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TEMPORAL-SPATIAL PATTERNS OF FOOD CACHING IN TWO SYMPATRIC SHRIKE SPECIES[1]

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Abstract. To study the temporal-spatial patterns of food caching in two sympatric shrike species (Northern Shrike *Lanius excubitor* and Red-backed Shrike *L. collurio*) in the northwestern region of the Iberian Peninsula, I sampled cached prey. Northern Shrikes cached food mainly during the non-breeding period, and Red-backed Shrikes during the breeding period, depending on prey availability and energy requirement. Rate of food cached by Red-backed Shrikes increased as number of nestlings increased. Most prey cached by Northern Shrikes was used within 9 days. Red-backed Shrikes usually utilized their caches within 24 hr, mainly at dawn and dusk. Northern Shrikes used 62% of cached prey, and Red-backed Shrikes 88%. At least 6% of the prey cached by Red-backed Shrikes was kleptoparasitized, chiefly by wasps.

Hawthorn (*Crataegus* sp.) and blackthorn (*Prunus* sp.) shrubs with cylindrical, thin and long thorns were preferred for caching, whereas rose (*Rosa* sp.) and bramble (*Rubus* sp.) shrubs with laterally flattened, wide and short thorns were avoided by both species. Red-backed Shrikes scattered their caches. The distance between the nest and the prey cached by the Red-backed Shrike depended on the availability of suitable thorny shrubs in the territory, with a tendency to cache close to the nest. Shrikes chose the upper and inner parts of the shrubs for caching, presumably to hide the food from kleptoparasites. I found an association between prey color and color of cache-shrub, suggesting that cryptic coloration influenced choice of cache site.

Key words: Food caching; temporal patterns; cache use; spatial patterns; Lanius excubitor; *Northern Shrike;* Lanius collurio; *Red-backed Shrike.*

INTRODUCTION

Bird species that cache food usually combine the following temporal and spatial patterns; they cache food while it is abundant in order to consume later during periods of shortage or when energy requirements are greater, and they scatter the caches to reduce the probability of being discovered by kleptoparasites (reviews by Roberts 1979, Smith and Reichman 1984, Andersson 1985, Sherry 1985, Källander and Smith 1990, Vander Wall 1990).

Most studies of food storage by *Lanius* shrikes have concentrated on the ontogeny of impaling and wedging of prey (Lorenz and von Saint Paul 1968; Wemmer 1969; Smith 1972, 1973) and on the variety of prey cached (for the western Palearctic see Cramp and Perrins 1993), rarely addressing the ecological and energetic aspects of this behavior. Carlson (1985), however, suggested that Red-backed Shrikes (*L. collurio*) selected cache sites by a compromise between maximizing the rate of food delivery to the young and minimizing both kleptoparasitism risk and location of nest by potential predators. Yosef and Pinshow (1989) demonstrated that increasing prey storage by male Northern Shrikes (*L. excubitor*) during the pre-reproductive period influenced female mate choice.

This study analyzes the seasonal variation of food caching, the time until utilization of cached prey, and their spatial distribution for Northern and Red-backed Shrikes in an area of sympatry. Energy demand, food availability and accessibility to suitable cache sites were considered.

METHODS

The study area is situated in the province of León, in northwest Iberia (42°35′ to 42°45′N, 5°25′ to 5°32′E). It is part of the supramediterranean bioclimatic stage in the Mediterranean biogeographic region, and the climax vegetation consists of deciduous oak (*Quercus pyrenaica*) with a few clusters of holm oak (*Q. rotundifolia*) (Rivas Martínez 1987). The landscape is a mosaic of cereal cropland, woodland, scrub, irrigated pastureland and hedges. In this area, Northern Shrikes are resident birds whereas Red-backed Shrikes are summer migrants.

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Presamplings indicated frequent prey storage by Northern Shrikes during autumn and winter and by Red-backed Shrikes during spring and summer, but caching by Northern Shrikes during the nesting period was rarely observed. Therefore, I systematically searched for caches in the first case, and unsystematically and unthoroughly in the second. In an area of 1.2 km^2 occupied by Northern Shrikes, I searched for caches at least every 3 days during the autumn and winter of 1987–1988 and 1988–1989. I did not differentiate between individuals (territories). I carried out sampling along two routes in two separate valleys with dispersed shrubs and trees. To search for prey cached by Red-backed Shrikes during the breeding period, I visited three territories, two in 1988 and the other in 1989, for a total of 72 days. I defined territories using the mapping method (see Bibby et al. 1992). At each stage of reproduction, the sampling effort remained the same and visits were daily. On each day I inspected all shrubs in the territory at 4 hr intervals. To identify family groups, I color-banded nestlings with plastic rings. After fledging, family groups split, one adult taking charge of one part of the progeny remaining in the territory, and the other looking after the remainder in a different place (Hernández 1993a).

In addition, between 1988 and 1990, I visited 42 Northern Shrike and 33 Red-backed Shrike breeding territories in the study area in order to research several aspects of their biology. On each visit, I searched for caches during a variable period of time. I also included cached prey found by chance in some of the analyses.

For each cached prey I noted prey type, time of day and date of storing and utilization, kleptoparasitism, as well as spatial location in relation to the nest and other stored prey. Cache longevity refers to the period of time between the sampling in which the prey (storage) or its absence (utilization) was recorded and the last sampling prior to it. The high visiting frequency allowed many of the cached prey to be found alive (Hernández 1994a). Some caching and use of prey was observed directly. Only directly observed kleptoparasitism events were recorded as such.

To estimate selection of shrubs for storage of prey, I used Jacobs's (1974) index:

$$D_{mi} = (r_{mi} - p_{mi})/(r_{mi} + p_{mi} - 2r_{mi}p_{mi}),$$

where r is the relative use for storage purposes and p the relative availability of the shrub type m located at site i. D_{mi} varies between -1 (maximum negative selection) and 1 (maximum positive selection), where 0 signifies an absence of selection. I calculated volume of cache-shrubs using height, length, and width measured at half the shrub height. To establish prey distribution, I divided shrubs in three height classes (lower, middle, and upper) and two depth zones (inner and outer). I noted two shrub colors: green (shrub with leaves) and brown (shrub lacking leaves).

I encountered 203 cached prey for Northern Shrikes and 556 for Red-backed Shrikes, although not all were used in all analyses because some of the necessary data were lacking. In the analyses comparing the two species, I used the total number of cached prey for which relevant data were recorded. Means were expressed (±SD). I used chi-square test instead of log-likelihood G-test only if there was any 0 value. I accepted $P < 0.05$ as statistically significant.

RESULTS

TEMPORAL STORAGE AND CACHE USE

In the area sampled regularly during autumn and winter, Northern Shrikes cached food mainly in winter (118 [61%] of 193 prey). Caching by Red-backed Shrikes, on the other hand, increased progressively from May through August (Table 1). Most prey cached in May was found during the nest building stage, and those found in June during the phases of laying-incubation, nestling and family group in the territory. In July, the proportion of prey cached during the phases of nestling and family group in the territory increased. Many of the prey cached in August were found when the family group was present in the territory, with moderate numbers during the nestling period. Throughout the breeding period, the number of cached prey increased during laying-incubation, nestling and family group in the territory phases. Three Red-backed Shrike nests in which nestlings hatched between 25 and 29 July, confirmed a positive relationship between rate of food storing and number of nestlings (Fig. 1). A marked increase in prey storage was observed during the second half of the nestling stage, and maximum values were reached before the family group split up (Fig. 1).

Most (97%) of 100 prey cached by Northern Shrikes were used within less than 9 days of storage (Fig. 2). Only 11 (2%) of 489 prey cached by

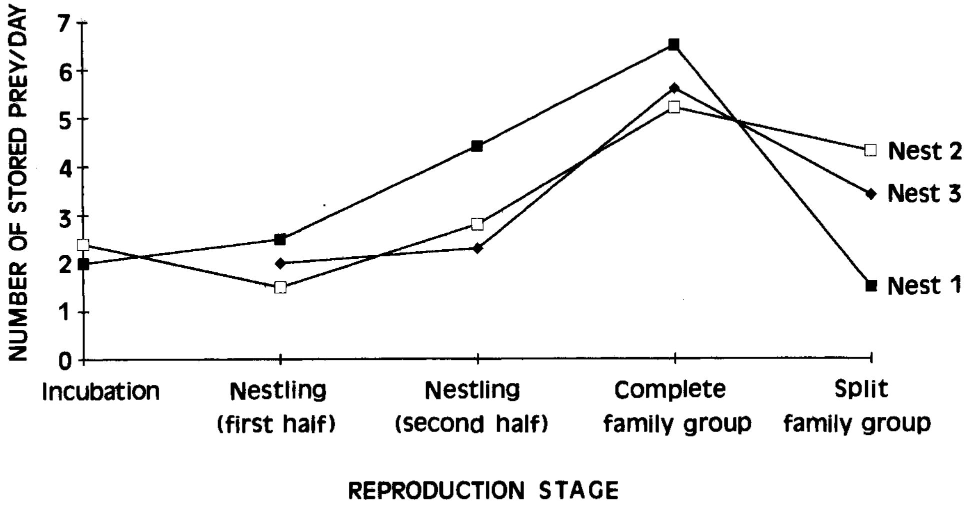

FIGURE 1. Mean number of prey stored per day by Red-backed Shrikes in the breeding territory. From the first reproduction stage until the last one, SDs for nest 1 were 0 (n = 1 day), 0.7 (2), 3.1 (5), 4.0 (8) and 0.7 (2); for nest 2 were 2.1 (5), 0.7 (2), 1.6 (5), 3.3 (4) and 2.5 (3); and for nest 3 were 0 (1), 0.6 (3), 2.6 (7) and 1.8 (5). In all nests chicks hatched between 25 and 29 July. In nest 1 there were four chicks. In nest 2 there were four chicks until the half part of nestling (second half) stage; at this moment two of them died. In nest 3 there were three chicks until complete family group stage started, since one chick died the day before its siblings left the nest.

Red-backed Shrikes were recovered later than 24 hr following storage. This species used its cached prey mainly at dawn and at dusk, with a peak in caching activity during mid-day (Fig. 3).

Northern Shrikes used 100 (62%) of their cached prey, and Red-backed Shrikes used 489 (88%) (n = 162 and 556 prey, respectively). The unutilized types of prey (dry or putrid) did not differ significantly from prey cached by the Northern Shrike ($\chi^2 = 15.80$, df = 10, $P > 0.05$), but did for the Red-backed Shrike ($\chi^2 = 36.49$, df = 15, $P < 0.005$) (Table 2). However, in the former, there were more pilose lepidopteran larvae among the unused prey. Red-backed Shrikes used pilose lepidopteran larvae, bumblebees (*Bombus* sp.) and beetles (especially Meloidae) to a small extent.

No kleptoparasitism of prey cached by Northern Shrikes was detected. At least 36 (6%) of 556 prey cached by Red-backed Shrikes were kleptoparasitized. The main pilferers were hymenopterans, especially wasps (*Vespula vulgaris* and *Dolichovespula sylvestris*) (26 cases), although ants also consumed caches (nine cases). Wasps cut up large pieces of the prey, usually the abdomen of grasshoppers, using their mandibles. Caches in

TABLE 1. Relative frequency of prey cached by Red-backed Shrikes in each reproduction stage and month. Data pooled for three territories.

Stage of breeding season	%				
	May	June	July	August	TOTAL
Unmated male	16.7	—	—	—	0.2
Pair before nest building	—	1.9	3.0	—	1.0
Nest building	83.3	7.5	8.1	—	4.0
Laying–Incubation	—	32.1	17.8	—	8.2
Nestling	—	24.5	31.1	20.8	23.7
Familiar group inside the territory	—	34.0	40.0	72.4	58.7
Familiar group outside the territory	—	—	—	2.3	1.4
Independent young	—	—	—	4.5	2.8
Number of prey (n)	6	53	135	308	502

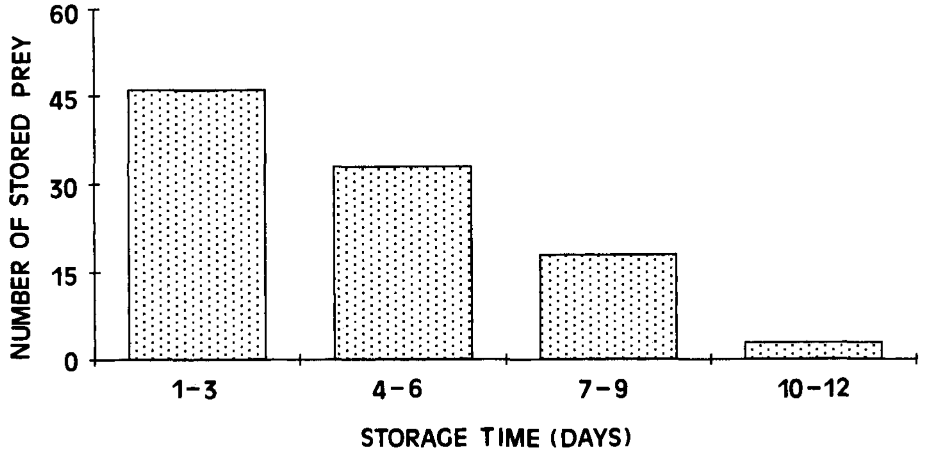

FIGURE 2. Time of prey storage until their use by Northern Shrikes. n = 100 prey.

shrubs colonized by ants tended to be taken by the ants if not consumed soon. On one occasion, immediately following impaling by a male Red-backed Shrike, a Blackbird (*Turdus merula*) removed and consumed an unidentified prey item.

SPATIAL DISTRIBUTION OF CACHES

Distribution of caches within the territory. Northern Shrikes cached 139 (87%) of 159 prey in thorny shrubs, including hawthorns (*Crataegus* sp.), blackthorns (*Prunus* sp.), roses (*Rosa* sp.) and brambles (*Rubus* sp.). Among the thorny shrub types, blackthorns and hawthorns were preferred, whereas roses and brambles were avoided (Table 3). The Red-backed Shrike cached 81 (99%) of 82 prey, 64 (83%) of 77 prey and 67 (97%) of 69 prey in thorny shrubs (n = 3 territories). This species also preferred hawthorns and blackthorns, and avoided brambles and roses (Table 3).

Northern Shrikes appeared to cache vertebrates more frequently in non-thorny shrubs (e.g., heaths [*Erica* sp.]) than invertebrates (7 [23%] of 31 and 11 [10%] of 105, respectively), but this tendency was non-significant so (G = 2.75, df = 1, $P > 0.05$). The difference between Northern Shrikes and Red-backed Shrikes in type of shrub chosen was significant for invertebrate prey (G = 8.24, df = 1, $P < 0.005$) but non-significant for vertebrate prey ($\chi^2 = 2.01$, df = 1, $P > 0.05$). However, the percentages of non-thorny shrubs used by Northern Shrikes were, in both cases,

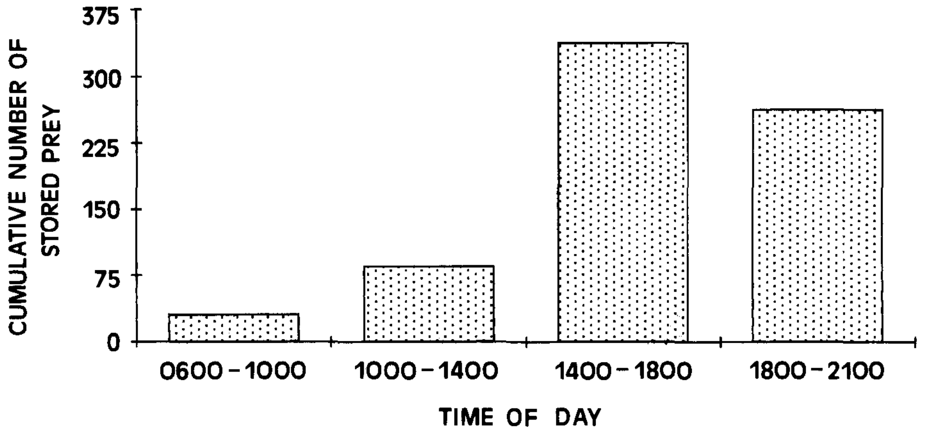

FIGURE 3. Cumulative number of prey stored by Red-backed Shrikes found during the day. Only prey subsequently used over the 72 day sampling period was considered. n = 489 prey.

TABLE 2. Taxonomic characterization of prey stored by shrikes, and of stored but subsequently unused prey.

	%			
	Northern Shrike		Red-backed Shrike	
	Stored prey	Unused prey	Stored prey	Unused prey
Haplotaxida	0.5	—	—	—
Stylommatophora	—	—	0.2	—
Julida	—	—	0.2	—
Odonata	—	—	0.9	—
Orthoptera	57.6	58.1	66.4	35.8
Dictyoptera	5.9	6.5	0.3	—
Homoptera	—	—	0.7	—
Lepidoptera	5.9	17.7	2.9	7.5
Diptera	—	—	0.7	—
Hymenoptera	1.0	—	14.6	32.8
Coleoptera	1.0	1.6	9.2	17.9
Araneae	—	—	0.9	—
Anura	0.5	—	0.2	—
Squamata	16.8	16.1	1.3	4.5
Passeriformes	5.9	—	0.3	—
Insectivora	1.0	—	0.3	—
Rodentia	3.9	—	0.9	1.5
Number of prey (*n*)	203	62	556	67

TABLE 4. Distribution of prey cached by Red-backed Shrikes at different distance intervals to the nest during the incubation, nestling and young in the nest-shrub stages.

Territory	Distance to the nest (m)	Number of available thorny shrubs	Number of available hawthorn and blackthorn shrubs	Number of cached prey
1	0–50	6	1	19 (23%)
1	50–100	9	4	62 (77%)
2	0–50	10	5	53 (83%)
2	50–100	6	1	11 (17%)
3	0–50	4	4	48 (72%)
3	50–100	4	4	19 (28%)

higher than those estimated for Red-backed Shrikes (11 [3%] of 357 invertebrates and 0 [0%] of 13 vertebrates).

In Northern Shrikes the maximum number of prey items cached simultaneously in the same shrub was only two, with mean of 1.1 prey/shrub (SD = 0.2, n = 192 cache sites). Red-backed Shrikes cached up to seven prey items in the same shrub before use, with means of 1.4 (SD = 0.8, n = 75), 1.8 (SD = 1.2, n = 62), and 2.2 (SD = 1.5, n = 80) for the three territories, and an overall mean of 1.7 prey/shrub (SD = 1.2). The correlation between the volume of thorny shrubs and the total number of prey cached in them by Northern Shrikes was positive and significant for brambles (Spearman rank correlation $r_s = 0.74$, $n = 12$, $P < 0.05$), but non-significant for hawthorns, blackthorns and roses. Neither was there such a correlation for the Red-backed Shrike's use of hawthorns ($r_s = 0.28$, $n = 14$, $P > 0.05$); sample size for other genera of shrubs was too small for analyses.

The average distances between available thorny shrubs were significantly greater (50–60 m) than between shrubs containing prey cached by Red-backed Shrikes (30–40 m) in all territories (two-tailed t-test = 2.93, df = 142, $P < 0.005$, territory 1; $t = 3.79$, df = 177, $P < 0.001$, territory 2; $t = 3.77$, df = 71, $P < 0.001$, territory 3), as measured at maximum storage each day. In Northern Shrikes it was impossible to identify the individual that stored each prey, but I noted some concentration of cache-shrubs.

In Red-backed Shrikes the distance of caches to the nest depended on the kind and availability of thorny shrubs in the territory, with a tendency to cache in hawthorns and blackthorns within 50

TABLE 3. Proportions of available shrubs used by shrikes to cache food. Available shrubs in parentheses. Jacobs's indices of selection (*D*).

	%			
	Hawthorn	Blackthorn	Rose	Bramble
Northern Shrike	46 (68)	63 (27)	18 (89)	22 (51)
D	0.26	0.41	−0.39	−0.23
Red-backed Shrike				
Territory				
1	100 (3)	100 (2)	17 (6)	25 (4)
2	75 (4)	100 (2)	60 (5)	0 (5)
3	100 (8)	—	—	—
Overall *D*	0.44	0.30	−0.31	−0.75

m of the nest (Table 4). For territory 2 the average distance to the nest of seven prey stored during incubation was 15.7 m (SD = 1.9). The average distance was 23 m (SD = 26, $n = 63$ prey) if both periods of incubation and nestling are considered together. Nesting shrubs (brambles in territories 1 and 2, heath in territory 3) were not used for food storage.

Distribution and concealment of cached prey within the shrub. Both Northern and Red-backed Shrikes cached prey mainly in the upper (45% and 49%, $n = 123$ and 380 prey, respectively) and middle (44% and 33%) parts of the shrubs, and small amounts in the lower part (11% and 18%). Northern Shrikes cached 63% of their prey in the inner part of the shrubs, whereas Red-backed Shrikes cached 42% in a similar manner. Both species cached vertebrates more frequently than invertebrates in the inner part of he shrubs (Table 5) with Red-backed Shrikes significantly so ($G = 6.18$, df = 1, $P < 0.05$).

TABLE 5. Types of prey cached by shrikes in the different shrub parts.

	%			
	Northern Shrike		Red-backed Shrike	
	Invertebrates	Vertebrates	Invertebrates	Vertebrates
Outer part	40.2	29.0	58.9	20.0
Inner part	59.8	71.0	41.1	80.0
Number of prey (n)	92	31	370	10

Red-backed Shrikes cached food significantly higher than did Northern Shrikes (1.1 ± 0.47 m compared to 0.9 ± 0.49 m, $n = 343$ and 137 prey; $t = 4.24$, df = 478, $P < 0.001$). Storage height was significantly correlated with shrub height (Northern Shrike, $r_s = 0.93$, $n = 31$, $P < 0.001$; Red-backed Shrike, $r_s = 0.44$, $n = 170$, $P < 0.001$).

The color of grasshoppers was significantly linked to color of shrubs in which they were cached by Red-backed Shrikes ($G = 44.43$, df = 1, $P < 0.001$). The proportion of green grasshoppers cached in brown shrubs (13%, $n = 126$) was lower than that of brown grasshoppers cached in similar shrubs (52%, $n = 109$). A significant link could be observed between the part of the shrub where the prey were cached by the Red-backed Shrike and the color of this shrub ($G = 4.11$, df = 1, $P < 0.05$); thus, the percentage of prey cached in the inner part of the shrub was greater in leafless brown shrubs (56 [49%] of 115 prey) than in green shrubs with leaves (92 [37%] of 246 prey).

DISCUSSION

TEMPORAL STORAGE AND CACHE USE

Why did Northern Shrikes in the study area cache food mainly during the non-breeding period whereas Red-backed Shrikes cached it during the breeding period? The number of prey cached by Red-backed Shrikes increased from May to August, parallel with an increase in food availability (Hernández 1993b, Hernández et al. 1993). Northern Shrikes bred earlier than Red-backed Shrikes, mainly in March–June (Hernández 1993a), when prey availability seemed to be too low to permit caching. In apparent contradiction to this, the storage of prey by Northern Shrikes peaked in winter, when food availability was lowest; however, a possible explanation is that the overall energy demand during this season was presumably less than in comparison to the stages of nestling and young care (but see Degen et al. 1992). On the other hand, the habitat occupied by this species in the study area was generally characterized by large areas of fallow and farmland, which were of poorer quality than the grassland habitat occupied by the Red-backed Shrike (Hernández 1993b, 1994b). Most of the prey cached by Northern Shrikes in autumn and winter was found in ecotones of forest edge.

Karasawa (1976) and Kobayashi (1980) described a food caching pattern similar to that of the Northern Shrike, with an increase during autumn and winter and a decrease during the reproduction period, for the Bull-headed Shrike (*L. bucephalus*) in Japan. Both species occur at the same latitude and have similar breeding phenology. Other authors have also found that Northern Shrikes cache food in winter (Olsson 1985, Grünwald 1993). In Alaska, this species specializes on vertebrates, and caches large amounts of birds and small mammals during the nesting period in June, when these abound (Cade 1967). In date palm groves in Algeria it stores dates (*Phoenix dactylifera*) during the breeding period in March (Parrott 1980). By contrast, both the Bull-headed Shrike, and, in my study area, the Northern Shrike, consume and cache mainly insects, whose availability is highest at the end of spring and in summer.

The amount of prey cached by Red-backed Shrikes increased as their energy requirements did, i.e., during the second half of the nestling stage (Diehl and Myrcha 1973). Caches also tended to be larger for pairs with larger broods, which is contrary to other food storing birds (Sperber and Sperber 1963, Korpimäki 1987; but see Vander Wall 1990). These differing results may be due to differences in food availability: if both energy demand and food availability are high, one might expect a high caching frequency, as in my study; if energy demand is high but food availability low, little caching might occur.

Northern Shrikes used their cached prey within a relatively short time period. Grasshoppers were cached to a greater extent on sunny days with high temperatures, when their activity and availability increased, and were utilized on subsequent days (pers. observ.). Low winter temperatures probably enabled their use several days after storage. Cade (1967) and Olsson (1985) estimated that most of the prey cached by Northern Shrikes was used within 7–10 days, similar to what was found in my present study.

Red-backed Shrikes usually used cached prey within 24 hr of storage. The use appeared to be related to fluctuations in food abundance during the day, with caching when prey availability was maximum (middle of the day) and cache use when prey availability was lowest (dawn and dusk). Carlson (1985) observed that this species used its caches in the early morning. Durango (1951, 1956) found that Red-backed Shrikes used cached food to dampen fluctuations in prey abundance caused by variations in weather. In the present study, prey was sometimes cached during favorable hours and used during unfavorable ones of the same day; no food was cached on rainy days (pers. observ.). High summer temperatures may have precluded the use of prey stored over longer periods.

Northern Shrikes used fewer of their cached prey than did Red-backed Shrikes. In Florida, Loggerhead Shrike (*L. ludovicianus*) left 48% of cached prey unused in the non-breeding period (Sloane 1991). This value is higher than the 38% noted for the Northern Shrike in my study area. Sloane (1991) suggested that unused caches acted as a warning to conspecifics that the territory was occupied. Yosef and Pinshow (1989) underlined the role of caches made by male Northern Shrikes in mate choice, females choosing males whose caches are better stocked. It is possible that unused prey cached by Northern Shrikes in my study area have the same role. However, almost 20% of the prey wasted by this species were pilose lepidopteran larvae which combine mechanical and chemical effects in their defense against predators (Margalef 1980). Among the few prey left unused by Red-backed Shrikes, besides pilose lepidopteran larvae most were pilose hymenopterans and meloid coleopterans which contain toxic cantharides (Forster 1968). In this matter, Loggerhead Shrikes impaling behavior serves as a preadaptation for overcoming the toxic defenses of *Romalea guttata* grasshoppers, because, apparently, *Romalea* toxins decline in potency with age after death (Yosef and Whitman 1992).

Prey cached by shrikes is often pilfered by insects (Owen 1948, present study), birds (Schön 1979, Olsson 1985, Yosef 1988, present study) and carnivores (Olsson 1985). The importance of kleptoparasitism seemed insignificant in my study area, but this phenomenon can be frequent and affect more than half the prey cached by the Northern Shrike (Schön 1979, Olsson 1985, Yosef 1988). The marked territoriality of shrikes may prevent food robbery by conspecifics.

SPATIAL DISTRIBUTION OF CACHES

In other portions of Europe, Red-backed Shrikes frequently use hawthorn and blackthorn shrubs to cache prey (Mielewczyk 1967, Lefranc 1979; but see Donovan 1929), and these were also selected by shrikes in my present study. The thorns of such shrubs are cylindrical, thin and long, so are better suited for impaling than thorns of roses and brambles which have laterally flattened, wide and short thorns. The more frequent use of non-thorny shrubs to cache vertebrates compared to invertebrates may have reflected the Northern Shrike's preference for wedging vertebrates into forks and for impaling invertebrates on thorns (Hernández 1994a). In Sweden, where Northern Shrikes cached vertebrates, they selected willows (*Salix* sp.) (Olsson 1985). Red-backed Shrikes utilized thorny shrubs more than did Northern Shrikes, as one might expect from the higher proportion of insects cached by the former.

Both shrike species scatter-cached the prey, so that in each shrub, regardless of its volume, more than two prey were not usually found at the same time. The maximum number of prey cached simultaneously in a shrub or tree by a Northern Shrike can be more than 10 (Cade 1967, Parrott 1980), whereas it may vary between three and seven in the Red-backed Shrike (Ash 1970, Lefranc 1979, present study). Scatter-caching decreases the probability that all of the food is discovered by conspecifics or other species (Smith and Reichman 1984, Källander and Smith 1990, Vander Wall 1990, Birkhead 1991). However, the shrubs used by the skrikes to cache food were more aggregated than the available shrubs, which perhaps facilitates caching and retrieval of prey.

Red-backed Shrikes showed a tendency to cache food close to the nest, as also observed by Owen (1948) and Durango (1956). Carlson (1985) suggested that the distance of the prey cached by this species to the nest is a compromise between maximizing the rate of food delivery to the young and minimizing both the risk of kleptoparasitism and the location of the nest by predators. Neither in Carlson's study nor in my present study was any prey cached in the shrub where the nest was built. In Alaska, Northern Shrikes cached prey more than 50 m from the nest probably to avoid attracting the attention of predators (Cade 1967). The Red-backed Shrikes cached prey at a shorter average distance from the nest during incubation than during the nestling stage. It is possible that the numerous prey items cached during the latter stage were scattered over a larger area to maintain densities low. Similarly, Gray Jays (*Perisoreus canadensis*) carried food farther when local cache density increased (Waite and Reeve 1992).

Many of the prey items cached by Northern and Red-backed Shrikes were wedged or impaled in the inner part of the shrubs (for the latter species, see Durango 1951, Carlson 1985). Concealment of stored food is one of the strategies used to guard it from competitors (Källander and Smith 1990, Vander Wall 1990). The lower parts of shrubs were used very little, presumably to keep the food away from terrestrial kleptoparasites. The Northern Skrikes used the inner zone of shrubs far more than did Red-backed Shrikes, perhaps because the larger size of their prey required greater concealment or because no leaves are found to provide concealment in winter. Other potential selective factors could influence the choice of cache location besides hiding from kleptoparasites, e.g., concealment of the shrike from its predators as it impales and searches for large thorns or forks needed for proper storing, which are usually within the shrub.

The association found between prey color and color of shrubs where cached suggests that choice of cache place was related to cryptic coloration. Green grasshoppers will be cryptic against a background of shrubs with leaves. Nevertheless, it is necessary to obtain more information about the availability of prey of different colors.

In conclusion, temporal variation in caching and cache use by shrikes depended on prey availability and energy demand. Air temperature affected preservation of food and, consequently, storage time period. Cache use was high, but influenced by the storing of unpalatable prey. Kleptoparasitism on caches was apparently low. Spatial distribution of caches was determined by availability of suitable shrubs, scattering of cached prey, distance to the nest and concealment of stored food within the shrub, which was in probable relation to correct impaling, kleptoparasitism, ability to recover cached prey and rate of food delivery to the young.

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