FAT RESERVES OF AN OPPORTUNIST AND OF A SPECIALIST SPECIES IN THE NEGEV DESERT

YEHOSHUA SHKEDY AND URIEL N. SAFRIEL

Department of Zoology, The Hebrew University of Jerusalem, Jerusalem 91904, Israel, and the Mitrani Center for Desert Ecology, Jacob Blaustein Institute for Desert Research, Sede Boqer 84990, Israel

ABSTRACT.—We extracted fat from samples of two sympatric lark species resident in the Negev Desert of Israel. The Crested Lark (*Galerida cristata*), which fed on a wide range of seed sizes, exhibited within-day but not seasonal fluctuations in fat content and carried on average 12.9% fat (of lean dry mass). The Desert Lark (*Ammomanes deserti*), which fed on a narrower range of seed sizes, exhibited smaller within-day fluctuations in the amount of fat, and carried on average 8.9% fat. We propose that although the two larks occupy the same environment and are of the same feeding guild, these differences are adaptive. When food becomes periodically scarce, feeding specializations of the Desert Lark may often suffice to overcome shortage, but their absence in the generalist Crested Lark may make it more dependable on fat reserves. *Received 9 July 1990, accepted 20 December 1990.*

SPECIES that utilize few food types are expected to exploit each of them more efficiently than species that utilize a wide range of resources (Pianka 1981a). If high efficiency is expressed in the ability to exploit effectively a resource even when it becomes rare, then food specialists should be less susceptible than food generalists to a simultaneous reduction in the level of most resources.

Fat storage, however, can be used as a buffer against fluctuations in food availability (King 1972), but the size of the fat reserve is expected to be determined by a trade-off between benefit (reduced probability of starvation) and cost (increased risk of predation) (King and Farner 1966; King 1972; Blem 1975, 1976; Stuebe and Ketterson 1982; Nolan and Ketterson 1983; Pienkowski et al. 1984; Lima 1986, 1988; Rogers 1987). It can be predicted that specialists and species of stable environments should deposit smaller fat reserves than generalists and species of variable environments.

We compared fat storage in two species of nonmigratory larks (Alaudidae). The distribution of the Crested Lark (*Galerida cristata*) extends from southern Sweden in the north to northern Kenya in the South (Hall and Moreau 1970). Most of this range is nondesert, hence desert might be marginal habitat for the Crested Lark. The distribution of the Desert Lark (*Ammomanes deserti*) is confined to arid regions (Hall and Moreau 1970). Both species are ground dwelling, and their diets comprise seedlings, insects, and a large proportion of seeds (Shkedy 1990). We found that in a region of sympatry within the Negev Desert of Israel, the Crested Lark consumed seeds that range from 0.3 to 53.5 mg in mass, whereas most of the seeds consumed by the Desert Lark were lighter than 1.0 mg. The Crested Lark generally was less tenacious and, depending on the time of year, moved between regions and habitats; but the Desert Lark was much more sedentary (Shkedy 1990). Thus, with respect to both food resources and habitat utilization where both species overlap, the Desert Lark is a specialist and behaves as if its environment is rather stable. The Crested Lark is a generalist, frequently changes food types and habitats, and behaves as if this same environment is rather variable. Specialization vs. generalization are regarded as adaptations to stable vs. unstable environment (Pianka 1981b, Futuyma and Moreno 1988). Because both species occur in the same environment, their different adaptations may reflect differences in the "interpretation" of environmental stability. We explore whether this implied difference in "interpreted" environmental stability and in mode of resource utilization by co-occurring species is reflected in differences between them in fat storage tactics.

METHODS

The study site was on Halouqim Ridge in the central Negev Desert of Israel near Sede-Boqer (30°52′N, 34°57′E; 475 m above mean sea level). The terrain consists of stony hillsides, with sparse shrubs (mostly *Artemisia herba alba*, *Hammada scoparia*, and *Zygophyllum dumosum*) (Evenari et al. 1982). Mean annual rainfall is 91 mm. Rainfall occurs only during winter (Sep-

TABLE 1. Mean (±SD) wet mass (WM), lean dry mass (LDM), fat content (F), and fat ratio (FR) of all birds. Level of significance: *** = $P < 0.001$.

Species	n	WM	LDM	F	FR (%)
Crested Lark	118	39.0 ± 2.7	11.5 ± 1.2	1.48 ± 0.71	12.9 ± 7.2
Desert Lark	103	22.0 ± 2.5	6.6 ± 0.8	0.59 ± 0.22	8.9 ± 3.2
Statistics		59.0***[a]	38.9***[a]	12.7***[a]	5.47***[b]

[a] t values.
[b] z value, Mann-Whitney U test.

tember to May). Mean monthly air temperatures vary from 9.8°C in January (the coldest month) to 25.5°C in July (the hottest month). During January, air temperatures might drop to −1°C (Zangvil and Druian 1983; data from meteorological station located 2 km from the study site).

We obtained our data from 118 Crested Larks and 103 Desert Larks collected from February 1987 to July 1989. Samples of both species were secured four times a year (hereafter seasons): before the breeding season (February through March, hereafter February), just after the breeding season (July), when Crested Larks return to the study site (September), and December. Each shooting expedition lasted approx. 2 weeks. Right after collection, we weighed each bird (wet mass, WM) to the nearest 0.5 g (50-g Pesola spring balance), measured its wing length (WL) to the nearest 1 mm (from carpal joint to wing tip; Newton 1969) and sexed it in the field by dissection. Because the gonads are small during nonbreeding seasons and there was damage caused by the shotgun pellets, we sexed only 56 Crested and 49 Desert larks. The birds were deep-frozen 1-4 h after death. We used Moreau and Dolp's (1970) methods for determining dry mass (DM), the amount of fat (F, extracted with petroleum ether), and lean dry mass (LDM). We then calculated the fat ratio by calibrating extracted fat with the bird's lean dry mass (FR = F/LDM) and with wing length (FR1 = F/WL). The results of the statistical analysis concerning both measures of fat ratio (FR and FR1) were similar, thus we only present the results with fat ratio of fat calibrated with lean dry mass.

RESULTS

On average, Crested Larks were heavier, they stored more fat, and their fat ratio (fat to lean dry mass) was higher than Desert Larks' (Table 1). In July lean dry mass of Desert Larks was 8.7% lower than average; in Crested Larks, wet mass was 4.4% lower than average and lean dry mass was 9.2% lower (Table 2). This is probably because juveniles (which we did not always distinguish from adults) were presumably part of the July samples, and juveniles are lighter than adults (Pätzold 1986). Desert Larks' mean lean dry mass was similar in all other seasons, but in Crested Larks it was lower in September than in December (Table 2). On average, fat ratio in both species was lower in September than in other seasons, but this trend was not significant (Table 2). There were no significant seasonal differences in fat ratio.

Fat ratio calculated over the entire study period increased during the day in Crested Larks. The highest fat ratio was between 1,500 and 1,700, and the ratio later decreased (Fig. 1). The mean increase of fat ratio over the entire study period was 0.5% per hour. In the pooled data of birds secured in December of 1987 and 1988, fat ratio increase during the day was higher than in all other seasons combined, and higher than that of the Desert Lark (Fig. 1, Table 3). The correlation between fat ratio and time of day was low and not significant in February and July (Table 3).

The daily increase in fat ratio of Desert Larks was much slower and not significant (only 0.03% per hour; Fig. 1, Table 3).

In February, lean dry mass in both species increased significantly during the day ($r_s = 0.37$, $n = 28$, $P < 0.05$, in the Desert Lark; and $r_s = 0.36$, $n = 37$, $P < 0.05$, the Crested Lark). Wing length also increased in the Desert Lark ($r_s = 0.33$, $n = 26$, $P < 0.05$) and in the Crested Lark ($r_s = 0.29$, $n = 36$, $P < 0.05$). In both species male wet mass was greater than female wet mass, and mean lean dry mass of Crested Lark males was greater than females (Table 4). There were no significant differences between sexes in any other index.

DISCUSSION

There are only a few studies of fat deposition in nonmigratory birds of nontemperate latitudes (Grant 1965, Ward 1969). The amount of stored fat (ca. 13% of the lean dry mass) as well as its seasonal fluctuations (with extreme deviation of a monthly mean from an annual mean of <0.3 g fat) in the tropical Yellow-vented Bul-

TABLE 2. Seasonal variation ($\bar{x}$ ± SE) in lean dry mass (LDM), fat ratio (FR), and wet mass (WM).[a]

	LDM	FR (%)	WM
	Desert Lark		
February	6.76 ± 0.12	9.2 ± 0.6	21.60 ± 0.36
July	6.06 ± 0.11[b]	9.3 ± 0.4	21.44 ± 0.37
September	6.81 ± 0.15	7.2 ± 0.6	21.80 ± 0.48
December	7.18 ± 0.17	9.5 ± 0.6	22.54 ± 0.49
	Crested Lark[c]		
February	12.01 ± 0.12	13.4 ± 0.9	39.24 ± 0.29
July	10.46 ± 0.16[b]	13.8 ± 1.5	37.29 ± 0.52
September	11.59 ± 0.21[d]	10.2 ± 1.0	38.69 ± 0.66
December	12.24 ± 0.10[d]	13.1 ± 1.2	40.26 ± 0.50

[a] Seasonal variation analyzed by two-way ANOVA. The year of study and the interactions between the year and the season did not affect significantly any of the independent variables. Comparisons between seasons were evaluated by Duncan's multiple range test only when the F values of the season effect were found significant by the two-way ANOVA.

[b] Different from all other seasons ($P < 0.05$).

[c] Wet mass in July was significantly lower than in February and in December ($P < 0.05$).

[d] Lean dry mass in September and December are significantly different ($P < 0.05$).

bul (*Pycnonotus goiavier*; fig. 2 *in* Ward 1969) are small when compared with temperate birds of similar sizes. For example, fat ratios of the American Goldfinch (*Carduelis tristis*) at Ontario in January and February was more than 30% (Middleton 1986, see also King and Farner 1966, King 1972, Visser 1978, Dugan et al. 1981, Nolan and Ketterson 1983, Pienkowski et al. 1984).

The Crested Lark's mean fat ratio (12.9%) was similar to that of the tropical bulbuls (13%; Ward 1969), but the fat ratio of the Desert Lark was even lower (8.9%). Seasonal fluctuations in fat ratio of both species were insignificant, even at times when lean dry masses were relatively low (July for both species and September for the Crested Lark). There were no significant differences between sexes in the pattern of fat accumulation in either species, despite differences in mass between the sexes in the Crested Lark (similar to the Sedge Warbler (*Acrocephalus schoenobaenus*); Baggott 1986). The only difference between sexes could have been that of a greater proportion of water contents in Desert Lark males than in females, as suggested by the significant difference between male Desert Larks' wet mass and the lack of significance in lean dry mass. As compared with birds in temperate, nondesert regions, the amount of stored fat is low in a climatically very stable and warm region (the tropics), as well as in the Negev Desert, where seasonal differences in temperatures are high and winter temperatures may drop to below 0°C (Zangvil and Druian 1983).

It is possible that the observed small fat storage serves as an energy source for overnight metabolism, as suggested for the tropical Yellow-vented Bulbul (Ward 1969). Indeed, the daytime buildup of fat in the Crested Lark may indicate an overnight utilization. The evening drop in fat ratio shown in Fig. 1 is probably an artifact. We shot only foraging birds, and the very few birds shot in the evenings were probably unsuccessful earlier in the day, and hence they were relatively lean. The daytime build up of fat in the Crested Lark was evident in December, when the nights are longest, and typified by low average minimum daily temperatures. No accumulation, however, was detected in February, though nights are still long and their temperatures are nearly as low as in December. Our February data may be misleading. Although February fat ratio did not increase during the day, lean dry mass and wing length did. This may mean that for some reason we caught larger birds late in the day in February.

Within-day changes in fat ratio never occurred in the Desert Lark. It is therefore possible that, instead of utilizing at night the fat stored during the day, the Desert Lark lowers its body temperature during the night, as birds often do during fasting (Baldwin and Kendeigh 1932, Biebach 1977, Ketterson and King 1977, Stuebe and Ketterson 1982) or during the night (Prinzinger et al. 1989). Only one desert bird, the Common Poorwill (*Phalaenoptilus nuttallii*), engages in long-term dormancy (Bartholomew et al. 1962), and we have no data on desert birds that depress their metabolic rate during the night. As an alternative for lower night metabolism, the Desert Lark may substitute daytime

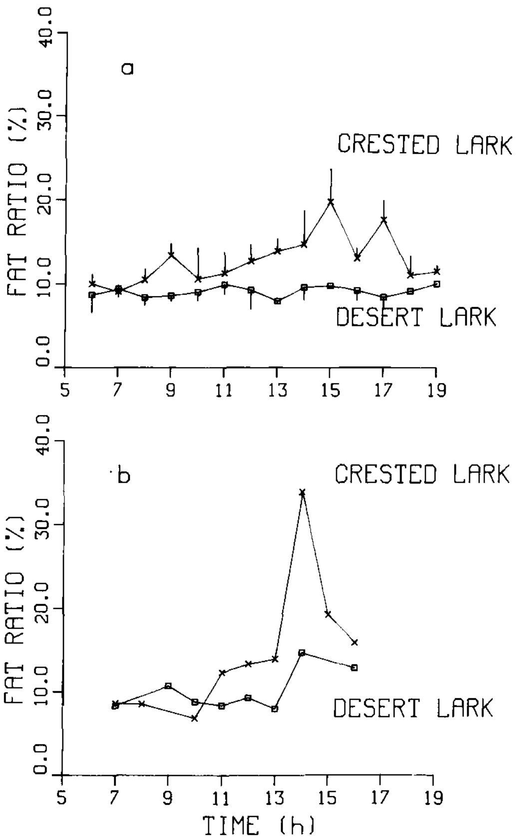

Fig. 1. Daily changes in mean fat ratio of Desert Larks and Crested Larks (a) for the entire study period and (b) only for birds collected in December 1987 and 1988. Vertical lines are 1 SE.

fat storage by liver glycogen storage for overnight utilization.

The stored fat in the two desert species we studied may also buffer between-days fluctuations in foraging success. This might be more significant for the Desert Lark than for the Crested Lark. The relatively stable body condition of the Desert Lark suggests an "interpretation" of the desert environment as a seasonally stable environment. The Crested Lark, on the other hand, had a low lean dry mass in September, after late-summer utilization of large desert valleys and patches of desert agriculture. Thus, even though it left its breeding habitats and utilized other desert habitats, it still did not maintain body mass the year round.

Calder (1974) suggested that large species are better buffered against environmental variability and should therefore, store less fat. But the larger Crested Lark stored on the average 45% more fat than the smaller Desert Lark. The overriding factor is presumably the difference in "interpretation" by the two species of the same environment, viewed by the opportunist species as unstable, and by the specialist as relatively stable. We propose that the food and habitat opportunism of the Crested Lark are safeguarded by reserve storage, at the cost of excessive mass, which may impair foraging and predator avoidance. The food and habitat specializations of the Desert Lark enable this species to be less dependent on fat storage. It may be more risky, at times of prolonged food scarcity, but the risk may be balanced by improved mobility.

It can also be argued that it is easier for a diet generalist than for a specialist to collect less preferred food types when the preferred ones suffice for maintenance only. When food becomes scare, the specialist is still sufficiently efficient to obtain its maintenance requirements, but it has difficulties in shifting to additional food types for fat storage. This may not apply to the Desert Lark because its main food type (small seeds) is more abundant by mass than large seeds, both in time and space (Shkedy and Safriel in prep.). Furthermore, if the Desert Lark barely managed to satisfy its maintenance requirement and the Crested Lark never experienced shortages, this should have been reflected not only by an average fat storage in the Desert Lark smaller than that in the Crested Lark, but also by a between-individuals variance around mean fat ratio in the Desert Lark larger than that in the Crested Lark. But, the between-individuals coefficient of variation (%) for Desert Lark's fat ratio (35.9 ± 2.81) was lower (data from Table 1, $z = 3.66$, $P < 0.001$) than that of the Crested Lark's (55.8 ± 4.63), although when analyzing each season separately (data from Table 2) the coefficients of variation of the

TABLE 3. Spearman rank correlation between fat ratio (FR) and time of day (h). Levels of significance: * = $P < 0.05$, ** = $P < 0.001$.

	Crested Lark	n	Desert Lark	n
February	0.15 NS	37	−0.001 NS	28
July	0.28 NS	30	−0.21 NS	27
September	0.41*	22	0.16 NS	25
December	0.75**	29	0.12 NS	23
Total	0.40**	118	0.04 NS	103

TABLE 4. Mean (±SD) wet mass (WM), lean dry mass (LDM), fat ratio (FR in %) and fat (F) of male and female Crested Lark and Desert Lark. Sample sizes are in parentheses. Levels of significance: ** = $P < 0.01$, *** = $P < 0.001$, NS = not significant.

	Crested Lark			Desert Lark		
	Males	Females	z	Males	Females	z
WM	39.9 ± 2.0 (44)	37.7 ± 2.6 (29)	3.8***	22.7 ± 2.3 (38)	21.0 ± 1.7 (32)	3.5***
LDM	11.9 ± 1.0 (35)	11.0 ± 1.1 (21)	2.9**	6.8 ± 0.8 (25)	6.6 ± 0.6 (24)	0.9 NS
FR	14.4 ± 8.8 (35)	15.1 ± 9.7 (21)	0.5 NS	8.7 ± 3.4 (25)	8.9 ± 3.7 (24)	0.3 NS
F	1.7 ± 0.8 (35)	1.6 ± 0.9 (21)	0.1 NS	0.6 ± 0.2 (25)	0.6 ± 0.2 (24)	NS

Desert Lark were significantly lower only in July ($t = 2.61$, df = 76, $P < 0.05$).

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