PREY CACHING IN THE HUNTING STRATEGY OF SMALL PREDATORS

by

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INTRODUCTION

Many granivorous birds and mammals store seeds and acorns (Smith, 1968, 1979; Roberts, 1979). The adaptiveness of this behavior seems obvious; the food preserves well in the cache sites and is variable in its availability. Food storing has been observed in predators, especially in small mustelids (Nyholm, 1959, 1961, 1972a, 1972b; Siivonen, 1975; Cahalane, 1947; Westman, 1972). Nyholm found rodent caches made by weasels (Mustela rixosa) and stoats (Mustela erminea). He also found a marten (Martes martes) in the same hole with its cache. Westman reports food stores made by minks (Mustela vison) containing fish. Erlinge et al. (1974a, 1974b) in their terrarium experiments found that both weasels and stoats tended to continue hunting after they had carried the prey to a cache. (The terrariums were mimics of forest and meadow where the rodents had spent some time, e.g., making burrows before the beginning of experiments.)

Some of these observations refer to situations where leftovers of large prey items have been stored (Nyholm, 1961). It is not hard to see how such behavior is helpful for the predator that has caught a larger prey than it can consume at once. However, the situation described by Erlinge et al. (1974a, 1974b) was different. The small mustelids in his terrarium stockpiled prey without eating them until their hunting period was over. The caches of weasels and stoats found by Nyholm also contained several prey animals. Why did the predators make such stores of perishable food?

One possible selective pressure is control over essential resources. During cool or hot and dry time periods, a predator has three ways of controlling resources: defending a territory, storing prey, or building up fat reserves. By defending a territory from others using the same prey species, a predator has a rather good control over living prey animals.

The more exclusive the defense, the more prey the predator has for its own needs. Preserving prey alive has the advantage of allowing the growth of the prey population, but has the disadvantage of losing prey energy due to maintenance, and death of potential prey items.

If territorial defense is not effective, a predator may instead kill as much prey as possible during periods of high availability, and store the excess for less optimal times. By making caches in safe places, it has control over a small amount of prey which may be enough for survival over bad times. Of course some of the potential growth of the prey population is lost but it is likely that a predator, unable to defend a territory against other predator species, would loose it anyway. When prey is scarce, a predator has to spend more time hunting, during which time it would be rather visible and in danger to be killed itself. The option to use *stored* food decreases this danger. In a case like this, there should not be real territories, except for sexual purposes, the species living instead in a home range. Dead prey, of course, continually loses some of its energy content and food value, this process going faster the warmer and moister the weather. The third option, to store *fat and hibernate*, seems incompatible with the requirements that an actively pursuing habit sets for predators, because an animal with much fat would not perform well in high-speed chases.

Thus there are two primary strategies: territoriality and food storing. What determines the adaptiveness of these two strategies? We can rank the predators which use the same prey species according to their size. The size per se is not the important factor, but size would be related to the probability that a larger predator might intrude the area that a given individual is using, even if that individual defended that area as a territory. This probability will be roughly proportional to the number of larger predator species in the same area. Even if there were only a slight difference in

size between animals in the lower end of the guild, there may be a pronounced difference in the optimal strategy depending on the numbers of predators of different sizes, because even a slightly larger predator is likely to be strong enough to enter the specifically defended territory.

I will make a clear distinction between two types of food storage. The marten has been observed hiding parts of its prey and returning to the cache (Nyholm, 1961). This observation is contrasted with the large food stores made by weasels (Nyholm, 1972b). The adaptiveness of the latter type of food storage is the problem that I will address. Indeed, all observed behavior need not be adaptive. Almost all predators on some special occasions kill more prey than they need at the moment and leftovers thereby, which they sometimes hide. Kruuk (1972) interpreted such behavior as a malfunctioning of a generally adaptive behavioral repertoire occurring because the situations are so rare that there is little selective pressure against such behavior. Hence, I must define food storage operationally so that it embraces only regular construction of caches, occurring whenever there is enough prey available because dead prey may be hidden and is thus unlikely to be lost even if the area is invaded by a larger predator. If food is continuously abundant, stores could be left uneaten, because stored food will freeze, dry or gradually rot. Hence, fresh food is probably preferred (type 1 food storing, e.g., weasel).

Stores made in cool or hot and dry climate are rather well retained but stores made in hot and humid climate are likely to rot too soon to be of any use as "emergency stores". Thus, storing should be found in every biotope where larger predators are present and the climate is appropriate.

In a seasonal environment, food is likely to be scarce during some part of the year. At this time, it is advantageous to store the possible leftovers for later use even when defending a territory. When food is once

again abundant, however, there is no need to use such leftovers. (Type 2 food storing, e.g, marten.)

In summary, I am hypothesizing that species which cannot easily defend live resources because of the presence of large competitors will evolve the habit of food storing as a strategy of maximizing the amount of resources in their control, if the climate is at all suitable for the retention of stored prey.

THE MODEL

In order to ensure that the logical structure of the above presented hypothesis is consistent and in order to make predictions, the hypothesis must be presented as a formal model.

First, I attempt to ascertain the relationship between the amount of time invested in territorial defense and the size of territory (which in turn, should be equivalent to the amount of live prey defended against other individuals). I simplify the situation in order to make broad interspecific comparisons easier and assume that the territories are circular in shape and defended either by moving along the perimeter or by back-and-forth movements from the center to the border. In either case, it is a linear variable which is assumed to be proportional to the time spent in defense, whereas the amount of resources controlled is proportional to the area of the territory.

Let A = area, c = circumference, d = diameter and r = radius. The area of a circle is $A = \pi r^2$. And because 2r equals the diameter and πd equals circumference of a circle, we write $A = (\pi/4)d^2 \Rightarrow A = (\pi/4)\ (c^2/\pi^2) \Rightarrow A = (c^2/4\pi)$. This formula we will leave now for later use.

Let D = the time spent in territorial defense, which defines the circumference of a territory. Thus $c = \beta_o D$, where β_o is a constant depending on the size of the predator thus describing the effectivity of defense.

We now write the relationship between area A and the time spent in territorial defense D, substituting $c = \beta_o D$ as follows: $A = (\beta_o D)^2/4\pi = \gamma D^2$, where $\gamma = \beta_o^{\ 2}/4\pi$, to shorten the equation. The formula $A = \gamma D^2$ is used in defining the relationship between area A in control and the amount of live prey in control, W_1. (W_1 being directly proportional to the area.)

$W_1 = \beta_1\ \gamma\ D^2$, β_1 = predator specific constant.

I assume that territorial defense and food caching are two mutually exclusive ways for a predator to spend its "spare time" (time left when the immediate needs of the animal are met). W_1 can now be presented graphically as a function of the way this available time is allocated between food caching and defense. The exact shape of this function depends on the value of β_1, but the general shape should be one of an upwards opening parabola (due to D^2 in the equation.) This family of curves is depicted in Fig. 1.

But what does the constant β_1 describe? It is predator-specific and should give some valid information between predators; what causes differences in β_1? One important variable is the probability of meeting larger predators in comparison to the probability of meeting conspecifics. Little information of this kind is available but β_1 can be roughly approximated by the number of larger predator species in an area. (Because smaller predators are more numerous than the bigger ones, the following graph is obtained when considering the absolute number of each predator species.) It is reasonable to believe that β_1 is equal to the likelihood that, during a given period, the predator does not meet a larger predator species that would enter the territory and consume the resources.

Thus, β_1 can be written as (k/φ) $(1/N)$, where k/φ is a constant and describes the max β_1 for a predator of a given type. N is the number of larger predator species (Fig. 2).

Now, let us consider how the allocation of the "spare time" between caching and defense effects the amount of stored food. Let W_s be the amount of stored food under the control of the predator. Because the caches can be hidden, the likelihood that other predators would rob them seems very small. Hence, it does not seem plausible that territorial defense would in any way increase the amount of stored food. W_s then becomes directly proportional to the time used in storing. Exactly how they are proportional

depends on the climate, which determines the rate at which stored food loses its value. Thus,

$W_s = \beta_2 S$, where S = the time spent in storing food

β_2 = a constant depending on climate

By plotting time against W_s we get the graph in figure 3.

Now we are ready to construct a fitness set (by plotting W_s against W_1) and the adaptive function, W_T. It is composed of the unweighed sum of the fitness components W_1 and W_s. (The decay of dead prey - depending on climate - has been incorporated in W_s.) The point where a fitness set touches the outermost possible adaptive function is the optimal solution for each curve (Levins, 1968) (Figure 4).

The two graphs give only two types of optimum solutions both in cool (or dry) and in hot and humid climates. All "spare time" has to be used either in storing or in defending a territory, depending both on the position of the animal in the guild and on the climate. The model suggests that in cool and in dry climates, the storing strategy should be more widespread than in hot and humid climate. In the latter, storing (if it occurs at all) should be only found in the smallest species in a competition guild.

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FIG. 1. The relation between the amount of live prey in control (W_1) and the allocation of time between territorial defense (D) and food storing (S).

FIG. 2. The relation between the coefficient β_1 (indicating the effectiveness of territorial defense) and the number of bigger competitors (N).

FIG. 3. The relation between the amount of stored prey (W_s) and the allocation of time between territorial defense (D) and storing (S). The steepness of the line depends on the climate (steep if cool or dry).

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Fig. 1.

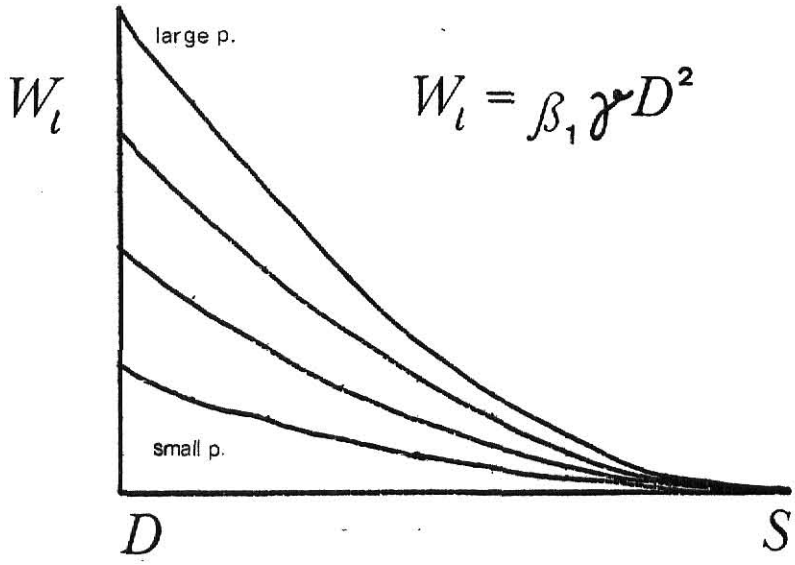


Fig. 2.

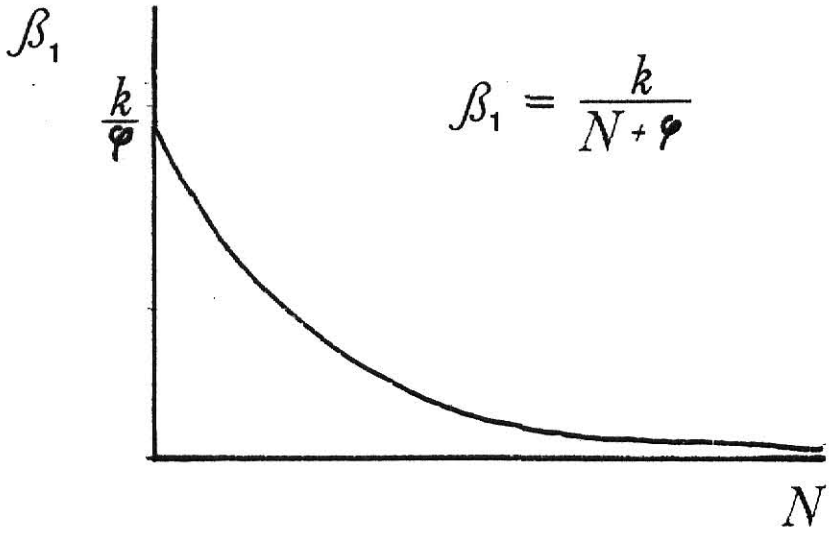


Fig. 3.

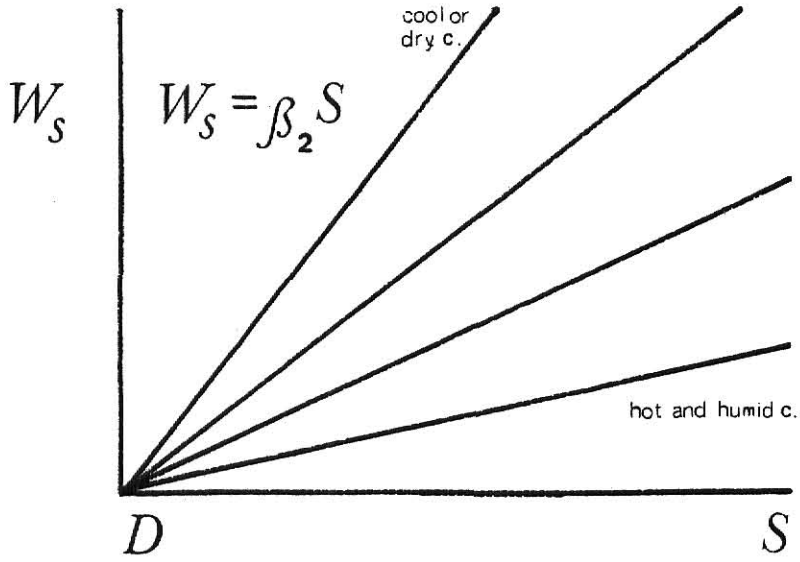


FIG. 4. A fitness-set relating the amount of live prey in control (W_l) to the amount of stored prey (W_s) for predators with different sizes and thus different positions in the guild. The adaptive functions are indicated by dashed lines, the dots indicate the optimal strategy of each predator.

4a. Cool (or dry) climate

4b. Hot and humid climate

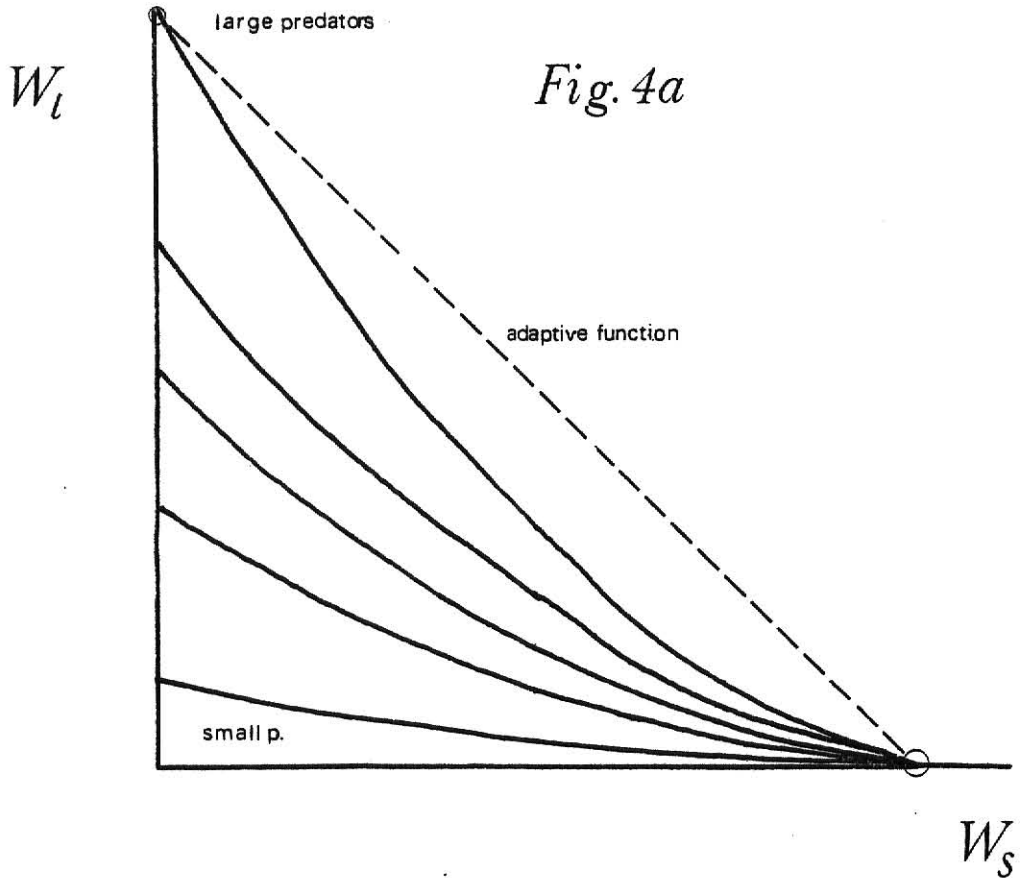

large predators
W_l
adaptive function
small p.
W_s

Fig. 4a

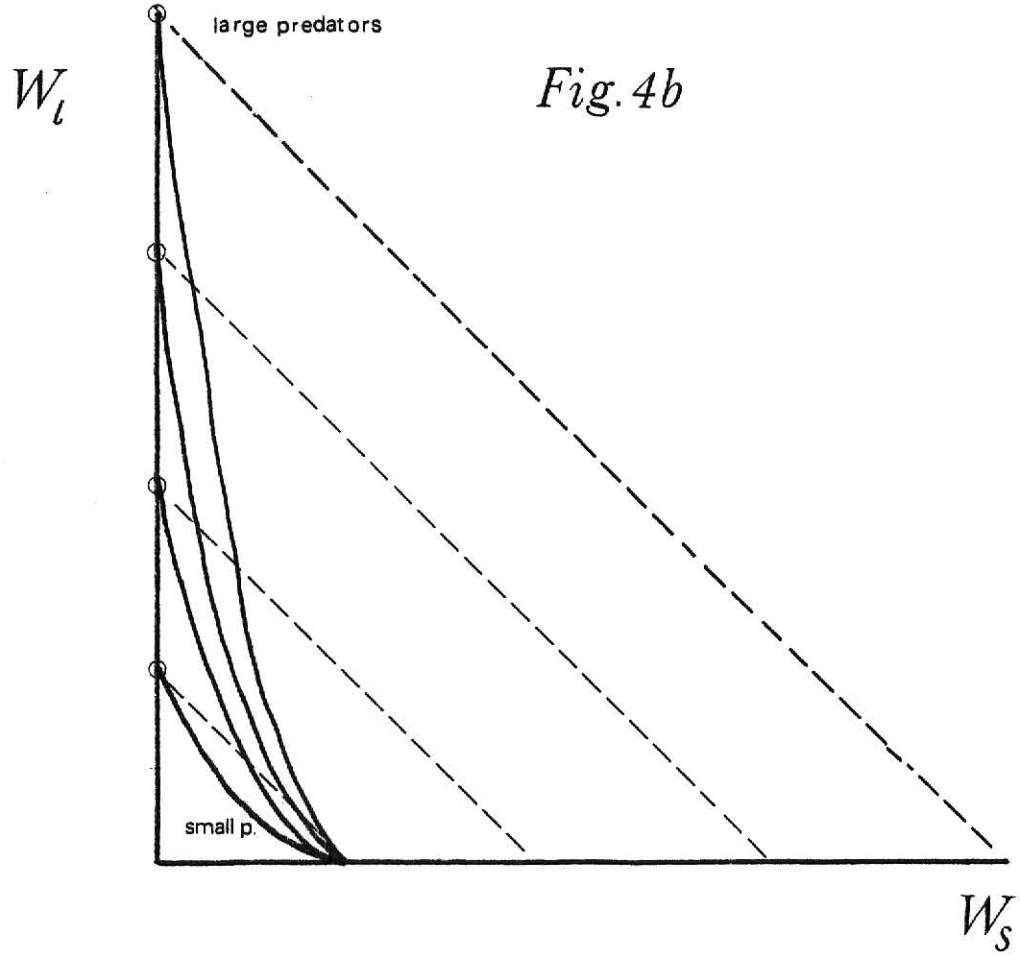

large predators
W_l
small p.
W_s

Fig. 4b

PRELIMINARY TESTS

Preliminary tests of the hypothesis were made from information from literature covering the terrestrial predators of Inari Lapland, Yukon Valley and Georgia (U.S.), and from predaceous birds of Inari Lapland.

The resident species of Inari Lapland (Tables 1, 4, 5) is taken from Iso-Iivari (1979). Regular visitor birds are included because owls tend to breed irregularly. The information from the Yukon Valley (Table 2) is based on the distribution maps by Burt and Grossenheider (1952). The list of Georgia's mammals (Table 3) was gathered from Golley (1962). The body sizes, living habits and natural enemies I checked from handbooks (Cahalane, 1947; Siivonen, 1972, 1975; van den Brink, 1967; and Burt and Grossenheider, 1952). The predators hunting mainly in water were excluded.

That the writers of handbooks have not paid equal attention to the same issues is a regrettable source of error. I tried to respond to inconsistency by comparing the American and European sources and assigning the habit of food storing to a species when it (or a closely related one) was noted as food storing in any handbook (e.g., Vulpes vulpes - Vulpes fulva). I did not meet the same kinds of problems when dealing with birds because the handbook of Haartman et al. (1963) offers a more systematic treatment. Because the observations of prey species and enemies are mainly from southern Finland I assume, e.g., that a predator occasionally killing a common jay (Garrulus glandarius) is dangerous for a Siberian jay (Perisoreus infaustus).

The only predators in Inari Lapland which do not store are wolf (Canis lupus) and lynx (Lynx lynx). They are also at the top of the ranking order (constructed on the basis of body weight). The stores of marten (Martes martes) are mainly leftovers (cf. Nyholm, 1961) and marten does not

have many enemies. All opportunists from bear (Ursus arctos) to arctic fox (Alopex lagopus) make food stores. For the two smallest predators (Mustela nivalis and Mustela erminea) the highest number of enemies was listed. The observations of food storing were most unambiguous in these two cases.

In Yukon Valley the number of species exceeds that of Inari Lapland by one and the set of species is a bit different. There are two species of bear (Ursus horribilis and Ursus americanus) and they are both opportunists making food stores. There was no mention of food stores made by lynx (Lynx canadensis) or wolf (Canis lupus). Also, other opportunists make food stores as well as the two smallest pursuers (Mustela nivalis and Mustela erminea).

In Georgia there are nine species of terrestrial predators and they are completely different from the Finnish ones. The occurence of enemies is distributed within the guild much in the same way as in the more northern areas. However, storing is rare and the main range of two storers (Ursus americanus and Vulpes fulva) is in more northern areas. Of pursuer-type animals only the very smallest - long tailed weasel (Mustela frenata) - makes caches. It is not even clear to what extent the statements of Cahalane (1947) referring to "weasels" collectively or the remarks of Hall (1951) about food storing in a more northern population of M. frenata are applicable to long-tail weasels of Georgia.

The above discussed observations of food storing among pursuers are mainly of Mustelidae. But storing should also occur in other predator guilds among the smallest members if climate is appropriate. I tested this idea with the predaceous birds of Inari Lapland. In both diurnal and nocturnal bird guilds the smallest species northern shrike (Lanius exubitor) and pygmy owl (Glaucidium passerinum) make caches. Opportunists are mentioned to make stores and short eared owl (Asio flammeolus) may store

voles in autumn. The daily caches of Tengmalm's owl (Aegolius funereus) are probably leftovers of big food items (type 2 food storing).

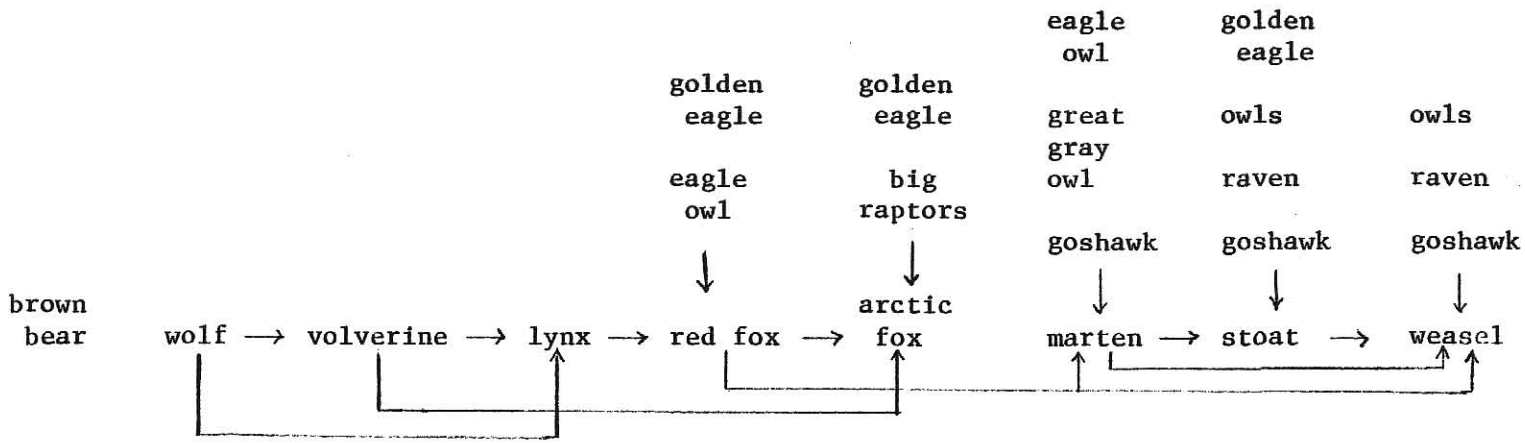
These results largely agree with predictions. Among pursuers food storing occurred in the lower ends of the guild and was more restricted in Georgia than in cooler areas. Omnivores seemed to store food irrespective their position in the guild, if only the climate was reasonably suitable for retention of food. This, indeed, is just what Roberts (1979) suggested. If an animal is adapted to shift from one diet to another one with changes in the relative abundance of different food types, the behavior of setting aside resources while they are abundant is to be expected to prevail. An attempt to preserve live resources by territorial defense would probably be futile, because opportunists are usually inefficient in utilizing but some particular fractions of their prey populations (juveniles, animals that are weak because of difficulties in obtaining food during the harsh conditions of late winter). Hence, a given population only intermittently offers resources for an opportunist, and having a big area with many prey to control might sometimes be useless (see above).

However, the source material used above is unfortunately ambiguous and often open to several interpretations. In order to test more specific predictions and to check the interpretation of literature, I have taken a closer look at three small predators. The details of the weasel study have been reported elsewhere (Oksanen and Oksanen, 1981). The outline is as follows. I introduced a male weasel (Mustela nivalis rixosa) into an island and compared the development of a vole population on this island with those of neighboring control islands on which weasels had not been introduced. (The experiment was performed on a tundra lake with low predator densities in surrounding areas. Hence, spontaneous presence of weasels on any island

was most unlikely.) The loss due to the introduced weasel was calculated on the basis of the difference between the population development on the experimental island and controls. Even the most conservative estimate of the impact of the weasel was in clear discrepancy with the maximum estimate of its energy needs, suggesting that killing in considerable excess to daily needs occurred.

To get an insight into the relationship of two successive predators of a guild I have selected kestrel (Falco sparverius) and loggerhead shrike (Lanius ludovicianus) as a test pair.

Table 1. Terrestrial mammalian predators of Inari-Lapland and their natural enemies. The arrows indicate predatory relationships within the guild. o = opportunist, p = pursuer



Storing:	+	-	+	-	+	+	-	+	+
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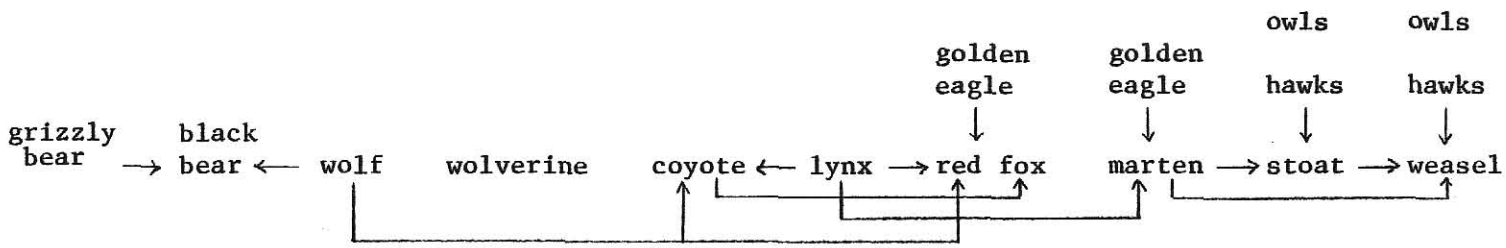
TABLE 2. Terrestrial mammalian predators of Yukon Valley and their natural enemies. The arrows indicate predatory relationships within the guild.



Storing:	+	-	-	+	+	-	+	+	+	+
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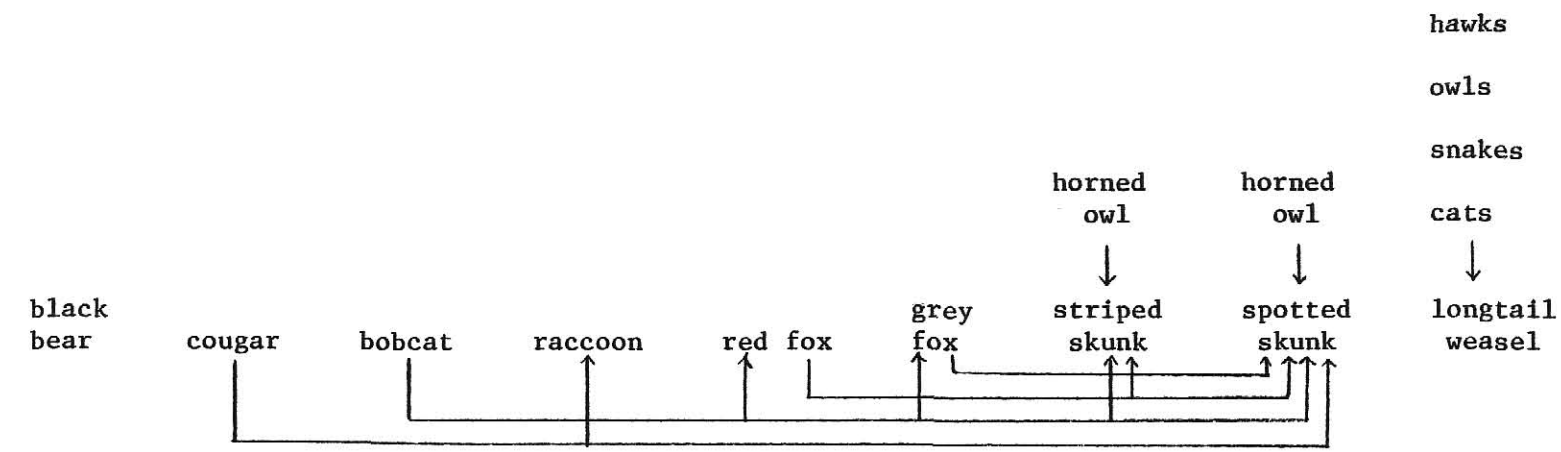
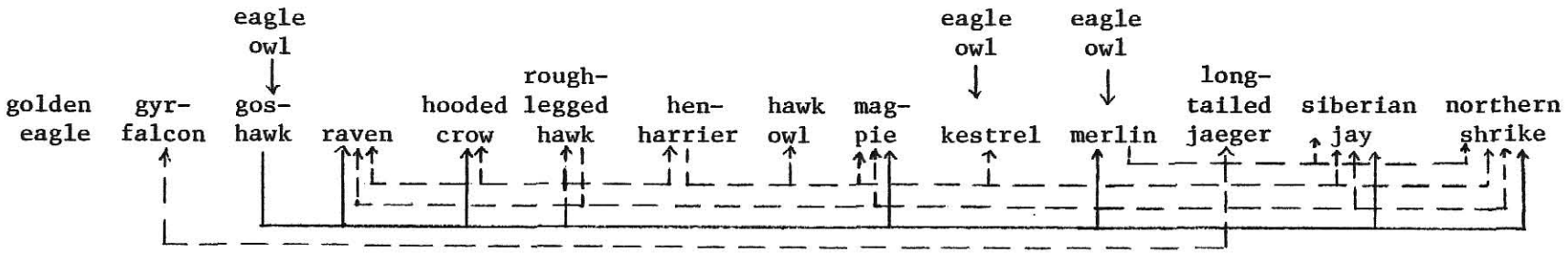
TABLE 3. Terrestrial mammalian predators of Georgia (US) and their natural enemies. The arrows indicate predatory relationships within the guild.



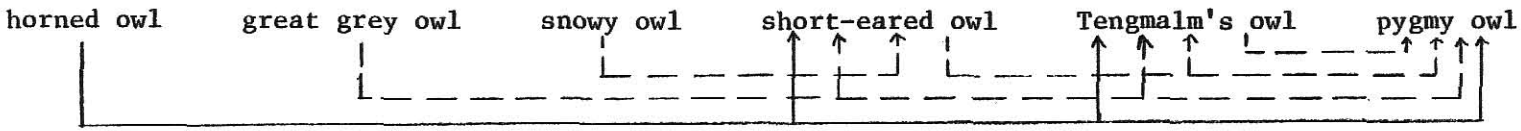
Storing:	+	-	-	-	+	-	-	-	+
Type:	o	p	p	o	o	o	o	o	p

TABLE 4. Diurnal raptors of Inari-Lapland and their natural enemies. Solid lines indicate predatory relationships within the guild directly mentioned in the source. Dashed lines indicate relationships inferred from reports referring to closely related (usually more southern) species.



Storing:	-	-	-	+	+	-	-	-	+	-	-	-	+	+
Type:	p	p	p	o	o	p	p	p	o	p	p	p	o	o

TABLE 5. Nocturnal raptors of Inari-Lapland and their natural enemies. Solid and dashed lines as in Table 4.



Storing:	-	-	-	- (+)	-(?)	+
Type:	p	p	p	p	p	p

THE CASE OF LOGGERHEAD SHRIKE AND KESTREL

Adult male kestrels weigh an average of 109 grams; females, 119 grams (Brown and Amadon, 1968). Adult loggerhead shrikes weigh an average of 50 grams (Craig, 1979). Thus the ratio is close to the limiting similarity for two adjacent members of a guild (Hutchinson, 1959).

According to Balgoyeen (1976), vertebrate prey make 68% of kestrels diet throughout the year in Colorado. (The 68% is divided as follows: birds 16.6%; mammals, 25.7%; reptiles, 26.0%; the remaining 32% is insects. Percents are calculated using approximated body weights of prey species.) According to Miller (1931) vertebrate prey never make 70% of the diet of the loggerhead shrike, even during winter in California. (There small mammals constitute from 3% to 55% of the food, depending on area and season.) Birds never comprise more than 15%, reptiles are represented by 7-8%. Most of insect prey are Orthoptera and they comprise 30-75% of the whole diet. (These values are derived from stomach contents of loggerhead shrike.) Thus also the utilization of resources seems typical for two relatively close competitors.

The size difference suggests that kestrel is superior to loggerhead shrike in aggressive encounters. Pursuer type raptors other than the kestrel, and utilizing the same kinds of prey are rather rare in Kansas. Thus the possibilities for Kansas kestrels to control live resources should be good in spite of its small size. Hence my hypothesis predicts a clear difference between these two species with respect to their behavior and food storing.

Observations of food storing of kestrel and loggerhead shrike in literature

The case of food stores made by kestrel is well analyzed in several studies and without exception food stores were considered as an adaptation against short-term food stress. Collopy (1977) found that during two winters, food caching represented 1.2 - 1.4% of all activities of female kestrels wintering in Areta Bottoms, California. Only vertebrate prey were stored. The prey was cached in grass clumps. Storing could happen anytime of the day, and retrieving happened during afternoons (minimum retrieving estimate was 70%). Hunting could be continued after storing. Stendell and Waian (1968) in California found a cache (in a tree) which was used from 10 December 1965 to 19 January 1966. During the observation period of 40 days, at least 17 prey items were stored. Often the store was empty and the maximum number of prey items cached at one time was five (1 lizard and 4 small mammals). The longest interval one prey (Reithrodontomys megalotis) remained was seven days. No stored prey was found after 19 January although the kestrel still hunted in the same area. Nunn et al. (1976) in Illinois made some laboratory experiments with one hand-reared male kestrel and white mice and rats and two field experiments with two female kestrels and white mice studying excess killing and caching behavior. In January, one wild female killed 19 of 20 offered mice in one run and cached 15 of them. The female was observed to use those caches at least during two following days. According to Mueller (1974) caching can happen any time of the year. He has made observations of caching behavior of kestrels in the laboratory and found a positive correlation between the time of deprivation and storing tendency. The kestrels were later able to spot the exact location of the caches. Balgoyeen (1976), in the California Sierras, found that storing started shortly after the arrival of the birds and ended one to two weeks

after hatching. The male hunted when the nesting cycle began and both male and female stored excess prey. (Sometimes the prey was cached totally uneaten.) The female had two to six storing places, the male had fewer. Typical caching places were tree trunks. Prey items tended to be cached singly and Balgoyeen estimated that those stores would satisfy the food needs of a female for two to three and a half days. Usually caches were used in two or three days. Insects were not cached. Tordoff (1955) observed storing of excess food and retrieval behavior in captivity and caching on two occasions in nature.

The case of food stores in the loggerhead shrike is much less clear. According to Miller (1931) and Craig (1979) insects are swallowed immediately but all other prey is impaled for handling. [The origin of impaling instinct has been discussed, e.g., by Wemmer (1966).] Miller speaks of special impaling stations which make returning to stored food easier. According to him, stored prey is useful for a day or two unless climatic conditions are favorable for longer preservation. Usually, the shrike returns to the prey during succeeding hours or as long as the prey is edible and no more recent kill occupies its attention. In California stores are rare during the middle of the winter and Miller never has found them where brooding females or young were being fed. He found the greatest abundance of stores is in the late summer and fall. Miller concluded that the shrike's habit of impaling is not truly storage.

Craig (1978) does not discuss the meaning of impaling in the loggerhead shrike because the return rate is very low. Bent (1950) stated that the impaled prey rots so quickly that it cannot have any real value as food reserves and that usually the impaled prey has been left untouched. On the other hand Applegate (1977) in southern Illinois during April and May 1975

observed one pair of loggerhead shrike: the male occasionally impaled spiders to the barbed wire fence and the female usually used them later the same day. The female did not hunt herself: the prey she provided to nestlings came from the fence. Also the male sometimes carried impaled prey to the nest. Applegate thinks that in this way the male just does its part in raising the brood decreasing the workload of the female.

Cade (1967) has studied northern shrike (Lanius exubitor) in subarctic Alaska. He found that during the breeding season, northern shrikes may maintain larders (usually in thorny bushes) in the nesting area. In one larder, there were as many as 12 vertebrate carcasses hanging. The impaled prey were with few exceptions used. Some prey items hung for a week or more but were eventually used. In winter, a carcass may freeze solid and Cade thinks it is probably abandoned. Watson (1910) found near Albuquerque, New Mexico, a loggerhead shrike feeding on dry, impaled lizards several weeks old. He states that in the dry climate of New Mexico an impaled prey cures rather than decays.

The observations cited above suggest that kestrels in general store excess prey for short time intervals (type 2 food storing) which does not conflict with my hypothesis if these kestrels are nesting in areas where there are no larger competitors. However, the information on the loggerhead shrike is ambiguous. My hypothesis suggests that food storing should be conspicuous among socially subordinant members of a guild and the use of the stores should depend on the availability of live prey. (The fact that the stores of loggerhead shrikes are sometimes not used at all is consistent with my predictions.)

PREDICTIONS

In my hypothesis I have made six predictions which should further test my thinking regarding the loggerhead shrike - kestrel situation;

1. Kestrels should defend larger areas than loggerhead shrikes, even accounting for differences in body size.

2. Kestrels should be territorial throughout the year. When territories are established there should be vigorous interactions between kestrels while the boundaries are being formed. Also, display behavior should be pronounced.

3. The home ranges of loggerhead shrikes should only have a weak territorial character. Displays should be less pronounced and no display behavior should be observed when a kestrel is in sight.

4. Kestrels should chase loggerhead shrikes away when the shrike intrudes into the kestrel's vicinity. Loggerhead shrikes should, therefore, avoid contacts with kestrels.

4a. Shrikes should avoid nesting in kestrel territories.

4b. When co-occurring with kestrels, loggerhead shrikes should perch much lower than when alone and clearly lower than kestrels.

5. To differentiate between type 1 food storing predicted for loggerhead shrikes and type 2 food storing predicted for kestrels, the following should be observed.

5a. Kestrels should make small stores only in times when there is considerable risk of poor hunting conditions and should use the stored prey items in a relatively short time. When hunting conditions are more dependable they should cease caching.

5b. Loggerhead shrikes should continuously store where ever they co-occur with kestrels for long periods.

5c. Loggerhead shrikes should store as much prey as they can and the use of the stores will depend upon the availability of live prey, which will be preferred.

6. Loggerhead shrikes should store the prey, making it unavailable for kestrels.

STUDY AREA AND METHODS

I observed kestrels from 15 February to 25 May, 1981 and loggerhead shrikes from 23 March (when the first individual was found) to 25 May, 1981 on grazed, tallgrass prairies around Manhattan, Riley County, Kansas. This area is intensively grazed, so that visibility was good down to ground level at distances of about 500 meters. Visibility in wooded places grew much worse by mid-April when trees were leafing out. For February I have anecdotal observations of different individuals wintering near the city of Manhattan and near Konza Tallgrass Prairie. In early March when migrating kestrels began arriving I concentrated my observations on rangeland of the Kansas State University north of Manhattan.

The topography is of gently rolling hills with trees (Populus, Celtis, Gleditzia, etc.) in valleys. The elevation varies from 315-420 m. Lone trees grew in gullies, red cedar (Juniperus) and locust (Gleditzia) on slopes seemingly invading overgrazed areas. The area contains farm ponds and dry creek beds. Ranges were fenced with barbered wire and a telephone wire ran across one loggerhead shrike home range. A dirt road ran through the main study area. In early May I extended observations eastwards to the Tuttle Creek Reservoir where I observed two nesting loggerhead shrike pairs. The home range of so called Dead Bush shrikes consisted of dead bushes and short grass. In the valley was a dirt road and a telephone wire and tall trees. The other pair (Meadow Pair) nested in a non-grazed meadow between a woody valley and a dirt road.

Observations were made using a telescope and 10 x 50 and 7 x 50 binoculars. The behavior was recorded using a stop watch and a watch with a second hand. Perching height was recorded. Duration of different types

of behavior and perching height distributions were calculated from these data. Home ranges of loggerhead shrikes and territories of the three most observed kestrels were mapped by recording the places where they were observed. Other kestrel territories were mapped by chasing the birds around and mapping the area they would use. The results yielded by these two methods were very similar.

TESTING PREDICTIONS AND DISCUSSION

Prediction 1. (Kestrels have larger territories.)

When calculating average maximum territory size for kestrels I have left out the consideration of the two biggest territories because large parts of these territories are agricultural land (see map). (This exclusion biases my data against my predictions, thus making the test conservative.) The average territory size for the three best known kestrel pairs was 2.20 km^2 and for the 10 kestrel mapped by chasing the average was 2.06 km^2. When these are combined we get the average of 2.12 km^2. I have only 7 loggerhead shrike home ranges mapped. Two of those seemed to be owned by a single bird. The home range of the so called pond pair seemed to be inside a solitary shrike's hunting area. When this solitary shrike entered the pond pair's home range it was never observed to be chased away. The average home range of these seven was 0.50 km^2. When taking the body sizes into account [kestrel, about 100 g (Brown and Amadon, 1968); loggerhead shrike, about 50 g (Craig, 1979)] in my study areas the territories of kestrels were 2.12 times larger than the home ranges of loggerhead shrikes.

In comparison to the range of kestrel territory sizes mentioned in literature the average size found in my study area falls to the middle of the variation. The smallest one, 0.80 km^2, is reported in Pennsylvania by Heinzelman (1964) and the biggest, 4.60 km^2, in Wyoming and Michigan reported by Craighead and Craighead (1956). The others are 1.0 km^2 (home range size) in Utah Valley by Smith et al. (1972), 1.1 km^2 in winter in Ohio by Mills (1975) and 4.0 km^2 (home range size) in Illinois by Enderson (1960). The mean of these six values is 2.16 km^2.

Miller (1937) gives 0.045 km^2 to 0.061 km^2 variation for loggerhead shrikes breeding territory. According to Porter et al. (1975) in short

LEGEND TO THE MAP

The territories and located nests of kestrels (solid lines, dots) and the home ranges and nests of shrikes (dashed lines, circles) in the study area. Other features represented in the map are water courses, outlines of hills and the location of KSU campus. The numbers indicate the pairs referred to in the text:

1 = Toramylly Shrikes

2 = Bachelor Shrikes

3 = White House Shrikes

4 = Pond Shrikes

5 = Solitary Shrike

6 = Dead Bush Shrikes

7 = Meadow Shrikes

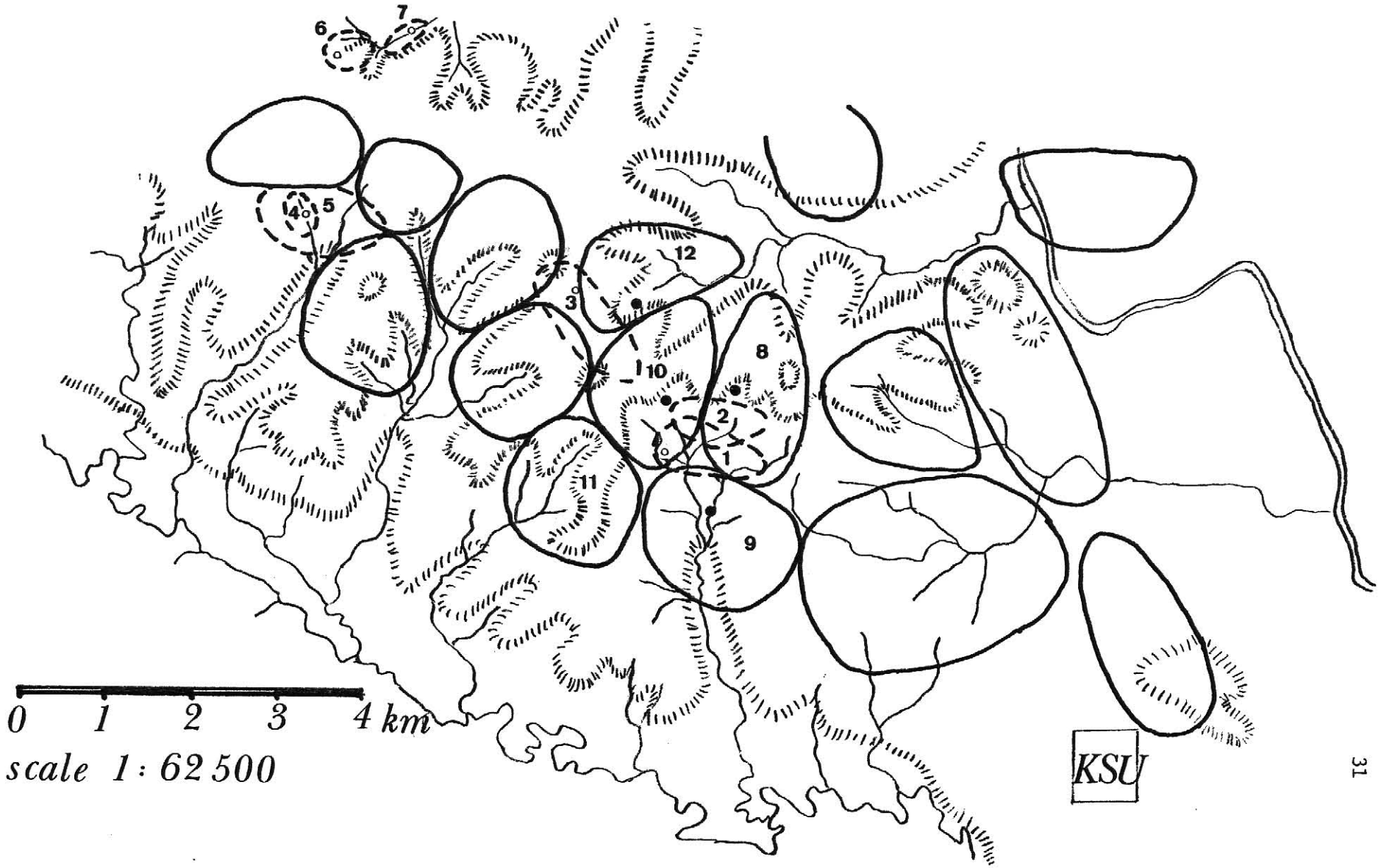
8 = East Valley Kestrels

9 = Woody Valley Kestrels

10 = Dead Poplar Kestrels

11 = Green Valley Kestrels

12 = North Valley Kestrels


7
6
4
5
12
3
8
10
2
1
11
9
0 1 2 3 4 km
scale 1 : 62 500
KSU

grass prairie, Colorado loggerhead shrike nests were never closer than 400 meters which would give a territory size of 0.50 km^2. However, Porter et al. say that the actual territory radii were much smaller (they do not give any values). In subarctic Alaska the hunting area of three northern shrikes was about 1.3 km^2 (Cade, 1967). Northern shrike weighs about 70 grams.

Thus, my data are in accordance to the predictions, and the kestrel territories of my study area do not seem exceptionally small or large, as compared to published data. The same seems to be true for shrikes, although the published data are very variable (as one would expect for a species whose home range does not have a strong territorial character). Literature suggests that the size of territories and home ranges may vary greatly from habitat to habitat, and in order to make comparisons between the two species, one must have data from the same habitats.

Prediction 2. (Kestrels are territorial all year, conspicuous displays and vicious fights are typical.)

I have observations from one spring and one area only. Thus, I cannot test the first part of the second prediction (kestrels are territorial year-around) with my own data. Published information suggests that kestrels are territorial throughout the year. Opinions of the degree of territoriality vary.

Mills (1976) suggests that the purpose of winter territoriality is to provide a sufficient food supply which corresponds to my conjecture that the strategy of kestrels is to store live prey by means of territorial defense. On the other hand, he could not observe any "definite territorial behavior" (border disputes?) during the winter in Arizona. A clear habitat separation between sexes was found. Mills (1975) studied winter territoriality of kestrels in Ohio, e.g., by releasing kestrels into the territories

of other ones. Four out of the five released birds were immediately chased. He saw five occasions when a male and a female shared the same territory, but the only time he observed two kestrels (both females) in an area of overlap between two territories the birds were fighting. According to Cade (1955), kestrels winter territories are defended from the end of August to the beginning of the breeding season (females being dominant over males) in California. In his opinion, only the vicinity of the nest is defended during the breeding season.

Kestrels arrive during the first half of April in California's Sierra Nevada (Sagehen Creek) (Balgoyeen, 1976). Prebreeding home range can be 200% larger than the one during the breeding season. (Possibly to be prepared for adverse conditions; snowfalls are possible in April.) The boundaries are defended against other kestrels (thus, the home ranges seem to have a territorial character). In Pennsylvania, kestrels seem to have definite hunting ranges around the nests (Heinzelman, 1964). Smith et al. (1972) found a clear tendency of kestrels to utilize the same areas as in previous year in Utah Valley, Utah. They did not observe any intraspecific territorial interactions, in spite of overlap between home ranges. The first males arrived in February and early March. The majority of males arrived between 12 April and 3 May. (May and June are the rainiest months of the year.)

In my study area, kestrel territories seemed to be clear-cut and well defended. Unfortunately, I was able to follow just two series of interactions where the boundary between two adjacent territories was formed, in early March. The pair whose territorial center (future nest tree) was slightly closer to the focus of the first battle (an old windmill) consolidated its hold of this point, but before this occurred, we observed the

pair (so-called Dead Poplar Pair) to chase the intruding one (so-called Woody Valley Pair) or either of its constituents 11 times from this battlefield. The so-called North Valley Female also had at least one intensive border fight with the Dead Poplar Female (the Dead Poplar Male was present but remained largely passive). The intruding female even perched in the nest tree but was immediately chased by the Dead Poplar Female. Within 30.2 minutes, the intruder was chased 12 times by the female and once by the male. Also East Valley Pair and Green Valley Pair were observed to intrude on the Dead Poplar Pair's territory. They were chased away. The Dead Poplar Pair thus had to defend its territory against intrusions from all sides. The female chased much more during March (21 times, for a total of 52.4 minutes) than the male (9 times, 22.3 minutes). The average duration of a fight was 2.5 minutes (2.50 minutes for the female, 2.48 minutes for the male). In April and May we did not observe the female of this pair fight. The male was observed fighting once in both months (both fights lasted for one minute). Four fights between Woody Valley Male and East Valley Male were observed in April and May. (The boundary between these pairs received little study in March.) In one fight, deep in the territory of East Valley Pair, the East Valley Female also participated in chasing. The average duration of three fights was 5.25 minutes, the fourth one only lasted a few seconds. Altogether during the 82.3 minutes when kestrels belonging to different pairs were seen together, 75.7 minutes were spent in fighting. The remaining 6.6 minutes were spent sitting and flying. The time used in fighting refers to periods during which either or both members of the co-occurring pairs were engaged in aggressive interactions. Both females and males were observed chasing opponents belonging to both sexes. Sometimes even bodily contact was involved. The Dead Poplar Pair was also once observed to be engaged in a fight with crows (Corvus brachyrhynchos)

when a flock of crows landed on their nest tree (in March). Chasing occurred both ways, and it was hard to see which species was aggressively the stronger one. Kestrels, however, seemed to be much more motivated, and the crows eventually left.

Display behavior was performed both when an intruder was in the vicinity and when the pair was alone. The Dead Poplar Female was a bit more actively displaying than the male. Usually, they were flying up and down simultaneously, crying "klee-klee" or "kikiki". This behavior was very conspicuous indeed.

Even if my material does not directly relate to the question of whether kestrels are territorial year-around and how the breeding territories change to winter territories, the time of arrival to breeding grounds is interesting in this context. In my study area, the breeding territories of kestrels were settled at least twenty days before the first shrike was observed. There was no comparable difference in the timing of the breeding cycle. The Dead Poplar Female was rarely observed after 20 March, and 11 April we scared it from the nest cavity. The East Valley Female was sitting visible for a longer time, but after 12 April it seemed to spend most of its time in the nest. At the end of the study period (25 May), no kestrel fledglings had yet been observed. The nest in East Valley was then checked, and the nestlings were still quite helpless (though having feathers). Shrikes, on the other hand, were observed start breeding about simultaneously with kestrels and fledge earlier (see discussion below). Hence, I suspect that kestrels arrive earlier than shrikes because kestrels invest more in territoriality and it is more important for them to be on breeding grounds as early as possible lest they would not stand a chance to get a reasonably good breeding territory.

Prediction 3. (Territoriality is weak in shrikes, displays inconspicuous and not performed when kestrel is in sight.)

According to Bent (1950: 142) "the loggerhead maintains definite territorial limits and protects them assiduously". Miller (1937) says that pairs tend to nest in the same place from year to year and he also claims them to be territorial (Miller, 1931). According to Zimmerman (1955), loggerhead shrikes have definite territories in winter. During the fall and winter, shrike territories were contiguous in California (Craig, 1978). When loggerhead shrikes started to arrive at Pawnee National Grassland (in Colorado), the males were aggressively defending territories according to Porter et al. (1975). However, the actual radii of territories were much smaller than the distance between nests, and Porter et al. thus suggest that the breeding density was not regulated by territoriality. According to Cade (1967), pairs of northern shrikes (Lanius excubitor) are widely spaced in subarctic Alaska and pairs do not keep exact territory boundaries.

I mapped seven loggerhead shrike home ranges, and in two cases there was a possibility for territorial conflicts. An intruder was observed for 71 minutes in a shrike's territory. Only 2.5 minutes of this time was the owner observed to chase the intruder. This 2.5 minutes consisted of two chasings when the so-called Bachelor was chasing one member of the Toramylly Pair. No bodily contact was observed. The area where one solitary shrike moved included the Pond Pair's home range. The solitary shrike was observed for 18 minutes inside Pond Pair's home range, but the only change in Pond Pair's behavior was that the male sang more than usual. Sometimes the distance between Pond Male and the solitary shrike was only ten meters.

Singing was the only display behavior I could observe. The song was rather quiet. The only pair that sang from a perch higher than six meters was the Pond Pair in the vicinity of which no kestrels were observed (see map). The others sang in bushes or other places lower than six meters.

In fact, only the Pond Pair, Toramylly Pair, White House Pair and the Bachelor were ever observed singing. This may partly result from the Dead Bush Pair and Meadow Pair observed only in May, whereas the singing period was clearly in March and April (see Appendix 1B). No singing was observed when a kestrel was in the vicinity (the so-called natural experiment) or when a kestrel model was there.

The first shrike was observed 23 March but more shrikes were not observed until 31 March. The Pond Female was observed to sit in the nest for the first time 9 April. 19 May, the juveniles of this pair were observed sitting in bushes near the nest tree. 30 April, at least five just hatched nestlings were observed in the White House Pair's nest. When the nest was checked for the last time 19 May, the juveniles were near to fledging. Dead Bush Pair was first observed 14 May. 17 May when the nest was checked, we found five nestlings. The nest was empty 24 May. 19 May, the Meadow Pair had six eggs in the nest, and 24 May when the nest was checked for the last time, there were six still rather small nestlings. Toramylly Pair also had six nestlings when the study ended. This fits with Miller's (1937) proposition that the time from egg laying to fledging in loggerhead shrikes is approximately 41 days. Porter et al. (1975) give the duration of this period as 33 days. Notice also that the breeding cycles of different pairs were far from synchronous.

As a conclusion concerning predictions 2 and 3, the following can be noted. My field data suggests that the territorial character of the home range is much stronger in the American kestrel than in loggerhead shrike. The existence of definite territory boundaries in shrikes seemed dubious. Both fighting and display behavior in shrikes was much less pronounced than in kestrels. Even if the breeding cycle of kestrels is not completed earlier than that of shrikes, kestrels had established territories before shrikes had even arrived and at least 20-30 days before they commenced

breeding. This seems to stress the need of being early on breeding grounds in order to secure a territory for kestrels and the lack of a corresponding need in shrikes.

Prediction 4. (Kestrels chase shrikes, shrikes avoid kestrels.)

I never saw a kestrel chase a shrike, but this was observed by Elmer Finck (pers. comm.) and his class saw a shrike fly behind a tree in the vicinity of a kestrel which immediately started to chase the shrike all around. Many times I observed a shrike to disappear to the ground or inside a bush when a kestrel was flying in the neighborhood (e.g., the natural experiment to be discussed later, the withdrawal of the Bachelor from a bush near the nest tree of the East Valley Pair (kestrels) when the male of this pair returned to the tree at 20 April). According to Cade (1967), the usual reaction of a northern shrike to the presence of a hawk is to disappear to the densest branches of a tree. Trautman (according to Zimmerman, 1955) has similar observations: when a flacon enters the territory of a "gray shrike" (northern shrike?), the shrike immediately leaves. Trautman, however observed loggerhead shrike and kestrel share the same territory which Zimmerman suggests indicates that there is no such competition between loggerhead shrike and kestrel.

Prediction 4a. (Shrikes avoid nesting in kestrel territories.)

I have mapped seven loggerhead shrike home ranges and fifteen kestrel home ranges which I would call territories on the basis of the behavior of the pairs that were most intensely watched (Dead Poplar Pair, East Valley Pair, Woody Valley Pair, Green Valley Pair, North Valley Pair). Two shrike pairs were nesting within kestrel territories (Toramylly Pair, White House Pair). Their nests were situated on the edge of kestrel territory. The

Bachelor was moving mainly in that part of East Valley kestrel's territory which was seldom visited by the kestrel (the southwestern edge). Also the nest of Toramylly pair was in an area rarely visited by kestrels later in the spring. (Toramylly was the very focus of the longest observed battle between two kestrel pairs, but the shrikes had not yet arrived by then.) The White House Pair was only once (during a period of very foggy and rainy weather) observed deep in the territory of Dead Poplar Pair. Usually it was observed near its nest bush, located in the seam of four kestrel territories. In the home range of the solitary bird, hunting in the surroundings of the Pond Pair, two kestrels were seen (each once). No kestrel was observed within the home range of the Pond Pair, although the kestrel living north of the pair sometimes flew over the open field immediately north of the home range. The Dead Bush Pair nested on the northern side of this kestrel territory, in an area where kestrels were not observed. The Meadow Pair bred further to the north and so far from the mapped area that nothing can be said with certainty about the kestrel situation there (no observations of kestrels were obtained).

Prediction 4b. (When co-occurring with kestrels, shrikes should perch low.)

When testing predictions referring to perching height distributions, I have treated both sexes of kestrels separately, whereas shrikes could not be sexed. I first calculated the perching height distribution of the more active shrike (probably mostly the male) for each month. For the Pond Pair, and Toramylly Pair the perching height distribution of the less active member was also calculated (pooled over the whole study period to get a reasonable total). Comparisons between shrikes occurring alone (Pond Pair, Solitary Shrike, Dead Bush Pair), shrikes co-occurring with kestrels (Toramylly Pair, Bachelor) and kestrels inhabiting the same habitats (Dead Poplar Pair,

East Valley Pair) was made by calculating the percent of time perched in different perching height categories (below 1.5 m, from 1.5 m to 3 m, from 3m to 6 m, above 6 m), using each individual for each month as a data point (except for the case of Pond Pair explained above). The Meadow Pair was disqualified from comparisons because of insufficient knowledge of the kestrel situation (corresponding time spent in North Valley yeilded no sightings of the resident kestrel, the habitat of the two places was similar and the time when the Meadow Pair was observed was most unsuitable for sighting kestrels as their display period was over). Also White House Pair was disqualified because its habitat offered few high perches, and those that were there were rather far from the nest.

The perching height distributions of kestrels and co-occurring shrikes were clearly different (Fig. 5). Only very low perches were used about equally as often. Low and medium sized shrubs were used more frequently by shrikes (two-tailed Mann-Whitney test yields, $p = .015$ in both cases), and perches higher than 6 m were used much more frequently by kestrels ($p = .015$, see Table 6a). There was also a significant difference in the use of high perches (more than 6 m) between shrikes that co-occurred with kestrels and shrikes that were alone (Table 6a). Between shrikes that were alone and with kestrels, there were no statistically significant differences at all, although the data suggest that kestrels used more often very low perches whereas medium-sized shrubs were more frequently used by shrikes.

In order to see whether kestrels really influenced the perching heights of shrikes, a stuffed kestrel male was installed to a top of some shrub or branch, about 75 meters from the nest of each shrike. The experiment was regarded as started when the shrike for the first time was in such a place from where it could see the model (which usually was the case in the very moment the model had been installed). Only the time when the shrikes were

FIG. 5. Perching height distributions of kestrels (triangles), shrikes co-occurring with kestrels (squares) and shrikes without kestrels in their vicinity (dots). The numbers on the vertical axis refer to the centers of the perching height classes. The standard error is given by the horizontal bars.

Fig. 5

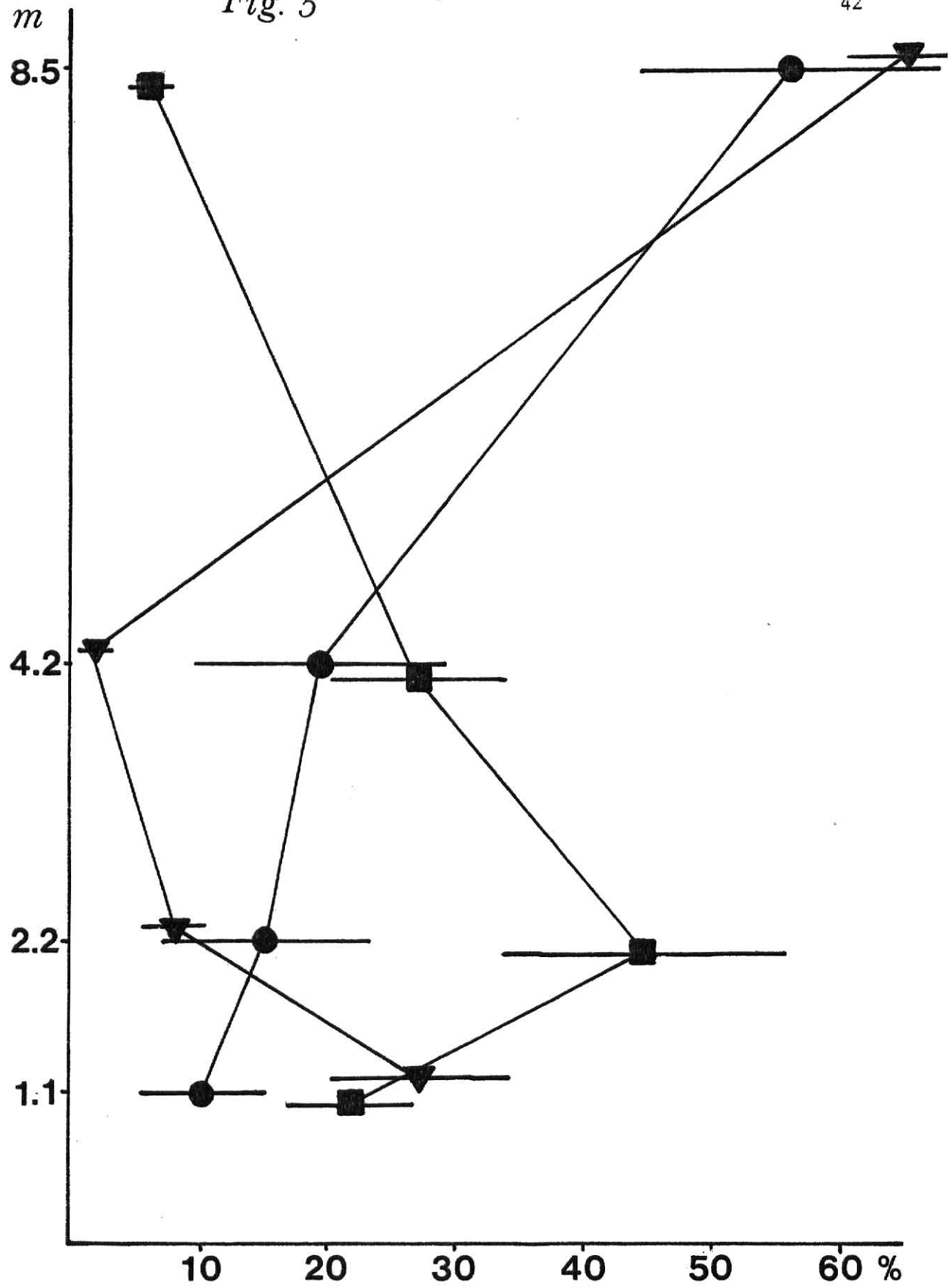


Table 6a. The U-values and corresponding probabilities of pair-wise comparisons between the use of each perching height class by kestrels, shrikes co-occurring with kestrels and shrikes that do not co-occur with kestrels (two-tailed Mann-Whitney test).

Perching Height	Kestrels vs. Co-occurring Shrikes		Kestrels vs. Shrikes Occurring Alone		Shrikes with Kestrels vs. Shrikes Alone	
	U	P	U	P	U	P
6 m	0	.015*	4	$.190^{NS}$	0	.029*
3-6 m	0	.015*	3	$.111^{NS}$	5	$.486^{NS}$
1.5-3 m	0	.015*	8.5	$.817^{NS}$	1	$.057^{o}$
0-1.5 m	6	$.413^{NS}$	3	$.111^{NS}$	3	$.200^{NS}$

Table 6b. Differences in the percentage of time spent out of sight between the normal situation and the experimental one (one-tailed t-test).

Shrike Pair	Experiment-Normal
White House	+14.33
Toramylly	-10.30
Toramylly (natural experiment)	+20.82
Pond	+34.20
Dead Bush	+11.60
Meadow	+17.25

$\bar{x} = +14.65 \pm 5.94$

$t = 2.466^{*}$

perching within the range of vision of the model was included. Also direct reactions to the model were excluded. (Typical reactions included disappearance to a distant part of the home range, and eventually an approach towards the model seemingly designed to detract its attention from the nest.) A natural experiment took place when the Dead Poplar kestrels twice were observed to hunt very close to the nest valley of Toramylly shrikes. During these visits, the behavior of the shrikes was recorded. For both designed experiments and the natural one, the perching height distribution in other times was used as a control.

During the time when the model was in view, the shrikes were significantly ($p < .05$, tested by using each experiment and each control as one data point , see Table 6b) more out of sight than normal. Perches higher than 6 m were never used during the experiments. I have calculated the perching height distributions during the experiments for each case, even if the total time used in perching was less than ten minutes in three cases. (For Dead Bush Pair, I pooled observations of both shrikes, and even so the total only amounted to 9.5 minutes. For the rest, only the more active constituent of the pair has been used in calculations.) Already the lack of use of high perches during designed experiments and the natural one is statistically significant, because the probability that they just by chance happened to have used these perches less than normal is $(0.5)^6=0.016$.

Because my perching height classes made a geometrical series (for the reason that smaller absolute differences can be detected when estimating the heights of low perches), the geometrical means of class limits were used in calculating average perching heights. These means themselves make up a geometrical series. Hence, the values for the tallest (>6 m) and lowest (<1.5 m) perches were taken by extending this series. The average reduction of perching height due to kestrel was 1.6 ± 0.39 m. Mean perching

height was reduced in each experiment which has the probability of $(0.5)^6 = 0.016$ of occurring just by chance. The normal and experimental perching height distribution for all six cases are presented in Fig. 6.

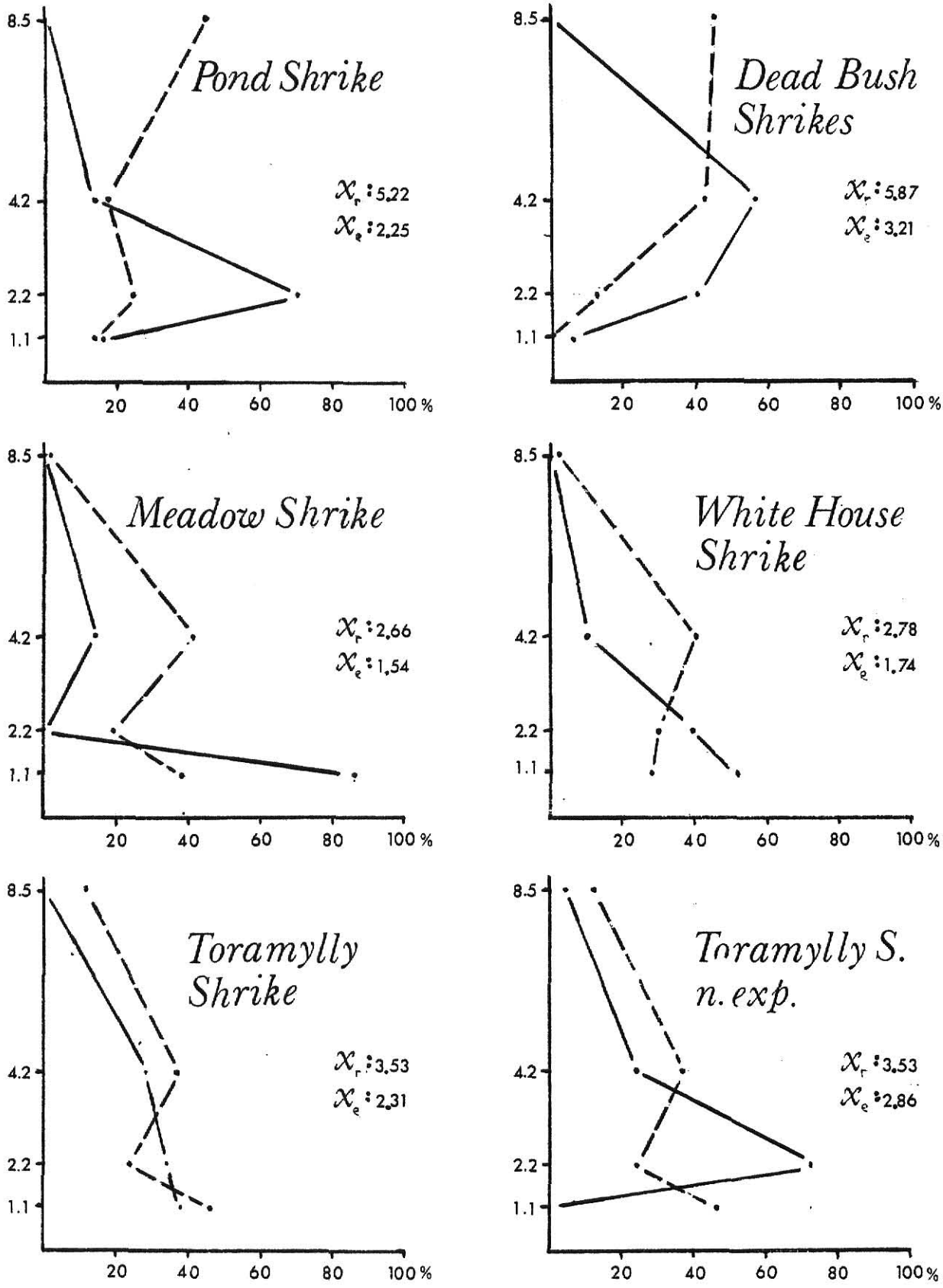
Following conclusions appear warranted. The over-all pattern of data was as predicted. Shrikes perch lower than kestrels where the two species occur together, whereas for shrikes not having kestrels in vicinity, no clear difference between the perching height distribution of the two species was obtained (Dead Bush Pair, Solitary Shrike, Pond Pair). The difference in the use of high perches was almost as clear between shrikes occurring alone and shrikes co-occurring with kestrels as it was between kestrels and co-occurring shrikes. The introduction of a kestrel model or the visit of a real kestrel caused all shrikes to abandon high perches. During the natural experiment, the shrike disappeared when kestrels flew over the nest. All this suggests that (at least during the breeding season), differences in hunting strategy (cf. Mills, 1979) only explain a minor part of the differences in perching heights between kestrels and shrikes. Avoidance seems to be a major cause.

Prediction 5a. (Kestrels cache only when hunting conditions are unreliable.)

I only could locate two storing places of kestrels. According to literature information reviewed earlier, they should occur in tree trunks, grass clumps and fence posts. I looked at such places in three kestrel territories, in the fourth one I only checked fence posts (as they were the only places where I had had any success). The two storing places located were in two fence posts, both in the territory of the Dead Poplar Pair. The first stored prey item (half of a snake) was found 15 March. When next checked 18 March, the store was empty. 19 March, two stores were found (one in the same fence post as the previous stores, very close to the nest,

FIG. 6. The regular (dashed lines) and experimental (solid lines) perching height distributions of different pairs of shrikes. The mean height under regular conditions ($\bar{x}_r$) and during the experiment ($\bar{x}_e$) is included in each graph.

Fig. 6


Pond Shrike
χ_r : 5,22
χ_e : 2,25
Dead Bush Shrikes
χ_r : 5,87
χ_e : 3,21
Meadow Shrike
χ_r : 2,66
χ_e : 1,54
White House Shrike
χ_r : 2,78
χ_e : 1,74
Toramylly Shrike
χ_r : 3,53
χ_e : 2,31
Toramylly S. n. exp.
χ_r : 3,53
χ_e : 2,86
8.5
4.2
2.2
1.1
20
40
60
80
100 %

the other one 30 meters to the north of this). This was the only time when the second storing place was observed being used.

Altogether seven prey items were found from these stores: six snakes or parts of snakes (usually the latter) and one hind portion of Peromyscus. These observations were made within two weeks (15 March - 29 March). A store never contained more than one prey item at a time. The same prey was never found more than once from a cache. There was unfortunately an interval of six days between the last observation of stored prey and the subsequent attempt to find stores of kestrel (6 April). Attempts to find cached prey of kestrels thereafter were all futile. (Stores summarized in Appendix 2).

Prediction 5b. (Shrikes cache continuously.)

The food storing observation of shrikes were made by trying to go through thorny bushes and to follow fences with barbed wire (in which case, the posts were also checked to find kestrel caches in their cracks; just one Microtus skull was found). This searching was done in the home ranges of shrikes as often as possible. In two home ranges, impaled prey marked from 13 May onwards to follow turnover rates. In the home range of White House Pair, observations were concentrated to a stretch of road of about 650 m, lined with fences on both sides.

As mentioned before, a shrike (the Bachelor) was first observed 23 March. The first impaled prey items (a grasshopper and three caterpillars) were found the same day in its home range (from thorny bushes). However, the Bachelor did not store regularly; at least we could not find impaled prey very often during the latter half of the study period (see Appendix 2). The first time when the Pond Pair was observed was 31 March, and when the second visit was made to the area 6 April, two impaled insects were found. The number of impaled prey in the central parts of its home range gradually

increased towards the end of the study period. The other member of the White House Pair also was observed 31 of March for the first time, but its location misled us about the place where its nest was, and there was a long period of futile searching before its nest was found 18 April. From 30 April onwards, stores were continuously found from the stretch of fence that we surveyed (cf. above) until the end of the study period (see Appendix 2).

The Toramylly Pair was observed for the first time on 30 April (although some observations that we thought to represent Bachelor might indeed have actually referred to either of its members). At the same time, 8 impaled insects were found from its home range. The last time its home range was checked was 25 May. Then only 3 insects were found impaled. Meanwhile, there were very few observations of impaled prey. The valley where this pair nested had a fair-sized woodlot (30 m by 70 m) of big Gleditzia triaconthos bushes and small trees which were almost impossible to be checked carefully without being torn in pieces, especially after the leafing of the trees reduced the visibility.

Dead Bush shrikes were observed for the first time on 14 May, and only one grasshopper was then seen impaled. After that, no sightings of impaled prey were made. Once we saw the shrike carry a snake over the gravel road, away from its nest, and it flew back without its prey. We never found where the snake had been carried. Thorny thickets and woodlots abounded in that direction, and there were many thorny shrubs and low trees near the nest as well.

The Meadow Pair was found the same day as the Dead Bush Pair. The second time we observed Meadow Pair (15 May), we also checked thorny bushes and barbed wires in the surroundings of its nest. Five impaled insects and a lizard were found hanging from a thorn of a Gleditzia. On 24 May, 26 items were found impaled, including a frog, three lizards, two snakes and two

prairie voles (see Appendix 2). In the meantime, the place was only visited twice, and the same rotten lizard was the only prey item found.

Prediction 5c. (Shrikes cache as much as possible, use caches only when necessary.)

My test of this prediction left much to be desired. In order to do a rigorous test, I should have gathered information about the availability of different prey groups. I should also have had information about the success rate of attacks, to know how much the shrikes could get in excess of their immediate needs, and of the rate at which prey were impaled. This would have taken tens of ours of observation time and the impaled prey should have been marked more consistently and in greater numbers than was done in the present study. As some of the impaling sites (fences) were such that shrikes have had them available for relatively short times (as compared to the rate of evolution), it is quite possible that their use was maladaptive for shrikes and other birds would keep cleaning these stores, so that even with a good effort and success in storing, little would be there at any time. If I were to have a good idea of the rate of prey storing in such places, I should also have needed to have observations about the impact of other birds on the amount of stored prey.

However, I will try to summarize the pieces of information that I managed to gather. The day temperatures were about +15°C when shrikes were first observed. The landscape was still brown and looked dead. In April, days were warmer but very little new growth was to be seen during the first half of the month. The greening of th prairie occurred in the later part of April, but simultaneously, the weather grew periodically very rainy and probably adverse for hunting, although no real backlashes of the winter occurred. An alteration of rainy and sunny weather continued throughout May without notable rises in temperature. Our attempts to see what the

birds were doing during rainy weather were largely futile. The little that we saw indicated great mobility, very low perching and few attempts to catch prey.

As mentioned earlier (and to be seen in Appendix 2), there was an increasing abundance of impaled prey towards the end of the study period in Pond shrikes. On the other hand, if only vertebrate prey is considered, the trend seems to be an opposite one (12 April: 3 snakes and one vole; 14 April: the same vole; 19 May: one vole). One reason for this might be that when snakes start to move, they were still clumsy enough due to cool weather to be relatively easy to catch. The sudden appearance of numerous impaled spiders starting 14 May is also interesting as it occurred about the time of fledging. Some prey was left where it had been impaled for long times. This was especially the case for the very early hairy caterpillars which were seen hanging in the same places for weeks. The vole found 12 April, was there still 18 April. (The next time the stores of Pond Pair were checked was 2 May; when the vole was no longer there.) We marked some impaled prey, but the method was poor, because the same places were not visited frequently enough and only one type of mark was used. However, grasshoppers and spiders usually disappeared within a couple of days. I saw a shrike taking an impaled prey three times.

In the White House Pair's home range, only insects were found impaled. Our observations concentrated to a stretch of road of about 650 meters, with fences of barbed wire on both sides. This place was regularly used for impaling, whereas only very few impaled insects were found near the nest. We marked the prey items from 13 May onwards. They disappeared within a couple of days, except for some beetles which remained untouched for the whole time. It is really impossible to say who used the impaled prey. Once I observed a red-bellied woodpecker take an impaled caterpillar from

a fence post (there was a "thorn" there), and many bird species (tyrant flycatchers, various sparrows) were observed perching on the barbed wire.

We had no evidence indicating that the Toramylly Pair ever stored very actively. Only 15 impaled insects were found during 25 days. The Bachelor remains a mystery. From 23 March to 2 May (when we stopped checking its home range regularly), only 25 impaled prey items were found. On 2 May, a tail of Eumeses obsoletus was found hanging from a fence, the tail was a couple of days old. In the last week of March and early April, the Bachelor was regularly observed, but in late April we got no observations of it and suspected that it had left the area. However, it (or a similar solitary shrike) was seen once more 7 May for two minutes. Before that, it had not been observed on 28 April, in spite of an intensive search throughout its home range. No impaled prey were found past 2 May and those found at 2 May were not fresh. Once more, the Bachelor seemed to be there in the vicinity of the Toramylly Pair on 25 May (three shrikes seen simultaneously).

As mentioned earlier, I had little evidence of prey storing for the Dead Bush Pair. The Meadow Pair stored both insects and vertebrates. One lizard, already starting to be rotten when first observed, was hanging at least for ten days. The five impaled insects observed 15 May had disappeared 17 May. On 24 May we found 8 impaled vertebrates (the rotten lizard, an extremely dry frog which we had probably missed earlier, two snakes, two lizards and two prairie voles). When these vertebrate preys were checked in the afternoon of 25 May, they were still all there.

Prediction 6. (Shrike stores in places not accessible for kestrel.)

The most common impaling sites of shrikes were thorny bushes while barbed wires were also used. While kestrels perched in thorny bushes, they usually used either higher or lower perches, (see Fig. 5), and they always

sat in the top. I never saw a kestrel inside a thorny bush. At least in these places, shrikes seemed to store their prey places inaccessible for kestrels. When kestrels were observed on fences, they always sat on posts. I do not know if a kestrel could even land on a wire, at least I never saw it occurring. I saw kestrels perching on telephone wires which are much thicker. As an impaling place, barbed wire is an unnatural mimick of a thorny bush and does not provide real protection for impaled prey as thorny bushes do.

Conclusions for Predictions 5 and 6

Kestrels did not seem to store very much. The only observations I have are in accordance to predictions and so are the cases reported in literature (discussed earlier). The storing was observed when hunting conditions seemed intermittently poor and a risk of winter backlash was still there. Storing ceased when the growing season really started. Stores were clearly leftovers and seemed to be used within short periods.

Shrikes started to store when they arrived and continued throughout the study period, although with great differences between individuals. However, individuals and pairs that did not seem to store during the later half of the study period either were not very successful in general (the Bachelor, which did not obtain a mate), or hunted in places where finding a store was especially difficult (Toramylly Pair, Dead Bush Pair). Some prey types remained untouched whereas others were used (or robbed, at least they disappeared) very soon. That suggests differences in prey preference. Unfortunately, I have too little for detailed conclusions about that. It would also suggest that usage of impaled prey depends on the availability of live prey. Literature information is in some respects in accordance to the prediction, in other ones against it. However what has been published on

prey storing in shrikes largely consists of casual observations and their interpretation, and also my own material relating to this question is rather vague. What would be needed would be a study entirely concentrated on quantifying prey storing.

The apparent differences in the intensity of prey storing between different shrikes is an open and intriguing question. Did the Bachelor not obtain a mate, because its territory was of such poor quality that it failed to make stores? Was the home range of the Pond Pair where the clutch fledged the earliest and was a large one (six, out of which one died shortly after fledging) and where stores were most regularly found also an especially productive one? It looked lush, but the answering of questions of this type would also have required quantitative studies on the availability of resources.

Over-all Conclusions Referring to the Predictions

The present material seems to make a strong case for the inferior position of the loggerhead shrike with respect to kestrel and for the consequent unability of shrike to secure resources by means of territorial defense. Conversely, territorial defense seems to be important for kestrels. Predictions referring to food storing obtained moderately strong support. Their more rigorous testing would be a natural next step.

ARISING QUESTIONS

The model explained food storing as a strategy of controlling resources and predicted that its occurrence ought to be an all-or-nothing phenomenon. This clearly was not quite correct. Even kestrels had some tendency of caching surplus food in early spring. Such "type 2 food storing" was discussed and it was regarded as a plausible behavior of any predator that faces the possibility of poor hunting conditions. However, this was verbal discussion only. It would have been better to have the model formulated so that this type of food storing would have also been incorporated.

Another observation which was discussed but not predicted by the model was the widespread occurrence of food caching among opportunists. It would be better to relate the parameters of the model to the position of the species on the pursuer-opportunist axis.

Besides these questions that reflect shortcomings of the model, there is the question how should a small pursuer-type predator behave in hot and humid climate where the retention of stored food is very poor. Should it rather evolve to become an opportunist? Should it specialize on something that no other predators "want" to use? Could it obtain control over resources by becoming social? (Mongooses seem to have "done" both of the last two mentioned things.) Or should it just rest when having satisfied immediate food needs?

The model is clearly not yet a comprehensive explanation for all food storing in any types of predators, nor does it provide answers for some important questions referring to the optimal strategy of small predators. Yet, I hope that is has helped in understanding the occurrence of seemingly wasteful caching behavior and in focusing more sharply on unanswered questions.

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APPENDICES

APPENDIX 1A. Time budgets of kestrels. The left-hand column indicates the perching height classes and types of activities other than perching. Fighting time is included in the time budget of those individuals on whose territory the event occurred. The units are percentages of total time.

	Dead Poplar Kestrels					East Valley Kestrel			Woody Valley Kestrel		North Valley Kestrel		Kestrel In Ogden	Kestrel On Konza
	March		April		May	March	April	May	March	April	April	April	Febr.	Febr.
	Male	Fem.	Male	Fem.	Male	Male	Male	Male	Male	Male	Male	Fem.		
Total Time (minutes)	923	923	127	127	243	374	175	12	22	275	48	48	26	50
0-1.5 meters	17.2	20.6	5.5	5.5	8.2		0.6							
1.5-3 meters	6.4	2.9			1.5		5.2							
3-6 meters	2.9									1.1		14.6		
>6 meters	30.7	33.9	9.1		16.7	43.3	35.8		17.8	52.4	62.5		15.4	75.6
Flight	7.4	3.5	2.4	0.8	5.4	26.1	18.9	56.5	11.3	0.6	20.8		45.1	17.7
Display Flight	1.4	1.8			0.2	0.4								
Fight with Kestrels	2.3	5.6	0.8		0.4			43.5		4.0				
Fight with Other Species	0.5	0.6								0.2				
Out of Sight	31.3	31.1	82.3	93.6	65.6	30.2	39.5		70.9	41.7	16.7	85.4	39.4	6.8

APPENDIX 1B. Time budget of shrikes. The markings are as in Appendix 1A. S1 refers to the more active individual, S 2 to the less active one. Normal and experimental situations are recorded separately. N. exp. refers to the natural experiment.

		Bachelor Shrike		White House Shrikes			Toramylly Shrikes			Pond Shrikes				Solitary Shrike	Dead Bush Shrikes			Meadow Shrikes	
		Mar.	Apr.	Apr.	May	May	May			Apr.	May	Apr. + May	May	Apr. + May	May			May	
		Nor.	Nor.	S1 Nor.	S1 Nor.	S1+S2 Exp.	S1 Nor.	S1 Exp.	S1 N. exp.	S1 Nor.	S1 Nor.	S2 Nor.	S1 Exp.	Nor.	S1 Nor.	S1 Exp.	S2 Exp.	S1 Nor.	S1 Exp.
Total Time (minutes)		193	564	46	56	37	308	33	37	279	182	460	170	18	44	28.0	30	120	30
0-1.5m	silent	20.7	10.1	2.2	31.9	24.2	8.9	18.7		3.3	9.2	1.6	2.6	11.1		1.8		21.2	25.0
	singing			1.1			3.1												
1.5-3 m	silent	34.2	26.4	23.3	18.0	20.2	7.0	15.9	12.3	28.1	4.0	2.2	12.2		8.1	2.8	10.0	10.6	
	singing		3.4																
3-6 m	silent	10.6	12.2	48.9	4.1	4.8	7.2	13.6	4.1	9.9	9.0	4.1	4.1		27.2	8.0	10.0	22.6	4.2
	singing	6.2	1.2	9.3			7.1												
6m	silent	6.7	0.7	2.2			3.6		0.7	32.7	16.7	7.7		88.9	28.7			0.7	
	singing									1.6	0.7								
Flight		0.8	1.7	2.0	1.8		1.1			0.6	2.2	0.1	0.3			1.2	1.4		
Fighting with shrike		0.7	0.4																
Fighting with other species											1.4				0.4				
Reaction to model						8.8							0.9			35.7	18.3		10.0
Out of sight		20.0	44.0	11.0	44.1	42.0	62.1	51.8	82.9	23.9	57.5	84.5	79.9		35.6	50.5	61.7	43.5	60.8

APPENDIX 2

STORED FOOD

Dead Poplar Kestrels

15	March	half of a snake
18	March	empty
19	March	half of a snake
20	March	snake
21	March	hind part of deer mouse
29	March	snake
6	April	empty
11	April	"
12	April	"
16	April	"
18	April	"
19	April	"

Bachelor Shrike

23	March	2 grasshoppers 3 caterpillars
29	March	1 grasshopper 7 caterpillars
12	April	1 spider 1 caterpillar
15	April	1 beetle
18	April	2 grasshoppers 1 moth
19	April	2 caterpillars
2	May	1 beetle 2 grasshoppers tail of lizard

Toramylly Shrikes

30 April 5 beetles
1 moth
1 grasshopper
1 grasshopper nymph

2 May 3 grasshoppers
1 moth

25 May 2 grasshoppers
1 beetle

White House Shrikes

30 April 12 grasshoppers
4 beetles
1 caterpillar
(8 of these were on the surveyed stretch of fence)

2 May 1 caterpillar
7 grasshoppers
2 grasshopper nymphs
1 spider

4 May 8 grasshoppers
1 grasshopper nymph
1 spider

13 May 1 old grasshopper
1 old grasshopper nymph
1 new grasshopper
1 old grasshopper

15 May 5 new grasshopper nymphs

19 May 8 new grasshoppers
3 new grasshopper nymphs
2 new crickets
3 new beetles

20 May 5 old grasshoppers
1 old grasshopper nymph
1 old cricket
3 old beetles
1 new grasshopper nymph
1 new beetle

21 May 4 old grasshoppers
3 old grasshopper nymphs
3 old beetles
4 new grasshoppers
3 new grasshopper nymphs

Meadow Shrikes

15 May
- 1 lizard
- 3 grasshoppers
- 1 cricket
- 1 caterpillar

24 May
- 3 lizards
- 2 snakes
- 1 frog
- 2 voles
- 5 grasshoppers
- 5 grasshopper nymphs
- 1 cricket
- 2 caterpillars
- 3 beetles
- 2 moths

25 May
- 3 lizards
- 3 snakes
- 1 frog
- 2 voles
- (invertebrates were not checked)

PREY CACHING IN THE HUNTING STRATEGY OF SMALL PREDATORS

by

TARJA MAARIT OKSANEN

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ABSTRACT

Some small carnivores store food in large quantities, in spite of the fact that their food spoils in nature. This caching behavior is explained considering their inferior position in the foraging guild. It is hypothesized that control of live prey by means of territorial defense is not feasible for animals whose resources are also utilized by bigger and more powerful carnivores, and that accumulation of fat for hibernation is not feasible for any pursuer-type carnivores. Hence, caching dead prey in well-hidden stores is the only remaining alternative and this behavior will be favored by natural selection if the climate is at all suitable for the preservation of cached prey.

This verbal hypothesis is translated into a formal model and preliminarily tested by data from literature concerning caching of prey. A detailed test was performed by comparing the behavior of loggerhead shrikes and American kestrels in the Flint Hills of Kansas. Territorial behavior was observed to be much stronger in kestrels than in shrikes. Shrikes perched lower than kestrels in areas where both species co-occurred but not so when shrikes were alone. Introduction of a kestrel model caused significant lowering in the perching heights of shrikes. Shrikes stored food during all parts of the study period. Food caches made by kestrels were found only in early spring and contained just a single prey item at a time. The prediction that the smaller member of the guild is less territorial and more inclined to caching was corroborated.