Weight lifting and health status in the black wheatear

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Male black wheatears *Oenanthe leucura* demonstrate an exaggerated sexual display by carrying many heavy stones (on average 3.1 kg per season for this 35-g passerine) to cavities inside caves before the start of each clutch. The energetic cost of this display is mainly determined by the size of stones, which gives rise to the largest power output of a muscle ever recorded for any species (400 W/kg), rather than the total number of stones carried, which only amounts to 1% of daily energy expenditure for a black wheatear male. We tested whether stone carrying reflected male health status by removing two primaries from a group of males, but not from controls. Experimental manipulation did not significantly affect stone carrying. Similarly, male health status measured as hematocrit, leukocyte concentration, and T-cell response to an injection with phytohemagglutinin (a lectin) was not affected by experimental manipulation. Male black wheatears that carried very heavy stones, each on average more than a quarter of their own body mass, had a stronger T-cell response to injection with a lectin than males that carried light stones. Furthermore, males that carried heavy stones had a reduced hematocrit level, which may have arisen from the effects of the extremely heavy work load. Rate of stone carrying and mass of stones was not significantly related to the abundance of two species of ectoparasites. Male black wheatears with high T-cell responses were significantly more likely to survive than males with low responses, but other measures of male performance did not differ significantly between survivors and nonsurvivors. The male stone-carrying display thus reflects male health status as demonstrated by a component of immunocompetence. *Key words:* hematology, immune response, *Oenanthe leucura,* phytohemagglutinin, sexual selection, survival, T-cell response, wheatears. *[Behav Ecol 10:281–286 (1999)]*

Secondary sexual characters and sexual displays are often condition dependent in their expression, with excessively displaying individuals having superior condition both before as well as after the display (review in Andersson, 1994). Receivers of a sexual signal may use information on the condition of the signaler to obtain direct fitness benefits in terms of fertility or costly parental care, or indirect benefits in terms of genetically based viability. Differences in condition may arise as a consequence of individual differences in parasitism, hypothesized to be caused by genetically based resistance to parasites (Hamilton and Zuk, 1982). Sexual selection based on condition-dependent secondary sexual characters may continuously reflect that ability of individuals to resist attacks from currently detrimental parasite genotypes because frequency-dependent selection maintains continuous variation in host resistance (Hamilton and Zuk, 1982). There is mounting evidence that parasites play an important role in host sexual selection (Hamilton and Poulin, 1997; Møller et al., 1999), particularly because host sexual displays reliably reflect host immunity rather than the burden of innocuous parasites often studied by behavioral ecologists (Møller et al., 1998a).

Host immunity has been hypothesized to be directly revealed by secondary sexual characters (Folstad and Karter, 1992), either because of the immunosuppressive effects of biochemicals necessary for development of the sexual displays (Folstad and Karter, 1992), or because reproductive effort cannot be used simultaneously for sexual display and immunity (Møller and Saino, 1994; Wedekind and Folstad, 1994). Comparative evidence suggests that bird species with extrav-

agant sexual coloration invest more heavily in immune function as assessed from the size of their immune defense organs and the circulating levels of leukocytes than bird species with sexually monomorphic displays (Møller et al., 1998a). Furthermore, there is a positive relationship between investment in immune function in birds and extrapair paternity, which constitutes a measure of intensity of an important component of sexual selection (Møller, 1997a). Male birds often have depressed immune function when adults, and the degree of immunodepression is positively related to the intensity of sexual selection as estimated from the frequency of extrapair paternity (Møller et al., 1998b). There is a growing number of intraspecific studies demonstrating associations between the expression of secondary sexual characters and various measures of immunity. For example, Saino and Møller (1996) demonstrated that a measure of B-cell–mediated immunity was depressed by experimentally increasing the size of a secondary sexual character in the barn swallow *Hirundo rustica,* and the measure of immunity was positively related to the original expression of the sex trait. These results are consistent with the secondary sexual character being a reliable signal of one component of immunocompetence. Studies of 12 species have so far investigated the relationship between immunity and morphological displays such as colors and the size of secondary sexual characters, and these studies found positive associations between immunocompetence and exaggeration of sexual displays (review in Møller et al., 1999). Currently, we are only aware of a single study investigating the relationship between a behavioral display and immunity (Saino et al., 1997e). Hence, there is a need for additional studies of the role of immunity in behavioral sexual displays.

The black wheatear is a small (about 35 g) passerine bird that is resident in Spain and Morocco. Some weeks before egg laying, males start to collect stones from the ground and place these in cavities in cliffs, caves, or buildings while the female

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mate is present (Moreno et al., 1994; Soler et al., 1996). Individual males carry stones that each weigh on average from 3.4 g to 8.2 g for different males, in total 0.3–10.1 kg, on average 3.1 kg of stones per season (Moreno et al., 1994). The stone-carrying activity is performed before each breeding attempt during the breeding season, although more stones are carried before the first breeding attempt (Soler et al., 1995). Male morphology is adapted to stone carrying: males have large wing areas that give rise to a low wing loading compared to that of females (Møller et al., 1995). Male stone carrying is inversely related to wing loading (Møller et al., 1995). Females mated to males that carry more stones start laying earlier, lay more eggs and clutches, and on average raise more offspring per season than females mated to males that carry few stones (Moreno et al., 1994; Soler et al., 1996). Experimental manipulation of the number of stones by addition or removal of stones demonstrated that males are able to compensate for stone removal, and they carry stones at a slower rate if stones are added (Soler et al., 1996). Handicapping of males by removal of primary feathers from each wing resulted in a reduction in stone-carrying activity, which in turn reduced female reproductive effort (Soler et al., 1996).

The aim of the present study was to test the hypothesis that males signal their current health status to their partner by carrying many heavy stones. We predicted that males that carry many heavy stones would have lower hematocrit levels, lower concentrations of leukocytes, lower erythrocyte sedimentation rates, stronger immune responses, and have fewer parasites than males that carry fewer stones. High levels of hematocrit are indicative of recent exercise, whereas excessive exercise caused by extreme work load will depress haematocrit (review in Birchard, 1997; Harrison, 1985). Hence, we predicted that the extremely heavy work load of male black wheatears during bursts of stone carrying should result in a reduction in hematocrit. Circulating levels of leukocytes reflect current infection status for a number of parasites and diseases, with high levels indicative of poor health (e. g., Dein, 1986). If male black wheatears that carry many heavy stones are particularly healthy, we would predict that they had lower concentrations of leukocytes than males that carry few light stones. The two main branches of the vertebrate immune system are cell-mediated and humoral immunity (Klein, 1990; Roitt et al., 1996; Wakelin, 1996). Here we assessed one component of immune function in black wheatears, a measure of T-cell–mediated immunity, based on the intensity of swelling of the skin of the patagium in response to an injection with a lectin (Cheng and Lamont, 1988). We used this method because it does not require extensive recapture of individuals. It is based on the observations that phytohemagglutinin has a strong mitogenic effect on T-lymphocytes, stimulating macrophage infiltration and dense perivascular accumulation of lymphocytes (Goto et al., 1978; McCorkle et al., 1980; Stadecker et al., 1977). The increase in thickness of the patagium of the wing has been shown to correlate with a number of components of fitness in free-living birds (e. g., Saino et al., 1997b). If male black wheatears carrying many heavy stones are healthy, we would expect them to have stronger T-cell responses than males carrying few light stones.

The predictions were tested by experimentally manipulating the working ability of male black wheatears by either removing primaries number four and five or by handling the wings without feather removal, and subsequently assessing the three health parameters of the males. Previous experiments have demonstrated that feather removal has a strong negative effect on stone-carrying ability of males because it increases wing loading and hence reduces the stone-lifting ability of males (Møller et al., 1995).

MATERIALS AND METHODS

Study area

We studied black wheatears in Hoya de Guadix, Granada Province, Spain, during March–July 1996. Breeding sites of this species are restricted to areas with nest holes in cliffs or deserted buildings. Based on our experience from a previous study, we located all potential breeding territories and captured the territory owners. We found 38 territories with black wheatears. Not all birds were captured due to practical difficulties, and the final sample size was thus reduced to 29.

We searched territories regularly for nests and recorded the breeding activities of pairs, including information on date of start of laying, clutch size, brood size at fledging, number of broods, and seasonal reproductive success. We obtained information on precipitation for the spring months January–March for the weather station at Guadix, which is in the center of our study site (Consejería de Medio Ambiente, 1997).

Capture, measurement, and blood sampling of adults

Adult black wheatears were captured in snap traps with a mealworm. After capture adults were measured (length of wing, outermost tail feathers, length of white part of seventh rectrix, all measured to the nearest 1 mm, length of tarsus to the nearest 0.1 mm) and weighed (with a Pesola spring balance to the nearest 0.1 g). When nestlings were approximately 13 days old, they were measured as described for adults.

We removed a sample of blood from the brachial vein of each adult black wheatear and placed the sample in two standard 100-μl capillary tubes. The capillary tubes were stored horizontally in a cooling box with frozen cooling blocks. Tubes were subsequently centrifuged for 10 min at 11,500 rpm, and the hematocrit and the buffy coat (which mainly consists of leukocytes and was used as an estimate of leukocyte concentration; e.g., Dein, 1986) were expressed as the percentage of the capillary (measured to the nearest 0.1 mm) occupied by erythrocytes and the buffy coat, respectively. The plasma and the erythrocytes were then separated and frozen.

We assessed T-lymphocyte immune responsiveness by injecting the patagium with phytohemagglutinin (PHA). The thickness of the left- and right-wing webs (patagia) of adult males at premarked sites was measured three times with a caliper to the nearest 0.01 mm. The right-wing web was injected with 0.2 mg of PHA (Sigma, L-8754) in 0.04 ml of phosphate-buffered saline (PBS). The left-wing web was injected with 0.04 ml PBS only. Males were kept in a cage for 12 h and provided with mealworms and water ad libitum. After 12 h we remeasured the thickness of wing webs at the inoculation sites. The measure of immune response is the difference in wing web thickness after 12 h and immediately after injection for the PHA-inoculated wing minus the difference in wing web thickness after 12 h and immediately after injection for the PBS-inoculated wing (see Saino et al., 1997b, for details). The measurements of PHA response of the same individuals were significantly repeatable ($F = 8.83$, df = 23,24, $p = .0068$). The assessment of immunity was performed during the prebreeding period in early spring during the time of stone carrying.

We assessed the abundance of two species of ectoparasites in adult males. The abundance of Mallophaga of the suborder Ischnocera was assessed from the number of holes in the primaries, secondaries, and rectrices because these feather lice chew large, clearly visible holes in feathers (e.g., Møller, 1991). This estimate of lice abundance is strongly positively correlated with the abundance estimated directly from counts of lice in another passerine (Møller, 1991). Black wheatears are parasitized by an unidentified species of hematophagous mite that sucks blood from the skin around the eyes and the
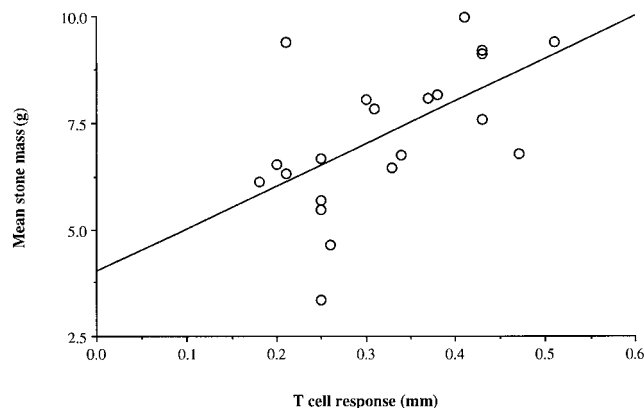
Figure 1
Mean mass of stones (g) carried by male wheatears in relation to their T-cell response (mm). The linear regression line has the equation $y = 4.00 + 9.98x$.

Figure 2
Mean mass of stones (g) carried by male wheatears in relation to their hematocrit. The linear regression line has the equation $y = 24.12–31.73x$.

bill. The abundance of this species of mite was estimated by carefully counting the number of mites around the eyes and the bill.

We repeatedly searched the study area during intensive field work during 1997–1998 for the presence of survivors from 1996. Male black wheatears are resident passerines that often stay in their territories throughout the year. Breeding dispersal is very restricted, usually being limited to movements to a neighboring territory (M. Soler et al., unpublished data). Hence it is unlikely that males that were not resighted in 1997–1998 were breeding elsewhere.
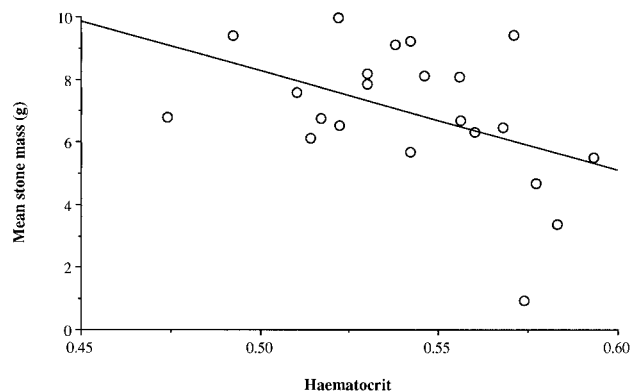
Experimental manipulation of stone-carrying ability

We manipulated the ability of males to carry stones by randomly allocating a sample of males captured before the start of stone carrying to either of two treatments: (1) removal of primaries number four and five by cutting the feathers at the base (manipulation) or (2) capturing the male and handling the wings as in the first treatment without cutting them (control). We did not use a sham manipulation by, for example, removing the tips of two feathers in some birds, as done previously (Møller et al., 1995) because a previous experiment demonstrated that there were no differences between males that were handled and males that were sham manipulated (Møller et al., 1995). Males were manipulated on average 14.9 days (SE = 4.3, $n = 29$) before they were tested for immune responsiveness, and there was no difference between experimental and control males [mean (SE), experimental: 15.1 (6.2), $n = 14$; control: 14.7 (6.0), $n = 15$]. The two groups of males did not differ significantly ($p > .05$) with respect to any of the morphological measurements recorded.

Statistical analyses

Hematocrit and leukocyte concentration were expressed as the proportion of erythrocytes and leukocytes, respectively, that constituted the entire capillary tube. We assessed the reliability of the estimates of hematocrit and leukocyte concentration in different capillary tubes with repeatability analyses that quantify the amount of within-individual as opposed to among-individual variation (Falconer and Mackay, 1996).

Differences between experimental treatments were assessed by means of one-way analyses of variance. When several analyses were made for a single data set, the level of significance of 5% was adjusted for the number of tests made using the sequential Bonferroni adjustment (Holm, 1979). Not all var-

iables were estimated for all males, and sample sizes thus differed slightly among the statistical tests. Values are reported as means ± SE.

RESULTS

Stone carrying and health status

Before the first clutch, male black wheatears carried, on average, 163 ± 2 stones ($n = 29$ males) weighing 6.54 ± 0.35 g, in total 1173 ± 184 g. The height of the nest, where most stones were located, was 148 ± 10 cm ($n = 29$). The experimental treatment did not significantly affect the number of stones carried ($F = 0.84$, df = 1,27, $p = .37$; experimental: 183 ± 35, $n = 14$; control: 137 ± 15, $n = 15$), average mass of stones ($F = 1.45$, df = 1,27, $p = .24$; experimental: 7.02 ± 0.360 g, control: 6.16 ± 0.56 g), total mass of stones ($F = 1.00$, df = 1,27, $p = .33$; experimental: $1,378\pm283$ g; control: 1.062 ± 238 g), or nest height ($F = 1.05$, df = 1,27, $p = .31$; experimental: 137 ± 15 cm; control: 155 ± 12 cm).

The total number of stones carried by males was positively correlated with the mean mass of stones ($r = .45$, $n = 29$, $p = .019$), but it was unrelated to the height of the cavity ($r = .08$, $p = .78$). Similarly, mean stone mass for individual males was unrelated to the height that the stones were carried ($r = -.08$, $p = .71$).

The experimental treatment did not significantly affect the phytohemagglutinin response ($F = 1.26$, df = 1,19, $p = .29$; experimental: 0.303 ± 0.035, $n = 11$; control: 0.354 ± 0.029, $n = 10$). The power of this test is low, so the null hypothesis of no significant difference cannot readily be accepted. Average mass of stones was positively correlated with the response to injection with phytohemagglutinin [Figure 1; $F = 9.27$, df = 1,19, $r^2 = .33$, $p = .0067$; mean stone mass (g) = $(4.00\pm1.10) + [(9.98\pm3.28)\times\text{T-cell response}]$ (mm)]. The total number of stones carried was not significantly related to immune responsiveness to phytohemagglutinin ($F = 0.002$, df = 1,19, $p = .96$).

Hematocrit estimates were significantly repeatable among blood samples collected from the same male ($F = 58.22$, df = 22,23, $p < .0001$). Hematocrit values were not affected significantly by the experimental treatment ($F = 0.12$, df = 1,20, $p = .73$). Male black wheatears that carried heavy stones had a low hematocrit value compared to males that carried light stones [Figure 2; $F = 5.13$, df = 1,20, $r^2 = .16$, $p = .035$; mean stone mass (g) = $(24.12\pm7.60)—(31.73\pm14.00) \times$ hematocrit]. The fit was not significantly improved by a polynomial
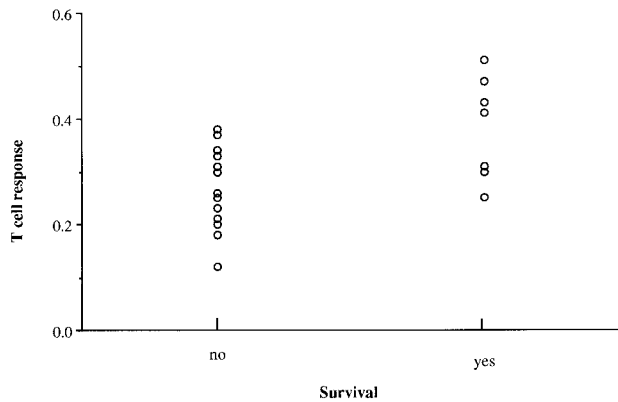
Figure 3
Survival of adult male black wheatears in relation to their T-cell response (mm).

regression. The total number of stones was not significantly related to hematocrit ($F = 1.44$, df = 1,20, $p = .24$).

Leukocyte estimates were significantly repeatable among blood samples collected from the same male ($F = 4.73$, df = 22,23, $p = .040$). Leukocytes were not significantly affected by the experimental treatment ($F = 0.27$, df = 1, 19, $p = .69$). The concentration of leukocytes in the blood was not significantly related to the two measures of stone carrying ($F < .29$, df = 1,19, $p > .60$).

The prevalence of the single species of *Mallophaga* was 0.86 in adult males ($n = 101$), and its abundance was 5.62 ± 0.41. The prevalence of the mite was 0.36 ($n = 101$), and its abundance was 3.03 ± 0.58. The abundance of the two species of parasites was not significantly related to the two measures of stone carrying ($F < 1.40$, df = 1,27, $p > .25$).

Health status and reproductive success

The experimental treatment did not significantly affect laying date, clutch size, or seasonal production of fledglings (laying date: $F = 3.04$, df = 1,35, $p = .09$; clutch size: $F = 0.06$, df = 1,35, $p = .81$; no. of fledglings: $F = 0.30$, df = 1,35, $p = .59$). The three measures of health status were not significantly related to the life-history variables. Laying date, clutch size, and seasonal production of fledglings were not significantly related to phytohemagglutinin response ($F < 1.08$, df = 1,19, $p > .31$). Similarly, hematocrit was not significantly related to the three life-history variables ($F < 0.22$, df = 1,19, $p > .38$). Males with a high leukocyte concentration started breeding later than other males ($F = 5.53$, df = 1,19, $r^2 = .19$, $p = .03$; laying date = $(10.18\pm9.03) + [(1600.54\pm680.73) \times$ leukocyte concentration]). There was no significant relationship between leukocyte concentration and clutch size or number of fledglings ($F < 0.69$, df = 1,19, $p > .42$). The single statistical significance disappeared after Bonferroni-adjustment for multiple tests of the hypothesis.

Health status and survival of adult males

Males that survived from 1996 to 1997 or 1998 had a stronger immune response than males that were not recorded in the study area in 1997 or 1998. The T-cell response of survivors was 0.366 ± 0.036 mm ($n = 8$), but males that were not subsequently resighted had a response that was more than 25% lower (0.269 ± 0.017 mm ($n = 17$; $t = 2.81$, df = 23, $p = .01$; Figure 3). The only variable that approached statistical significance was leukocyte concentration, which tended to be elevated among nonsurvivors (survivors: 0.011 ± 0.002, $n = 8$;

nonsurvivors: 0.015 ± 0.001, $n = 17$; $t = 1.75$, df = 23, $p = .09$). None of the other measures of male performance differed significantly between survivors and nonsurvivors.

Weather conditions in 1996

The spring of 1996 was characterized by extreme precipitation in our study area, with 453.1 l/m² of rainfall in this otherwise extremely dry area (Consejería de Medio Ambiente, 1997). The average for 1990–1995 was only approximately half of that recorded in 1996 (233.7 ± 25.0 l/m², minimum 174.6 l/m², maximum 342 l/m², $n = 6$). The average for the 1990s was slightly lower than that for the period 1970–1996 (292.0 l/m², $n = 26$), and only one other year had precipitation as high as 1996 (1989, 468 l/m²).

DISCUSSION

Health status and sexual display

Sexual displays have been hypothesized to reveal the health status of males because male phenotypic or genotypic quality in terms of parasite resistance affects the display ability of an individual (Hamilton and Zuk, 1982; review in Møller et al., 1999). Most intraspecific studies have considered morphological displays such as color or exaggerated traits like elongated feathers or antlers, but relatively little attention has been paid to behavioral displays (Møller et al., 1999). Behavioral displays differ from morphological ones in that the costs of display are only paid when the individual is displaying, whereas morphological traits generally are subject to natural selection pressures both during and outside periods of display. Hence, we might expect behavioral displays to be less costly than morphological ones.

The present study of stone carrying in the black wheatear concerns an extreme behavioral display—males carrying heavy stones to cavities inside caves—and the functional significance of this display is that it affects the parental investment of their mates (Moreno et al., 1994; Soler et al., 1996). This display is not very costly in terms of metabolism because males carry only an average of 21 stones per day, each stone weighing an average of 5.8 g. This equals an increase in energy expenditure of only 1% of daily energy expenditure (Møller et al., 1995). Because individual stones (which weigh 3.4–8.2 g for different males) are heavy relative to the bird (which weighs about 35 g), males may display their maximum working ability during stone-carrying displays. Consistent with this expectation, Møller et al. (1995) calculated that males experience an increase in power output due to stone carrying of 55kJ/h, or 28 times their basal metabolic rate. This estimate equals an energy output of 400 W/kg, which is close to the upper limit of sustainable power of any muscle (Goldspink, 1977).

In the present study we found that a measure of immunocompetence was significantly positively related to the average mass of stones carried by each male, implying that males carrying very heavy stones were better able to raise a strong immune response to a novel antigen than males carrying light stones (Figure 1). The T-cell response to injection with phytohemagglutinin provides an important measure of a component of immune function that is directly related to condition of chickens (Glick et al., 1981, 1983), a measure of immunocompetence that has a genetic basis in chickens and barn swallows (Cheng and Lamont, 1988; Saino et al., 1997b), and this measure of immune function provides reliable information about long-term viability of male barn swallows (Saino et al., 1997a) and black wheatears (Figure 3). Hence, an aspect of the stone-carrying display reliably reflected the im-

munocompetence of male black wheatears. This finding is consistent with the hypothesis that stone carrying reveals the maximum working ability of a male, thereby reflecting male health status. We did not find any correlation between immunocompetence and total number of stones carried, which is as expected, as total stone-carrying activity mainly reflects the working effort during the extended stone-carrying period rather than the maximum stone-carrying ability of an individual.

Two species of ectoparasites were commonly found in adult black wheatears. Their abundance was not significantly related to the expression of the stone-carrying display. This observation adds to an increasing number of studies showing that sexual displays are much more weakly correlated with the abundance of parasites than with measures of immune defense (Møller et al., 1999). The abundance of different kinds of parasites is generally not positively correlated for hosts of a given population (Møller et al., 1999). Thus, it is unlikely that the abundance of different kinds of parasites of a host species should, in general, be negatively correlated with the expression of sexual displays (Møller et al., 1999). Measures of general antiparasite defenses such as measures of immunocompetence are likely to provide reliable information about the ability of males to cope with the currently most detrimental species of parasites, and their abundance is thus more likely to be related to the expression of secondary sexual characters (Møller et al., 1999). In accordance with this suggestion, the correlation between the expression of secondary sexual characters and parasite load was on average only $-.06$ for 52 samples, whereas the correlation between the expression of secondary sexual characters and measures of immune function was on average .43 in 17 samples (Møller et al., 1999). The strong, positive relationship between T-cell response in male black wheatears and stone carrying and the weak relationship between parasite load and stone carrying is in agreement with this general trend.

Excessive exercise is known to depress the relative amount of erythrocytes measured as the hematocrit (reviews in Saino et al., 1997c,d). For example, several studies of animals and humans performing excessive exercise show a reduction in hematocrit (Birchard, 1997; Harrison, 1985; Escribano et al., 1995; Riera et al., 1983; Saino et al., 1997c,d). An experimental study of the barn swallow demonstrated that tail elongation decreased hematocrit (Saino et al., 1997c). Male black wheatears that carried heavy stones had a reduced hematocrit value compared to males that carried few stones (Figure 2). Because the work load of stone-carrying males is the largest ever reported for any muscle, we can be confident that the stone-carrying display is close to the maximum amount of work possible. The reduction in hematocrit among males carrying very heavy stones is consistent with the prediction that increased workload depresses hematocrit. A negative relationship between stone carrying and hematocrit was not repeated for the total number of stones carried, which supports the suggestion that males are displaying maximum working ability during a short burst rather than working ability during extended periods.

Previous experimental work on the black wheatear revealed that experimental manipulation of the stone-carrying ability of males by removal of primary feathers from experimental males caused a significant reduction in the number and the mass of stones carried (Møller et al., 1995). The present study found no evidence for such an effect. This difference in the effect of wing feather removal on the stone-carrying display in different years may be explained by extreme among-year variation in environmental conditions. Hoya de Guadix is a particularly warm and dry area with summer temperatures exceeding 45°C and sparse precipitation falling in winter. The warm and dry climate results in a low abundance of invertebrates in most years. The present study was performed in 1996, which was a year with considerable rainfall (Consejería de Medio Ambiente, 1997). The relationship between invertebrate abundance and precipitation has not been investigated specifically in the Guadix area, although the relationship between precipitation and primary productivity and between primary and secondary productivity are well known from many terrestrial ecological studies (Polis et al., 1997, and references therein). Hence, the vegetation and the abundance of insects may have been considerably elevated in 1996 compared to 1991 and 1992, when the first two experiments were made. Hence, we hypothesize that any effects of the experimental treatment on stone carrying, health status, and reproductive success may have been compensated by readily available food during this favorable year.

Immune response and survival of adult males

Parasites are often presumed to play a significant role in determining fitness of their hosts by competing for resources from maintenance and reproduction (Price, 1980). This assumption is founded on observational and experimental studies demonstrating reduced fitness of heavily infested hosts (reviews in Lehmann, 1993; Møller, 1997a). If parasites impose severe selection pressures on their hosts, this should result in the evolution of efficient host defenses. The immune system is supposedly one such efficient host defense (Klein, 1990; Roitt et al., 1995; Wakelin, 1996). However, there is little empirical evidence for the efficiency of the immune system. For example, a recent study of male barn swallows provided one of the first field demonstrations of a strongly positive correlation among B-cell–mediated immune response, tail length, and survival prospects to the subsequent year in this long distance transequatorial migratory bird (Saino et al., 1997a). T-cell response to injections with phytohemagglutinin is also positively correlated with tail length in male barn swallows (S. Merino, personal communication).

In the present study of the black wheatear, we found that adult males recorded in the study area in a subsequent year had a significantly greater T-cell response than males that were not resighted in subsequent years (Figure 3). The increased concentration of leukocytes in nonsurvivors is also consistent with the interpretation that survivorship was related to health status (Dein, 1986). None of the other measures of performance by adult male black wheatears differed significantly between survivors and nonsurvivors. Hence, it seems likely that a strong immune response by male black wheatears provides an advantage in terms of survival prospects. Females may benefit from mating with immunocompetent males because such males may provide more resources for their offspring (Moreno et al., 1994) and because immunocompetent males may provide genetic benefits in terms of parasite resistance to their offspring (Hamilton and Zuk, 1982).

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