

PARALLEL VERSUS SERIAL BREEDING STRATEGIES IN THE GREAT GREY SHRIKE AT SEDE BOQER, ISRAEL

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ABSTRACT.—In the Negev Desert Highlands we observed two different breeding strategies for Great Grey Shrikes (*Lanius excubitor*). Males with naturally large or artificially augmented caches used a different breeding strategy than conspecifics with small caches. In pairs with large caches, females laid a second clutch soon after the first hatched and males cared for the first brood (parallel strategy). In pairs with small initial caches, both parents cared for the young until fledged, with the male doing all provisioning; females laid their next clutch after fledging (serial strategy). Six pairs that adopted the parallel strategy had significantly more nestings (80%), produced more eggs (93%), and fledged more young (96%) than pairs that adopted the serial strategy.

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The Great Grey Shrike (*Lanius excubitor*) is the most widely distributed of all shrikes, and has a Holarctic distribution (Cade 1967). In Israel, it is a permanent resident in the Arava, the Golan Heights, Samaria, and the Negev Desert (Paz 1987). The Great Grey Shrike's behavior of impaling prey on pointed objects has been much studied (e.g. Morris 1851, Donovan 1929, Miller 1931, Amadon 1951, Lorenz and St. Paul 1968, Wemmer 1968, Beven and England 1969, Smith 1972, Olsson 1986). However, studies of its breeding biology are limited to migratory populations in Europe (e.g. Huhtala et al. 1977, Bassin 1982, Solis and Reboilo 1985) and North America (Bent 1965, Cade 1967). Ours was the first study of a partially-sedentary population.

We studied 15 male Great Grey Shrikes and observed nesting attempts in 6 others. During 1987–1989 we investigated the influence of cache size on the reproductive strategy of the Great Grey Shrike. We hypothesized that females evaluate male parental worth based on the size of the male's cache and use it to decide on a reproductive strategy for the season. We predicted that females would choose males with larger caches and that the larger the cache, the more progeny the pair would produce. We tested these predictions by observing pairs where the males had different sized caches at the beginning of the season and by artificially

manipulating cache sizes (Yosef and Pinshow 1989).

During the 1987 breeding season we discovered that (1) male Great Grey Shrikes were resident in their territories throughout the year (Yosef and Pinshow 1989); (2) females arrived at varying periods of time prior to the breeding season and some males paired earlier than others; (3) two males had polygynous relations with two females each (Yosef and Pinshow 1988b); and (4) differences existed in nesting frequency between pairs. Furthermore, in all cases, the male initiated nest building by bringing the first twigs and commencing nest building, although the female ultimately did most of the building by herself (Yosef 1992d).

STUDY AREA AND METHODS

The study was done on Sede Zin, a loess-covered plateau, near Sede Boqer (30°52'N, 34°47'E; 475 m) in the Negev Desert highlands. The region is arid with mild winters and warm summers (UNESCO 1977). Rainfall occurs in winter and averages 90 mm annually. Dew occurs on about 190 nights, amounting to 18 mm annually (Zangvil and Druián 1986). The plateau supports a sparse dwarf-shrub community dominated by *Hammada scoparia*, *Zygophyllum dumosum*, *Raoumia hirtella*, *Anabasis syriacus*, and *Artemisia herba alba*. The major woody species are *Januaris niletica*, *Atriplex halimus*, *Retoum lacum*, and *Tymonaea hirsuta*. Regional flora includes a large variety of herbs and geophytes (Darin et al. 1975).

Birds were trapped during the 1988 breeding seasons (mid-January to mid-June) using a modified Bal-Chatri trap baited with a mouse (Clark 1967, Kridelbaugh 1982). They were banded with an aluminum

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hand on one leg and one colored plastic band on the other. Offspring were banded with two colored plastic bands on the same leg, such that the color of the upper band was the same as that of the male parent.

Territories of males in the study were mapped and dimensions recorded through observation of their occurrence and spatial limits of their response to taped songs of other males and a mounted specimen. All prey items taken were identified.

RESULTS

Two different breeding strategies were observed during the breeding seasons. Great Grey Shrikes with naturally large or artificially augmented food caches (Yosef and Pinshow 1989) used a different breeding strategy than conspecifics with small caches. In pairs with large caches, females laid a second clutch soon after the first hatched while males cared for the first brood (parallel strategy). In pairs with small initial caches, both parents cared for the young until fledged, with the male doing all provisioning; females laid their next clutch after fledging (serial strategy).

Males had between two to five caches each in their respective territories. During the 1987 breeding season, three (caches untouched) of the nine pairs adopted the parallel breeding strategy, and six the serial strategy (Table 1). Pairs adopting the parallel strategy averaged 3.0 nestings for the season, laying 18.33 eggs/pair. Of these, 13 hatched (hatching success of 80.7%) and 10 young fledged (fledging success of 65.25%). In contrast, pairs that adopted the serial strategy nested on average 1.66 times, laying 9.5 eggs/pair for the season. Of these an average of 6.83 eggs hatched (hatching success of 71.03%) but only 3.67 young fledged (37.52% fledging success). A comparison of the two strategies, for the 1987 breeding season, shows that pairs adopting the parallel strategy had significantly (80.72%) more nestings ($U_{3,6} = 20, P < 0.05$), produced significantly (92.95%)

more eggs ($U_{3,6} = 15, P < 0.05$) and although their hatching success was only 13.54% greater, fledged significantly (73.91%) more young ($U_{3,6} = 12, P < 0.05$). No parallel breeding was observed during the 1989 breeding season.

The overall results for 1987–1988 indicate that the six pairs (all with either naturally large or artificially augmented caches) that adopted the parallel strategy had significantly (80.2%) more nestings ($U_{6,15} = 99, P < 0.05$), produced significantly (92.6%) more eggs ($U_{6,15} = 96, P < 0.05$) and fledged significantly (96.5%) more young ($U_{6,15} = 94, P < 0.05$) than pairs that adopted the serial strategy.

DISCUSSION

For many species of birds, breeders with fully dependent young do not typically begin a new nesting attempt. Yet pairs that raise two broods concurrently may rear more young than pairs that do not (Burley 1980, Hill 1984). Therefore, parents that do raise concurrent broods face the problem of partitioning their care between young of the first clutch and eggs from the second. Siegfried and Frost (1975), Burley (1980), and Hays (1984) reported cases of clutch overlap and showed that investment in two concurrent broods occurred during the least demanding phase of development of the first.

Finke's (1984a) model proposes existence of variation in male help, in response to which females must adjust their reproductive effort to maximize their lifetime reproductive output. In some species, male help has been shown to increase fitness of the pair (Dyrce 1977, Alatalo et al. 1981, Muldal 1986), but it may be difficult for females to immediately assess males at the time of their arrival (Wittonberger 1981) and they may have to rely on features (e.g. courtship feeding) that could indicate male parental quality.

In birds, the behavior of the male feeding the

TABLE 1. Number of nestings, number of eggs laid for the whole season, and hatching and fledging success for each pair of Great Grey Shrikes (*Lanius excubitor*) adopting either the 'parallel breeding strategy' or the 'serial breeding strategy' during the 1987 breeding season.

Nesting attempts	Number of eggs	Eggs hatched	Hatching success (%)	Young fledged	Fledging success (%)
Parallel strategy ($n = 3$ pairs):					
3 ± 1	17 ± 6	13 ± 3	81	10 ± 5	65
Serial strategy ($n = 6$ pairs):					
2 ± 1	10 ± 3	7 ± 3	71	4 ± 3	38

female before or during breeding season is generally known as courtship feeding. Lack (1940) explained this behavior as being symbolic and for maintaining or strengthening the pair bond. But Curio (1959) observed in the Pied Flycatcher (*Muscicapa hypoleuca*) that females received too great an amount of food from their mates to consider it only symbolic. Royama (1966) studied the Great (*Parus major*) and Blue tit (*P. caeruleus*), and suggested that this behavior was significantly valuable to the female, especially during egg laying and incubation periods, and to have a nutritional function rather than a symbolic one. Similar views were adopted by Krebs (1970) for the Blue Tit and by Kilham (1972) for the White-breasted Nuthatch (*Sitta carolinensis*).

Nisbet (1977) showed in Common Terns (*Sterna hirundo*) that prior to egg-laying, females depend on males to provide all their food, and that they use this provisioning as an indicator of future male parental quality. The females are liable to desert if the supply is inadequate. Trivers (1972) proposed that the courtship period could provide an opportunity for females to assess male quality. Yamagishi and Saito (1985) showed in the Bull-headed Shrike (*L. bucephalus*), that the high frequency of courtship feeding in the cold season and in the critical breeding stages is crucial to females and they interpreted it as a behavior that is not symbolic, but necessary to the success of breeding attempts early in the season.

In Israel, Great Grey Shrikes usually begin laying at the end of January or in early February, and such early laying is most unusual compared to other Israeli passerine birds which eat mainly terrestrial insects. As mentioned above, females arriving early are fed fresh prey which is augmented by some food from the male's cache. This suggests that a male shrike may be indicating to a courted female that there is a predictable, quality food supply available on its territory. Females fed in this manner are likely to start the breeding season in enhanced body condition. Females in better body condition than their neighbors can, we suspect, adopt the more strenuous, parallel breeding strategy.

The advantages of the parallel strategy are quite obvious. Our manipulation of food caches indicated that cache size and the males' ability to provide food to the female prior to her laying the first clutch may together serve as cues by which the females judge male quality, and decide upon their strategy for the forthcoming breeding season. It is particularly important to determine if and how females are able to alter their reproductive effort if males vary in the aid they provide.

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