CACHE SIZE IN SHRIKES INFLUENCES FEMALE MATE CHOICE AND REPRODUCTIVE SUCCESS

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ABSTRACT.—Male Northern Shrikes (*Lanius excubitor*) in Israel create conspicuous caches of impaled prey. We found that cache size increased before the breeding season, peaked when nests were completed and eggs laid, and declined sharply when males fed impalings to mates and young. We hypothesized that cache size reflects the quality of the male and his territory, thereby influencing mate selection. To test this hypothesis, we manipulated cache size of male Northern Shrikes. Male shrikes with experimentally augmented caches mated earlier and sired more offspring than controls, and males without caches remained unpaired and deserted their territories. We concluded that cache size affects mate selection by female Northern Shrikes and that reproductive success is increased in individuals with larger caches.

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AMONG passerines, true shrikes (Laniinae) are noted for their behavior of impaling prey on pointed objects. Male shrikes impale prey at preferred sites within their territories forming prominent caches which may be retained for long periods (Owen 1948, Cade 1967). They may impale throughout the year (Beven and England 1969).

Impaling aids the shrike in prey manipulation and dismemberment (Morris 1851-1857, Olsson 1985), and may possibly increase the size of exploitable food items (Smith 1972). Furthermore, impaled prey serve as a larder (Donovan 1929, Beven and England 1969). Applegate (1977) suggested that impaling serves to divide labor between sexes, i.e. males do the hunting and impaling, and females butcher the prey and feed themselves and their young. Oksanen et al. (1985) proposed impaling to be the best use of "leisure" time (the time available after immediate food needs of the shrike and its dependents are fulfilled).

Although cached impalings serve as a larder to the shrike, their conspicuousness makes them subject to kleptoparasitism (Olsson 1985, Yosef 1988). Also, the fact that most long-term impaling is done by males (Owen 1948, Beven and England 1969, pers. obs.) does not, in itself, substantiate the suggestion that impaling divides labor between sexes. Shrikes often impale small organisms (e.g. wasps, bees, beetles, etc.) (Hegazi 1981, Olsson 1986, pers. obs.) that do not necessitate immobilization for butchering, and sometimes they impale inedible objects (Owen 1948, pers. obs.). We suggest, therefore, that the above reasons for impaling by shrikes do not fully explain the behavior's functions.

Male Northern Shrikes (*Lanius excubitor*) in the central Negev, Israel, reside permanently in breeding territories and some males are polygynous (Yosef and Pinshow 1988). Females are not permanent residents and leave immediately after their broods fledge. Although males cache prey regularly, females may impale but do not cache. These observations led us to hypothesize that prominent caches play a role in mate attraction. Presumably, they reflect the quality of the male and its territory, and thus affect mate selection by females.

This hypothesis led to three predictions. First, concentrations of impaled prey in prominent places should be greatest at the onset of the breeding season. Second, when females arrive, males with richer caches will pair before those with poorer ones. Finally, males with bigger caches will beget more offspring.

METHODS

We tested the predictions by experimentally manipulating cache size of male Northern Shrikes near Sede Boqer (34°47′N, 30°52′E, 475 m ASL) in the Negev desert, Israel. This area is classified as arid, with 250-300 biologically dry days per year and a precipitation to evaporation ratio of <0.2 (UNESCO 1977). Rain falls during the winter and averages 104 mm annually, with large annual differences in total precipitation and in its temporal and spatial distribution. Dew occurs on ca. 190 nights/year and daily relative

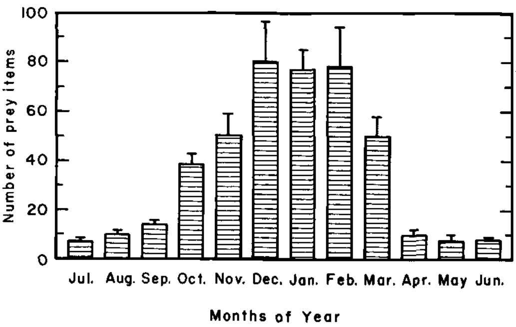

Fig. 1. The number of prey items cached by 6 male Northern Shrikes monthly. Histogram and bars denote monthly $\bar{x}$ ± SD.

TABLE 1. Number of nestings, eggs laid, young fledged in control groups of Northern Shrikes during the 1988 breeding season in the Negev desert. Values are $\bar{x}$ ± SD. There are no differences between groups.

Group	Nests	Eggs laid	Young fledged
Northern (3 pairs)	1.67 ± 0.58	6.0 ± 0.0	3.4 ± 3.13
Southern (3 pairs)	1.67 ± 0.58	5.6 ± 0.55	4.6 ± 1.52

humidity averages 58%. Maximum and minimum daily air temperatures range between 40°C and 9°C over the year and daily air temperature averages 32°C during August, the hottest month, and 5°C in January, the coldest month (Zangvil and Durian 1983). The predominant perennial plants are the shrubs *Artesmia herba-alba, Gymnacarpos decander, Hammadia scoparia, Noaea mucronata, Raemuria negevinsis, Zygophyllum dumosum* and *Atriplex halimus*. In addition, a variety of herbs and geophytes occur (Danin et al. 1975).

From June 1987 to June 1988, we mapped territories of 12 male Northern Shrikes by general observation of their activity and observation of the reaction of the males to taped songs of other males and to a stuffed dummy. Their favored cache sites were noted, but no measure of territory quality was made. All birds were captured with a bal-chatri noose trap (Clark 1968) and each was marked individually with colored leg bands and released. Birds were sexed by observing mating and other behavior. Visual observations were made with binoculars (10 × 20) and a telescope (×20).

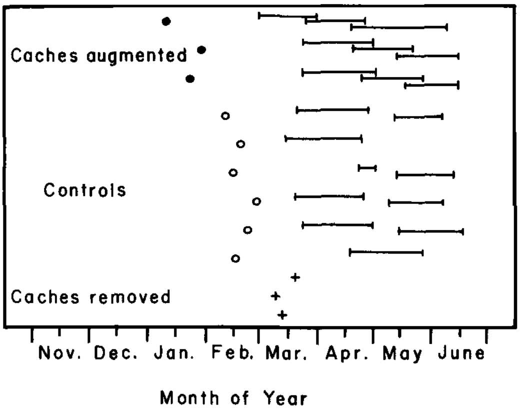

Fig. 2. Time when females were first observed in the territories of male Northern Shrikes with artificially augmented caches (●) and in control birds (O). The times of departure (+) of shrikes whose impalings were removed and remained unpaired are shown. Horizontal bars adjacent to symbols represent time from laying to fledging for each nesting.

Six males served as controls and their caches were counted weekly for an entire year. On the same day, all prey from the caches of 3 experimental males were collected and the caches of 3 others were augmented by increasing each by 25% over the mean number of prey in control caches. Prey species, which consisted almost entirely of arthropods, were added to the augmented caches in the same proportions as found in the controls. To avoid the possible effect of females returning to the breeding area from a particular direction and pairing with males they discover first, 3 control birds were chosen with territories in the north of the study area and 3 in the south.

Means are expressed (±SD), but groups were compared using the Mann-Whitney *U* test (Zar 1984). We chose $P < 0.05$ as the minimum acceptable level of significance.

RESULTS

Males had between 2 and 5 caches each in their territories. From June to September 1987, the monthly mean of impaled items of the 6 controls varied between 6 and 14 (Fig. 1). In October there was a sharp rise which peaked from December through February. During this period, males also impaled inedible objects (e.g. snails, feathers, crusts of bread). For the next 2 months, the number of cached prey remained high with fluctuations when males supplemented their diets from their caches during inclement weather.

The first females arrived in January, and the males with augmented caches paired first (Fig. 2). Females were first seen in the cache-augmented territories between 8–26 January, which was significantly earlier than the first appear-

TABLE 2. Time of first observation of females in control and cache-augmented territories of male Northern Shrikes and number of nestings, eggs laid, and young fledged by pairs in the territories during the 1988 breeding season in the Negev desert. Values are $\bar{x} \pm$ SD; those in columns followed by the same letter are significantly different.

Territory	Females first seen	Nests	Eggs laid	Fledglings
Control (6 pairs)	12-27 Feb. 1988	1.67 ± 0.52A	9.67 ± 2.94B	6.70 ± 1.97C
Cache-augmented (3 pairs)	8-26 Jan. 1988	3.00 ± 0.00A	18.00 ± 1.00B	17.0 ± 1.73C

ance of females in the six control territories (12-27 February) ($U_{3,6} = 18$, $P < 0.025$). Thus, on average, males with augmented caches paired 1 month before controls. All three males deprived of their caches remained unpaired and left the study area in mid-March.

We found no significant differences between the control groups in the number of times pairs nested ($U_{3,3} = 11$, $P > 0.05$), the number of eggs laid by females ($U_{3,3} = 10$, $P > 0.05$), or the number of young fledged by pairs ($U_{3,3} = 4$, $P > 0.05$) (Table 1). Therefore, we combined the results of the two control groups and tested these against those of the cache-augmented pairs (Table 2).

The first male to pair was also the first to have completed nest building on 25 February (Fig. 1). The other two males with augmented caches and the six controls all began nesting between 13 and 20 March. Males with augmented caches fathered 3 broods each, which was significantly more than the 1 or 2 broods fathered by controls ($U_{6,3} = 46$, $P < 0.05$). On the average, 87.5% more eggs were produced by pairs with augmented caches than by controls ($U_{6,3} = 31$, $P < 0.05$), and cache-augmented pairs fledged 60% more young ($U_{6,3} = 21$, $P < 0.05$).

DISCUSSION

As predicted, we found that cache size of male Northern Shrikes increased prior to their breeding season, peaked when nests were completed and eggs laid, and declined sharply when impalings were fed to mates and offspring. Also, males with larger caches mated first and sired more offspring. We concluded that female Northern Shrikes apparently selected males that had larger caches and that their reproductive success was increased when they paired with such males. Although females in cache-augmented territories did not breed earlier than females in control territories, they produced more eggs, which suggests that they began to breed in enhanced body condition. The overall importance of the cache is emphasized by the fact that cache-deprived males failed to breed.

There are at least three reasons why female shrikes may select males that have larger caches. A large cache might indicate that its owner holds a territory abundant in resources (Dobzhansky 1937, Mayr 1972, Searcy and Yasukawa 1983), or is more proficient at finding prey than the other males in the area (i.e. has "good genes") (Borgia 1979, Kodric-Brown and Brown 1984). Alternatively, a large cache might simply be attractive to females without indicating either of the former (Darwin 1871, Lande 1981, Kirkpatrick 1982). Holding a better territory does not necessarily mean that the male is genetically superior, only that his mate can feed herself and her offspring better. The "good genes" option means that males with larger caches generally have genes for higher viability, which will be transferred to the offspring. The "attractiveness" option would have no viability benefit. It would only enhance the male's probability of mating. We could not discriminate between these possibilities as the experiment was designed to answer the question of whether concentrations of prey impaled in prominent places affects female choice.

In contrast to cases in which female mate choice in birds may be influenced by the size of a male's adornment, as in birds of paradise (LeCroy et al. 1980), in pheasants (Davison 1981), or in widow birds (Andersson 1982), or by constructed decoration, as in bowerbirds (Borgia et al. 1987), cache size as a cue for mate selection in shrikes may serve as a direct measure of male and territory quality—its function as a larder being an additional benefit.

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