



The functional significance of sexual display: stone carrying in the black wheatear

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Abstract. Male black wheatears, *Oenanthe leucura*, carry on average almost 2 kg of stones to cavities inside caves before each clutch is laid. This costly behaviour may play a role in post-mating sexual selection, if females adjust their reproduction to the amount of stones carried by their mates, an hypothesis tested in two field experiments. First, breeding sites with many new stones also contained many old stones from previous breeding seasons. In a stone removal experiment, in which all old stones were removed from half of the territories, but not from control territories, males carried the same amount of stones following the two treatments. Reproductive success was similar in the two treatments, and the number of old stones carried was thus an unimportant feature of the display. Second, either the number of new stones present or those carried could be the important cue of the display; this was tested by manipulating stones during the display period. When the number of new stones was doubled every second day, males reduced their stone-carrying activity, and when the number of new stones was halved every second day, males compensated for the removal. Laying date and annual reproductive success were positively affected by the treatment and the number of stones carried, but not by the number of stones present, suggesting that females pay attention only to the number of stones carried.

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Sexual selection, particularly pre-mating sexual selection, has been the subject of intense study in recent years (reviews by Andersson 1994; Møller 1994a), but post-mating sexual selection has been relatively neglected. Under social monogamy, however, the quality of parental care is a very important determinant of reproductive success (Clutton-Brock 1990), and females that are able to acquire mates with high parenting ability will experience a considerable selective advan-

tage (Heywood 1989; Hoelzer 1989; Price et al. 1993).

Theoretical treatments of direct fitness benefits such as parental care have traditionally assumed that sexual displays directly reflect the ability of signallers to provide parental care (Heywood 1989; Hoelzer 1989; Price et al. 1993). However, Burley (1986, 1988) has shown that males may experience sexual selection advantages through access to mates of high parenting ability because of either differential access or differential parental investment. Differential female access applies when attractive males acquire mates of high fecundity or parenting ability, because such females start breeding earlier, or are better able to compete for access to attractive males, than other females. This was clearly the situation envisaged by Darwin (1871) and Fisher (1930) in their models of sexual selection under monogamy, and several studies have provided evidence for this mechanism (e.g. Burley 1986; Møller 1994a).

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Differential parental investment occurs when the partners of attractive individuals invest differentially in reproduction because the offspring of such males may experience increased viability or mating success. An increasing number of studies have described phenomena that can be interpreted as the result of differential parental investment (Burley 1986, 1988; Møller 1992, 1994a, b; Hoi-Leitner et al. 1993; de Lope & Møller 1993; Petrie & Williams 1993). A better understanding of the role of post-mating sexual selection can be obtained only when a diverse array of examples has been carefully analysed.

A particularly bizarre example of a sexual display involved in post-mating sexual selection is stone carrying by male black wheatears, *Oenanthe leucura*. This species is unique because males (and to a small extent females) carry huge amounts of stones to potential nest sites, and stone carrying is involved only in post-mating sexual selection because males are already mated when they perform their display (Moreno et al. 1994). The black wheatear is a 35–40-g bird with slight sexual size dimorphism and sexual dichromatism (Cramp 1988; Glutz von Blotzheim 1988; Møller et al. in press). Black wheatears are socially monogamous: males defend exclusive territories of a few hectares around potential nest sites, and pairs often remain together throughout the year (Richardson 1965; König 1966; Prodon 1985; Cramp 1988; Glutz von Blotzheim 1988; personal observations).

Approximately 2 weeks before the initiation of egg laying males start to collect stones from the ground and fly with them to cavities or horizontal surfaces situated 0.3–2.7 m above ground usually inside caves. Preceding the first clutch, a male carries on average 277 stones weighing 1.8 kg during a 1-week period (Moreno et al. 1994). The evolutionary origin of this behaviour remains obscure, because males of species of the genus *Oenanthe* or the family Turdidae do not contribute to nest building. Very few stones are carried at the beginning and the end of the stone-carrying period, while most stones are carried during a few days of intensive work (Moreno et al. 1994). Møller et al. (in press) estimated peak energy output during stone carrying to be approximately 400 W/kg, which is close to the upper limit of sustainable power by any type of muscle and, for example, by far exceeds the energy output of hovering hummingbirds at 240 W/kg (Goldspink

1977). Females may carry some stones later just before they start building the nest. The stones are carried in the beak, and so are relatively small and flat (Moreno et al. 1994), features that make it easy to discriminate between stones carried by black wheatears and stones from the environment. The major stone pile in a territory usually serves as the foundation of the nest (82% of 113 breeding attempts), and old stone piles thus serve as indicators of old nest sites. The mass of stones carried is considerable, and many potentially suitable nest sites high above ground level are not used, perhaps because the birds are unable to lift stones that high. The stone-carrying behaviour may thus constrain the use of potential nest sites, which are either natural holes in canyons and gullies or cavities inside abandoned buildings or man-made caves. Females lay 3–6 eggs per clutch (Soler et al. 1995), which they incubate alone. Both sexes feed the nestlings, but males are particularly active early during the nestling period (Moreno et al. 1994). Individual pairs initiate up to five breeding attempts and rear three broods between late March and late August. Similar amounts of work are performed before the initiation of subsequent clutches by the same pair during the same season, and males are consistent in the amount of stones carried before each clutch in some years, but not in others (Moreno et al. 1994). The stone piles have no obvious function in terms of nest support, nest insulation, or nest protection against potential predators, but the amount of stones carried appears to be used by females to assess mate quality (Moreno et al. 1994).

In this paper we test the adaptive significance of this display. Females may use the display to assess male phenotypic quality in terms of working ability. Black wheatears re-use cavities for breeding, and large amounts of stones may thus accumulate in frequently used territories. The number of new stones carried by males is positively correlated with the number of old stones present from previous breeding seasons (Moreno et al. 1994), perhaps because males that are able to carry many stones prefer sites that are frequently occupied. Females may thus use the amount of new stones carried, the amount of old stones, or both, to assess male phenotypic or genotypic quality.

First, we determined the effect of the presence of old stones on current stone carrying and

female reproductive decisions. If the presence of old stones is important for the amount of stones carried by males and hence for female reproduction, then experimental removal of old stones from some territories should delay laying and reduce female reproductive success. Second, we tested whether it is the presence or the actual carrying of new stones that affects female reproductive decisions in terms of timing of laying and seasonal reproductive success. To test this, every second day during the stone-carrying period we either removed half of all new stones or added as many new stones as had been carried by the male during the preceding 2 days.

METHODS

Study Site

We worked during the breeding seasons 1988–1992 in the Hoya de Guadix, South Spain (37°18'N, 3°11'W). This is an area of deep canyons and ravines with eroded slopes, which cut into high plateaux (altitude of approximately 1000 m) covered by sparse vegetation and agricultural crops. Annual precipitation is very scarce and irregular (below 300 litres per m²) and temperatures vary widely from freezing during the long winter and spring to maxima above 40°C during the hot, dry summer. Diurnal fluctuations in temperature are also large from frost during the night to above 25°C during daytime in spring. We studied 20 areas, several of them in more than 1 year depending on the presence of black wheatears.

Capturing and Ringing Adults

Most males were caught at the beginning of the season by mist netting, using playback of song and a male stuffed decoy. Most females were captured with baited spring traps or mist nets while feeding nestlings. A number of roosting birds were captured during winter at night inside caves and buildings. All birds were provided with an individual combination of colour rings and a numbered aluminium ring from the Spanish Institute for Nature Conservation (ICONA), and this allowed recognition of captured individuals both within and between seasons.

Recording Reproductive Parameters

Reproductive success was measured during repeated visits to the nest sites. We recorded the

following variables: (1) laying date which was the date when the first egg of the first clutch was laid; (2) clutch size; (3) number of fledglings measured as the number of nestlings present when ringed at an age of 11–13 days; (4) the annual number of breeding attempts (successful or unsuccessful) initiated by a pair; and (5) the annual reproductive success as the total number of fledglings in all the breeding attempts of a year.

Removal of Old Stones

Territories were randomly assigned to each of two treatments in late February 1992 well before the start of stone carrying and reproduction: (1) removal of all stones from old sites; and (2) manipulation of all stones in old sites as a control treatment. One of us (M.S.) collected all old stones in cavities and on the ground below cavities in 14 territories assigned to the removal treatment, and deposited them outside the territories. The old stones were manipulated, but not removed, in 12 territories assigned to the control treatment. We recorded the number of new stones collected during the first breeding attempt as described above. Reproductive parameters were subsequently recorded throughout the reproductive season.

Manipulation of New Stones

We manipulated the number of new stones present in a number of territories in 1989 at all sites to which stones were carried. All old stones were sprayed with a grey colour before the start of the breeding season to allow us to distinguish between old and new stones. Territories were randomly assigned to one of three treatments: (1) stone addition, (2) control and (3) stone removal. Territories were randomly assigned to addition or control, or to removal or control. Eight territories were assigned to each of the addition and the removal treatments while 15 were assigned to the control treatment. We visited all territories every second day from the start of the breeding season; stone carrying mainly took place during periods of 2–19 days, on average 6.9 days (Moreno et al. 1994). The entire stone-carrying period was sampled, and individual males were recorded carrying stones on 2–10 visits at 2-day intervals. In territories receiving the addition treatment, we added as many stones as had been collected by the black wheatear during the previous 2 days, while

Table I. Effect of removal of all stones from old sites on stone carrying and reproduction in the black wheatear in 1992

	Treatment		<i>t</i>
	Removal	Control	
Stone carrying			
No. of stones carried	161 (53)	165 (60)	0.76
Reproduction			
1st laying date	105 (3)	102 (5)	0.42
1st clutch size	4.00 (0.00)	4.00 (0.17)	0.00
Fledged young 1st clutch	2.36 (0.58)	1.23 (0.52)	1.50
No. of breeding attempts	2.40 (0.16)	2.55 (0.15)	0.64
Annual no. of fledged young	6.88 (1.10)	6.25 (0.85)	0.43
<i>N</i>	11	12	

Values are means (\pm SE).

we removed half of the stones collected by the birds during the previous 2 days in the removal treatment. In the control treatment we just checked for and counted new stones. The experiment ended in each replicate as soon as the first egg had been laid, and stone carrying had ceased. Reproductive parameters were subsequently recorded as described above.

Statistical Analyses

Different measures of stone carrying are positively correlated. For example, the total number and the total mass are strongly positively correlated with each other (Moreno et al. 1994). In the present study we used the total number of stones carried before laying of the first clutch as a measure of the intensity of the display.

The number of stones carried and the various reproductive parameters were compared in unpaired *t*-tests in the experiment in which old stones were removed. The number of stones present and stones carried were \log_{10} -transformed before analysis. The number of fledged young in the first clutch, the number of breeding attempts, and the total number of fledged young were \log_{10} -transformed before analysis.

In the manipulation of new stones, the number of stones carried and the number of stones present were compared between experimental treatments using one-way analysis of variance after \log_{10} -transformation. The number of fledged young in the first clutch, the number of breeding attempts, and the total number of fledged young were \log_{10} -transformed before analysis. The linear

relationships between reproductive parameters and the number of stones carried and the number of stones present, respectively, were determined in analyses of covariance with treatment as a factor and the number of stones present and carried, respectively, as covariates.

All tests are two-tailed. Values reported are means (\pm SE).

RESULTS

Removal of Old Stones

All the territories were already occupied when treatments were applied. Three territories were abandoned after the manipulation, but all of these received the control treatment. If the presence of old stones was important for stone carrying, we predicted that males would carry more stones in territories without old stones. This was not the case (Table I). Male black wheatears in control territories carried as many new stones as males in removal territories. The experimental treatment thus did not affect the stone-carrying behaviour of males.

If the presence of old stones was important for the reproductive decisions of female black wheatears, we would predict that females would reproduce at a higher rate in control than in removal territories. There was no indication that reproduction differed between removal and control treatments, and most of the reproductive parameters were almost identical (Table I). This suggests that female black wheatears do not respond to the presence of stones collected in previous breeding attempts.

Table II. Effect of manipulation of the number of new stones on stone carrying and reproduction in the black wheatear in 1989

	Treatment			<i>F</i>	<i>P</i>
	Addition	Control	Removal		
Stone carrying					
No. of stones present	447 (107)	309 (44)	227 (58)	0.60	NS
No. of stones carried	240 (48)	309 (44)	426 (43)	4.18	0.026
Male morphology					
Wing length (mm)	98.9 (0.9)	98.5 (0.7)	99.1 (0.8)	0.81	NS
Body mass (g)	37.4 (0.8)	37.5 (0.6)	37.5 (0.9)	0.72	NS
Reproduction					
Nest height (m)	1.61 (0.24)	1.66 (0.17)	1.58 (0.33)	0.33	NS
1st laying date	128 (5)	123 (5)	110 (7)	3.35	0.048
1st clutch size	3.75 (0.10)	3.80 (0.11)	3.88 (0.13)	0.19	NS
Fledged young 1st clutch	1.50 (0.33)	1.60 (0.34)	1.75 (0.59)	0.07	NS
No. of breeding attempts	1.50 (0.19)	1.80 (0.28)	2.25 (0.41)	1.11	NS
Annual no. of fledged young	2.50 (0.61)	2.80 (0.52)	4.13 (0.17)	4.14	0.030
<i>N</i>	8	15	8		

Values are means (\pm SE). *F*-values are from one-way analyses of variance.

Table III. Analyses of covariance between reproductive variables and treatment, number of stones present, and number of stones carried, respectively

Reproductive variable	Model	Treatment	Stones present	Stones carried	Residual
1st laying date	599.53**	256.42*	47.72	238.30*	67.96
1st clutch size	0.020	0.028	0.015	0.016	0.183
Fledged young 1st clutch	1.41	0.99	4.41	2.49	1.68
No. of breeding attempts	0.584	0.163	0.043	0.040	1.071
Annual no. of fledged young	4.286**	6.318***	0.294	3.000*	0.643
<i>df</i>	4	2	1	1	26

The number of stones present and the number of stones carried were \log_{10} -transformed before calculations. Values are mean squares.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Manipulation of New Stones

Our manipulation successfully generated significant differences in the number of stones carried, but not in the number of stones present at the end of the experiment (Table II). There were no statistically significant differences in male morphology or in nest height above ground level between treatments (Table II).

There was a statistically significant difference in laying date and annual number of fledged young between experimental groups, with laying date being advanced and annual reproductive success being increased by stone removal (Table II). The laying date of the first clutch was strongly negatively related to the number of stones carried by

males (Fig. 1a; $r^2 = 0.26$, $F_{1,29} = 11.52$, $P = 0.002$). Treatment and the number of stones carried, but not the number of stones present, appeared to affect the timing of laying directly, the negative relationship indicating that laying was earlier when many stones were carried (Fig. 1). The size of first clutches and the size of first broods at fledging were not significantly related to the number of stones (Table III). Similarly, the annual number of breeding attempts was weakly positively, but non-significantly related to the number of stones (Table III). However, the annual number of fledglings was significantly positively related to the number of stones carried (Fig. 1b; $r^2 = 0.12$, $F_{1,29} = 5.17$, $P = 0.03$). Only

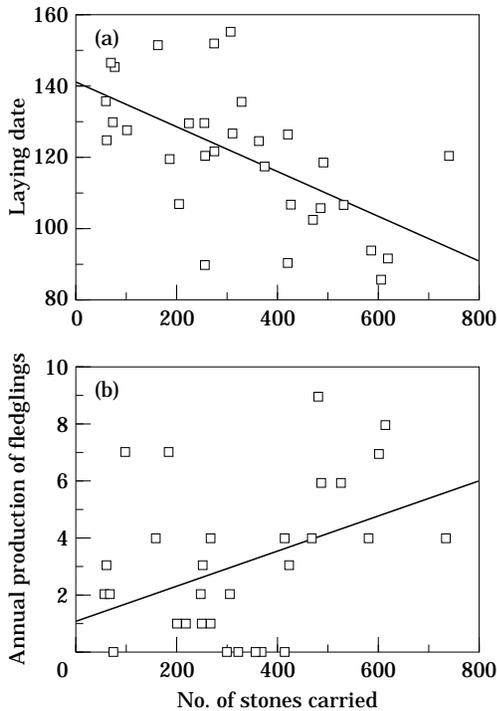


Figure 1. The relationship between stone carrying and (a) laying date (1=1 January) and (b) annual production of fledglings. The lines are the regression lines with the equations Laying date = $134.8 - 0.007$ (SE = 0.002) No. of stones carried, and Annual production of fledglings = $1.67 + 0.001$ (SE = 0.0003) No. of stones carried.

treatment and the number of stones carried, but not the number of stones present, appeared to affect the annual production of offspring directly (Table III). In conclusion, the number of stones carried by males, but not the number of stones present, appeared to affect laying date and annual reproductive success.

DISCUSSION

Our stone-removal experiment clearly demonstrated that old stones from previous breeding seasons were irrelevant to females. Males carried as many new stones when old stones were removed, as when old stones remained in the territory (Table I). Female reproduction did not differ between territories with old stones removed and territories with old stones present (Table I), suggesting that females, if anything, pay attention

to the number of new stones rather than the number of old stones from previous breeding seasons.

In the second experiment we tested whether females use the number of stones carried or the number of new stones present as a cue in their reproductive decisions. We found statistically significant differences in laying date and annual reproductive success between treatments (Table II) and a strongly negative relationship between laying date and the number of stones carried (Fig. 1, Table III). Laying date is an important reproductive parameter because early laying increases the probability of recruitment in many bird species (e.g. Lack 1966), including the black wheatear (Soler et al. 1995). Annual production of fledglings increased with an increasing number of stones carried (Table III), either because females put more effort into reproduction when mated to males that carried many stones, or because males that carried many stones provided more food for the offspring. The relationships between stone carrying and female reproductive parameters suggest that the expression of the stone-carrying display directly affects female reproductive decisions in terms of laying date and annual reproductive effort. However, there was no effect of the number of new stones present on reproduction. This suggests that females must observe the stone-carrying display before it affects their reproductive decisions. This suggestion is consistent with our observations of the stone-carrying display during which males carry stones from the ground, while females observe them and sometimes lift a few stones that have been carried, as if assessing their mass (Moreno et al. 1994).

The experimental treatment had an effect only on the number of stones carried, and not on the number of stones present (Table II). The analyses of covariance also indicated that it was the number of stones carried that was the important determinant of laying date and the annual production of fledglings (Table III). Of course, we cannot with this experiment identify the exact cue used by females in their reproductive decisions. However, the direct relationships between reproductive parameters and the number of stones carried (Fig. 1), and the fact that females observe males during the stone-carrying events, suggest that the important cue is the number of stones carried rather than the number of stones present in a territory. This interpretation is also supported by the results

of the first experiment, which demonstrated that reproductive performance was independent of whether old stones from previous breeding seasons were present or absent.

The fact that the manipulation of old stones present does not affect male stone-carrying activity, while manipulation of the number of new stones recently carried does, seems contradictory. However, while the first experiment manipulated the number of old stones from the previous breeding season, the second experiment manipulated the number of stones carried recently by the specific male. Males thus appear partially to adjust their stone-carrying activity to the number of stones present of those carried by themselves. However, the extreme variance in the number of stones carried by different males, which ranges from 0.2 to 10.1 kg (Moreno et al. 1994), suggests that features other than the number of stones present are important determinants of the number of stones carried.

It may seem absurd that females base their reproductive decisions on extravagant male sexual displays. However, our result is not different from that of a number of other studies demonstrating that females invest more in reproduction when mated to a male with an extreme secondary sexual character (Burley 1986, 1988; Møller 1992, 1994a, b; Hoi-Leitner et al. 1993; de Lope & Møller 1993; Petrie & Williams 1993). Which benefits may females acquire from responding to the male display? They could obtain direct fitness benefits if, for example, the expression of the display directly reflected the ability of males to provide parental care. This possibility is partly supported by a weak, but positive, relationship between the intensity of male parental care and the number of stones carried by males (Moreno et al. 1994). Alternatively, females may obtain indirect fitness benefits if the intensity of the stone-carrying display reflects heritable male attractiveness or viability. It would seem obvious that males in good body condition could carry more stones than males in poor condition, and that stone carrying would be a reliable, condition-dependent display. Differences in condition might reflect genetic, environmental and genotype-environmental effects. Female differential investment resembles what one would predict from the sexy son hypothesis, which is based on the assumption that a fecundity cost of a sexual display is reimbursed in terms of an increased

attractiveness of offspring (Weatherhead & Robertson 1979). Females that invest relatively more in the offspring of males carrying many stones might rear offspring that are also able to carry many stones or offspring of higher viability.

In conclusion, the stone-manipulation experiments demonstrated that females adjust their reproductive decisions to the number of new stones carried by males, but not to the number of new stones or old stones present in a breeding territory. Females may benefit from paying attention to the stone-carrying display in terms of direct or indirect fitness benefits.

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