

Determinants of Reproductive Success in a Mediterranean Multi-brooded Passerine: the Black Wheatear *Oenanthe leucura*

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SOLER, M., J. MORENO, A. P. MØLLER, M. LINDÉN & J. J. SOLER (1995): Determinants of reproductive success in a Mediterranean multi-brooded passerine: the Black Wheatear *Oenanthe leucura*. *J. Orn.* 136: 17–27. — The factors affecting individual variation in reproductive success in a multibrooded passerine, the Black Wheatear *Oenanthe leucura*, were studied during five years in a dry inland depression in SE Spain. Black Wheatear pairs initiated 1–5 breeding attempts in a season, including relayings, and managed to raise 0–3 broods and 0–13 fledglings. The onset of breeding for different pairs spanned several months. The number of breeding attempts and the proportion of young resulting in fledged young (excluding predated broods) were the best predictors of seasonal reproductive success. Clutch size showed a quadratic relationship with laying date. Female age and time of residency and indexes of parental condition such as discontinuities in feather growth or prevalence of ectoparasites had significant effects on breeding productivity. Repeatabilities of breeding performance for males, females or in territories were not significant.

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Introduction

Breeding seasons of birds are usually longer in the tropics than in temperate regions (BAKER 1939). This probably reflects a relationship between latitude and the dynamics of the food supply, the yearly period of favourable day length and temperature decreasing from the tropics towards cold temperate areas. In subtropical latitudes at many locations, rainfall is low and variable, restricting primary production and determining „opportunistic breeding“ at practically any time of the year (IMMELMANN 1970, 1971, MACLEAN 1971, WYNDHAM 1986). Some high inland areas of the Mediterranean basin are characterized by large seasonal temperature fluctuations and low and irregularly distributed precipitation. Vegetation growth is restricted during the cold winters and the dry, hot summers in these areas (NAHAL 1981), which in turn determine low and variable arthropod abundances (HODAR unpubl.). Only a few avian insectivores remain as residents in such barren habitats. One of them, the Black Wheatear *Oenanthe leucura*, inhabits ravines and canyons in the driest regions of the Western Mediterranean (CRAMP 1988). The scarce resource base throughout the year (small chitinous prey during winter, nocturnal habits of prey during summer) and the absence of marked increases in arthropod abundance in spring (HODAR unpubl.)

probably do not allow large reproductive efforts. On the other hand, the resource threshold for breeding may vary locally and temporally. How have residents like the Black Wheatear adjusted to these constraints for breeding?

Low clutch sizes do not allow fine-tuning of parental effort to individual or territory quality. On the other hand, long breeding seasons allow individual pairs to time their effort according to their parental capacity. A strategy of laying a variable number of small clutches may be favoured in habitats with scarce resources and limited fluctuations in prey abundance (THIOLLAY 1991). As a consequence we would expect a large variation in reproductive timing and success. The variation in seasonal productivity would be determined not only by the variation in the productivity of each brood, but also by variation in the number of broods raised (CRICK et al. 1993). The factors affecting individual variation in reproductive success may become clearer in such a situation than in the synchronously breeding populations studied in more seasonal and productive temperate areas. In the present study, we have studied the factors determining the variation in reproductive success of individuals in a population of Black Wheatears focussing on the following questions:

- 1) Which breeding variables explain reproductive success in this species?
- 2) Is there a seasonal trend in breeding success?
- 3) How is parental care related to breeding success?
- 4) Which characteristics of breeding adults are associated to differences in breeding success?

Materials and methods

The Black Wheatear is the largest species of the genus *Oenanthe* (35–40 g) and has a very slight sexual size and colour dimorphism (CRAMP 1988, GLUTZ & BAUER 1988). It is resident throughout its breeding range (CRAMP 1988, GLUTZ & BAUER 1988). Individuals are observed in loose pairs throughout the nonbreeding season and breed monogamously (RICHARDSON 1965, KÖNIG 1966, PRODON 1985). Only females incubate and brood ectothermic chicks, while both sexes feed nestlings and fledglings. Black Wheatears feed on arthropods during most of the year (RICHARDSON 1965, SOLER et al. 1983, HODAR unpubl.). Its most distinctive behaviour is the stone carrying display enacted prior to each breeding attempt (FERGUSON-LEES 1960, RICHARDSON 1965, KÖNIG 1966, STÖBENER 1979), which has been shown to allow adjustment of reproductive effort to the phenotypic quality or physical condition of mates (MORENO et al. 1994).

The study was made during the 1988–1992 breeding seasons in the Hoya de Guadix, southern Spain (37° 18' N, 3° 11' W), an area of deep canyons and ravines with eroded slopes, which cut into high plateaux (1000 m) covered by sparse vegetation and agricultural crops. Annual precipitation in the area is very low (310 mm), and temperatures vary widely throughout the year, from freezing during the long winters to maxima above 40° C during the hot, dry summers. Black wheatears breed in the canyons and gullies, and around ruined buildings and abandoned man-made caves (people lived in caves until recently in this area). There is a marked preference for nesting in abandoned caves, if available, and the highest breeding densities are reached in areas with abundant caves. These caves offer constant moderate temperatures in an environment characterized by thermal extremes.

We studied 24 areas with one to eight breeding pairs in at least one year. Of these, five areas were included in all years, four in 4 years, three were included in 3 years, six in two years and six in only one year. The numbers of sites and breeding pairs included in different years were 10 and 22 in 1988, 14 and 28 in 1989, 15 and 34 in 1990, 16 and 37 in 1991 and 13 and 32 in 1992. Sites were included depending on the presence of Black Wheatear pairs in early spring. Between 1989 and 1992 we performed a number of field experiments, but only data for unmanipulated pairs (pairs were marked) have been included in the analyses of the present paper.

We visited territories at least weekly throughout the breeding season (end of March to beginning of August) to find nests and record breeding success. By closely following the breeding activities of pairs and looking for nests in caves, ruined buildings or suitable natural sites, we were able to classify breeding attempts as first, repeat of first (after predation or desertion), second (young having fledged from the previous attempt), repeat of second (all attempts after predation or abandonment of second clutches/broods), and third (very rare). The laying date was defined as the day when the first egg was laid assuming that one egg was laid daily. Clutch size was defined as the number of eggs in the nest after the start of incubation. Incubation period was estimated as the number of days between laying of the last egg and hatching. Brood size at hatching is defined as the number of nestlings present on the first day after hatching. Number of fledged young is defined as the number of nestlings present during the last visit to the nest (11–13 days after hatching). Hatching success is defined as brood size at hatching divided by clutch size in nests which survived until hatching, and fledging success as brood size at fledging divided by brood size at hatching in nests which survived until fledging. On the other hand, the proportions of eggs hatched and young fledged include clutches and broods which did not survive until hatching or fledging. Nesting success is defined as the number of young fledged divided by clutch size in nests which survived until fledging. Productivity is defined as the seasonal number of fledged young.

Unmarked males were caught at the beginning of the season by luring them into mist nets with the aid of taped song and a decoy. Unmarked females were captured with spring traps or mist nets while feeding nestlings. Most birds were individually colour-banded as well as provided with aluminium rings (Spanish Institute for Nature Conservation-ICONA), which allowed recognition of captured individuals in successive years. The permanence of individuals in their territories from one year to the next will be considered as site-fidelity, due to observations of individuals changing territories between seasons. Male and female age was classified as one year or more according to plumage characteristics (SVENSSON 1984). To estimate adult condition we used the number of easily visible discontinuities in the pattern of growth bars in primaries and rectrices (GRUBB 1989). This index refers to condition during the previous moult, which presumably is correlated with present condition. Another index of condition may be the prevalence of external parasites. We counted the holes in primaries and rectrices due to malophagous parasites, and noted the presence of ticks around the bill and eyes. Chicks were ringed with aluminium rings at the age of 11–13 days, weighed with Pesola spring balances accurate to 0.1 g and their tarsi measured with dial calipers.

We recorded feeding rates at six nests of first broods in 1989 when chicks were 10 days or older. The number of visits with food by the male and the female was recorded during a 4-hour period in the afternoon (16–20 h). There were highly significant between-pair concordances of rankings of male and female feeding rates between periods of 4, 3, 2 and 1 h (Kendall coefficients of concordance, $p < 0.01$), which indicates that hourly observation periods may be sufficient to explore between-pair variability. Thus, in 1991, we observed feedings of seven broods of 10 or more days of age for only one h in the afternoon. In 1991, we also observed male

and female feeding rates to fledglings of 20–28 days of age in 10 territories during periods of one hour.

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Results

1. Variation in breeding parameters

Black Wheatears raised on average more than one brood per season in Guadix, but initiated between one and five breeding attempts (Table 1). Many breeding attempts were relayings due to relatively frequent nest predation or abandonment (Table 2). Although the incidence of predation was lower for second than for first or repeat clutches (Table 2), the distribution of mortality factors did not differ between the three types of clutches (Log-likelihood test for small frequencies, $G = 4.54$, d. f. = 4, n. s.). The type of nest-site, artificial cave or natural cavity, did not significantly affect the probability of nest predation (20 % of 135 nests in caves and 31 % of 45 nests in natural cavities were predated, $\chi^2 = 1.78$, d. f. = 1, n. s.). Incubation periods were surprisingly variable, indicating marked differences in incubatory efficiency or thermal characteristics of the nest (Table 3). Second clutches were laid between one and four weeks after

Tab. 1. Different measures of breeding success for first, second and repeat clutches and for all clutches. Number of breeding attempts, number of broods raised and productivity (number of young fledged) are for the whole breeding season. Means \pm SD and ranges (for breeding attempts, number of broods and productivity) are represented with sample sizes in brackets. Three third clutches have not been included.

	First	Second	Repeat	All clutches
No. of attempts				2.15 \pm 0.76 (93) 1–5
Prop. eggs hatched	0.65 \pm 0.40 (81)	0.78 \pm 0.35 (44)	0.81 \pm 0.29 (27)	0.72 \pm 0.37 (155)
Hatching success	0.84 \pm 0.21 (62)	0.88 \pm 0.21 (39)	0.88 \pm 0.18 (25)	0.86 \pm 0.20 (129)
Prop. young fledged	0.50 \pm 0.41 (85)	0.61 \pm 0.39 (47)	0.62 \pm 0.39 (29)	0.56 \pm 0.40 (164)
Fledging success	0.92 \pm 0.17 (54)	0.90 \pm 0.16 (34)	0.90 \pm 0.19 (22)	0.91 \pm 0.17 (113)
Nesting success	0.76 \pm 0.24 (54)	0.81 \pm 0.22 (35)	0.78 \pm 0.25 (23)	0.79 \pm 0.23 (115)
No. of broods raised				1.42 \pm 0.71 (100) 0–3
Fledged young	1.94 \pm 1.68 (104)	2.45 \pm 1.78 (53)	2.08 \pm 1.61 (39)	2.14 \pm 1.70 (199)
Productivity				4.65 \pm 2.73 (95) 0–13

Tab. 2. Frequency of nest desertion, destruction of eggs by non-predators, clutch predation, brood predation and predation under unknown phase for first, second and repeat clutches. Three third clutches not included.

	Surviving	Deserted	Eggs destroyed	Clutch predation	Brood Predation	unknown phase
First clutches	59	11	1	7	8	7
Second clutches	38	4	1	1	3	1
Repeat clutches	23	3	1	2	2	3

fledging of the first brood (Table 3). Clutches were normally of four eggs and broods contained normally 3–4 young (Table 3). First, second and repeat attempts did not differ significantly with respect to any breeding variable (Tables 1 and 3, ANOVAS, n. s.).

The seasonal breeding productivity per pair was 4–5 fledglings (Table 1). However, there was a striking variation between pairs in annual breeding success, some pairs raising 13 young to fledging while others fledged none (Table 1). Some females laid only one clutch per season, while others were able to raise 3 broods in a breeding season extending from late March to mid August (Table 1). There was also a range of variation of three months in the initiation of breeding in different pairs throughout the study years (Table 3). While some pairs began laying in early March, others waited until June. Two variables explained more than 40 % of the variation in seasonal productivity, namely number of breeding attempts initiated and quality of parental care as estimated by the proportion of eggs resulting in fledged young in all unpredated nests (nesting success), while clutch size seemed less important (Stepwise multiple regression with number of attempts, initial laying date, size of first clutches and parental care index as independent variables: $F = 16.92$, d. f. = 45, $P < 0.001$, $r^2 = 0.44$, Productivity =

Tab. 3. Laying dates, relaying intervals after raising the first brood, clutch sizes, duration of incubation periods and brood sizes for first, second and repeat clutches. Means are presented with SD and range, sample sizes are in brackets. Three third clutches are not included.

	First clutches	Second clutches	Repeat clutches
Laying date (1 = January 1)	112.6±15.0 (94) 64–156	155.9±14.3 (48) 118–189	147.2±26.4 (34) 102–193
Relaying interval (days)	17.2±6.9 7–31		
Clutch size	3.99±0.60 (87) 3–6	4.04±0.75 (47) 2–5	4.03±0.73 (29) 3–6
Incubation period (days)	14.9±1.6 (44) 10–19	14.2±1.7 (30) 10–17	14.5±1.4 (17) 11–17
Brood size	3.43±0.95 (62) 1–5	3.74±1.12 (39) 1–5	3.48±0.92 (25) 2–6

$-1.37 + 2.21$ [no. attempts] $+ 3.37$ [nesting success]). The number of breeding attempts depends significantly on initial laying date (No. attempts = $4.99 - 0.02$ [initial laying date], $r = 0.25$, d. f. = 81, $P < 0.001$). Productive pairs were those able to lay many clutches and efficiently care for eggs and nestlings. Productivity as measured by the seasonal number of fledged young was positively correlated with the recruitment of young to the study population ($r = 0.37$, d. f. = 48, $P < 0.01$).

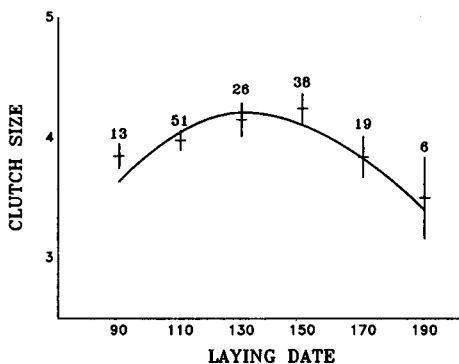


Fig. 1. Mean clutch sizes (\pm S. E. bars) laid for 20-day periods throughout the breeding season. The quadratic regression of clutch size on laying date ($y = -1.174 + 0.080 \pm 0.019 (x) - 0.0003 \pm 0.00006 (x^2)$, $F = 9.71$, $P < 0.001$, both coefficients significant, t -tests, $P < 0.001$) is also depicted.

2. Effects of year and breeding area

Laying dates of first clutches and seasonal productivity of young differed significantly between years (laying date: ANOVA, $F = 7.13$, d. f. = 93, $P < 0.001$; productivity: $F = 3.84$, d. f. = 93, $P < 0.01$). Thus, in 1992 breeding was significantly earlier than in 1988, 1989 and 1991 and productivity significantly greater than in 1989 (Scheffé F -tests, $P < 0.05$). As some study areas were used in some years but not others, the inter-year differences could be due to differences between areas. However, a two-way ANOVA on breeding productivity with year and area as classifying factors revealed a significant effect of year but not of area, and no significant interaction between year and area (year: $F = 8.67$, d. f. = 31, $P < 0.001$; area: $F = 1.70$, d. f. = 31, n. s.; interaction: $F = 0.71$, d. f. = 31, n. s.).

3. Seasonal variation in breeding success

Clutch size increased with laying date for first clutches ($y = 2.74 + 0.011x$, $r = 0.26$, d. f. = 79, $P < 0.05$) and decreased for second clutches ($y = 7.70 - 0.023x$, $r = 0.41$, d. f. = 43, $P < 0.01$), while repeat clutches showed no significant trend. Over all clutches, there was a significant quadratic relationship of clutch size with laying date (Figure 1). The number of fledged young, hatching success and fledging success did not correlate with laying date for first, second or repeat clutches (regression analyses, n. s.), although there was a significant negative trend of mean fledgling mass with date for second clutches ($r = -0.39$, d. f. = 28, $P < 0.05$). Thus, there are no clear indications of a significant increase or decrease in the capacity to raise nestlings throughout the protracted breeding season.

There was no correlation between the interval between fledging of the first brood and laying of the second clutch and the size of the second clutch ($r = -0.15$, d. f. = 27, n. s.). Intervals were not significantly related with fledging date of first broods ($r = 0.10$, d. f. = 34, n. s.). There was no significant trade-off between the size of the first and second clutches ($r = 0.23$, d. f. = 43, n. s.) or between the size of first and repeat clutches ($r = 0.05$, d. f. = 13, n. s.).

The duration of incubation decreased with laying date ($r = 0.22$, d. f. = 92, $P < 0.05$), probably in relation with the seasonal increase in ambient temperature. Incubation length also decreased significantly with clutch size ($r = 0.25$, d. f. = 92, $P < 0.05$). The effect of clutch size was still significant when controlling for laying date in a multiple regression ($r = 0.32$, d. f. = 92, $P < 0.01$; $b[\text{date}]$: $t = 1.98$, $P = 0.05$, $b[\text{clutch size}]$: $t = 2.38$, $P = 0.02$). Small clutches may cool faster during female absences due to the larger exposed surfaces of their eggs. No effect of the type of nest-site (man-made caves or natural cavities in clay cliffs, MORENO et al. 1994) on incubation period was noted (Unpaired t-test: $t = 0.51$, d. f. = 91, n. s.).

4. Variation in parental care

Males fed nestlings as much as females during and after the nestling period (Table 4, paired t-tests, n. s.). Feeding rates of first broods had no significant effect on fledging mass or tarsus length (mass: $r = 0.17$, d. f. = 13, n. s.; tarsus: $r = 0.19$, d. f. = 13, n. s.), on the proportion of young raised to fledging ($r = 0.24$, d. f. = 13, n. s.) or on the number of fledged young ($r = 0.02$, d. f. = 13, n. s.). However, there were positive associations of total feeding rate and female feeding rate to first broods with seasonal productivity (total rate: $r = 0.59$, d. f. = 13, $P < 0.05$; female rate: $r = 0.62$, d. f. = 12, $P < 0.05$).

Parental care before fledging was significantly correlated with postfledging care (feeding rates before and after fledging: $r = 0.67$, d. f. = 8, $P < 0.05$). Postfledging care had a significant negative effect on the period before laying the second clutch (total feeding rate: $r = -0.93$, d. f. = 4, $P < 0.05$, female rate: $r = -0.93$, d. f. = 4, $P < 0.05$). The duration of this period was also significantly related to fledging success ($r = -0.50$, d. f. = 28, $P < 0.01$). Long relaying intervals after fledging the first brood have a marked effect on laying dates of second clutches ($r = 0.44$, d. f. = 33, $P < 0.01$).

Tab. 4. Hourly rates (means \pm SD, ranges) of feedings by males, females and pairs to nestlings of 10–13 and fledglings of 20–28 days of age. Number of observation periods are in parentheses.

	Male	Female	Total
Feeding rate nestlings	4.6 \pm 3.2 0–12	4.6 \pm 1.4 3–7	9.3 \pm 3.9 (16) 4–19
Feeding rate fledglings	7.8 \pm 5.8 2–19	5.5 \pm 2.6 2–9	21.2 \pm 12.3 (8) 8–46

Thus, parents feeding more at the nest are the most productive, continue feeding intensively after fledging and are still able to reduce the period before laying the second clutch.

5. Effects of parental age and site-fidelity

Females paired to yearling males laid significantly smaller clutches which resulted in significantly smaller broods than those paired to males older than one year (clutch size: 3.5 ± 0.5 vs. 4.1 ± 0.6 , $t = 2.68$, d. f. = 45, $P < 0.05$; brood size: 2.5 ± 1.0 vs. 3.6 ± 0.9 , $t = 2.72$, d. f. = 32, $P < 0.05$). Females older than one year raised significantly more young in first broods than yearling females (2.7 ± 1.4 vs. 1.6 ± 1.4 , $t = 2.29$, d. f. = 40, $P < 0.05$). They suffered less predation (13.6%, $n = 59$) than first-year females (25%, $n = 28$), although the difference was not significant ($\chi^2 = 1.03$, d. f. = 1, n. s.). There were no differences in any breeding parameter comparing newly formed pairs with pairs established in a previous breeding season (Unpaired t-tests, n. s.).

Females breeding for the first time in a territory laid their first clutch two weeks later on average than females having bred in the territory before (April 15 + 12 days vs. May 1 ± 14 days, $t = 3.11$, d. f. = 25, $P < 0.01$). This led to an almost significant difference in productivity (5.8 ± 2.2 versus 3.9 ± 2.8 , $t = 2.0$, d. f. = 27, $P = 0.054$). No effect of previous breeding of males in the territory were detected (unpaired t-tests, n. s.). The proportion of marked individuals which were not found from one year to the next in the study area was 49.5% ($n = 107$), 44.8% for males ($n = 58$) and 55.1% for females ($n = 49$). No effects of any breeding parameter on the probability of not breeding further in the study area (through decease or dispersal) were noted (unpaired t-tests, n. s.).

6. Effects of parental size and condition

Assuming that the discontinuities in the pattern of growth bands (observed by eye as lighter bands across the feathers) in primaries and rectrices indicate low nutritional condition during moult (GRUBB 1989), we can use their number as an index of prior condition and therefore of individual proficiency. The number of light bands in males had a very strong positive association with the duration of the interval between fledging of the first brood and laying of the second clutch ($r = 0.74$, d. f. = 14, $P < 0.01$). The number of light bands in females had a significant negative association with the number of broods raised ($r = -0.50$, d. f. = 21, $P < 0.05$) and with seasonal productivity ($r = -0.54$, d. f. = 21, $P < 0.01$). Condition during the last moult seems to indicate impaired reproductive capacity in females and a reduced ability to induce further reneating by females in the males. The presence of malophagous parasites showed no association with any breeding variable in males and females. However, the presence of ticks around the bill and eyes of males was associated to lower numbers of fledged young in first broods (0.2 ± 0.4 vs. 2.2 ± 1.8 , $t = 2.42$, d. f. = 20, $P < 0.05$), a lower proportion of eggs resulting in fledged young (0.05 ± 0.11 vs. 0.55 ± 0.47 , $t = 2.33$,

Tab. 5. Repeatabilities (R) of seasonal productivity of young between years with S. E.s and results of ANOVA tests for males, females and territories. S. E.s calculated according to BECKER (1984). Degrees of freedom are between and within groups.

	F	d. f.	P	R	S. E.
Males	2.51	11, 14	n. s.	0.41	0.23
Females	2.12	9, 11	n. s.	0.35	0.28
Territories	1.96	12, 30	n. s.	0.23	0.18

d. f. = 16, $P < 0.05$) and a lower productivity (2.0 + 2.8 vs. 5.4 + 2.6, $t = 2.27$, $p = 18$, $P < 0.05$). No such associations were found for females.

7. Repeatability of breeding performance for individuals and territories

Repeatabilities of seasonal productivity have been calculated for males and females, including only individuals for which we had data for more than one year in the sample (12 males and 10 females). Repeatabilities were not significant (Table 5). The repeatability of seasonal productivity for the 13 territories for which we have data for more than two years was not significant and was intermediate between the values for males and for females (Table 5). Environmental variation seems more important than the identity of breeders or their territories in explaining seasonal breeding success.

Discussion

The present results agree with the scant information about the breeding biology of the Black Wheatear (CRAMP 1988). They confirm its suggested multibrooded reproduction (RICHARDSON 1965, KÖNIG 1966, PRODON 1985) and the low clutch sizes attained (CRAMP 1988). They indicate that clutch size variation is very slight, while the number of breeding attempts may vary from 1 to 5. The number of nesting attempts is the strongest predictor of reproductive success in this species. Like in other multi-brooded species, reproductive success is more a function of the number of broods raised to fledging than of clutch size (BURLEY 1980, WESTMORELAND et al. 1986, ROWLEY & RUSSELL 1991). We also find that for multi-brooded species typical quadratic relationship between laying date and clutch size (CRICK et al. 1993). The different measures of reproductive success do not reflect any clear trend with date, suggesting that early initiation of breeding has no important costs.

The two variables which affect the number of breeding attempts which a pair might initiate are the date of onset of breeding and the intervals between raising a brood and laying another clutch. Early onset of breeding and shortened relaying intervals allow pairs to make more breeding attempts in the face of frequent nest predation (FINCH 1984). Years with early onset are also the most productive for the study population. The large variation between pairs in breeding productivity can be associated to a large variation in these two variables. Both onset of breeding and relaying intervals may be related to parental condition: females breeding for the first time in a territory delay

onset of breeding, and females paired to males with indications of low condition during the previous moult have longer relaying intervals.

The other factor explaining reproductive success is parental care quality: yearling females have lower fledging success than older females (SAETHER 1990) and female and total feeding rates to nestlings are associated to higher productivity. Again, condition seems to determine parental care: females with lower condition during moult show lower productivities, and males with signs of parasitism have lower fledging success and productivity. Parental care to nestlings is prolonged after fledging: parents feeding their fledglings intensely are also able to shorten relaying intervals. The capacity to attain a sufficient condition for breeding seems to vary between years for individuals, as shown by relatively low repeatabilities of breeding success between years for males and females.

Areas and territories may be unpredictable with respect to food resources and predation risks as shown by low repeatabilities of breeding success for territories between years. Decisions to breed or not may depend on individual condition and on that of their mate. The intensity of the stone carrying display by males in this population has been shown to be associated to timing of breeding, clutch size, breeding success and male feeding rates (MORENO et al. 1994). Stone carrying as a display of present condition may be necessary to allow females to adjust reproductive decisions not only to their own condition, but to that of their mates. Such costly displays may be typical of populations with long and variable breeding seasons and strong effects of condition on the ability to produce or care for eggs and young.

Zusammenfassung

Am Beispiel des Trauersteinschmätzers, einem Singvogel mit mehreren Jahresbruten, wurden in einer trockenen Inlandniederung Südostspaniens die Faktoren untersucht, die individuelle Unterschiede im Fortpflanzungserfolg bedingen. Die Paare unternahmen einschließlich Ersatzgelege ein bis fünf Brutversuche pro Saison und können maximal bis 3 Bruten aufziehen. Hieraus ergibt sich eine große Variation der Produktivität. Der Legebeginn zog sich bei den einzelnen Paaren über mehrere Monate hin. Die Zahl der Brutversuche, die vom Termin des ersten Legebeginns abhängig waren, und die Qualität der elterlichen Brutpflege, gemessen an dem Anteil der Eier, die flügge Junge ergaben (ohne Fälle von Nesträuben), ließen den Bruterfolg pro Saison am besten bestimmen. Gelegegröße variierte nur gering (4 Eier im Mittel) und zeigt die quadratische Beziehung zum Legedatum, wie für mehrfachbrütende Sperlingsvögel typisch. Eltern, die intensiver am Nest fütterten, waren die produktivsten, fütterten auch intensiver nach dem Flüggewerden der Jungen und zeigten kürzere Intervalle zwischen aufeinanderfolgenden Bruten. Einjährige Weibchen oder Weibchen, die mit einjährigen Männchen verpaart waren, hatten geringeren Erfolg gemessen an Zahl der flüggen Jungen; Weibchen, die das erste Mal in einem Revier brüteten, begannen später zu legen. Unregelmäßigkeiten in der letzten Mauser, wie sie an Ungleichmäßigkeiten der Wachstumsbänder der Federn zu erkennen waren, hatten negativen Effekt auf die Produktivität der Weibchen und auf die Abstände zwischen aufeinanderfolgenden Bruten bei Männchen. Männchen mit vielen Ektoparasiten waren weniger produktiv. Die Wiederholbarkeit des Fortpflanzungsverhaltens von Männchen, Weibchen oder in einzelnen Revieren war relativ niedrig und nicht signifikant. Die langen und

variablen Fortpflanzungsperioden und die starken Einflüsse auf die individuelle Kondition bei Produktion und Fürsorge der Eier und Jungen ist wohl für trockene und wenig produktive Landschaften des Mittelmeerbeckens typisch.

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