 5.6% of nests incubated by males ($n = 18$).

Unhatched eggs

We further analysed variation in hatching success using clutches that reached the hatching stage (i.e. excluding total losses). Hatching success did not

vary between sites ($\chi^2 = 2.28$, $df = 2$, $P = 0.320$), but did vary between years ($\chi^2 = 9.24$, $df = 3$, $P = 0.026$) and according to incubating sex ($\chi^2 = 3.26$, $df = 1$, $P = 0.045$), the interaction year \times sex being not significant ($\chi^2 = 1.32$, $df = 2$, $P = 0.516$). Hatching success was lowest in 2007 and was lower for nests incubated by males (Fig. 1d).

For nests incubated by females, hatching success did not differ significantly between years ($\chi^2 = 0.48$, $df = 3$, $P = 0.923$; Fig. 1d), and did not vary with laying date (lay date: $\chi^2 = 0.00$, $df = 1$, $P = 0.957$; lay date \times year interaction: $\chi^2 = 2.23$, $df = 3$, $P = 0.526$; Fig. 3) or clutch size ($\chi^2 = 0.10$, $df = 1$, $P = 0.757$). In contrast, for nests incubated by males, hatching success differed between years ($\chi^2 = 21.48$, $df = 2$, $P = 0.001$; Fig. 1d) and decreased with increasing laying date ($\chi^2 = 26.58$, $df = 1$, $P < 0.001$; Fig. 3) and with clutch size ($\chi^2 = 9.73$, $df = 1$, $P = 0.002$), the interaction year \times laying date being not significant ($\chi^2 = 3.05$, $df = 2$, $P = 0.217$). Clutches that were larger, laid later and incubated by males had a lower hatching success (Fig. 3).

DISCUSSION

Male incubation rate was estimated with regard to the total number of males that were radiotagged, instead of using the number of nests located (see Green 1984). Our data are therefore the first to document the proportion of males that take care

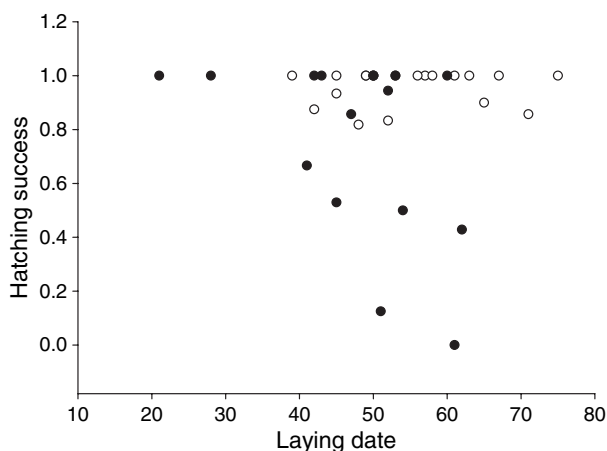


Figure 3. Relationship between hatching success (proportion of eggs hatched, excluding clutch losses due to predation) and laying date according to the sex of the incubating bird [white dots (○), females; black dots (●), males].

of a clutch in a natural Red-legged Partridge population in the species' natural range. We found that almost all females surviving until late breeding season incubated a clutch independently of yearly conditions. In contrast, the proportion of males incubating was highly variable among years, from none in one of the years to approximately 50% in the other three study years. We followed 12 pairs with both members tagged throughout breeding, and in four of these both males and females incubated (33%, Table 1). Given that almost all (95%) females and 41% of males incubated a clutch, our data suggest that double-nesting behaviour occurs frequently. Furthermore, nests incubated by males had larger clutches and lower losses due to predation than those incubated by females, a result that stresses the likely importance of the male contribution to Partridge reproduction in natural populations.

There was a marked year-to-year variation in the laying dates of nests incubated by males or females. In the 2 years with apparently the best breeding conditions (2003 and 2007), laying dates of nests incubated by males were earlier than or similar to those of females. In contrast, clutches incubated by males were laid later than those incubated by females in 2004, a year with a drier spring (Appendix 1), in which Partridges laid relatively smaller clutches later in the season. Thus, under good breeding conditions (higher spring rainfall and milder temperature, see Appendix 1), females laid more eggs and did so earlier, with males taking charge of the first clutch, while under less favourable conditions females started incubation of the first clutch.

Predation has been considered a major force driving double-nesting behaviour in Partridges (Green 1984). No males were found incubating clutches in 2005, a year of marked drought in our study area (Appendix 1), in which vegetation growth, including cereals, was poor. Vegetation cover is a key factor for nesting success in this species (Ricci 1985, Rands 1987, Ricci *et al.* 1990), so weather could affect nest predation probability through differential vegetation growth (Díaz & Carrascal 2006, Pescador & Peris 2007). Partridges may therefore adjust their nesting behaviour to perceived nest predation risk. There was no significant variation among years in clutch losses due to predation, but predation rate was overall lower for nests incubated by males. Moreover, the higher predation rate observed for nests incubated by females was not related to different habitat selection or

differences in predator density (Casas 2008). However, it is possible that females are less able to avoid predators (because of their greater reproductive effort), or that their behaviour during laying (laying in two nests requires females to visit nests more often than males) makes them more conspicuous.

An alternative explanation for the observed inter-annual differences in the occurrence of double-nesting behaviour could be that females can lay more eggs in wet-spring years, and that a better breeding strategy is to split these into two clutches, to increase the probability that at least one of these will not be predated, or to maximize the number of eggs laid and the pair's reproductive output. The Mediterranean climate is characterized by a high inter-annual variability of temperature, rainfall regimes, environmental productivity and food supply (Peinado & Rivas-Martínez 1987, Lucio 1990, Blondel & Aronson 1999). Previous studies showed a strong influence of climatic conditions on Red-legged Partridge productivity, with a wetter spring being associated with larger clutch sizes (Rueda *et al.* 1993) and greater chick survival rates (Lucio 1990). We found large differences in clutch size among years, with smallest clutch sizes and no double-nesting in 2005, a year with marked drought in late winter and spring (Appendix 1). Thus, in years with more rainfall in spring the greater occurrence of double-nesting could be primarily explained by a greater laying capacity of females.

Clutches incubated by males were larger than those incubated by females, and this was consistent across years. The simplest explanation for differences in clutch sizes incubated by males and females might be that the larger body size of males allows them to cover a greater number of eggs. However, this rarely seems to be a factor limiting clutch size in birds, particularly in Galliformes (Lack 1947, Skutch 1982), and such sex-related differences in clutch size were not found in another study (Green 1984). Another explanation could be that several females lay eggs on the same nest, a behaviour relatively common in Galliformes (Filchagov 1996, Storch & Segelbacher 2005), including the Red-legged Partridge (Casas *et al.* 2006b). Clutches incubated by males could be larger if they are more susceptible to egg dumping by females (Casas *et al.* 2006a). On the other hand, differences in laying onset between male and female nests could arise from differences in nutrient reserves that females allocate to egg

production between early and late season, a general rule in birds (Martin 1987), including precocial species (Winkler & Walters 1983). Also, it is possible that females lay a higher number of eggs in nests incubated by males because these nests have a lower likelihood of predation, a strategy that could increase pair fitness (see above).

Clutches incubated by male Partridges had poorer hatching success (partial losses). Green (1984) found a similar pattern in what he defined as 'delayed' and 'undelayed' nests (mostly male- and female-incubated nests, respectively). Hatching success in nests of females can be considered within the natural values for birds, at about 90% (Koenig 1982). However, hatching failure in nests incubated by males was abnormally high, particularly late in the season (20–90% of eggs unhatched). Lower hatching success in male-incubated nests may be explained by incubation capacity (Fernández & Reboreda 2007). Dumped eggs appear more frequently in nests cared for by males (Casas *et al.* 2006a), and these eggs could have lower hatchability, particularly if their development is not well synchronized with those of the host clutch. Finally, lower hatching success of nests incubated by males could be a consequence of the longer period that eggs remain un-incubated in the nests. This would be consistent with the negative relationship between clutch size and hatching success found, given that larger clutches imply longer periods of exposure until clutch completion (males do not start incubating until females finish their second clutch; Green 1984; Table 1). Late in the season, temperatures are higher and humidity lower, thus increasing the probability of hatching failure as the breeding season advances. This would suppose an additional constraint on the female's decision to leave a clutch under the care of her mate, which would be particularly stringent in years with delayed laying; if laying starts late, a good deal of the investment devoted to eggs cared for by males could be lost.

Phylogenetic analyses (Owens 2002) and experimental work (Kentish Plover *Charadrius alexandrinus*; Székely *et al.* 1999) suggest that population density and associated re-mating opportunities are critical factors behind the appearance of female or male uniparental care. When the benefits of deserting a clutch are higher for females than for males, due to poor re-mating opportunities for males under conditions of low population density, male-only parental care would appear. When the opposite is true, female-only parental care would be

favoured. Red-legged Partridge population density can vary greatly (Vargas *et al.* 2007), but often around the threshold of density proposed by Owens (2002) as the limit between species exhibiting male- or female-only parental care (one nest every 10 ha). We have also observed a high rate of divorce and re-mating within the same breeding season, as well as cases of polygyny, EPPs (extra-pair paternity) and intraspecific parasitism (Casas *et al.* 2006a, 2006b). Male care appears only under good breeding conditions, whereas in poor years, female-only care emerges. Red-legged Partridges could be in a situation near the female-only stage of parental care, which is a common breeding system in Galliformes (Owens 2002), but depending on the environmental conditions, male care can also be favoured. This system could be considered a flexible and intermediate stage in the evolution of breeding systems. However, further research, particularly on the occurrence and success of male care of nests under similar environmental conditions but different population densities or predation pressures, is needed to better understand the evolution and maintenance of this breeding system. A longer study with marked individuals across years would also be necessary to better understand the costs and benefits of the peculiar parental behaviour of Partridges.

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APPENDIX 1

Weather conditions during the study period. Winter (22 December–21 March) and spring (22 March–21 June). Temperature (°C) calculated as average for each period, humidity (% water saturation) calculated as average for each period; and rainfall (L/m²) calculated as the accumulation for each period (data taken from the agrometeorological station of Ciudad Real of the SIAR, Servicio Integral de Asesoramiento al Regante <http://crea.uclm.es/siar/datmeteo/datosmet.php>).

	Temperature	Humidity	Rainfall
2002–2003 winter	5.99	79.93	149.8
2003 spring	13.22	64.27	158.2
2003–2004 winter	5.98	82.01	116.4
2004 spring	10.71	72.46	78.4
2004–2005 winter	3.48	72.24	50
2005 spring	13.42	54.9	98
2006–2007 winter	5.31	83.55	66.6
2007 spring	11.41	68.98	203.8