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SURPLUS KILLING IN THE HUNTING STRATEGY OF SMALL PREDATORS

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Studies on the impact of vertebrate predators on a prey population are often based on estimates of the numbers of predators and prey (e.g., Pearson 1966, 1971; Goszczynski 1977; Phelan and Robertson 1978; King 1980; Erlinge et al. 1983). This approach includes assumptions about the functional response of predators, that is, about the changes in hunting effort for different prey species and about the factors that determine the handling time (Holling 1965). Changes in the preference for different prey species, often called switching, have an important effect on the functional response curve, especially at relatively low prey densities (Greenwood and Elton 1979). The lower part of the functional response curve also will probably be influenced by transit time (Murdoch 1977; Oaten 1977) and by the costs of activity (Abrams 1982). The upper part of the functional response curve is largely determined by handling time, that is, the time between the capture and the resumption of searching behavior (Holling 1965).

The extent of switching can be estimated by using scat analysis (e.g., Day 1968; Phelan and Robertson 1978; Tapper 1979; Erlinge 1981), and weight loss of predators can be used for estimating inadequate feeding rates. Handling time could be estimated readily if all predators were characterized by rigid hunting behavior in which a prey is attacked when seen within a fixed attack radius and consumed before the predator starts to search for new prey items. If, however, predatory behavior is more flexible, handling time becomes more difficult to estimate. Such flexibility may be created, for example, by selective feeding and consequently decreased consumption per prey with increased prey density (Mysterud 1980; Stenseth 1981; Abrams 1982). It is also possible for predators to kill prey without immediately consuming them (Nyholm 1961; Kruuk 1972; Curio 1976; Mysterud 1980; Elgmork 1982). Such behavior substantially shortens the handling sequence by eliminating the time used for feeding activities. This can make the functional response curve nearly linear or only slightly convex at even high prey densities. Consequently, the numerical predator-to-prey ratio advocated by Pearson (1966, 1971) might not reflect the intensity of predation, and estimates of predation based on identifiable prey remains found from predator scats could be far too low.

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Killing without immediate consumption hardly can be a significant factor in predator-prey dynamics if such behavior is only based on malfunctions in a normally adaptive behavioral mechanism (see Kruuk 1972). In the cases discussed by Kruuk, circumstances were unusually unfavorable for the escape behavior of the prey and virtually no searching effort was required for making the additional kills. We are instead focusing on the eventual existence of surplus hunting in which the normal searching behavior of a predator is activated even if the amount of prey already captured is sufficient to satisfy the immediate energy needs of the predator and its dependent young. Such hunting activities have costs (risks of injury and secondary predation, reduction of the time available for other activities) and it appears implausible that such surplus hunting would persist if the advantages of that behavior did not outweigh the costs. Below, we will develop a hypothesis on this cost-gain balance and discuss some data related to predictions derived from this hypothesis.

SURPLUS HUNTING AS A STRATEGY TO UTILIZE UNPREDICTABLE OR INDEFENSIBLE RESOURCES

The Rationale

When the energy balance of a predator and its dependent young is negative, each gram of prey consumed will make a substantial contribution to the fitness of the predator. When the threat of starvation is removed and zero energy balance is ensured, additional food can be consumed for growth and fat accumulation. These processes, however, have their physiological limits, and even the option of selective feeding cannot contribute much to the fitness of a predator whose food already contains the balanced mixture of nutrients needed for building up and maintaining its body (Stenseth 1981). We therefore must expect that when the amount of prey captured during a given activity period increases sufficiently, the value of consuming the next prey item captured approaches zero.

The optimal behavior in a situation in which the immediate value of a captured prey item is close to zero must depend on the reliability of live prey as a resource, which, in turn, is affected by the predator's position on the generalist-specialist axis. The ability of a generalist to use many types of resources, often including carrion and high-quality vegetable food, implies structural compromises which will probably lower the pursuit efficiency and make the costs of capturing live prey sensitive to environmental variation. When conditions become favorable for the escape strategy of a prey type, costs of capture should rise drastically, making the net energy value of a live prey low (possibly negative). Consequently, the predator should have little to lose and much to gain from surplus killing and prey caching when the costs of making a kill are at their lowest.

For a specialist adapted to hunt one prey type under varying environmental conditions, the costs of making a kill once prey are located should be more constant and the expected hunting success will probably be more directly related to the abundance of the preferred prey type. Consequently, the contribution of surplus killing to the fitness of a specialist appears ambiguous: surplus killing can transfer resources from times of plenty to times of shortage, but such behavior can also contribute to create the shortage, as pointed out by Kruuk (1972). Therefore, we expect that the net impact is influenced by the predictability of future access to live prey. This, we suppose, will be most influenced by defensibility of the prey resource.

When evaluating the defensibility of a specialist's resource basis, it appears useful to consider the asymmetry in competition between predators of different sizes. The upper limit of a predator's food spectrum is determined by the problems involved in killing a large prey, whereas the main problems with a small prey are the probable existence of refuges inaccessible to the predator and the low yield per prey killed as compared with the costs of searching and capturing. Consequently, there is more reason to expect changes in the lower limit of acceptable prey sizes than in the upper limit, since increased abundance of prey lowers the costs of searching but does not affect the problems of killing a prey. Thus, we can expect the potential food niches of predators to be (and they are often shown to be) nested so that the food of a smaller predator is also potential food for a larger one (see Erlinge et al. 1983). Now, a small predator cannot prevent an aggressively superior larger predator from entering the territory and capturing live prey, whereas hidden food caches are relatively well protected from potential invaders. We thus hypothesize that the relative advantages of surplus hunting are largest for the smallest members of predator guilds. In the following fitness-set model the consequences of this asymmetry for the adaptive value of surplus killing are analyzed more rigorously.

The Model

Consider a predator which has already captured so many prey items that the immediate food value of the next prey would not exceed the costs of capture. To minimize the energy expenditure and risks of secondary predation, the predator could then cease to be active. This response, however, would also leave the prey supply undefended so that competing predators could enter the territory at low risk. Such invasions must be expected if the home range has higher prey density than its surroundings. Thus, passiveness during the ''leisure time'' obtained when the immediate energy needs are satisfied is only a way of minimizing costs. Passiveness does not help the predator improve its future prospects of finding food.

Alternatively, the predator may remain active after satisfying its immediate food needs and divide its leisure time between hunting and other activities. In order to obtain robust conclusions, we will consider two extreme cases. In the first, we assume that the other activities are such that the allocation of time between hunting and these unspecified activities is neutral from the standpoint of territorial defense. The allocation of time should thus only influence the predator's own impact on its prey supply and this impact should be directly proportional to the time used for hunting. The expected future prey density should then be a linearly increasing function of the time used for other activities, and the slope of the line should depend on the degree to which the predator controls its prey supply (zero if prey dynamics are not affected by predation). In the second case, we assume that the likelihood of detecting competitors during the hunting time is negligible and that the other activities are strictly territorial, performed by moving along the perimeter of a circular territory frequently enough to detect intruders. The length of the perimeter traveled with sufficient frequency should be proportional to the time used for territorial activities, and the area of a circle is proportional to the square of its perimeter. This consideration suggests that the amount of prey protected against conspecifics and aggressively inferior competitors should increase with the square of the time invested in territorial defense. We are inclined to regard this latter case as more realistic, but similar conclusions can follow from both assumptions.

Since we are studying how the allocation of time between surplus hunting and other activities influences the future availability of resources, it is preferable to use a formulation which yields both extreme and intermediate assumptions when appropriate parameter values are chosen. Let M be the (minimum) future live-prey density to be expected if all available time is allocated to hunting; a (≥ 0), the effect on the prey of the predator's refraining from hunting; b (≥ 0), the additional positive impact on the prey supply caused by strictly territorial activities; and t ($0 \leq t \leq 1$), the fraction of available time not used for hunting. The expected prey density (N) after a fixed time period then should obey the equation

$$N = M + at + bt^z \tag{1}$$

where $1 \leq z \leq 2$. The former extreme assumption is obtained by setting $b = 0$; the latter by setting $b > 0$ and $z = 2$. For elongate territories (which are common for some predators, see Erlinge 1974, 1977), $1 < z < 2$, and for one-dimensional territories, $z = 1$. Situations in which a change of behavior from hunting to strictly territorial activities only slightly improves the efficiency in fending off competitors can be represented by giving a small but positive value for b.

If a fraction t of the available time is used for other activities, the fraction available for surplus hunting will be $1 - t$. The amount of cached food (C, to be measured in obtainable calories) after a fixed time period should be proportional to the time used for surplus hunting, which yields the equation

$$C = c\,(1 - t) \tag{2}$$

where c represents the favorability of the circumstances for acquiring and retaining food caches.

The parameters a, b, c, and M will be affected by many factors, but in evaluating the relative advantages of alternative activities, we should concentrate on factors which do not have a similar impact on the value of both equations (e.g., prey density, which increases both C and N, is thus relatively uninteresting in the present context). The parameters a and b reflect the defensibility of live prey, which should be highest for the largest specialist predator. The main resources of such predators should be inaccessible to most other predators, because of the problems of handling large prey; also, the largest predator can fend off or even kill its eventual competitors. The converse should hold for the smallest predator of the area. Whenever the resources of the smallest predator are abundant, they should be attractive to almost all the other predator species and an attempt to fight against the larger competitors should be both futile and dangerous. Medium-sized predators should have intermediate values of a and b so that these parameters are positively correlated to this aggressive rank order of predator in its guild. The parameter c in equation (2) should not show a similarly increasing relation to the rank order. Instead, c should be sensitive to the prevailing weather conditions. If the killed prey freezes or dries quickly, its caloric value is retained in the long run (although freezing causes an initial loss of net caloric value), whereas cached prey decays rapidly in humid and warm weather.

To decide what kind of behavior is optimal under different circumstances, we start by constructing a relative graph on which the expected future amount of live prey (N) is graphed against the allocation of leisure time and the position in the guild. (Because the position in the guild is a discrete variable, this 3-dimensional graph can be presented in 2 dimensions.) On this graph we can superimpose another graph on which the amount of cached prey (C) is presented as a function of time allocation (fig. 1). Figure 1*a* corresponds to the alternative $b = 0$, that is, the change of behavior from hunting to other activities is neutral from the standpoint of territorial defense. Figure 1*b* corresponds to the alternative $b > 0$ and $z = 2$; that is, hunting and defense are mutually exclusive activities, and territory shape is circular. Since both N and C are functions of the same argument (t) and represent resources which can contribute to the fitness of the predator, the information incorporated in figure 1 can be reconstructed in the form of fitness sets (see Levins 1968) in which N is graphed against C (fig. 2 for cool or dry conditions, fig. 3 for warm and humid conditions). The fitness sets in figures 2*a* and 3*a* that are derived from figure 1*a* are straight, and the fitness sets in figures 2*b* and 3*b* that are derived from figure 1*b* are concave. This implies also that fitness sets conforming to intermediate assumptions must be nonconvex.

In a fitness set, the optimal solution can be found only after the adaptive function has been deduced. (The adaptive function is usually presented in the form of lines of equal fitness; see Levins 1968.) In the present case, the fitness components (N and C) are two types of food which are interchangeable in the sense that a predator can satisfy its energy needs with either fresh or cached prey. Consequently, the adaptive functions should be straight lines, the inclination of which depends on the relative value of the two resource types, providing that the costs of making a kill remain constant. We have argued in the preceding section that these costs should be normally rather constant for a specialist predator, but that this should not apply under extremely stressful weather conditions when exposure to the weather is already a major cost. When such conditions are possible, the adaptive function must incorporate a cost factor for insufficient "buffer caches" required for a positive energy balance under adverse weather conditions. This cost factor should approach zero when caches become large enough to last for the longest periods of adverse weather that can be expected.

The above consideration suggests that the adaptive function has the form represented by the equation

$$W = C + \alpha N - \beta e^{-\gamma C} - K \tag{3}$$

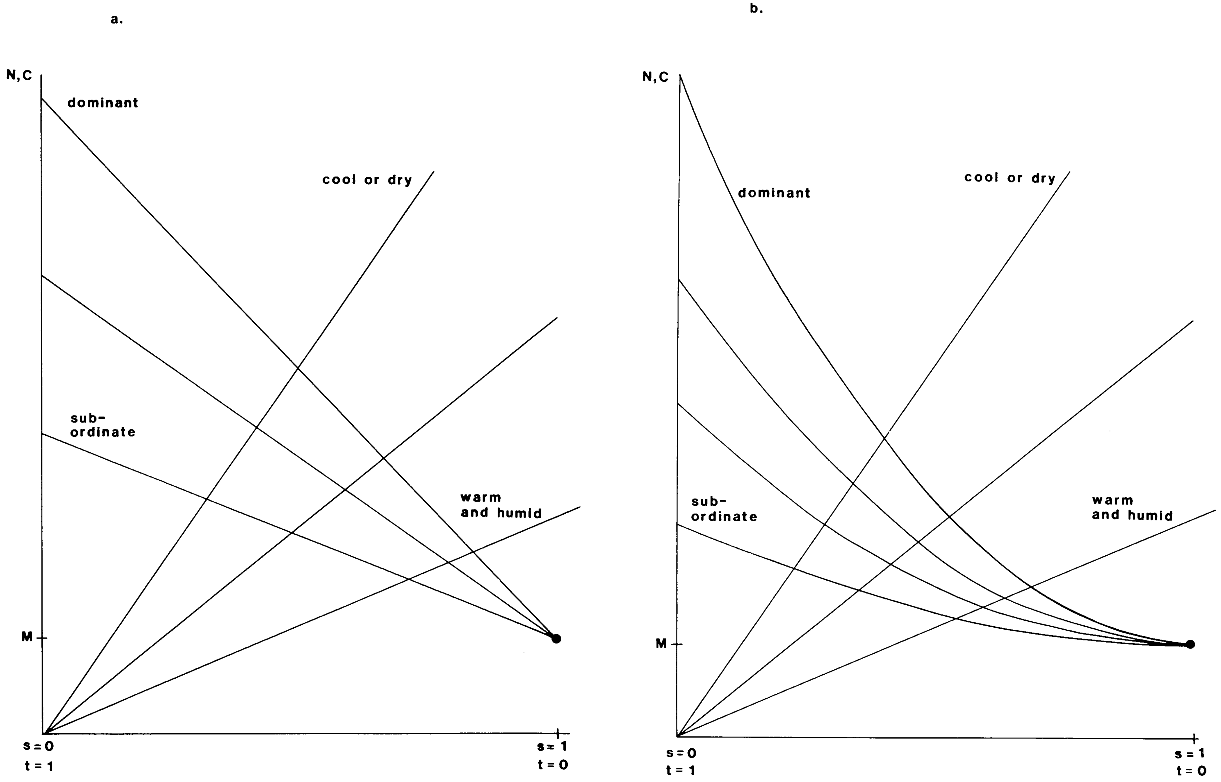

FIG. 1.—Amount of cached prey (C, ascending lines) and expected amount of live resources (N, descending curves) as functions of time allocation between surplus killing ($s = 1 - t$) and other activities (t). Different positions in the guild and climates with different retention of cached prey are simultaneously represented in the figure (M = minimum expected density of live prey). *a*, Detection of intruders is assumed to be equally probable during hunting and other activities. *b*, No detection of intruders while hunting, "other activities" consist of active defense of a circular territory.

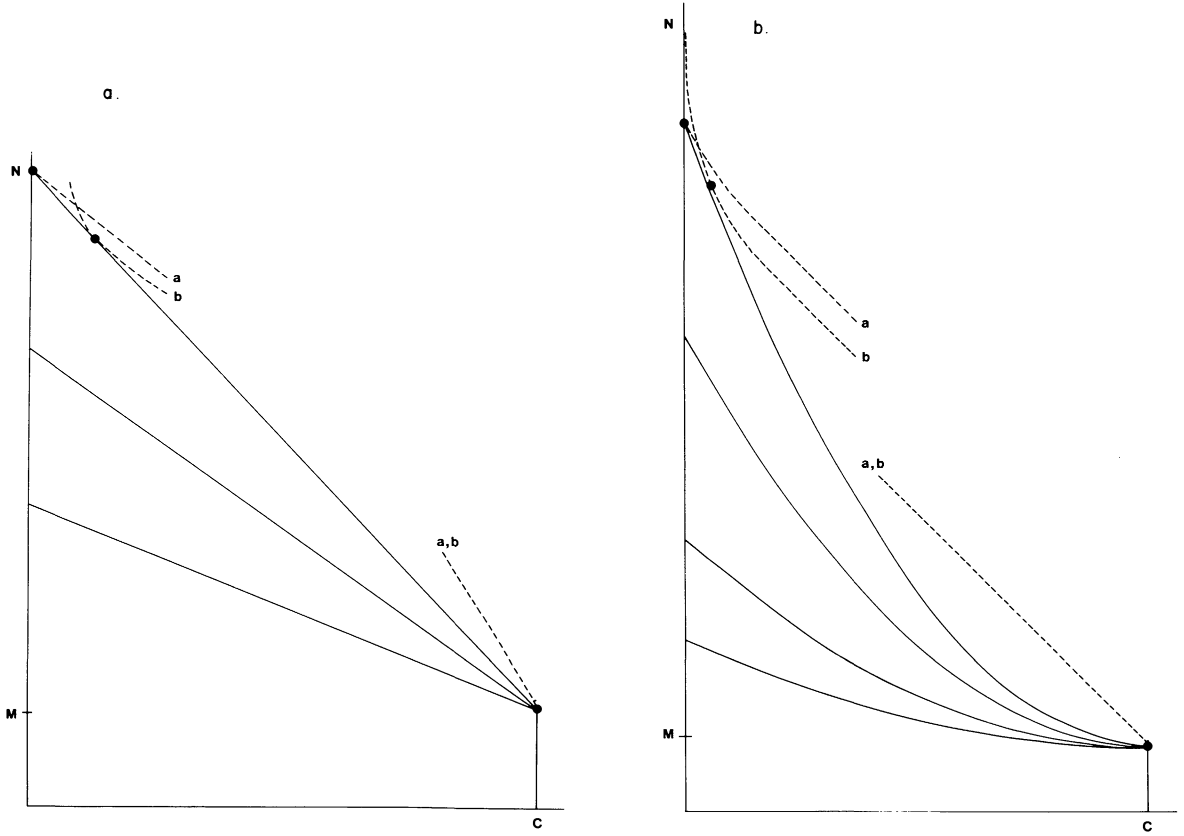

FIG. 2.—Fitness sets depicting expected amount of live prey (*N*) against amount of cached prey (*C*) for the aggressively dominant predator (uppermost solid line) and for the subsequent members of the guild (successively lower solid lines). Adaptive functions (dashed lines) are presented separately for situations in which buffer caches for periods of adverse weather are relatively unimportant (*a*) and for cases in which the importance of buffer caches is substantial (*b*). For each fitness set and adaptive function, the optimum strategy (outermost adaptive function touched by the fitness set) is marked by a dot. *a*, Fitness set derived from fig. 1*a*; *b*, fitness set derived from fig. 1*b*.

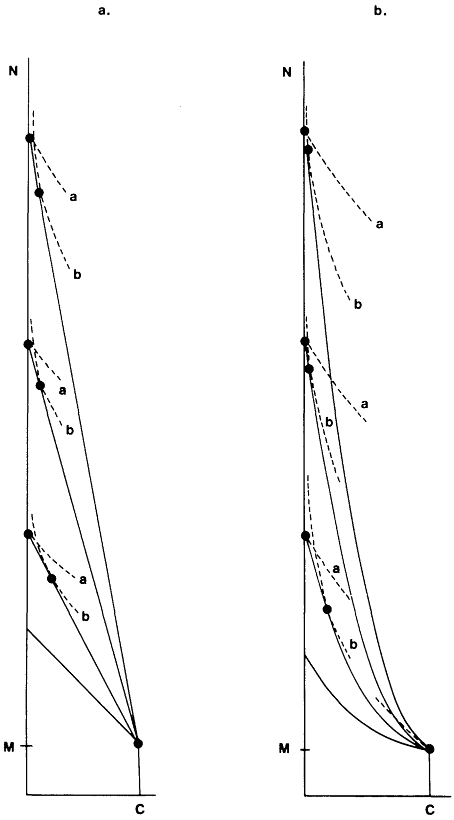

FIG. 3.—Fitness sets comparable with fig. 2 for predators in a warm and humid area. Symbols as in fig. 2.

where α represents the value of live prey in relation to a caloric equivalent of cached food and β represents the costs of having no "buffer caches" for times of adverse weather. (Because of the high per-gram metabolism of small predators, β should be negatively correlated to body size; see Iversen 1972.) γ represents the expected length of periods with adverse weather, and K represents the basic costs of activity.

When the fitness sets are combined with the adaptive functions thus obtained, three types of optimal solutions are found. The aggressively dominant members of each guild should prefer to retain their prey alive, although some surplus killing can occur as a precaution against adverse weather (figs. 2, 3, uppermost fitness sets). The smallest, aggressively inferior members of the guilds should use their leisure time for surplus hunting if the gain exceeds the costs of activity, that is, if $c - K > 0$ (see eqs. 2, 3 and figs. 2, 3). The point in the predator guild at which unlimited surplus killing becomes optimal should lie higher in the aggressive rank order of the guild if the area is cool and dry, and thus favorable for the retention of cached meat (fig. 2), than if the area is warm and humid (fig. 3). The choice between the two extreme cases (figs. 2*a*, 3*a* and 2*b*, 3*b*) has little influence on predictions, which suggests that the model is robust.

Notice that the model does not imply that food caches resulting from surplus killing are always used. Caches can be mainly wasted in that only a small fraction of cached food actually contributes to the fitness of the predator. The implications of our model nevertheless differ from the proposition that surplus killing is a malfunction of the behavioral mechanism of predators (Kruuk 1972). We suggest that the possibly small advantage of the behavior exceeds its short- and long-term costs, so that a tendency for surplus hunting has positive selective value for aggressively inferior predators. When a period of low prey density starts, the presence of food caches may become critical for survival, and the onset of such periods is difficult to anticipate. The wastage of cached food during periods of sustained high prey densities should be considered with this in mind.

Like all optimization models, our model presumes that the animals are actually adapted to the prevailing situation. This restricts the applicability of our model to situations that are typical for a given population. Predators should be adapted to predictable changes in guild structure and retention of cached prey, but a predator meeting aberrant conditions can be expected to behave in a way that is adaptive in the normal situation. When the fitness of a predator is strongly affected by factors other than the supply of resources, the relevance of the present model is also limited. For example, males of a polygynous species meet situations in which exclusive access to females is crucial to fitness. During the reproductive season, our model thus should be only adequate for females, whereas the optimal hunting behavior of potentially polygynous males cannot be predicted without considering the eventual conflict between hunting and female control.

Within the limitations discussed above, our model can be extended to embrace generalist predators as well. For them, the fitness sets become flatter, because their diverse resource base decreases the impact of surplus killing on the expected density of live prey. The adaptive functions would be steeper and more curved than in figures 2 and 3 because of the higher costs of capturing live prey and the greater sensitivity of hunting success to environmental conditions (see "The Rationale," above). Consequently, the optimum for a generalist would almost inevitably lie in the lower right corner of the fitness set, corresponding to the use of all leisure time for surplus hunting (or resting if $c - K < 0$). The fitness-set approach thus sustains the conclusion that surplus hunting and prey-caching should be an advantageous behavior for generalists living in cold or dry environments, regardless of the size of the predator.

RELATION TO EMPIRICAL EVIDENCE

Occurrence of Surplus Killing in Predator Guilds of Northern Europe

This model was inspired by Nyholm's (1961, 1972*a,b*) reports of food caches constructed by weasels (*Mustela nivalis rixosa*) and stoats (*Mustela erminea*), which are the smallest members of the mammalian predator guild in northern Europe. After deriving the model, we found still more impressive records of prey caches accumulated by stoats and weasels (Rubina 1960; Johnsen 1969). The tendency for surplus hunting in weasels and stoats has also been shown experimentally by Erlinge, Bergsten, et al. (1974) and Erlinge, Jonsson, et al. (1974; see also Oksanen and Oksanen 1981).

The studies of Goszczynski (1977) and Erlinge et al. (1983) suggest that weasels and stoats living in the northernmost parts of the temperate zone are subjected to intense competition by mammalian and avian predators. Also, in truly boreal areas the number of predator species utilizing the same resources as weasels and stoats is high, at least during periods of high prey density when the question of time division between surplus hunting and territorial activities is relevant (Källander 1964; Enemar et al. 1965; Ulfstrand 1965; Pulliainen 1980; Korpimäki 1981; Nilsson 1981; Mikkola 1983; Angelstam et al. 1985).

Territoriality in small mustelid populations of northwestern Europe appears to be restricted to reproductive competition between males. In dense populations, such territorial interactions may become intense (Lockie 1966), but Erlinge (1974) found that the territory system breaks down when food becomes scarce. In a woodland population, subject to persistent food shortage, King (1975) found virtually no evidence of territoriality among weasels. Moreover, the data of Erlinge (1974, 1977) suggest that the home ranges of female stoats and weasels are so spread out that contacts between females should be rare. In arena tests, female stoats avoided each other and became inactive after having watched each other for a while (Erlinge 1977). The behavior of small mustelids in northwestern Europe thus seems to correspond to the implications of our model, that a tendency to surplus hunting is associated with a competitively inferior position and the absence of food-related territoriality.

To further test our model, we reviewed available evidence on the occurrence of food-caching in predator guilds in boreal Fennoscandia. We only accepted records which clearly referred to active caching of entire prey items because storing the leftovers of a single prey does not indicate surplus hunting. As a reference area, we chose the Oulanka National Park, Finland, which lies in the middle of the boreal zone. The list of resident mammalian predators, breeding owls, and raptors is based on Siivonen (1975) and von Haartman et al. (1963); borderline cases were checked from Sulkava and Helle (1983) and Helle et al. (1983). To simplify the interpretation, species using aquatic prey were excluded. Predators were divided into three guilds: carnivorous mammals, diurnal raptors (including predaceous passerines), and owls. Each guild was arranged on the basis of body weight. The importance of size in the interspecific dominance hierarchy was checked with information on natural enemies of each predator. This information and records of food-caching were obtained mainly from von Haartman et al. (1963), van den Brink (1967), Siivonen (1972), Pulliainen (1974), Newton (1979), and Mikkola (1983). Additional information was found from Nyholm (1961), Haglund (1966), MacDonald (1976), Pulliainen (1980), Rijnsdorp et al. (1981), and Elgmork (1982).

The result of this literature survey, summarized in table 1, supports the existence of a dominance hierarchy based on body size, and corroborates our predictions. Copious prey-caching and/or direct evidence of pronounced surplus killing were reported for the smallest specialists and for all generalists with low pursuit

TABLE 1

Guilds of Terrestrial Predators of Fennoscandian Central Taiga, Arranged According to Body Weight

Species	Type	Caching	Recorded Natural Enemies
A. Carnivorous Mammals			
Ursus arctos	G	+	
Canis lupus	S	−	
Gulo gulo	G	+	8
Lynx lynx	S	−	8
Vulpes vulpes	G	+	8, 13, 4, 6
Martes martes	S	+	19, 1, 16, 16
Mustela erminea	S	+	14, 4, 1, 10, 6, 16, 17, 5, 12
Mustela nivalis	S	+	19, 14, 15, 1, 10, 6, 16, 17, 5, 12
B. Diurnal Raptors Including Predaceous Passerines			
Aquila chrysaetos	S/G	−	
Accipiter gentilis	S	−	6
Corvus corax	G	+	1*
Falco peregrinus	S	−	6
Buteo buteo	S/G	−	1, 6, 17
Circus cyaneus	S	−	6
Accipiter nisus	S	−	1, 6
Falco tinnunculus	S	−	1, 6
Falco columbarius	S	−	1, 6
Lanius excubitor	S	+	6*
C. Owls			
Bubo bubo	S	−	
Strix nebulosa	S	−	4, 1
Strix uralensis	S	−	4, 1, 6
Asio flammeus	S	−	4, 1, 11, 7, 9, 6
Surnia ulula	S	−	4, 1, 11, 6, 17
Aegolius funereus	S	−	14, 4, 1, 11, 2, 6, 16, 17, 18
Glaucidium passerinum	S	+	14, 1, 2, 6, 16, 3

Note.—On the basis of natural history information, the predators are divided into three types: specialists (S, species with high pursuit efficiency for some prey category); generalists (G, species with a broad spectrum of prey, but always low pursuit efficiency); and intermediate predators (S/G). Plus sign (+) refers to unambiguous records of large-scale prey caching, indicating a pronounced tendency to surplus hunting. Information on pronounced food-caching was also found for weakly predaceous passerines which could have been included in table 1*B*: *Corvus corone*, *Pica pica*, *Perisoreus infaustus*, *Garrulus glandarius*. Species of recorded natural enemies: 1, *Accipiter gentilis*; 2, *Accipiter nisus*; 3, *Aegolius funereus*; 4, *Aquila chrysaetos*; 5, *Asio flammeus*; 6, *Bubo bubo*; 7, *Buteo buteo*; 8, *Canis lupus*; 9, *Circus cyaneus*; 10, *Corvus corax*; 11, *Falco peregrinus*; 12, *Glaucidium passerinum*; 13, *Lynx lynx*; 14, *Martes martes*; 15, *Mustela erminea*; 16, *Strix nebulosa*; 17, *Strix uralensis*; 18, *Surnia ulula*; 19, *Vulpes vulpes*.

* The number of natural enemies is underestimated because the species is not included in taxonomically organized raptor literature.

efficiency. The situation thus suggests that the tendency for copious surplus killing and prey-caching is not a peculiarity of the genus *Mustela*, but a common feature of generalists and small specialists inhabiting the central taiga of Fennoscandia.

We also found some evidence which suggests that copious prey-caching is less prevalent in warmer areas. Mikkola (1983) does not describe the smallest owl of the Mediterranean region, *Otus scops*, as caching prey, and the caching habit appears to be weakly developed or absent in two more-southern shrike species, *Lanius minor* and *L. senator* (Ulrich 1971; Lefranc 1978). The relevance of these rather anecdotal comparisons is somewhat weakened by the fact that southern Europe has a relatively dry climate. Thus, it cannot be stated that the climate of the area would be very hostile for the retention of cached food. A corresponding absence of caching records, however, is also characteristic for the predator guilds of the warm and humid areas in the southeastern United States, according to Bent (1937, 1938, 1946, 1950) and Cahalane (1947). The only species of the area for which indications of pronounced prey-caching were noted (*Ursus americanus*, *Mustela frenata*, and *Lanius ludovicianus*) have their range centers in considerably more northern or continental areas.

The Case of the American Kestrel and the Loggerhead Shrike

The information reviewed above can be regarded as a relatively weak test. Thus, the correspondence between predictions and data only amounts to a modest increase in the plausibility of our hypothesis. We have not refuted the alternative explanation that surplus hunting and prey caching is only a means for a small predator to buffer itself against the occurrence of adverse weather conditions, as proposed by Hagen (1960). Since the idea of buffer caches implies that surplus hunting only occurs to a limited extent and under certain weather conditions, a distinction between our proposal and the hypothesis of Hagen is essential for finding out the relevance of surplus hunting to the functional response of predators.

A critical test is most readily performed in a guild in which even the aggressively dominant constituents are small (hence, the need for buffer stores is similar for all predators) and in which the predators can be observed in action. The breeding diurnal raptors of the Flint Hills prairie near Manhattan, Kansas, conform to these criteria. In our study performed in spring 1981 (a detailed report is provided by T. Oksanen et al., in prep.), we found the following numbers of home ranges or territories from our study area of ca. 50 km^2: *Buteo jamaicensis*, 1; *Falco sparverius*, 16; *Lanius ludovicianus*, 7. In spite of the very small body size of the American kestrel (about 100 g; Brown and Amadon 1968), its breeding population thus seems to have few larger avian competitors in this prairie area. (In winter, the number of larger raptors is much higher.) Conversely, loggerhead shrikes (about 50 g; Craig et al. 1979) coexist with an abundant larger competitor, the kestrel. The assumed aggressive dominance of the kestrel was substantiated by the following observations. (1) Shrikes arrived later and settled on the periphery of kestrel territories. (2) In areas frequently visited by kestrels, shrikes used perches much lower than those in areas where kestrels were not seen. (3) Even in areas of the latter type, high perches were not used when a kestrel mount was installed in the center of the home range. (4) We observed direct avoidance and distraction reactions to the kestrel mount and a real kestrel.

As predicted by our model, the interspecific difference in the aggressive rank order was reflected in a different level of aggressiveness and territoriality within the species. The diffuse home ranges of shrikes contrasted with the clear-cut kestrel territories which only overlapped in their margins (details will be presented by T. Oksanen et al., in prep.). Of the 82.3 min that kestrels belonging to different pairs were seen within a distance of 100 m, we observed overt aggression during 75.7 min. Both sexes actively participated in the disputes. For shrikes, corresponding coexistence was observed during 71.0 min, whereas overt aggression was seen only during 2.5 min. (The figure for observed coexistence in shrikes is a minimum estimate, because positive identification of coexistence required simultaneous location of three individuals or observation of display or aggression.)

To obtain quantitative data on prey-caching we surveyed suitable caching places: cracks in fence posts, holes in trees, and grass clumps in places inside those kestrel territories where the location of the nest was known to us, and thorny bushes and barbed wire in places where shrikes were seen during March, April, and May 1981. All prey items which were not impaled were assumed to have been cached by kestrels. Such prey items were only found in small numbers in March (fig. 4, Appendix) and we observed the same prey item only once during two surveys. Most prey items observed in the caching sites of kestrels were relatively fresh vertebrates. Conversely, impaled prey items were found all the time when shrikes were present. Both fresh and partially decayed prey items were found, which suggests varying retrieval rates. Fifteen vertebrates and numerous invertebrates were found impaled (fig. 4, Appendix). There was no tendency for the amount of impaled food to decline when the risk of late blizzards and cold, rainy periods was over in May. The picture is somewhat complicated by the fact that one of our shrikes disappeared after May 2 and we therefore extended the study area northward. However, the last caching record of the missing shrike (no. 1 in the Appendix) was rather similar to the first caching record of the new pair (no. 7 in the Appendix), so that the increase in cache levels at the onset of summer could not be attributed to the change in shrike home ranges under survey.

It is indeed possible that the caching sites of kestrels are less conspicuous than those of the shrikes, thus biasing our data. Even those caching sites of kestrels where prey were found in March were empty later, suggesting that the observed decline in caching activity was in fact real. Moreover, during 2080 kestrel min of observations, we never saw any prey-caching performed, whereas caching behavior was observed in 1830 min of shrike observations. It seems reasonable to conclude, therefore, that prey-caching by breeding kestrels in the Flint Hills prairies was modest in extent and restricted to early spring, when the risks of adverse weather were considerable. Corresponding behavior in loggerhead shrikes was much more persistent (fig. 4, Appendix).

In agreement with the above interpretation of our data, the most impressive published information on prey-caching in the American kestrel (Tordoff 1955; Stendell and Waian 1968; Nunn et al. 1976; Collopy 1977) refers to winter conditions, when the invasion of raptors breeding at higher latitudes is likely to create a different guild structure than in the case reported here. In winter also the risk of adverse weather is considerable. Balgooyen's (1976) observations seem comparable to ours: caching occurred in the spring, and caches (which were estimated to correspond to food needs of 2–3.5 days) were retrieved in a few days.

For the loggerhead shrike, the published reports on caching behavior are rather conflicting. Very low retrieval rates are reported by Bent (1950) and Craig (1978),

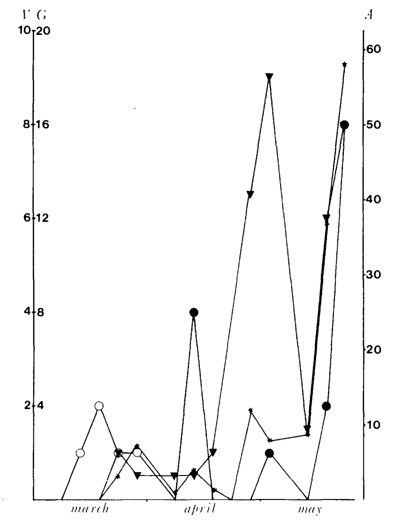

FIG. 4.—Numbers of prey cached by kestrels (open circles) and shrikes (solid symbols) in the regularly checked areas during different 5-day periods of spring 1981. Vertebrates, open and solid circles (scale *V*); grasshopper imagos, triangles (scale *G*); other arthropods, stars (scale *A*). If the same place was checked twice during the same 5-day period, the lower count was ignored.

leading to the conclusion that caching is largely a waste of potential food (but see Watson's [1910] observation of retrieval of very old prey items). On the other hand, retrieval has sometimes been observed to occur so rapidly that impaling is considered to be a way of handling the prey (Miller 1931) or dividing the labor between the sexes (Applegate 1977), rather than a form of genuine food-storing. Both types of observations are understandable, however, if shrikes cache in accordance with their prey situation and retrieve in accordance with their food needs, as we have predicted for a predator in an aggressively inferior position. We do not claim that surplus killing and prey-caching would necessarily have a great impact on the fitness of these predators; such behavior is just predicted to be the best use of what we have called leisure time, the time available when the immediate food needs of the predator and its dependent young are satisfied. If the density of the prey population is not high, leisure time should not exist and accumulation of prey caches should not occur.

CONCLUSIONS AND SUMMARY

Our model is based on the assumption that surplus hunting is an activity with substantial immediate costs, and future costs, in the form of its impact on the density of live prey. Compared to propositions in which predation is regarded as a minor factor in the dynamics of the prey population (see, e.g., Krebs and Myers 1974), our assumptions are maximally negative for the evolution of surplus hunting. In spite of our conservative starting point, our model predicts that a tendency to participate in surplus hunting under periods of high prey density is evolutionarily plausible for the smallest members of predator guilds (and for generalists) in cool or dry environments. We arrive at this prediction by assuming that surplus hunting and territoriality are mutually exclusive activities and that these activities are perfectly compatible with each other. Thus, the prediction appears to be robust. A review of records related to surplus killing among predators in the taiga zone of Fennoscandia corroborates this prediction. The results of a case study with breeding American kestrels and loggerhead shrikes in the Flint Hills prairie, Kansas, supports the idea that an animal's rank order in the guild is more important than size per se.

The model does not provide a sufficient basis for constructing a functional response curve for any given small predator. Our main point is that in studies on small predators and their prey, time should be devoted to the construction of the functional response curve by means of experiments performed under as natural conditions as possible. Assumptions derived from a predatory schedule in which capture is always followed by consumption and digestion appear to be inaccurate for small predators under periods of high prey density, and using immediate energy needs as the basis for estimates of predation can be even more misleading.

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APPENDIX

PREY CACHES OF AMERICAN KESTRELS AND LOGGERHEAD SHRIKES OBSERVED ON THE FLINT HILLS PRAIRIE, KANSAS, DURING MARCH, APRIL, AND MAY 1981

Kestrel Pair No. 10
March 15: half of a snake
March 18: no records
March 19: 1 snake + half of another snake
March 21: hind parts of a deer mouse
March 29: 1 snake
April 9 and later: no records

Shrike No. 1
March 23: 2 grasshoppers
3 caterpillars
March 29: 1 grasshopper
7 caterpillars
April 12: 1 spider
1 caterpillar
April 15: 1 beetle
April 18: 2 grasshoppers
1 moth
April 19: 2 caterpillars

Shrike No. 1 (*continued*)
May 2: 1 beetle
2 grasshoppers
tail of a lizard

Shrike Pair No. 2
April 30: 5 beetles
1 moth
1 grasshopper
1 grasshopper nymph
May 2: 3 grasshoppers
1 moth
May 25: 2 grasshoppers
1 beetle

Shrike Pair No. 3
April 30: 12 grasshoppers
4 beetles
1 caterpillar

(*continued*)

APPENDIX (*Continued*)

Shrike Pair No. 3 (*continued*)
May 2: 1 caterpillar
7 grasshoppers
2 grasshopper nymphs
1 spider
May 4: 8 grasshoppers
1 grasshopper nymph
1 spider
May 13: 2 grasshoppers (old)
1 grasshopper nymph (old)
1 grasshopper (new)
May 15: 5 grasshopper nymphs (new)
May 19: 8 grasshoppers (new)
3 grasshopper nymphs (new)
2 crickets (new)
3 beetles (new)
May 20: 5 grasshoppers (old)
1 grasshopper nymph (old)
1 cricket (old)
3 beetles (old)
1 grasshopper nymph (new)
1 beetle (new)
May 21: 4 grasshoppers (old)
3 grasshopper nymphs (old)
3 beetles (old)
4 grasshoppers (new)
3 grasshopper nymphs (new)

Shrike Pair No. 4
April 6: 1 grasshopper
1 caterpillar
April 12: 1 deer mouse
3 snakes
1 grasshopper
2 caterpillars
May 2: 5 grasshoppers
1 beetle
1 Arctidae moth
May 14: 4 caterpillars
4 spiders

Shrike Pair No. 4 (*continued*)
May 19: 1 prairie vole
1 grasshopper
23 spiders
1 caterpillar
1 beetle
May 20: 1 grasshopper
1 grasshopper nymph
28 spiders
4 caterpillars
1 cricket
1 bumblebee

Shrike No. 5: nest or activity center not located

Shrike Pair No. 6: caching activity observed (flew away from the nest with a snake); caching place not found

Shrike Pair No. 7
May 15: 1 lizard
3 grasshoppers
1 cricket
1 caterpillar
May 24: 2 prairie voles
3 lizards
2 snakes
1 frog
5 grasshoppers
5 grasshopper nymphs
1 cricket
2 caterpillars
3 beetles
2 moths
May 25: 2 prairie voles
3 lizards
3 snakes
1 frog
(invertebrates were not checked)

NOTE.—The numbers for shrikes and kestrels refer to the territory or home-range map in T. Oksanen et al. (in prep.). For kestrel nos. 8 and 9, no prey caches were observed. "Old" and "new" in the cached prey items of shrike pair no. 3 refer to our attempt to study retrieval rates by marking impaled prey items. These particular prey items, impaled on barbed wire, appeared to be subject to robbing by other birds and do not give a reliable picture of retrieval rates. Barbed wire is a novelty in the habitat and the shrikes apparently have not yet adapted to the presence of "spines" which are very accessible to robbers.

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