



# The possible function of stone ramparts at the nest entrance of the blackstart

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(Received 30 May 1997; initial acceptance 6 August 1997;  
final acceptance 3 December 1997; MS. number: 5556)

## ABSTRACT

Blackstarts, *Cercomela melanura*, Turdidae, construct a rampart of stones at the entrance to their nests. These ramparts may reach remarkable proportions, containing hundreds of flat rocks. We investigated several hypotheses regarding the function of stone ramparts, by monitoring individually marked blackstarts at the En-Gedi Nature Reserve, Israel. Stones were collected solely by females, who carried them in their beaks, while flying to the nest, at a rate of up to one stone per min, after pair formation had occurred. The number and total weight of stones as well as rampart height showed a highly positive correlation with the size of the nest cavity opening. The rampart decreased the size of the cavity entrance to some nests by as much as 67%, which suggests an antipredator barrier function. Survival rates of eggs and chicks were extremely low and the major cause of reproductive failure was predation. Successful nests tended to be located higher off the ground than predated nests, and often contained fewer stones. Furthermore, larger females in terms of wing and tail length nested in cavities higher off the ground and built smaller ramparts containing lighter stones. An artificial nest predation experiment did not reveal a difference in predation rates between nests with and without stone ramparts. Spiny mice, *Acomys* sp., were the main egg predators. However, in 37% of nests with ramparts that were predated, the perpetrator flattened the rampart, suggesting that they may serve as a barricade, forcing the predator to invest time in clearing the stones in order to gain access to the nest, and perhaps allowing the nesting female sufficient time to escape. We propose, therefore, that owing to such high nest predation rates, females nesting close to the ground build stone ramparts as an 'early warning' mechanism to prevent themselves from being trapped inside nest cavities and predated.

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At least 29 species of ground-nesting, mostly desert-dwelling, passerine birds are known to build a rampart of small stones at the entrance to their nests. These species belong to four families: Turdidae, Alaudidae, Fringillidae and Troglodytidae (Cramp & Simmons 1988; Afik et al. 1991; Roberts 1993; Merola 1995). The scope of building activity in these species ranges from the construction of a small, encircling wall of pebbles around the rim of the nest, a shallow depression or scrape on the ground, lined with vegetation, usually in the shelter of a tussock or small rock (Alaudidae), to the accumulation of hundreds of small, flat rocks, whose total weight may exceed 1 kg, as in species of the genus *Oenanthe* (Turdidae), which typically nest deep in rock crevices, under boulders and rock piles (Cramp & Simmons 1988). In these latter species, the rocks are piled up in front of the nest, to form a flat mosaic, three or four layers deep and 10–40 cm

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wide, extending outward from the nest tunnel for as much as 1 m (Fischman 1977; Cramp & Simmons 1988; Palfrey 1988). The bird carries stones in the beak while flying to the nest in intense carrying bouts during the first stage of nest building (Fischman 1977; Palfrey 1988; Moreno et al. 1994).

Stone carrying appears to be a costly activity in terms of time and energy. Several functional explanations for the maintenance of this behaviour have been suggested, yet relatively little research has been conducted to test them. Until recently, most of the information accumulated on rampart building behaviour was based on observations alone. The rampart has been suggested to function: (1) as a support for the nest, preventing it from sliding off a sloping surface and thus allowing the birds to use higher nests which are potentially less accessible to ground predators (Richardson 1965); (2) as protection from wind, rain or dust storms (Ferguson-Lees 1960), by anchoring the nest structure to the substrate and possibly stabilizing the soil in the vicinity (Afik et al. 1991); (3) as

camouflage for the nest entrance reducing nest predation rates (Etchecopar & Hue 1967), or as a physical barricade, making access for predators difficult (Ferguson-Lees 1960; Richardson 1965); (4) as a mechanism to regulate and limit the maximum temperature inside the nest, since most rampart builders are small desert birds nesting on the ground in early summer, when diurnal temperatures can be extremely high and the stone rampart at the nest entrance may then be a poor conductor of heat into the nest cup, as a result of the large quantity of air trapped between the stones (Orr 1970; Afik et al. 1991); (5) as an advertisement display as part of pair formation and nest site selection (Ferguson-Lees 1960; Richardson 1965).

Recent investigation of the stone-carrying behaviour of the black wheatear, *Oenanthe leucura* (Moreno et al. 1994; Møller et al. 1995; Soler et al. 1996) has revealed that it may function as a postmating but prenesting sexual display which allows females to adjust reproductive effort to the parental and/or phenotypic quality of their partner. This species, however, may be unique in that it is the male that performs this behaviour; in other species it is assumed that it is usually the female that carries the majority of the stones to the nest (Fischman 1977; Zachai 1984; Cramp & Simmons 1988; Palfrey 1988; Afik et al. 1991). However, in only a few species of rampart builders has the sex of the builder been determined (Cramp & Simmons 1988).

Our purpose in this study was to determine the extent of stone rampart building in the blackstart, *Cercomela melanura*, Turdidae, and to assess the possible functions of the stone rampart.

## METHODS

### Study Species

The blackstart is a small (14–16 g), common resident of the Saharo-Sindian desert belt. The local subspecies *C. m. melanura* is widespread along the Dead Sea depression south to the Sinai and northwest and central Saudi Arabia (Bundy 1986; Cramp & Simmons 1988). In the En-Gedi area, this species is a very common resident, especially at the mouths of desert wadis and boulder-strewn slopes (Paz 1986; Shai 1990). Although quite abundant in desert regions of Israel, this species has been poorly investigated and many aspects of its social organization and behaviour are not known (Cramp & Simmons 1988).

The blackstart is monogamous and remains paired on the territory throughout the nonbreeding season (Paz 1986; Cramp & Simmons 1988). The breeding season in En-Gedi is from February to July, during which time up to three broods may be reared (this study). The nest is usually situated in a rock crevice, up to 0.8 m from the entrance, which is usually covered with a platform of small, flat pebbles, two to three layers deep. Building is done by the female alone (this study) and takes 4–5 days (Cramp & Simmons 1988). Three to four eggs are laid, one every day, and incubation, carried out solely by the female, lasts 13–14 days (Paz 1986). Both parents feed the

nestlings and the young fledge after about 14 days (Paz 1986).

### Study Site

We conducted field work during the breeding seasons of 1994–1995 in the oasis of En-Gedi, a nature reserve on the west shore of the Dead Sea, Israel (31°28'N, 35°23'E) at 400 m below sea level. The area is rocky terrain, with steep cliffs ranging up to 200 m above sea level. Annual precipitation in the area is about 75 mm and falls mostly in winter. In spite of this low precipitation, local rains cause an average of two floods a year, and some water flows in two wadis within the reserve all year long. The temperature varies from an average minimum of 13°C in winter to more than 40°C in summer. We studied blackstarts in 20 territories between the mouth of Nahal (wadi) Arugot and the slopes north to Nahal David.

### Capturing and Ringing Birds

We captured birds with walk-in box traps baited with fly larvae along with playback of song and a stuffed decoy. All birds were individually ringed with coloured and numbered aluminium rings. Males are slightly larger than females (Cramp & Simmons 1988), and we determined the sex of birds from body measurements (wing, tail, bill, tarsus and weight) with the addition of observational data (copulation behaviour was observed in all pairs, only females have a brood patch and only males perform territorial displays).

### Recording Reproductive Parameters

We conducted daily observations during the breeding season in order to locate nests and measure reproductive success of different pairs. We discovered nests mostly by continuous observations of females carrying nesting material or food to the nest.

Upon discovery of a nest, we recorded its stage (rampart building, nest cup building, laying, incubation, hatching or nestlings) and identity of parents. Any changes in pairs that took place, such as disappearance of one pair member and its replacement by a new bird, were noted.

We monitored territories and nests throughout the breeding season in order to measure the reproductive success of each pair. We classified breeding attempts as first, repeat of first (after predation of eggs or young, or abandonment of eggs from 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).

We examined nests immediately after the end of breeding attempts in order to examine nest site parameters. Nest sites were classified according to their placement: (1) nests built under or between rocks on the ground; (2) cavity nests built inside holes on rock faces or artificial walls lacking a horizontal surface at the entrance; and (3) nests built inside old irrigation pipes.

For each nest we used a compass to measure the orientation of the nest opening and a steel ruler to measure the following to the nearest 0.5 cm: (1) height of the opening from the ground; (2) maximum height and width of the cavity opening; (3) distance from the entrance opening to the nest cup; (4) distance from the beginning of the stone rampart to the nest cup; and (5) maximum height of the stone rampart from the entrance floor. Stones from the rampart were individually weighed to the nearest mg. In addition, we measured to the nearest 0.05 mm the length, width and breadth of 132 stones sampled randomly from different nests, using a calliper ruler.

### Nestling Feedings

We recorded feeding rates at seven nests of first broods in 1995 when chicks were approximately 10 days old. We recorded the number of times the male and female brought food to each nest, as well as the size of the food item (compared with the bird's beak) during one 2-h observation period per nest between 1700 and 1900 hours.

### Artificial Nest Predation Experiments

To assess the possible contribution of the stone rampart in lowering nest predation, we compared egg predation rates in artificial blackstart nests containing and lacking a stone rampart. The experiments were conducted on the eastern slopes of En-Gedi spring, a few hundred metres outside the study area. The experimental plot measured 300 × 250 m, and was divided by 10 small, east-facing rock terraces. Each terrace was 250–300 m long.

We constructed artificial nests from elongated plastic boxes (50 × 9.5 × 9.5 cm) closed at one end, in which a nest cup from an old blackstart nest was fitted. The front of the nest cup was 35 cm from the opening of the box. These dimensions closely resemble those of real blackstart nests found in the study area. Behind the nest cup we placed a small mirror on a hinge. We could temporarily raise the mirror, which lay face down on the box floor, by pulling a long nylon cord from the outside. Shining a flashlight at the raised mirror from the opening allowed us to observe the contents of the nest cup without touching the nest itself. We built 24 artificial nests and placed them in the field for a month before starting the experiments in order to remove any traces of our odour. The artificial nests were placed alongside eight terraces in the experimental plot, three nests per terrace, at a spacing of 70–100 m. This distance is similar to the spacing of real blackstart nests in the study area. For half of the artificial nests (12 nests) we added a stone rampart similar to the ones constructed by blackstarts (250 stones, collected from old blackstart nests). The remaining 12 nests did not contain a rampart.

The choice of suitable eggs for such an experiment should be made after taking into consideration the potential predators in the study area, and the cues (visual or olfactory) they use for locating nests. The only predators

in our study area capable of entering blackstart nest cavities were small rodents and reptiles. Preliminary egg predation experiments in the Tel-Aviv University Zoological Garden showed that potential predators such as spiny mice, *Acomys* sp., cannot eat commercially available eggs (e.g. quail, *Coturnix coturnix*), owing to their large size. We therefore used fresh budgerigar, *Melopsittacus undulatus*, eggs supplied from a local breeder. These eggs are only slightly larger than blackstart eggs (126% by weight), and can be grasped easily by small mammalian predators. To identify predators by tooth marks left on the eggs, we used a plaster egg the size of a real blackstart egg, which was painted to resemble the spotted brownish-red appearance of a real egg. We inserted one budgerigar egg and one plaster egg in each nest, and covered the box with rocks so that only the opening was exposed. All nests were put in place early in the morning (0500–0700 hours). We wore rubber gloves and boots while handling the nests in order to minimize human scent marks.

We left the artificial nests in the field for 14 days (imitating the incubation period of blackstarts), and checked them every 2–3 days for signs of predation. A nest was considered as predated upon if one of the eggs disappeared or we could see tooth marks on the plaster egg.

We conducted five experiments between 28 February and 12 July 1995, parallel to the blackstart breeding season. During each experiment we changed the location of the nests and switched the nests containing stone ramparts. In total, 120 artificial nests were tested.

In addition to identifying egg predators from tooth marks left on the plaster eggs, we photographed several predation attempts on artificial nests. We used a passive infrared detector ('Lynx' model, Crow Alarm Systems, Tel-Aviv, Israel) connected to a Canon EOS 650 camera through the camera's cable release connector. The camera and detector were placed on a tripod 2 m from an experimental nest that had been predated the day before, in which we deposited a number of eggs. This procedure was done in order not to interfere with the results of the predation experiments by possibly attracting predators to our equipment. We placed a small clock near the nest entrance to record the time of predation, and left the camera for periods of 24 h.

### Statistical Methods

Data were analysed with nonparametric statistics (Statistica for Windows, version 4.3) because they were significantly nonnormal in distribution and had unequal variances that could not be transformed to satisfy the requirements for parametric statistics. Probabilities obtained from repeated tests of the same hypothesis using the same data (i.e. Spearman rank correlation matrices) were Bonferroni adjusted to correct for the number of statistical tests performed (Sokal & Rohlf 1995). To avoid pseudoreplication we included only first breeding attempts in cases where parameters of stone carrying by a pair or measures of reproductive variables per attempt were relevant variables. Nesting success was calculated according to the Mayfield method (Mayfield 1975;

Hensler & Nichols 1981); and nest orientation analysis was performed using circular statistics (Batschelet 1981; Zar 1984). All tests were two-tailed and the significance level was set at 5%. Values reported are means and standard errors.

## RESULTS

### Nest Building

The breeding season lasted about 5 months in both years, from the middle of February to the middle of July, during which up to three successful clutches were reared in 1994 and only two in 1995. When a nesting attempt failed, females started building a replacement nest as soon as 4–5 days after terminating the previous attempt. Some females built as many as four replacement nests after abandoning the previous one. During the 2 years of this study we found 54 active nests. In addition, we found 35 old nests for which there is no information regarding the season they were active. In 10 old nests where we removed their contents (stones and nest cup) at the end of 1994, nesting activity was observed in the 1995 season. Active nests were found in cavities under big rocks, between rocks in old terraces, inside holes in wadi walls, abandoned little bee-eater, *Merops orientalis*, nests, and artificial walls. Nests were also discovered in old aluminium irrigation pipes scattered in the study area.

In 1995 males and females started examining potential nesting holes in their territory 2 weeks ( $13.8 \pm 2.3$  days,  $N=5$  pairs) before the start of nest building. The members of a pair took equal part in hole checking. Nest building included the construction of a stone rampart, followed by the construction of a nest cup at the end of the nest cavity. Only females were observed bringing nesting material ( $N=12$  pairs,  $N=21$  nests). The male took no active part in nest construction, but on many occasions followed the female or perched close by and sang.

Stone ramparts were found in 49 of 50 active nests examined during the two breeding seasons. Four additional nests were inaccessible because of their height, but we could observe stones at their entrance. In most cases, the rampart was constructed as a mosaic of stones extending from the nest cup to the cavity entrance, the stones being piled up in a few layers and narrowing both the opening and the cavity itself. In some nests the rampart extended outward beyond the opening in a fan shape. The number of stones in ramparts was significantly different between nesting attempts (Kruskal–Wallis ANOVA:  $H_{2,47}=7.29$ ,  $P<0.05$ ). Multiple comparisons between groups (Siegel & Castellan 1988, page 181) indicate that replacement clutches contained significantly fewer stones than first-clutch nests (first:  $222.0 \pm 33.9$ ,  $N=20$ ; replacement:  $105.3 \pm 23.4$ ,  $N=14$ ;  $|R_u - R_v|=11.7$ ,  $P<0.05$ ), and fewer than second clutches (second:  $224.6 \pm 43.6$ ,  $N=13$ ;  $|R_u - R_v|=12.0$ ,  $P<0.05$ ). There was no significant difference in number of stones between first and second clutches ( $|R_u - R_v|=0.3$ , NS).

A similar trend (although not significant) was found for total weight of ramparts (first:  $475.3 \pm 72.2$  g,  $N=19$ ; replacement:  $239.0 \pm 56.0$  g,  $N=14$ ; second:  $516.2 \pm$

$125.1$  g,  $N=13$ ; Kruskal–Wallis ANOVA:  $H_{2,46}=5.68$ ,  $P=0.058$ ), and rampart height (first:  $2.79 \pm 0.32$  cm,  $N=19$ ; replacement:  $1.81 \pm 0.22$  cm,  $N=13$ ; second:  $2.86 \pm 0.48$  cm,  $N=11$ ;  $H_{2,43}=5.94$ ,  $P=0.051$ ).

The mean weight of individual stones in ramparts was not significantly different between nesting attempts (first:  $2.01 \pm 0.05$  g,  $N=19$ ; replacement:  $2.09 \pm 0.17$  g,  $N=14$ ; second:  $2.18 \pm 0.15$  g,  $N=13$ ;  $H_{2,46}=4.82$ , NS).

### Stone Characteristics

Ramparts consisted primarily of limestone, dolomite, flint and pieces of pottery. There was no preference for particular stones and those found in ramparts represented the abundance in the immediate vicinity of the nest. Nests containing large quantities of pottery fragments, for example, were located in areas near an archaeological site. Other objects found in small quantities in ramparts were metal scraps, nails and bolts, bottle caps, sticks and bits of broken glass. Rampart stones were highly regular in appearance, their main feature being their flatness. A clear difference was found between the length, width and breadth of 132 stones taken at random from different nests (length:  $24.8 \pm 0.4$  mm; width:  $17.1 \pm 0.4$  mm; breadth:  $6.2 \pm 0.1$  mm). As stones are carried in the bird's beak, flat ones are the easiest to transport. The weight of stones in ramparts was highly variable. The mean weights of the smallest and biggest stone found in each nest were  $0.25 \pm 0.05$  g and  $6.51 \pm 0.47$  g ( $N=28$  nests), respectively. Thus, females carried stones up to 43% of their own weight.

We observed stone carrying on five territories on eight occasions during the entire research period. Only females were observed carrying stones in their beaks, while flying to their nest. Males took no part in stone carrying, and were either perched nearby or were absent. Females collected stones from the ground within 10 m of the nest, although one female was observed flying 25 m with a large stone in her beak. Stone carrying reached a rate of almost one stone per min, as one female brought 57 stones in 1 h and 17 stones in a period of 20 min the next day.

### Nest Site Characteristics

The majority of nests (29 nests or 54% of the 54 nests found) were under or between large rocks on the ground, 15 (28%) in cavities in rock faces, wadi or walls, lacking a horizontal surface outward from the entrance, and 10 (18%) inside metal pipes.

There were significant differences between the nest types in their dimensions and ramparts (Table 1). Cavity nests were significantly higher off the ground than nests under rocks, and contained ramparts that were significantly shallower and consisted of smaller stones than the other two nest types. Cavity nests also showed an overall tendency (although not significant) for containing smaller ramparts both in terms of stone quantity and total weight.

Nest cups of birds nesting in pipes were placed significantly deeper from the entrance than nests built under



**Table 1.** Summary of nest site characteristics and rampart dimensions ( $\bar{X} \pm SE$ , range,  $N$ ) of the three nest types of blackstarts and statistical differences between nest types

Parameter	Nest type			Kruskal–Wallis test		Multiple comparisons*	
	Rock (1)	Cavity (2)	Pipe (3)	$H$ ( $N$ )	$P$ ( $df=3$ )	$ R_u - R_v $	Different pairs
Entrance height (cm)	9.4±0.8 4–22 29	8.9±1.1 4–16 10	9.5±1.0 6.5–16	0.2 (49)	NS		
Entrance width (cm)	12.7±1.2 3.5–30 29	10.0±1.1 6–17 10	7.9±0.8 4.5–14	8.7 (49)	<0.05	15.2	1,2
Nest height (cm)	8.3±3.1 0–72 29	606.1±242.1 0–2500 15	24.8±7.5 9.5–89 10	24.6 (54)	<0.001	23.2 14.5	1,2 1,3
Nest depth	24.8±2.2 7–66 29	28.1±1.5 20–38 10	39.3±4.6 19–72.5 10	11.3 (49)	<0.01	17.4	1,3
Rampart depth (cm)	24.4±2.2 7–60 26	22.3±3.1 0–30 10	39.9±4.8 19–70 9	10.1 (45)	<0.01	15.5 15.5	1,3 2,3
Rampart height (cm)	2.8±0.3 1–7 26	1.5±0.3 0–2.5 10	3.0±0.3 2–5 9	10.5 (45)	<0.01	11.9 18.5	1,2 2,3
Number of stones	195.2±29.5 14–556 29	118.1±24.1 0–209 10	228.2±40.6 94–440 10	2.4 (49)	NS		
Stone weight (g)	2.2±0.1 1.3–2.9 29	1.5±0.2 0.9–2.2 9	2.2±0.1 1.7–2.4 10	11.1 (48)	<0.01	17.6 15.7	1,2 2,3
Rampart weight (g)	446.5±71.6 32.9–1470.6 29	203.3±33.8 23.2–310.2 9	493.8±89.5 219.2–968.4 10	4.8 (48)	NS		

\*Calculated according to Siegel & Castellan (1988).

**Table 2.** Spearman rank correlations between various components of stone rampart size

	Number of stones	Stone weight	Rampart weight
Rampart height	0.69* (45)	0.24 (44)	0.68* (44)
Number of stones	—	0.15 (48)	0.95* (48)
Stone weight		—	0.38* (48)

Sample size in parentheses.

\*Statistically significant at the 0.05 level after Bonferroni adjustment.

rocks. As nest depth was positively correlated with length of the stone rampart (Spearman rank correlation:  $r_s=0.75$ ,  $N=45$ ,  $P<0.0001$ ), pipe nests also had significantly longer stone ramparts.

The number of stones and total weight of ramparts were highly correlated, and both were positively correlated with rampart height (Table 2). Mean stone weight was positively correlated with the total weight of ramparts.

Nests containing a larger (higher) opening contained more stones (Spearman rank correlation:  $r_s=0.56$ ,  $N=49$ ,

$P<0.0001$ ), and heavier ramparts ( $r_s=0.53$ ,  $N=48$ ,  $P<0.0001$ ). Entrance size was also positively correlated with the height of the stone rampart ( $r_s=0.34$ ,  $N=45$ ,  $P=0.021$ ), yet was not significant after Bonferroni adjustment for the number of statistical tests.

The stone rampart narrowed and partially blocked the entrance of most nests up to a maximum of 67% of the entrance. Examination of the proportion of the opening blocked by stones (rampart height/entrance height) revealed a significant difference between nest types (Kruskal–Wallis ANOVA:  $H_{2, 46}=8.75$ ,  $P<0.05$ ). The proportion of the opening blocked by stones in cavity nests was significantly less than in nests built under rocks (cavity:  $0.18 \pm 0.04$ ,  $N=10$ ; under rocks:  $0.31 \pm 0.03$ ,  $N=26$ ;  $|R_u - R_v|=11.8$ ,  $P<0.05$ ), or pipe nests (pipe:  $0.36 \pm 0.05$ ,  $N=9$ ;  $|R_u - R_v|=16.8$ ,  $P<0.05$ ). Nests built under rocks and pipes did not differ significantly ( $|R_u - R_v|=4.9$ , NS).

## EVALUATION OF THE HYPOTHESES

### The Nest Support Hypothesis

This suggests that stone ramparts function as a support for the nest, preventing it from sliding off a sloping surface and thus allowing the birds to use higher nests

which are potentially less accessible to ground predators. It predicts that larger ramparts would be built at crevices and similar sites, lacking a horizontal surface outward from the entrance, where there is obvious need for nest support. Our data do not support this hypothesis.

Not only was there no significant difference in the number of stones or rampart weight in cavity nests and nests built on the ground under rocks (Table 1), the trend was in an opposite direction: cavity nests tended to have fewer stones than other types. Furthermore, stones were arranged all along the length of the nest hole (Table 1), with the majority piled up at the entrance and not just concentrated at the base of the nest cup as would be expected. Therefore, a much greater quantity of stones was collected than needed for an optimal support function. Finally, while inspecting nests and collecting the stones of 49 nests, we did not find any nest whose surface was sloping in such a way that removal of the stones made the nest cup unstable.

### The Weather Protection Hypothesis

This suggests that a large quantity of stones may serve to protect the nest from wind, rain or dust storms. It predicts that the effect of such weather conditions on breeding success will be negatively related to the quantity of stones in the nest. Our data do not support this hypothesis.

We did not record any cases of nesting failure as a result of inclement weather during the two breeding seasons ( $N=54$  nesting attempts). All nests examined were built deep enough that the nest cup was in fact protected from external weather influences even without the stone rampart. Two nests built on the ground in the middle of Nahal Arugot, in places at risk of flooding, were built late in the breeding season, when such danger no longer existed.

### The Thermoregulation Hypothesis

This suggests that the stones function in regulating and limiting the maximum temperature in the nest. At high ambient temperatures, the stone rampart at the nest entrance will be a poor conductor of heat into the nest cup because of the large quantity of air trapped between the stones.

It predicts: (1) a preference for nesting in orientations where the nest opening is less exposed during the day to direct solar radiation, and therefore requires less investment by birds in stone carrying; (2) that fewer stones will be carried to nests situated deeper inside holes, where the microclimate is more constant and less vulnerable to changes in ambient temperatures; and (3) that birds should nest in deeper cavities or carry more stones to nests built later in the season when diurnal temperatures can reach harmful levels.

The orientation of nest openings of cavity and pipe nests did not differ from a uniform distribution, whereas the opening of nests built under rocks showed evidence of a preferred east-northeast direction (Table 3). Although

**Table 3.** Orientation of nest opening of the three nest types of blackstarts and statistical analysis of nest distribution

Parameter	Rocks	Cavity	Pipes
Mean vector ( $\mu$ )	61.12°	301.77°	55.02°
Length of mean vector ( $r$ )	0.41	0.39	0.26
Circular standard deviation	76.70°	78.15°	93.83°
Rayleigh test of uniformity ( $Z$ )	4.83	2.33	0.68
$P$	0.007	0.096	0.516
Number of observations	29	15	10

this may indeed represent preference for thermoregulatory optimal nest orientation, we believe that this derives from the topography of the study area. Nests built under rocks were usually located on moderate slopes strewn with rocks. In our study site such slopes are situated mostly at an approximate northeastern orientation. Furthermore, a circular-linear rank correlation analysis (Batschelet 1981) did not reveal any significant correlation between the nest orientation of nests built under rocks and number of stones ( $U=5.59$ ,  $N=29$ , NS), weight of stones ( $U=0.42$ ,  $N=29$ , NS), rampart weight ( $U=5.45$ ,  $N=29$ , NS), rampart height ( $U=0.79$ ,  $N=29$ , NS), or breeding success measured as number of young fledged ( $U=1.37$ ,  $N=29$ , NS).

Inside a cavity 30 cm deep under a rock the temperature was highly constant (34.6–36.5°C), with fluctuations between night and day of only 1.9° ( $N=1454$  temperature readings, 4 days of continuous measurements between 14 and 17 July 1995), whereas ambient temperature fluctuated between 28.6 and 44.2°C (range 15.6°; R. Elvert, personal communication). This confirms that the microclimate at such depths (which is close to the mean depth of blackstart nests built under rocks) is indeed fairly constant. Not only is the temperature in such a cavity constant, but also the physical properties of such a cavity provide a stable environment well within the range of optimal nest temperatures required for successful incubation in other passerine species (Drent 1976). Such favourable conditions may also require minimum attentiveness at the nest on the part of the female (White & Kinney 1974; Yom-Tov et al. 1978). Our findings raise the question whether birds breeding in such cavities are ever faced with the problem of overheating of the nest contents.

In contrast to prediction (2), however, nests built deeper inside holes did not contain fewer stones. Deeper nests contained longer ramparts (see above), and nest depth was not significantly correlated with number of stones (Spearman rank correlation:  $r_s=0.25$ ,  $N=49$ , NS), or rampart weight ( $r_s=0.24$ ,  $N=48$ , NS).

We found no difference in depth of nests built under rocks between the first breeding attempts of the season (March–April) and second-clutch nests (June–July; first:  $26 \pm 4.12$  cm,  $N=12$ ; second:  $26.61 \pm 3.7$  cm,  $N=9$ ; Mann–Whitney  $U$  test:  $U=47.5$ , NS). The number of stones in nests built under rocks did not differ between early and late clutches (first:  $237.9 \pm 46.7$ ,  $N=12$ ; second:  $225.2 \pm 62.1$ ,  $N=9$ ;  $U=47.5$ , NS), and no difference was

found for rampart weight either (first:  $488.3 \pm 99.2$  g,  $N=12$ ; second:  $580.7 \pm 170.5$  g,  $N=9$ ;  $U=53.0$ , NS).

Preliminary data obtained from temperature measurements in the field using model nests (thus enabling us to control all other variables except the presence or absence of a stone rampart) suggest that small differences in the nest cup structure (i.e. a bit more grass or feathers) may contribute to insulation of the nest contents far more than a stone rampart composed of 250 stones (Leader 1996).

The fact that some pairs chose exposed metal pipes (usually old aluminium irrigation pipes) does not support this hypothesis (10 active and 35 old nests were discovered in pipes). Although pipe nests tended to contain larger quantities of stones, and have a deeper placement of the nest cup, nest contents in these nests were exposed to external temperature fluctuations from all sides. The stone rampart may transfer heat less effectively into the nest only from the entrance, yet the thin metal layer separating the nest cup from the environment was not thermally insulated, and caused heating of the nest from all directions during the day. The temperature inside an aluminium pipe exposed to direct solar radiation can reach high values even at the beginning of the season in En-Gedi and dangerous levels soon afterwards ( $47^\circ$ =air temperature 2 cm above the nest cup in an old aluminium pipe nest oriented at  $40^\circ$  compared to ambient temperature of  $37^\circ$ , measured at noon on 30 May 1994). A 'thermal buffer' function of the stone rampart is therefore unlikely to work in the case of nests built inside metal pipes. Not only can there be no contribution by the rampart to the cooling of the nest contents because the pipe heats up from all sides and not only the entrance, the rampart may also function to the disadvantage of the nesting female by delaying the dispersal of accumulated heat inside the nest through the opening, thus creating a possible 'heat-trap'.

### The Sexual Display Hypothesis

This hypothesis suggests that (1) a stone-carrying display is part of pair formation or (2) pair members use the stone-carrying display to assess the quality of their partner and adjust their parental effort accordingly. Following Moreno et al. (1994), this predicts a negative correlation between the size of the rampart (number of stones) and the laying date as well as positive correlations between stone number and clutch size and number of clutches laid per season. Furthermore, the extent of parental care or its consequences measured as number of fledged young can be predicted from the intensity of stone carrying. It also predicts that larger birds will accumulate more and heavier stones to build larger ramparts.

Possibility (1) is not likely because birds were already paired before the breeding season. Blackstarts have a long-term pair bond (nine of 13 pairs observed together at the beginning of the 1994 breeding season remained together for three consecutive seasons). A new bird appeared in a territory only after one of the resident birds disappeared. Furthermore, the fact that stone ramparts

are constructed before each breeding attempt during the season, with no difference in stone quantity between first and second clutches does not support this suggestion.

Possibility (2) is more feasible, although only females participate in stone carrying; yet none of its predictions is supported by our data. The laying date of first clutches was not significantly correlated with the number of stones carried to the nest prior to that breeding attempt (Spearman rank correlation:  $r_s = -0.12$ ,  $N=12$ ,  $P=0.72$ ). Females carrying a larger mean number of stones per season did not initiate more breeding attempts ( $r_s = -0.31$ ,  $N=23$ ,  $P=0.15$ ), and did not produce more fledglings ( $r_s = -0.20$ ,  $N=21$ ,  $P=0.38$ ). The total amount of stones brought by females per season was also not correlated with total number of young fledged ( $r_s = -0.02$ ,  $N=21$ ,  $P=0.93$ ). Female and male feeding rates to nestlings were not associated with the total number of stones brought before that breeding attempt (female:  $r_s = -0.60$ ,  $N=6$ ,  $P=0.21$ ; male:  $r_s = -0.06$ ,  $N=6$ ,  $P=0.91$ ), weight of stones (female:  $r_s = -0.66$ ,  $N=6$ ,  $P=0.16$ ; male:  $r_s = -0.49$ ,  $N=6$ ,  $P=0.32$ ), or rampart weight (female:  $r_s = -0.54$ ,  $N=6$ ,  $P=0.27$ ; male:  $r_s = -0.23$ ,  $N=6$ ,  $P=0.66$ ).

To test the possibility of a female sexual display, we analysed morphological characters of females and their investment in rampart construction. We found no support for this as it seems that, contrary to the prediction, it was the females with short wings and tail, characteristics that seem to be important in flight performance (see Møller et al. 1995), that invested more in such displays: wing and tail lengths of females were negatively correlated with the mean total weight of ramparts built per season (Spearman rank correlation:  $r_s = -0.46$ ,  $N=19$ ,  $P<0.05$ ;  $r_s = -0.61$ ,  $N=19$ ,  $P<0.01$ , respectively) and the mean stone weight in ramparts was also negatively correlated with wing and tail lengths ( $r_s = -0.76$ ,  $N=19$ ,  $P<0.0001$ ;  $r_s = -0.59$ ,  $N=19$ ,  $P<0.01$ , respectively).

Furthermore, females with wings equal to, or longer than, the median ( $\geq 77$  mm) carried significantly smaller stones to their nests than females with smaller (below median,  $<77$  mm) wings (large:  $1.84 \pm 0.14$  g,  $N=10$ ; small:  $2.31 \pm 0.04$  g,  $N=9$ ; Mann-Whitney  $U$  test:  $U=6.0$ ,  $P=0.001$ ). The total weight of stones in nests of larger females tended to be less, but was not significantly so (large:  $385.8 \pm 107.8$  g,  $N=10$ ; small:  $594.4 \pm 99.7$  g,  $N=9$ ; Mann-Whitney  $U$  test:  $U=22.0$ ,  $P=0.06$ ). A similar difference was found for tail length. Females with tails equal to, or longer than, the median ( $\geq 61$  mm) carried significantly smaller stones to their nests than females with smaller (below median,  $<61$  mm) tails (large:  $1.87 \pm 0.14$  g,  $N=10$ ; small:  $2.28 \pm 0.05$  g,  $N=9$ ; Mann-Whitney  $U$  test:  $U=14.0$ ,  $P<0.05$ ), and the total weight of stones in their nests was significantly less (large:  $370.6 \pm 97.1$  g,  $N=10$ ; small:  $611.2 \pm 108.4$  g,  $N=9$ ; Mann-Whitney  $U$  test:  $U=19.0$ ,  $P<0.05$ ).

### The Antipredation Hypothesis

This suggests that the stone rampart contributes to lowering nest predation rates by (1) camouflaging the nest entrance, or (2) functioning as a physical barricade.

**Table 4.** Number of successful and unsuccessful blackstart nests during the incubation and nestling stages, and daily survival estimates

Nesting stage	Successful nests	Unsuccessful nests	Total days observed*	Daily nest survival ( $p$ )†	Standard deviation‡
Incubation	20	8	198.5	0.9597	0.0140
Nestlings	21	12	308.5	0.9611	0.0110

Incubation and nestling stages did not differ:  $Z=0.079$ , NS;  $Z=|P_1-P_2|/\sqrt{(v_1^2+v_2^2)}$ .

\*The total number of days all nests (successful and unsuccessful) of that group were observed.

†Daily nest survival,  $p=1-\{(\text{no. unsuccessful nests})/(\text{total days observed})\}$

‡Calculated by methods of Hensler & Nichols (1981);  $v^2=p(1-p)/(\text{total days observed})$ .

Both predict that nests suffering from predation have fewer stones than successful nests.

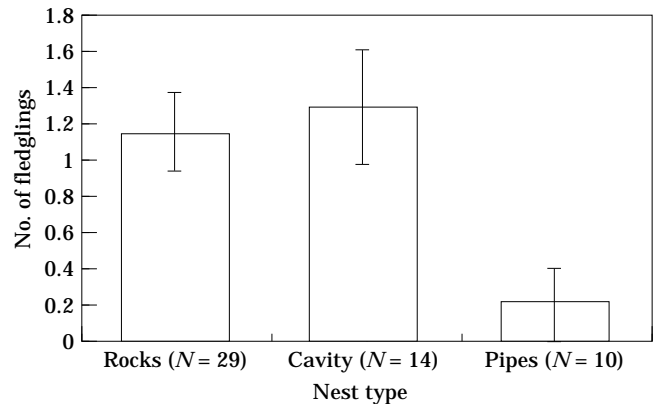
We did not directly witness any act of predation during the two breeding seasons, yet in all failed nesting attempts (except two nests abandoned in the incubation stage) the nest contents disappeared. In addition, three females in two territories disappeared during incubation. This pattern of nest failure can only be attributed to predation of nest contents, as there is no evidence to suggest that disappearance of nest contents was caused by other factors, such as exceptional weather, winds or floods.

Predated nests showed little signs of disturbance suggesting that most predators are small. Only one nest was dug up in a pattern suggesting predation by a red fox, *Vulpes vulpes*, whereas most nests were inaccessible to predators of this size. Potential nest predators may be snakes, *Echis coloratus*, *Telescopus dhara* and *Coluber rhodorhachis*, which we observed on many occasions inside or nearby old blackstart nests; we usually spotted them only after witnessing extensive mobbing behaviour by blackstarts. Small mammals observed near nests included two species of spiny mouse, *Acomys russatus* and *A. cahirinus*.

### Nest Survival

The daily Mayfield mean survival rate of blackstart nests during the incubation stage was 0.9597 (SD=0.0140), while that of the nestling stage was 0.9611 (SD=0.0110; Table 4). Assigning a period of 14 days for each stage reveals that the probability of successfully completing each stage was 0.5622 and 0.5738, respectively (daily nest survival to 14 days), and the probability of a nest surviving from initiation to fledging (a period of 28 days) is only  $0.5622 \times 0.5738 = 0.3226$ . Nest survival rates during the two periods did not differ (Table 4).

Nest and rampart dimensions did not differ significantly between successful and failed nests. Successful nests, however, were almost significantly higher than failed nests (successful:  $224.8 \pm 135.9$  cm,  $N=30$ ; failed:  $145.40 \pm 87.8$  cm,  $N=23$ , Mann-Whitney  $U$  test:  $U=241.0$ ,  $P=0.053$ ). In addition, pairs that reared at least one fledgling in a season nested at a greater mean height than pairs that reared none (successful:  $219.4 \pm 132.1$  cm,



**Figure 1.** Number of young ( $\bar{X} \pm SE$ ) fledged from different nest types.

$N=19$ ; failed:  $89.4 \pm 52.0$  cm,  $N=9$ , Mann-Whitney  $U$  test:  $U=43.0$ ,  $P<0.05$ ).

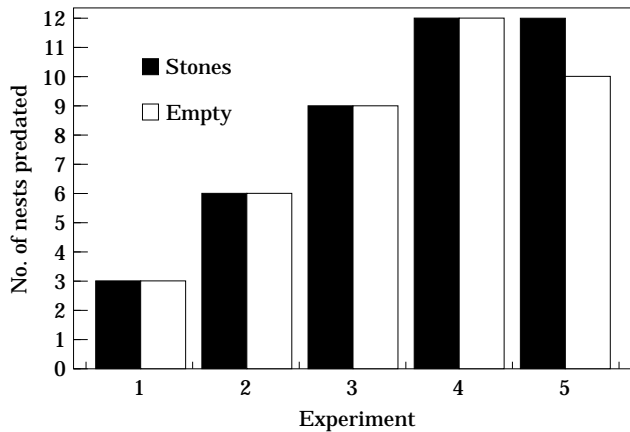
The mean number of young fledged from pipe nests was less (although not significantly) than from nests under rocks or cavity nests (pipe:  $0.2 \pm 0.2$ ,  $N=10$ ; under rocks:  $1.14 \pm 0.23$ ,  $N=29$ ; cavity:  $1.29 \pm 0.32$ ,  $N=14$ ; Kruskal-Wallis ANOVA:  $H_{2, 53}=5.69$ ,  $P=0.058$ ; failed nests included in the analysis; Fig. 1).

There was a significant difference in wing length of females between nest types (Kruskal-Wallis ANOVA:  $H_{2, 22}=7.51$ ,  $P<0.05$ ). Females nesting in cavity nests had longer wings than females nesting under rocks (cavity:  $78.3 \pm 0.25$  mm,  $N=4$ ; rocks:  $76.27 \pm 0.36$  mm,  $N=15$ ;  $|R_u - R_v|=8.8$ ,  $P<0.05$ ), but not significantly longer than females nesting in pipes (pipes:  $75.7 \pm 0.67$  mm,  $N=3$ ;  $|R_u - R_v|=11.5$ , NS). Wing length of females nesting under rocks and in pipes did not differ ( $|R_u - R_v|=2.8$ , NS). Tail length followed the same trend, but there was no significant difference (cavity:  $61.3 \pm 0.75$  mm,  $N=4$ ; rocks:  $60.5 \pm 0.42$  mm,  $N=15$ ; pipes:  $59.3 \pm 1.20$  mm,  $N=3$ ; Kruskal-Wallis ANOVA:  $H_{2, 22}=2.90$ , NS). Hence it seems that the larger females nested in cavities, a type of nest that fledged the highest proportion of young.

### Artificial Nest Predation Experiments

The number of artificial nests predated during each 14-day experiment did not differ between nests with and





**Figure 2.** Number of artificial nests predated in each experiment by nest type. Stones: nest containing a stone rampart; Empty: nests lacking a stone rampart. Number of nests of each type in each experiment=12.

**Table 5.** Mean survival ( $\bar{X} \pm SE$ ; days) of artificial nests with and without ramparts, in five experiments

	With ramparts	Without ramparts
1	11.4 $\pm$ 1.5	11.7 $\pm$ 1.3
2	10.1 $\pm$ 1.5	9.4 $\pm$ 1.6
3	10.1 $\pm$ 1.5	9.4 $\pm$ 1.6
4	10.1 $\pm$ 1.5	9.4 $\pm$ 1.6
5	2.8 $\pm$ 0.2	4.5 $\pm$ 1.4
Mean	8.8 $\pm$ 0.7	8.9 $\pm$ 0.7

Number of nests of each type=12 in each experiment.

without a stone rampart (Fig. 2). The mean number of days artificial nests survived in the field until they were predated (or until each experiment ended after 14 days) was not different between rampart and empty nests (Table 5; Wilcoxon signed-ranks test:  $T=6$ ,  $N=5$ , NS).

While checking artificial nests for signs of predation, we observed in some nests that the stone rampart was flattened and the stones scattered. The number of nests where the rampart had been moved was quantified in only three of the five experiments. In 37% (10 nests of the 27 artificial nests containing ramparts that were predated in these experiments) the predator was forced to move the pile of stones away from the entrance to gain access to the nest. In no nest however, was the rampart effective in completely blocking the entrance from predators, as the nest contents were eventually taken.

Based on tooth marks left on the plaster eggs, rodents were responsible for 68.3% of 82 artificial nest predation events. Most plaster eggs showed extensive chewing and many had perfect imprints of incisors. In some nests we also found eggshells and mouse droppings. In the 31.7% of remaining nests no remains were found that could identify the predator. In 10 of these nests only the real egg disappeared while the plaster egg was left untouched. We strongly suspect snakes as being responsible for at least some of these cases.

Photography of artificial nest predation events using an infrared triggered camera identified the rodent egg predators as *A. russatus* and *A. cahirinus*. Some of the photographs show the mice carrying whole eggs out of the nest. As spiny mice are known to carry their prey (i.e. snails) to their burrows rather than eat them on the spot, this may explain some of the cases of nest predation where no traces were found.

## DISCUSSION

Stone rampart construction in the blackstart is a peculiar phenomenon which appears costly to maintain. Females alone carry stones in their bill while flying to the nest in series of intense stone-carrying bouts before each nesting attempt. Such collecting flights have been calculated as being energetically demanding (Møller et al. 1995).

We have examined five functional hypotheses for the maintenance of rampart building behaviour. Our results, however, do not support any of the existing hypotheses. There was no evidence that the stones support the nest. Similarly, we were unable to find any evidence for the weather protection or thermoregulation hypotheses. We also reject the sexual display hypothesis proposed by Moreno et al. (1994), primarily because it is solely females who participate in stone carrying and rampart construction. Furthermore, it was the smaller females in terms of wing and tail length that invested more in stone carrying, both by the total weight of their ramparts and by carrying heavier stones. This is much harder to explain by means of some kind of advertisement display with no additional utilitarian function, and perhaps implies that the stone rampart is of real importance for successful breeding. Such a situation may well arise if the ramparts function as protection from nest predation.

It has long been known that a shortage of cavities can limit the numbers of hole-nesting nonexcavating birds (Lack 1954; Newton 1994). Although most of the information accumulated involves species nesting in tree cavities, it is safe to assume that the availability of cavities on cliffs or rock faces inaccessible to ground predators is a limiting factor as well. As we observed that it is the larger females that nest in cavities higher off the ground and build smaller ramparts, it is quite possible that smaller females are forced to breed in territories where nest sites are more accessible to ground predators and therefore need bigger ramparts to protect their nests. Indeed the major factor influencing blackstart reproductive success in this study appeared to be nest predation. Nest survival rates of this earth cavity nester were extremely low (only 32% according to the Mayfield method). These values are comparable to survival rates of ground-nesting, desert-inhabiting passerines which build open-cup nests (e.g. crested lark, *Galerida cristata*, and desert lark, *Ammomanes deserti*, Shkedy & Safriel 1992). Suarez & Manrique (1992) reported similar low Mayfield survival rates for a closely related species, the black-eared wheatear, *Oenanthe hispanica*. This species, which nests in similar places as the blackstart (Paz 1986; Cramp & Simmons 1988), is also reported to construct a large rampart of sticks and twigs at the nest hole entrance (Cramp & Simmons 1988).

Such a high predation pressure in the case of the blackstart may well explain the large energetic investment involved in constructing stone ramparts beforehand, if these structures assist in lowering future predation risk. In spite of reports of high predation rates of nest contents recorded in other rampart-building species as well (Richardson 1965; Zachai 1984; Palfrey 1988; Shkedy & Safriel 1992; Moreno et al. 1994; Merola 1995), this hypothesis has not been examined experimentally in the past and has simply been ruled out by researchers because of the supposedly increased visibility of nests with ramparts to the investigator's eyes in the field, and therefore to nest predators (Afik et al. 1991; Moreno et al. 1994). This argument loses some of its strength if we examine the type of predators to which these researchers attribute the acts of nest predation. The majority of predators listed (snakes, lizards and small mammals) most probably locate food primarily by olfactory rather than visual cues. The main predators of eggs in our artificial nests were spiny mice, *Acomys* sp., and snakes which we often observed near nests. The fact that no significant difference in daily survival rates was apparent between the incubation and nestling periods in natural nests suggests that predators do not use visual cues, such as increased parental nest visits during the nestling stage, to locate nests. Furthermore, artificial nests containing or lacking stone ramparts were detected by predators with equal ease. All these suggest that blackstart nest predators did not locate nests using vision as a primary cue. This information weakens the camouflage theory, but still does not allow us to reject the nest predation hypothesis.

The structure and size of ramparts in relation to the nest type and location strongly suggest that the rampart may function as a physical barricade which narrows the nest entrance, thus preventing predators from gaining access to the nest contents. Cavity nests usually have small openings. Some cavity-nesting species modify the cavity entrance to the minimal size enabling entry and exit of the bird, a practice that has reached perfection in hornbills, Bucerotidae (Collias & Collias 1984). An ingenious form of barricade against nest predation is the excavation of resin wells by woodpeckers in the immediate vicinity of their nest cavity entrances, which produces a smooth, sticky resin barrier that prevents snakes from gaining access to active nests (Rudolph et al. 1990).

On average, in 37% of artificial blackstart nests containing a stone rampart examined in various experiments, the rampart at the entrance was flattened and the stones scattered during predation. This means that while the predator entered the nest, it was forced to move the stones in order to gain access. In none of these nests, however, did the rampart prove effective in stopping the entry of small predators, as the nest contents were taken eventually. This is the main downfall of the antipredator barricade hypothesis.

Successful nests tended to be higher off the ground than predated nests and pairs that managed to rear at least one fledgling in a season nested significantly higher off the ground than pairs that did not rear any fledglings. Although those nests built higher off the ground (cavity

nests) tended to contain fewer stones and incorporated significantly smaller stones, the dimensions of the nest and rampart did not differ significantly between successful and failed nests. It is possible that the blackstart's ability to renest in a short time (as early as a few days) after premature termination of their present nesting effort is the real adaptation to high nest predation pressures.

We propose a different mechanism through which such structures may still function in reducing predation risk, not of the eggs or nestlings, but of the female attending the nest. The effect of predation on parents at the nest has received scant attention considering its potential importance. Anecdotal reports suggest that predation on incubating adults may be common (Magrath 1988), and may influence parental incubation patterns (i.e. late incubation and thus more synchronous hatching, to reduce time spent incubating and brooding; Hussell 1972; Magrath 1988).

A nest deep in cavities or shelters, especially close to the ground, may not allow the bird to escape if danger arrives. A predator that has entered through the opening would block any means of escape, and the shelter may turn into a trap. This problem has received little attention in the literature, yet Moreno et al. (1994) reported four cases where female black wheatears were predated while attending the nest and we recorded three cases where females disappeared while incubating.

It is quite possible that potential predators of eggs and nestlings will also pose a threat to adult birds. Many species of snake prey on birds (Skutch 1976), and a situation where the bird is trapped deep inside a narrow cavity without the ability to escape by flying out is only bound to make things simpler for the snake (i.e. Fry 1984; Brown & Brown 1996). There are also numerous accounts of small rodents such as *Mus domesticus* preying on small caged passerines, and this may hold true for relatively large omnivorous rodents (40–60 g) such as spiny mice. Mice can also inflict serious bites which may prove fatal for a female blackstart.

Unlike some hole-nesting species (i.e. great tits, *Parus major*; Perrins 1979), blackstarts do not seem to employ any active defensive measures from within the nest to deter predators and to allow the bird sufficient time to escape. An ability to detect predators beforehand, however, may help the nesting female to escape from the cavity in time. We observed that females quickly fly out from nests after hearing noise made by humans or other animals walking near their nest. While approaching nests for inspection, we have never been able to surprise an incubating female. We always observed the female fly out of the nest when we were still over 10 m away, even though there was no direct field of view of the nest entrance. As our whole study site is strewn with large quantities of small stones, walking without making noise is physically impossible. Incubating females no doubt used auditory cues as a sign of our approach. Potential predators of blackstarts do not make as much noise as a human being while moving in the field. Blackstarts, therefore, cannot rely on the natural characteristics of their surroundings and need a way to perceive auditory

information on approaching predators. This could be achieved by having a stone pile at the nest entrance.

If the rampart serves as a barricade (although ultimately an ineffective one), forcing the predator to invest time in moving the stones in order to enter the nest, the noise created and the time the predator is still outside may warn the female early enough to allow her to escape quickly, before the predator has managed to enter the nest itself. Such an early detection ability of danger may be especially important at night, when the female attends the nest for long periods of time yet cannot rely on the blocking of light from the entrance as a sign of the appearance of a predator.

Preliminary examination of this hypothesis has revealed that the females immediately burst out of nests in which we mimicked a small predator moving stones in the stone pile by gently pulling a long nylon cord tied to a stone planted in the stone rampart beforehand. The 'early warning' hypothesis may explain the huge investment of energy involved in carrying stones to the nest, but requires thorough investigation in order to validate it.

### Acknowledgments

We thank the Society for Protection of Nature in Israel (SPNI) En-Gedi field school and the staff of the En-Gedi Nature Reserve for their warm hospitality and great help, and R. Elvert and Y. Wyner for assistance in the fieldwork. We are very grateful to A. Lotem, J. Wright and A. P. Møller for helpful comments and discussions and to J. Moreno and an anonymous referee for comments that helped improve the manuscript. The research was supported by a grant to N.L. from the Inter-University Ecology Fund.

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