The function of stone carrying in the black wheatear, *Oenanthe leucura*

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Abstract. Mated pairs of the black wheatear, but particularly the males, carry large numbers of relatively heavy (3–9 g on average) stones in flight to nest cavities and other sites in caves and cliffs during the prelaying period of each clutch. The 40-g birds carry on average 1–2 kg of stones during periods of 2–22 days (average 7·8), and stone carrying is therefore costly in terms of time and energy. Five functional explanations for the maintenance of this behaviour are considered. (1) The nest support hypothesis, that stones form a solid base for the nest, is refuted because large horizontal nest cavities with no need for nest support contained as many stones as those in other sites, nests were frequently situated in sites without stones, and stones were carried to sites not subsequently used for nests. (2) The thermoregulation hypothesis, that stones may moderate large diel temperature fluctuations and thus reduce the cost of incubation and brooding, is refuted because nests were frequently situated in sites without stones, there were as many stones in caves where temperatures fluctuated little as in natural cavities where temperatures varied widely, hatching success was unrelated to the number of stones and the cooling rate of nest contents was not affected by the presence of stones. (3) The weather protection hypothesis, that a large number of stones may protect the nest from wind, rain, or dust, is refuted because nests were frequently situated in sites without stones, and no case of nest failure owing to inclement weather was recorded. (4) The anti-predation hypothesis, that stones may prevent predation of nest contents or incubating females, is also refuted because stone carrying prevented use of relatively safe nest sites above 3·5 m, and nests suffering from predation had as many stones as successful nests. (5) The sexual display hypothesis, that pair members use the stone-carrying display to assess the quality of the partner and adjust their relative parental investment accordingly, does account for the behaviour since clutch size was positively and laying date negatively correlated with the number of stones carried to cavities other than nest sites, and the seasonal production of young was positively associated with the seasonal number of stones carried to cavities other than nest sites. The number of stones carried to nest sites had less predictive capacity. Stone carrying was also associated with the extent of paternal care. The behaviour showed a relatively high repeatability within and between seasons, implying strong and consistent differences between individuals. Stone carrying in the black wheatear can therefore be considered a post-mating but prenesting sexual display which allows adjustment of reproductive effort by females to the parental and/or phenotypic quality of partners.

Black wheatears carry large numbers of stones, which combined weigh many times their own body weight, to nest cavities above ground level (Fig. 1a). This activity is bound to be costly in terms of time and energy use. Stones are deposited even in sheltered sites and in places without nests (Fig. 1b). Since males carry stones during their courtship activities, Ferguson-Lees (1960) suggested that the collection of stones might play an important part in nest site selection and courtship in the black wheatear (the sexual display hypothesis). In the first detailed field study of the black wheatear, Richardson (1965) pointed out that males were the more active sex performing this behaviour, and concurred with Ferguson-Lees (1960) that stones rarely served to protect the nest
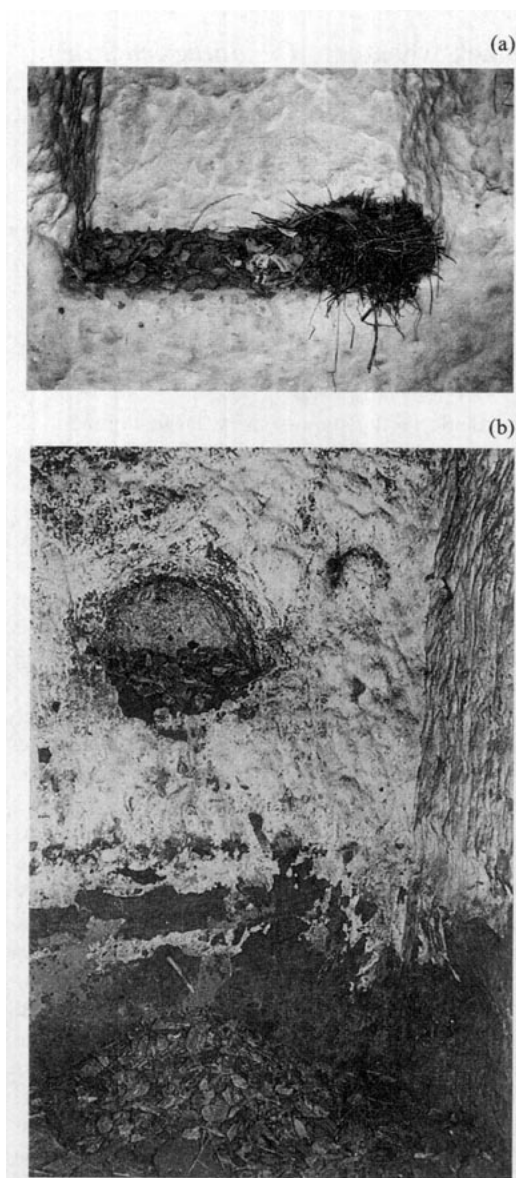
Figure 1. (a) Nest on horizontal ledge in artificial cave, with stones deposited to one side. (b) Stones on horizontal cavity and on the ground in an artificial cave. No nest was built here.

from weather or predators. He proposed that the habit of stone carrying originated from the need to build a foundation for the nest on uneven substrates, but that it has subsequently become a sexual display by the male in the context of nest site selection.

What is the function of stone carrying? Black wheatears may carry stones precisely because this is an energetically costly behaviour that can be performed only by individuals in good condition (Zahavi 1987). Stone carrying takes place after pair formation and preceding all breeding attempts, and it does not, therefore, have a mate-attraction function. However, there are many mechanisms of sexual selection that operate after pair formation (Kirkpatrick et al. 1990; Møller 1992). For example, according to the 'differential allocation hypothesis' (Burley 1986, 1988), females may be willing to invest more heavily in young sired by high quality males. If stone carrying reflects male quality, we should expect display intensity to affect female reproductive decisions such as when to breed, how many clutches to lay, how many eggs to lay in each clutch, or how hard to work while caring for young. Alternatively, a costly display could indicate the male's willingness to invest in offspring in species with paternal care such as the black wheatear (e.g. Heywood 1989; Hoelzer 1989). If this is the case we should expect a positive correlation between stone carrying and paternal care.

There may, however, be alternative explanations for the evolution and maintenance of stone carrying in black wheatears. Stones might support the nest (Panow 1974; Cramp 1988), be used to construct piles that might discourage predators (Verner 1909; Brehm 1913; König 1966) or protect the nest from wind, rain or dust. Finally, wheatears often live in habitats such as deserts and steppes with large diel temperature fluctuations. Many stones at the nest site could potentially moderate large temperature shifts, and have a thermoregulatory function.

Here we address these five different functional hypotheses for the maintenance of stone carrying in the black wheatear. More specifically we (1) describe the behaviour and the four different components of stone-carrying effort (number of stones, rate of stone carrying, average weight of stones, and height of the cavity above ground level to which the stones are carried), (2) determine the consistency in stone carrying by males and females during subsequent breeding attempts in the same and in different breeding seasons, and (3) provide tests of the predictions and assumptions of the functional hypotheses for the maintenance of stone carrying.

METHODS

Study Species

The black wheatear is the largest species of the genus *Oenanthe* (35–40 g) and has slight sexual size and colour dimorphism (Cramp 1988; Glutz & Bauer 1988). It is normally monogamous and remains paired on the territory throughout the non-breeding season (Richardson 1965; König 1966; Prodon 1985). Only females incubate, without being fed by males, but both sexes feed the young (Cramp 1988; Glutz & Bauer 1988). Individual pairs may initiate as many as five breeding attempts, up to three successful ones, in a reproductive season, which may last up to 5 months.

Study Area

We studied wheatears during 1988-1992 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 sparse and falls mostly in winter, and temperatures vary from freezing in the winter to more than 40°C in the summer. Black wheatears breed in the canyons and gullies, and around ruined buildings and abandoned artificial caves. There is a marked preference for nest sites in abandoned caves, and the highest breeding densities are reached in areas with many caves. These caves offer fairly constant moderate temperatures in an environment characterized by thermal extremes.

We studied 24 areas with one to eight breeding pairs in at least 1 year. Of these, five areas were included in all years, four in 4 years, three in 3 years, six in 2 years and six in only 1 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 or not depending on the presence of breeding pairs early in the season. Between 1989 and 1992 we performed a number of field experiments, but only control (unmanipulated) pairs have been included in the analyses of the present paper.

General Methods

We visited territories at least weekly throughout the breeding season (end of March to early August) to find stone piles and nests and record breeding success. By closely following the breeding activities of pairs and looking for nests, we were able to classify breeding attempts as first, repeat of first (after predation of eggs or young, or abandonment of eggs of the previous attempt), second (young 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. Brood size at hatching was defined as the number of nestlings present on the first day after hatching. Brood size at fledging was defined as the number of nestlings present during the last visit to the nest before fledging (11–13 days). Hatching success was defined as brood size at hatching divided by clutch size, and fledging success as brood size at fledging divided by brood size at hatching.

We recorded feeding rates at six nests of first broods in 1989 when chicks were 10 days or older. The numbers of visits with food by the male and the female were recorded between 1600 and 2000 hours. There were highly significant concordances of rankings of male and female feeding rates between periods of 4, 3, 2 and 1 h (Kendall coefficients of concordance, $P<0.01$). Thus, in 1991, we observed feedings of seven broods of 10 or more days of age for 1 h in the afternoon.

Males were caught in mist nets with playback of song and a decoy at the beginning of the season. Most unringed females were captured with spring traps or mist nets while feeding nestlings. All captured birds were individually ringed with coloured and numbered aluminium rings (Spanish Institute for Nature Conservation-ICONA). Males and females were classified as yearlings or older according to plumage characteristics (Svensson 1984).

We visited potential nest sites, especially caves and buildings, to find recently deposited stones. Nests in natural cavities were often found at a later stage than cave nests, most frequently during incubation or brood-rearing. Old stone piles were sprayed with grey paint at the beginning of the season to detect the addition of new stones. The paint was renewed in successive years, if necessary.

We counted the number of stones daily in some territories in 1988 and 1989, and the rate of accumulation of stones was determined by painting new stones with small marks during each visit. At the end of each season, we counted all stones and weighed them for each of the breeding attempts separately. Stones were partitioned into those placed next to the nest (nest), those lying on the ground under the nest (ground), and those carried to other locations (other). In 1988 and 1992, we quantified only stones at the nest or on the ground below (stones at nest sites hereafter). All stones carried during a particular breeding season were removed at the end of the season, but stones carried in earlier years were left untouched. The height of the nest site above ground level was measured to the nearest cm. Nest sites were classified as crevices, if the cavity did not have a horizontal surface, or other sites.

In 1989, we measured the maximum length, width and height of 10 old stone piles in territories outside our study area, and the number of stones was subsequently counted. The regression of the number of stones on the product of the three linear measures was highly significant:

No. of stones $= 69.25 + 0.0686$
[length (cm) × breadth (cm) × height (cm)],
$F_{1,8} = 56.67$, $r^2 = 0.86$, $P < 0.001$.

We used this regression equation to estimate the number of stones in old piles in 13 territories without having to destroy them.

Nest-cooling Experiment

We estimated the cooling rate of nest contents in 19 nests during mid July 1991 (after the breeding season). Between 1200 and 1600 hours, a small plastic bag filled with hot water was placed inside the nest cup with a thermocouple adjacent to the bag. We then measured the time it took for the water to cool from 40 to 30°C. All stones were then removed, the nest was placed in the same site, and the cooling rate estimated a second time.

Statistical Methods

All stone-carrying variables were $\log_{10}$-transformed and tested for normality before applying parametric statistics. Hatching success was arcsine-transformed before statistical analysis. Correlations between stone-carrying par-

ameters were Pearson product–moment correlations. To avoid including in the analyses several breeding attempts by the same pair in the same year, we have only considered first breeding attempts in cases when the number of stones carried by a pair or measures of reproductive variables per attempt were relevant variables.

We estimated the consistency in stone-carrying behaviour by determining the repeatability of variables and their standard errors (Becker 1984). This was done for successive breeding attempts within a year and in different years, respectively. Means (and SE) are presented. All tests are two-tailed.

RESULTS

Stone-carrying Behaviour

Pairs are already formed when stone carrying occurs. During February–March 1988, several weeks before stone carrying was initiated, we observed 48 individuals in pairs and eight single males. In a survey of 21 territories in November 1989, we observed the same pairs which had bred during the previous summer on seven territories, one pair member together with an unknown individual in four territories (in all cases the previous mate was not seen the following year), and the breeding male alone in two territories. Also, stones were carried before repeat and second breeding attempts (Table I). Mate changes were recorded in four out of 72 possible observations between subsequent breeding attempts.

We have observed stone carrying by eight different pairs. The black wheatears collected stones from the ground within 10 m of the cavity. From one to 82 stones were carried during a continuous observation period. Only males carried stones on five of these occasions, while females participated on three occasions. The female was always present and frequently picked up stones that had been carried by the male, but immediately dropped them again. The average proportion of stones carried by males in all instances mentioned above was $86.7 \pm 9.0\%$ ($N = 11$). Females particularly carried stones during actual nest building, when the nest was incorporated into the stone pile.

Black wheatears started to collect stones from 21 to 3 days before the start of laying (11.1 ± 0.9 days, $N = 27$) and ceased between 12 and 0 days before the start of laying (4.0 ± 0.8 days, $N = 23$).

Table I. Number of new stones ($\bar{X} \pm$ SE, range and sample size) found at the nest site, on the ground below and at other sites, and total number and weight (g) of stones collected before first, repeat of first and second attempts, and the seasonal total number and weight of stones collected during the season

	Nest	Ground	Other sites	Total number	Total weight (g)
First clutches	94·2 ± 14·7	82·8 ± 13·1	107·4 ± 32·3	319·9 ± 37·8	2019·4 ± 270·4
	0–840	0–543	0–1300	47–1366	241–10 109
	79	74	44	43	58
Repeat of first	32·3 ± 9·7	58·6 ± 20·6	20·7 ± 12·4	124·6 ± 120·0	820·3 ± 715·3
	0–168	0–387	0–151	13–399	105–2 232
	24	24	14	12	11
Second clutches	70·8 ± 15·4	52·2 ± 10·3	72·8 ± 29·3	253·9 ± 42·2	1508·6 ± 1282·4
	0–388	0–279	0–313	6–534	47–3 363
	40	39	13	15	15
Sum of all attempts per season, 1988–1992*				316·2 ± 31·1	2011·5 ± 209·1
				6–1204	46–7 481
				60	56
Sum of all attempts per season, 1989–1991†				503·4 ± 57·3	3092·7 ± 390·1
				62–1366	288–10 109
				34	34

*Only stones at nests or below them are included, as stones in cavities other than nest sites were not quantified in 1988 and 1992.
†Stones in cavities other than nest sites also included.

Intense stone carrying (defined by the appearance of more than five new stones per day) was performed during periods of 2–19 days ($6·9 \pm 0·8$ days, $N=25$). Stones were found in the nest cavity, on the ground below the cavity, and also frequently in a number of other sites within the breeding territory (Table I).

The number of stones carried before a breeding attempt varied widely (Table I, Fig. 2a). Significantly more stones were carried before the first clutch than before the second (Table I; ANOVA: $F_{2,135}=6.99$, $P=0·001$, Scheffé F-test, $P<0·05$) or before first repeat clutches (Table I; Scheffé F-test, $P<0·05$).

The rate of stone carrying ranged from three to more than 70 stones per day ($21·0 \pm 3·5$, $N=25$ sites) during the period of intense stone carrying (Fig. 2b). Single stones appearing on the piles weighed from less than 1 g to 25 g. The average weight of stones carried ranged from 3·4 to 8·2 g (Fig. 2c). The total weight of stones carried before the different categories of breeding attempts paralleled the number of stones carried. Each black wheatear pair carried on average slightly more than 3 kg of stones per season (Table I).

The height of the cavity above ground level varied between ground level and 3·6 m (Fig. 2d). Many cavities were present at greater heights, but were never used for placing stones. The four components of stone-carrying effort (number and weight of stones, carrying rate and cavity height) would be reliable indicators of the ability of individuals to carry heavy objects only if they were not negatively correlated with each other. The different components of stone carrying were not significantly correlated with each other, except the rate of stone carrying and the number of stones carried, which showed a highly significant positive correlation (Table II). This suggests that a large effort in terms of one component of stone carrying was not compensated by a lesser effort in terms of other components.

Repeatability of Stone Carrying

We checked for consistency in stone carrying for the same pair between different attempts during a breeding season by calculating the repeatability of the total number of stones carried. There were statistically significant repeatabilities within years in stone carrying for 3 of the 5 years of the study (Table III).

We also checked for consistency in stone carrying by individuals from one year to another. Stones carried by a pair in a certain season were assigned to both members of the pair, as we have
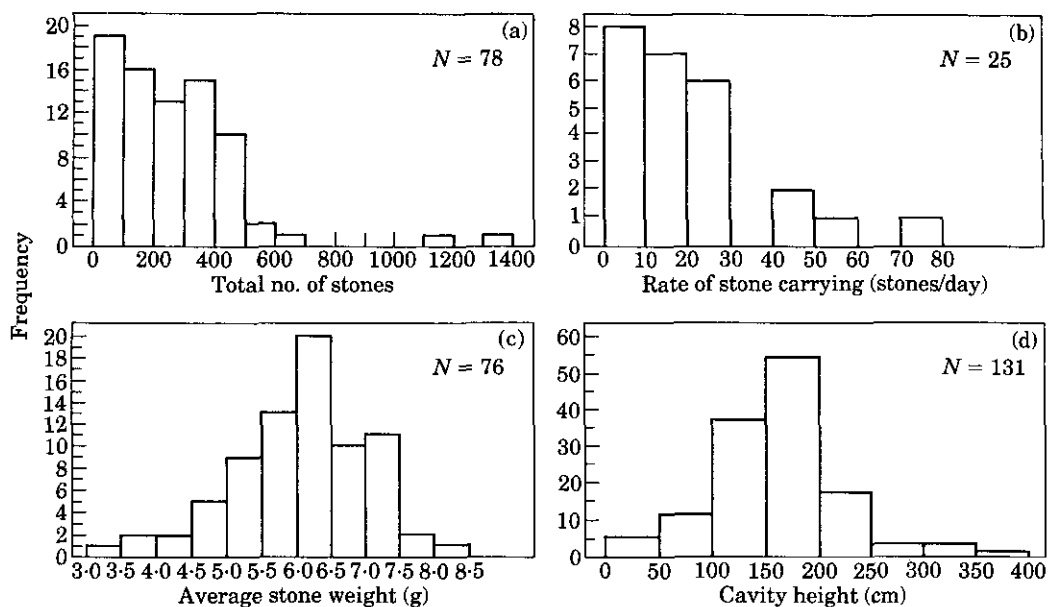
Figure 2. Frequency distribution of (a) the total number of stones per breeding attempt (1989-1991), (b) the rate of stone carrying (1988-1989), (c) the average weight of stones carried per attempt (1989-1991), and (d) the height of the cavity above ground level to which the stones are carried (1988-1992).

Table II. Correlations between the four components of stone-carrying behaviour

	No. of stones†	Stone-carrying rate	Mean stone weight†	Cavity height
No. of stones	—	0·68*	0·03	− 0·13
N		25	121	113
Rate of carrying			0·23	− 0·17
N			20	22
Mean stone weight				− 0·11
N				93
Cavity height				—

†Stones placed at nest sites.
*$P<0·001$.

no information about the proportion of stones carried by each member in most cases. We performed this analysis for males and females separately for stones carried before the first clutch and for stones carried per season to nest sites (data for 1988–1992) and to all cavities (data for 1989–1991 only). Repeatabilities for males were high for the seasonal total of stones carried to nest sites and to all sites, but were statistically significant only for the seasonal total number of stones carried to nest sites (Table III). Repeatabilities for females were very high and highly significant for the seasonal total number of stones (Table III). The relatively

high consistency in stone carrying between years suggests marked individual differences in the propensity to carry stones in both sexes. There was no effect of male or female age (first year or older) on the total number of stones carried before first clutches or during the season (Table IV).

Evaluation of Hypotheses

The nest support hypothesis

This suggests that stones are collected to form a solid base for the nest. It predicts that (1) more stones are carried to crevices and similar sites

Table III. Repeatabilities (r) of stone-carrying variables (logarithmically transformed) with ses and results of ANOVA tests for pairs within years, and for males and females between years, assigning stones carried by pairs to both members

	r	se*	F	df†	P
Within years for pairs					
Total no. of stones					
1988	0·571	0·159	3·58	19, 19	0·004
1989	− 0·301	0·354	0·61	14, 11	0·813
1990	0·697	0·174	4·26	17, 8	0·021
1991	0·606	0·185	3·99	12, 13	0·010
1992	− 0·058	0·257	0·95	14, 16	0·536
Between years for males					
Total no. of stones, first clutches	0·473	0·393	2·09	15, 4	0·248
Total no. of stones at nest sites‡	0·689	0·198	3·88	18, 6	0·050
Total no. of stones per season§	0·831	0·188	6·67	14, 2	0·138
Between years for females					
Total no. of stones, first clutches	0·569	0·310	2·86	11, 5	0·128
Total no. of stones at nest sites‡	0·171	0·417	1·29	15, 7	0·381
Total no. of stones per season§	0·940	0·052	20·50	11, 4	0·005

*Calculated according to Becker (1984).
†Between groups, within groups.
‡Includes only stones at nest sites and on the ground below in 1988–1992.
§Includes stones carried at sites other than nests in 1989–1991.

Table IV. Comparison of stone-carrying behaviour ($\bar{X} \pm$ se) between 1-year-old and older individuals, assigning stones carried by pairs to both members

	Young	Old	t*	P
Males				
Total stones, first clutches	231·0 ± 35·4	319·7 ± 52·6	0·30	0·764
N	6	25		
Total stones at nest sites†	311·0 ± 70·9	287·1 ± 39·2	0·85	0·399
N	6	28		
Total stones per season‡	381·2 ± 63·7	451·4 ± 75·8	0·10	0·918
N	5	20		
Females				
Total stones, first clutches	242·8 ± 51·2	349·3 ± 99·2	0·14	0·891
N	6	15		
Total stones at nest sites†	405·2 ± 124·9	380·5 ± 70·1	0·76	0·456
N	6	19		
Total stones per season‡	554·4 ± 362·7	528·3 ± 107·5	0·26	0·795
N	5	14		

*t-Tests performed on logarithmically transformed data.
†Includes only stones at nest sites and on the ground below in 1988–1992.
‡Includes stones at cavities other than nest sites in 1989–1991.

where there is an obvious need for nest support, (2) nests are located only in sites with stones, and (3) stones are carried only to sites subsequently used for nests.

There was no significant difference in the number of stones at nest sites in crevices and at sites in cavities with horizontal surfaces (crevices: 66·3 ± 12·0, N=34; other sites: 78·8 ± 10·7, N=123; t-test: t=1·24, P=0·11). Similarly, the total weight of stones at nest sites in crevices did not differ from that at other sites (crevices: 137·4 ± 26·9 g, N=32; other sites: 146·0 ± 14·3 g, N=123; t-test: t=0·65, P=0·52). These results do not support the prediction.

Nests were not always placed in cavities with stones (16·3% of 159 nests). Some of the stones were deposited in places without nests and often where there was no possibility of building nests. Frequently, more stones appeared at sites unsuitable for nesting than around the actual nests (in 27% of 73 breeding attempts for which all stones were counted, 1989–1991). At some of these sites stones were found on the ground only as a consequence of the small size or sloping surface of the cavity to which they had been transported (in 10 of 139 sites with stones, these were found only on the ground).

Many stones (on average 37·8%) were found at the nest site, on the ground below the nest-site (on average 36·3%) or in other sites in the breeding territory (on average 27·7%). The number of stones left on the ground and the number associated with the nest were positively correlated ($r=0.33$, $N=151$, $P<0.001$). This indicates that the number of stones on the ground was not the result of small cavities or ledges preventing stones from being deposited at the nest site, but the consequence of more intense stone carrying.

In conclusion, the three predictions derived from the nest support hypothesis were not confirmed.

The thermoregulation hypothesis

This posits that stones may moderate large diel temperature fluctuations and thus reduce the cost of incubation. It would be supported if (1) nests are placed only in sites with stones, (2) there are fewer stones in caves with relatively constant temperatures than in natural cavities, (3) hatching success is positively related to the number of stones and (4) stones reduce the cooling rate of the nest contents. Prediction (3) assumes that although birds may adjust the number of stones to environmental conditions (prediction 2), this number is constrained below optimal levels by carrying costs.

Nests were sometimes found in cavities without any stones (see above), so the presence of stones is not a necessary condition for building a nest. The temperature in natural nest sites fluctuates more and is often lower early in the season and higher later on than the temperature in caves (personal observation), so we should expect fewer stones to be collected at nest sites within the caves. There was no difference in the number or

total weight of stones carried between pairs nesting in caves and natural cavities (number of stones: caves: 324.6 ± 34.5, $N=32$; natural cavities: 313.4 ± 103.2, $N=12$; $t=1.20$, $P=0.23$; weight of stones: caves: 1981 ± 231.9 g, $N=32$; natural cavities: 2111.9 ± 771.4 g, $N=12$; $t=1.00$, $P=0.32$).

The thermoregulation hypothesis predicts that nest temperature should decrease less rapidly in the presence of stones since they would be able to buffer large temperature fluctuations. The cooling rate of a plastic bag with water placed inside nest cups was the same in the presence and the absence of stones (with stones: $0.16 \pm 0.03°C/s$; without stones: $0.14 \pm 0.02°C/s$; paired t-test: $t=1.72$, $df=18$, $P=0.10$).

There was no relationship between stones at nest sites and the proportion of eggs hatching (number of stones: $r=0.07$, $N=47$, $P=0.65$; weight of stones: $r=0.10$, $N=47$, $P=0.50$). Similarly, the hatching success of nests placed in sites without stones was as high as for nests with stones (hatching success: without stones: 0.73 ± 0.21, $N=4$; with stones: 0.84 ± 0.03, $N=43$; $t=1.16$, $P=0.25$). Predated and deserted nests were excluded from these analyses.

In conclusion, we could find no support for the thermoregulation hypothesis.

The weather protection hypothesis

This suggests that a large number of stones may protect the nest from wind, rain, or dust. It predicts that (1) nests are placed only in cavities with stones, and (2) hatching and fledging success as affected by weather are negatively related to the number or the total weight of stones.

Nests were sometimes placed in cavities without stones (see above). We did not record any cases of nesting failure as a result of inclement weather during 1988–1992 ($N=167$ breeding attempts). This suggests that weather conditions are an uncommon cause of reproductive failure in the black wheatear, and that they therefore cannot explain the maintenance of stone-carrying behaviour.

The anti-predation hypothesis

This suggests that stones may prevent predation by mammals or reptiles, or result in an early warning of predation risk to females. Predation of

nest contents in this study was a common cause of reproductive failure (20·6% of 92 first clutches, 23·3% of 30 replacements and 15·6% of 45 second clutches were predated at some stage). We recorded four cases of females being killed while attending nests. The anti-predation hypothesis can be considered to be supported if (1) stone carrying does not prevent the use of the safest nest sites at high altitudes, (2) the presence of stones does not render nest sites more visible to visually searching predators, and (3) nests suffering from predation have fewer stones than successful nests.

Black wheatears use cavities at a variety of heights above the ground with a normal distribution (Fig. 2) but we have never recorded the use of cavities more than 3·7 m above ground level. Cavities close to the ground may be more exposed to mammalian and reptilian nest predators. The use of cavities relative to those available within the same cave suggests that black wheatears strongly prefer cavities above a certain height (M. Lindén, unpublished data). Stone carrying may therefore prevent the use of the safest nest sites at the higher elevations.

The assumption that the presence of stones does not render nest sites more visible to visually searching predators is not likely to apply because we actually used the presence of stones as a cue when searching for nests. The assumption could not be tested directly, but if it applies we predict that territories with more stones should not suffer from increased levels of nest predation. The risk of nest predation was actually higher in territories with more stones (territories where we estimated the number of old stones included in the different years; depredated nests: $3677·6 \pm 973·4$, $N=7$; other nests: $1893·7 \pm 330$, $N=54$; $t=1·68$, $P=0·049$). The assumption is therefore not valid.

Nests suffering from predation did not have fewer stones than other nests (depredated nests: $159·3 \pm 31·8$, $N=29$; other nests: $140·6 \pm 14·0$, $N=123$; $t=0·33$, $P=0·37$).

In conclusion, the anti-predation hypothesis was not supported by our tests.

The sexual display hypothesis

This posits that pair members use the stone-carrying display to assess the quality of their partner and adjust their parental effort accordingly. It can be considered to be supported if (1) laying date is advanced when many stones are

carried, (2) clutch size increases with an increasing number of stones, (3) the number of clutches increases with an increasing number of stones, and (4) the extent of parental care or its consequences measured as number of fledged young can be predicted from the intensity of stone carrying.

Laying date of first clutches was not significantly related to the total number of stones carried before first breeding attempts (1989–1991: $r=0·08$, $N=42$, $P=0·60$). The same was observed for the stones carried to nest sites (nest and ground below, data for 1988–1992: $r=0·03$, $N=74$, $P=0·81$). However, there was a significant negative relationship of laying and hatching dates of first clutches with the number of stones carried to sites other than nests (1989–1991: $r=0·31$, $N=42$, $P=0·048$ and $r=0·43$, $N=33$, $P=0·012$).

Although there is a positive tendency, females did not lay significantly more eggs when a large number of stones was carried to the nest site before first clutches (1988–1992: $r=0·21$, $N=67$, $P=0·089$) or when a large total number of stones was carried (1989–1991: $r=0·30$, $N=37$, $P=0·072$). However, there was a significant positive correlation between the size of first clutches and the total number of stones carried to sites other than the nest before first attempts (1989–1991: $r=0·34$, $N=37$, $P=0·04$).

Females initiated more breeding attempts when large numbers of stones and large total weights of stones were carried to nest sites during the whole breeding season (1988–1992: number of stones: $r=0·32$, $N=55$, $P=0·017$; weight of stones: $r=0·31$, $N=51$, $P=0·026$). However, given the absence of relationships between the total number and weight of stones carried per season and the number of attempts (1989–1991: $r=0·01$, $N=32$, $P=0·94$ and $r=0·03$, $N=32$, $P=0·89$), the association with stones at nest sites may be a mere consequence of the increase in the number of nests built with number of attempts.

Pairs carrying no stones produced fewer fledglings per season than those carrying stones (no stones: $2·29 \pm 0·86$, $N=7$; stones: $4·65 \pm 0·31$, $N=66$; $t=2·31$, $P=0·022$). Annual number of fledged young was not significantly correlated with the total number and the weight of stones carried to nest sites throughout the breeding seasons (1988–1992: number of stones: $r=0·23$, $N=57$, $P=0·08$; weight of stones: $r=0·25$, $N=53$, $P=0·067$) or with the seasonal total number and weight carried to all cavities (1988–1991: number

of stones: $r=0.26$, $N=34$, $P=0.14$; weight of stones: $r=0.23$, $N=34$, $P=0.20$). However, there was a significant association between the seasonal total number and weight of stones carried to sites other than nests and number of fledged young per season (1989–1991: number: $r=0.37$, $N=32$, $P=0.036$; weight: $r=0.39$, $N=32$, $P=0.029$).

Male feeding rate to nestlings was positively associated with the total number of stones carried before that breeding attempt ($r=0.56$, $N=13$, $P=0.048$), while no significant relationship with stone carrying was found for female feeding rate ($r=-0.31$, $N=13$, $P=0.30$). Previous stone carrying was positively associated with the proportion of feeding visits by males (total number of stones: $r=0.64$, $N=13$, $P=0.019$) and negatively with the proportion of feedings by females ($r=-0.64$, $N=13$, $P=0.018$). The intensity of stone carrying did, therefore, reliably reflect the disposition of males to provide parental care.

In conclusion, the stone-carrying activity associated with sites other than nests was a good predictor of female reproductive investment and of reproductive success. Therefore, stone carrying in the black wheatear can be considered to be a post-mating sexual display which is associated with greater reproductive success throughout a protracted reproductive season. Also, stone carrying to all sites reliably reflected the extent of future paternal care. Stone carrying could help females adjust their level of investment to the feeding capacity of their partners.

DISCUSSION

Stone carrying in the black wheatear seems to represent an extreme effort with no obvious utility. Members of both sexes, but particularly males, carry an average of 2 kg of stones before their first clutch, and they repeat this effort before each subsequent clutch. Why should black wheatears spend so much time and energy collecting and carrying stones? We considered five different functional explanations for the maintenance of this costly behaviour. The four hypotheses that attributed a utilitarian function to stone carrying were not supported. There was no evidence that the main function of stones was support for the nest. Similarly, we were unable to find any evidence for the thermoregulation, weather protection and anti-predation hypotheses. If any-

thing, there is a predation cost of the presence of stones because of the increased predation rate in territories with more stones, and because stone carrying prevents utilization of safe nest sites at greater heights above the ground (M. Lindén, unpublished data). All four hypotheses predict that old stones may be just as useful as new stones. Large numbers of old stones were present in cavities and crevices in almost every territory, but females never used these as a foundation for their nests. This suggests that it is the new stones of the current reproductive attempt that are important.

The remaining sexual display hypothesis was supported by some analyses of stone-carrying behaviour. Laying and hatching dates were advanced and clutch size increased when more stones were carried to sites other than nests. These relationships were not significant for the stones carried to nest sites. Also, seasonal reproductive success was positively related to the total number of stones carried to sites other than nests. Again, the number of stones carried to nest sites showed no significant association with reproductive success. The fact that it is the stones with no practical utility with regard to nest construction that are predictors of reproductive investment by females and of reproductive success strongly indicate that stone carrying is a post-mating display and not merely nest-building behaviour. Female black wheatears may invest relatively more in reproduction in response to sexual displays because of the direct (parental care) or the indirect (offspring fitness) benefits acquired from the male. Sexual displays such as courtship feeding or courtship singing may advertise the willingness of males to invest in offspring (e.g. Nisbet 1973; Niebuhr 1981; Greig-Smith 1982; Heywood 1989; Hoelzer 1989). Although male black wheatears do not provide their mates with courtship food, the intensity of the display is positively related to the feeding of young by males, both absolutely and relative to females. Thus, the prediction of direct benefits through paternal care can explain the maintenance of the stone-carrying display. This function does not exclude the possibility that indirect benefits are also involved in the maintenance of the display.

Sexual selection can be considered to consist of a number of different components such as mating success, extra-pair copulation success, differential infanticide, differential abortion, parental

investment, and differential parental investment (Møller 1992). The differential parental investment hypothesis posits that individuals invest relatively more in reproduction if mated to highly attractive partners (Burley 1986, 1988). Differential allocation of parental effort may result in enhanced attractiveness (Darwin 1871; Fisher 1958; Iwasa et al. 1991) or in increased viability and fertility of offspring (Trivers 1972; Zahavi 1975; Pomiankowski et al. 1991) accruing to birds mated to attractive individuals. Differential reproductive investment by females mated to more attractive males has been reported in a number of different bird species (Burley 1986, 1988; Møller 1992; de Lope & Møller, in press; R. Johnston, personal communication; M. Petrie, personal communication; H.-U. Reyer, personal communication). Females of all these studied species have been shown to increase their investment in reproduction in relation to the presence of larger or brighter secondary sexual characters. The stone-carrying display of the black wheatear is special in this context because it is, to our knowledge, the only sexual display described that has a function solely outside the context of mate acquisition.

Another possibility is that females may use the stone-carrying activity of their mates when making decisions about whether to engage in extra-pair copulations with neighbouring males. This possibility appears unlikely for a number of reasons. First, it is unlikely that neighbouring females could use the stone-carrying behaviour of males to assess their quality. We have seen only the female mate and not neighbouring females attend the male during bouts of stone carrying. Second, we have never seen extra-pair copulations or extra-pair copulation attempts during 5 years of intensive field work. Third, we have very infrequently seen within-pair copulations, and these copulations are generally frequent when the likelihood of extra-pair copulations is high (Birkhead & Møller 1992). Fourth, intrusions by males during the fertile period of neighbouring females may indicate a sexual interest in females (Birkhead & Møller 1992), but we have recorded few intrusions. Extra-pair copulations are therefore not likely to explain the maintenance of stone carrying.

The origin of stone carrying in the black wheatear remains unknown. Stones placed around the nests of several species of desert larks have been proposed to maintain the heat balance of

nests in hot desert habitats (Orr 1970), insulate nest contents from the excessive heat of the desert floor (Valverde 1957), or prevent the nest from being covered with sand during storms (Maclean 1970; Harrison 1975). A similar behaviour has been described in the cavity-nesting rock wren, *Salpinctes obsoletus* (Smith 1904) and the New World flycatcher, *Sayornis phoebe* (Richardson 1942). Females of at least seven species of wheatear are known to carry stones to nest sites when actively nest building (Panow 1974). It is possible that stone carrying in the black wheatear originally had a function in supporting the nest or protecting it from inclement weather. Stone-carrying behaviour in the black wheatear differs from that of other wheatears in two respects: males play a major role and the amount of stones carried is highly exaggerated. This is also consistent with a sexual selection explanation for the function of stone carrying in the black wheatear.

Intense bouts of stone carrying must be energetically costly. Stones are carried in the bill in flight, which must be more costly than normal flight owing to the higher wing loading, the forward shift in the distribution of weight, and the added cost of holding the stone. Even if flight distances are usually short (a few metres), stones are carried upwards to cavities or ledges, implying an important lift component. The display is performed in intense bouts, during which as many as 82 stones can be carried without interruption during 30 min (personal observations). The display may be a reliable signal of strength or physical condition (Zahavi 1987; Grafen 1990; Pomiankowski et al. 1991), in the sense that individuals in impaired condition would be unable to carry as many or as heavy stones as individuals in prime condition.

High quality individuals should be able to carry many and heavy stones during subsequent breeding attempts, unless the quality of individuals varies temporally. There was in some years a relatively high repeatability in stone carrying between subsequent breeding attempts by the same pair. There was no significant effect of age on stone carrying, which indicates that the ability of individuals to carry stones does not improve after the first year of breeding. However, there were moderate to high between-year repeatabilities of performance for both males and females. This suggests important inherent differences in stone-carrying ability between individuals.

Stone carrying in the black wheatear appears most similar to ritualized nest building in other species (Newton 1979; Collias & Collias 1984). We suggest that extreme forms of addition of nest materials after courtship in other species may also be driven by post-mating forms of sexual selection. Careful attention should be given in this context to displays that have traditionally been interpreted as serving pair bond reinforcement. To conclude, stone carrying by the black wheatear is a post-mating but pre-nesting sexual display which probably originated from nest-building behaviour, and is maintained because it allows females to adjust their parental investment to the willingness of males to invest in their offspring and/or to their phenotypic quality.

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