Chapter 2. Modeling Subsistence Change in Southern New Zealand

Foraging theory consists of a set of models that assume that the choices foragers make maximize foraging efficiency using a currency, such as calories captured per unit foraging time, that is highly correlated with fitness (Stephens and Krebs 1986). In other words, in the long run, natural selection should favor foragers that maximize their rate of energy capture. In this chapter, I describe several foraging theory models that are used to generate predictions about subsistence change in response to declining populations of prey taxa. In particular, I examine the prey choice, patch choice, and central place foraging models which predict what resources foragers will choose to exploit, how foragers exploit resources across space and time, and how foraging from a central place can alter these expectations. I then describe how the predictions generated from these models can be tested archaeologically.

Prey Choice Model

The foraging decision analyzed by the prey choice model is whether a forager will pursue or ignore a prey item when encountered (Stephens and Krebs 1986). In this model, prey types are ranked based on the net energetic return they provide given the costs of capturing and processing them (post-encounter return rate). Resources are added to the diet according to rank by this measure, starting with the highest ranked resource. *Diet breadth*, or the range of resources taken, will expand, incorporating the next resource in the ranking, until it becomes inefficient to add lower ranked taxa. This point occurs when the return rate for the next ranked resource is less than the mean foraging return rate, or overall *foraging efficiency*, for the set of resources taken into the diet, including search time (Kaplan and Hill 1992). Incorporating a resource with a lower

return rate into the diet would lower the mean foraging return rate, decreasing foraging efficiency. In other words, it is more efficient to concentrate foraging effort on the higher ranked taxa than to pursue resources with return rates lower than the mean foraging return rate even when those lower ranked resources are encountered.

The number of resources incorporated into the diet will depend on the encounter rate with high-ranked prey (Stephens and Krebs 1986). The prey choice model predicts that high-ranked taxa will be pursued whenever they are encountered. Thus, when high-ranked prey are abundant, they should comprise a major part of the diet to the near exclusion of lower ranked prey items (Figure 2.1). Conversely, if high-ranked resources are rare, the diet should expand to include more low-ranked prey. Because the range of resources in the diet will depend on the abundance of high-ranked taxa, the prey choice model can be used to predict how diet will change when abundances of high-ranked taxa in the environment decline.

An important assumption of the model is that prey items are randomly distributed across the landscape so that the probability of encountering a prey type is constant (Stephens and Krebs 1986; Smith 1991). However, resources are often not distributed randomly across the environment, but instead tend to clump into spatially discrete areas. When the distribution of resources is patchy, the probability of encountering a prey type increases after an encounter rather than remains constant. In such cases, patches must be defined that create a spatial distribution of resources that is relatively homogeneous so that prey encounter within patches is random. The expectations of the prey choice model can then be assessed separately for each patch.

Patch Choice Models

Patch choice models examine how foragers select the patches or environments they exploit and how much time they should allocate to each patch. There are two types of patch choice models. The patch use model examines how foragers select the patches in which they will search in a manner that is analogous to how prey are selected in the prey choice model (MacArthur and Pianka 1966). Patch types are ranked on the basis of the net returns that can be gained from within a patch. The number of patches that are exploited increases until the gains from adding a new lower-ranked patch are zero.

A major criticism of the patch use model is that it does not take into account resource depression, or the depletion of resources as a predator forages within a patch. The Marginal Value Theorem (MVT) was developed to deal with the problem of resource depression, and also addresses the issue of how long a forager should remain in a patch. The MVT assumes that depletion occurs and predicts that foragers should leave a patch when the net return rate for the patch drops below the average return rate for all exploited patches, taking into account the costs of moving between those patches (Charnov 1976). As foragers move from one patch to the next, they should leave behind a trail of patches that have been depleted to similar marginal return rates. Any patch with return rates less than the average return rate will not be exploited.

Figure 2.2 is a graphical representation of the Marginal Value Theorem. The x-axis represents time; the y-axis is energy gained. Curves A, B, and C represent the energetic gain function, or return rates, for each of three patches. The slope of line R is the average return rate for all patches exploited, including travel time. The distance between the origin and the point on the x axis where the gain curve is tangent to the average return rate marks the optimal time spent in the patch. Staying in the patch longer would cause the average return rate to decrease. Therefore, it would be more efficient to move on to a

different patch even when the cost of traveling to that patch is considered. Some patches are not exploited because the net energetic return rate is less than the average return rate. For example, line R is not tangent to the gains curve for patch C. The allocation time for the patch is zero and thus it is not exploited.

The Marginal Value Theorem is useful in understanding how foragers should react to changing prey abundances. The model assumes that resources are being depleted as a forager moves through a patch (Charnov 1976). The MVT was designed to address changing encounter rates within a single foraging bout. However, the model can be extended to longer time scales to predict how patches may be added as foraging efficiency declines.

If resource depression is lowering encounter rates during a single foraging bout, encounter rates may also be lowered between foraging bouts if sufficient regeneration time has not passed (Cannon 1999). A decline in encounter rates within a patch will result in a decrease in the gains curve for that patch. This, in turn, will lead to a decrease in the average return rate for the set of patches being exploited. Given this, we can predict that declines in the average return rate may lead to more intensive use of each patch and/or an increase in the number of patches used. Graphically, a decrease in the average return rate would be represented by a decrease in the slope of line R (Figure 2.3). In addition, the gain functions for patches A and B will also decrease because of depletion within these patches. In this example, the average return rate has declined to the point where exploitation of patch C has become profitable. Note also that the residence times for patches A and B have increased, and exploitation within these patches becomes more intensive with more time and effort expended to extract resources (Broughton 1999).

The decline in the encounter rates of prey resulting from the foraging behavior of predators is known as *resource depression*. Three types of resource depression have been proposed: exploitation, behavioral, and microhabitat depression (Charnov *et al*. 1976). Exploitation depression is the direct result of harvesting of prey that causes declines in population abundances. This type of depression is analogous to the concept of 'overexploitation' as presented in the archaeological literature (e.g., Anderson 1997; Kirch and Yen 1982). People exploit resources to the point where their foraging efforts deplete population abundances. Explanations such as the 'Pleistocene Overkill' hypothesis assume that this type of predation pressure is the cause for mass population declines and extinctions (Martin 1973, 1984; Mosimann and Martin 1975).

The other two types of resource depression differ from exploitation depression in that declining encounter rates result from a decrease in prey availability rather than prey abundance (Charnov *et al*. 1976). Behavioral depression is caused by changes in prey behavior, such as increased alertness, that reduces prey availability and thus encounter rates. With the third type of resource depression, microhabitat depression, prey availability declines because prey relocate to areas that are less likely to be impacted by predators.

Central Place Foraging

The models I have discussed above are relevant for foragers who consume their prey at the point of capture. However, in many situations, humans are better characterized as central place foragers, who forage from a 'home base' and return prey to that base before consumption (Cannon 1999). Expectations of the prey choice and patch choice models

must be modified for central place foraging because this kind of foraging entails a distinctive pattern of depletion and incurs additional travel costs.

In their model of central place foraging and resource depletion, Hamilton and Watt (1970) propose that resources are first depleted locally around the central place. Over time, the depleted zone will expand, radiating out to regions farther from the central place. The radius of depletion will depend on the population size. In general, larger populations will have a wider effect on their surroundings.

The increasing travel costs incurred as foragers travel farther from the central place will affect the kinds of prey that are deemed profitable to exploit because of increasing transport costs. There are several models that examine how distance to prey affects foraging decisions in a central place model. In Schoener's (1979) "encounter by distance model", foragers sit and wait in one location for prey to pass by. Size, specifically length, is used by the predator as an indication of a prey's net return rate. The larger the prey, the greater the returns. Schoener predicted that as distance traveled increases, the size range of the prey taken narrows to focus on mainly larger, more profitable prey as long as post-encounter pursuit costs are not changing.

Orians and Pearson (1979) have developed two central place foraging models that may be more appropriate for human foragers than either the prey or patch choice models: the single loader and multiple loader models. Their single loader model is similar to Schoener's model in that foragers are expected to take higher return items as distance increases, assuming they pursue and capture a maximum of one prey item per foraging bout. Their multiple loader model differs from the "encounter by distance" and single loader models in that foragers are capable of returning more than one item per foraging trip. Thus, how much a forager can carry and still forage effectively becomes an issue.

The multiple loader model predicts that given these constraints foragers will make choices that maximize returns per foraging trip.

Orians and Pearson (1979) also modify the MVT to model how distance affects patch choice and time allocation for a central place forager (Figure 2.4). The difference between their central foraging patch choice model and the MVT, as shown graphically, is that the net energetic gain function for each patch does not start at the origin of the graph Instead, the gain curves are plotted at a distance from the origin along the X axis, which represents the round trip travel time for the patch. In addition, the average return rate line is fixed through the origin. So, as distance to patches increase, the gain curve must be steeper (i.e., the patch must be more productive) for those distant patches to be included in the foraging round. Despite these differences, the Orians and Pearson model and the MVT both predict the same thing: as patches are depleted and the overall foraging efficiency declines, low-ranked patches may be added.

Predictions

These models as a group provide two sets of predictions concerning changes in subsistence resulting from resource depression. The first set, derived from the prey choice and patch choice models, specifies the kinds of changes in diet and foraging efficiency that will occur as populations of high-ranked resources are depleted. Over time, foraging will result in a decline in the encounter rates of prey. High-ranked prey are particularly susceptible to resource depression because they are always taken when encountered. As encounter rates with high-ranked resources decline, these taxa contribute less to the diet. As a result, the mean foraging return rate may drop to the

point where adding lower ranked taxa to the diet becomes profitable. With less focus on higher return prey, foraging efficiency should also decline.

If overall foraging efficiency declines, then the number of patches exploited may increase as well. As predicted by the marginal value theorem and the central place foraging patch choice model, the number of patches exploited will depend on the mean foraging return rate (Charnov 1976; Orians and Pearson 1979). Those patches with return rates less than the mean foraging return rate will not be exploited. However, if the mean foraging return rate decreases significantly as postulated in the first prediction, then patches that were previously unprofitable may now be added to the subsistence regime. Initially, the resources exploited in these lower-ranked patches will tend to be narrowly focused on higher ranked resources within those patches. As resource depression occurs in these newly added patches, foraging efficiency will decrease within the patch.

The second set of predictions examines changes in the use of individual prey items that result from declining overall foraging efficiency. This entails shifting the scale at which the patch choice models are applied. Instead of examining prey types within patches (Charnov 1976; Orians and Pearson 1979), individual prey items that have already been harvested are treated as patches (Broughton 1999). When the scale shifts from prey types to individual prey items, patch choice models examine how much time a forager spends extracting resources from large prey items before moving on to the next one. When the patch choice models are applied in this way, the assumption is that the prey captured must be large enough so that the animal must be processed to transport. For such large animals, as foraging efficiency declines, the proportion of each individual animal that is utilized is expected to change.

The expected changes will differ depending on whether transport costs are increasing significantly. If transport costs are not changing significantly over time, then the MVT predicts that as encounter rates of prey and overall foraging efficiency decline, the amount of time a forager spends extracting resources from a carcass should increase (Broughton 1994, 1999; Charnov 1976). Thus, foragers may exploit an increasing proportion of each individual animal.

The alternative situation occurs when resource abundances near the site decline to the point where foragers will need to go farther afield to obtain resources, which causes transport costs to increase (Hames and Vickers 1982; Hamilton and Watt 1970). Models of central place foraging predict that as transport costs increase due to increasing distance to prey, foragers will become more selective not only about what is pursued, but also about what portions of those prey items are returned to the central place. That is, they will tend to forage for larger, higher return items in order to maximize their returns per trip (Orians and Pearson 1979; Schoener 1979). When the scale at which the model is applied shifts so that individual prey items are treated as patches, then the exploitation of more distant areas within a patch may lead to a decrease in the proportion of each animal returned, focusing on the parts of the animal that provide higher return rates.

Measuring Predicted Changes in the Archaeological Record

The models and predictions described above were developed for use in ecological time in circumstances where foraging behavior and its outcomes are directly measurable. Because archaeologists do not study human behavior (or prey encounter rates, etc.) directly, but rather the remnants of the physical manifestations of that behavior, applying these models to archaeological situations requires modification (see Grayson and Cannon

1999 for a discussion of archaeological applications of foraging models). Below I

describe the means for testing these predictions archaeologically.

Archaeological Measures of Changing Diet and Patch Use

The first prediction I have made is that foraging efficiency *will* decline as high-ranked

resources are depleted. If the decline in foraging efficiency is sufficient, diet breadth *may*

also increase. These changes in diet breadth and foraging efficiency should be reflected

by a shift in the proportion of high and low-ranked resources in the diet (Broughton

1999). A diet that is broad and for which foraging efficiency is low will be comprised of

more lower ranked taxa than one that is narrow with high foraging efficiency. To test

this first prediction, I must examine changes in the relative abundance of high and low-

ranked resources. In addition, since it is likely that prey are distributed in a non-random

manner, resource patches must be defined and the predictions applied to each patch

separately.

As foraging efficiency within patches declines, overall foraging efficiency for all

patches is also expected to decline. If overall foraging efficiency drops significantly,

then lower-ranked patches will be begin to be exploited. To determine if patches are

being added to the subsistence round, the relative abundance of resources from each

patch can be measured. If patches are defined in terms of resources exclusively found

there, then additions of patches can be detected through the appearance of those defining

resources within the diet.

In addition, with resource depression and patch expansion, there should be a change

in resource use across patches. While the relative abundance of high-ranked resources

utilized within patches declines, the relative abundance of high-ranked resources from the

newly added patch should abruptly increase with its initial use. Thus, the proportion of high-ranked patch-specific taxa should measure this shift in patch use as foraging efficiency declines (Broughton 1999).

To determine the proportions of high to low-ranked resources, prey must first be ranked. In ecological or ethnographic studies, prey ranks are determined directly by measuring return rates and handling costs (costs of capture and processing prey) using a currency such as kilocalories per hour (e.g., O'Connell *et al*. 1988; Smith, 1991). However, because these variables cannot be measured in the archaeological record, a proxy measure must be used to rank resources. A number of studies suggest that body size provides a valid estimate of prey rank (e.g., Hames and Vickers 1982; Hawkes *et al*. 1982; Hill *et al*. 1987; Schmitt and Lupo 1995). The relationship between body size and prey rank appears to be curvilinear with a point of diminishing returns at very large body sizes (e.g., elephants, whales) due to the significant handling costs of these very large animals relative to their returns (Bayham 1979; Broughton 1994, 1999). Assuming body size is an appropriate proxy for prey rank, then diet breadth and foraging efficiency can be measured archaeologically by examining the relative abundance of large- and small-bodied resources.

While body size appears to provide a good estimate of prey rank, other variables may influence such ranks. For example, improvements in procurement technology can affect the ranking of prey by lowering handling costs (Alvard and Kaplan 1991; Hames and Vickers 1982; Smith 1981, 1991; Winterhalder 1981). With more efficient pursuit technology, in particular, the handling costs may decline enough so that the net returns, and thus the relative ranking, for a particular prey increases. If the prey's rank increases significantly, then it may be added to the diet. Some examples of such technological

improvements include the bow and arrow (Hughes 1998), nets (Broughton 1999), and guns (e.g., O'Connell and Marshall 1989; Smith 1991; Winterhalder 1981). Each of these technologies decreases handling costs by decreasing pursuit time and effort.

An important kind of technological innovation is the use of mass capture techniques. When prey are captured *en masse* instead of individually, the prey item is no longer the individual animal. Rather, the prey item becomes the group of individuals that are captured by the technique. Some examples of mass capture are the use of nets in rabbit drives (Steward 1938), buffalo jumps (Frison 1991), or netting of fish (Broughton 1999). If prey are taken through the use of mass capture techniques, then the returns per capture are expected to be much higher than predicted by the size of the individual animal (Grayson and Cannon 1999; Madsen and Schmitt 1998). Thus, the rank of mass captured prey needs to be adjusted accordingly. The role of technological change in determining prey ranks can be examined by studying artifact data and adjusting the ranks accordingly.

Archaeological Measures of Changing Prey Use

With the decline in high-ranked prey abundances, and thus, foraging efficiency, the pattern of prey exploitation may also change. Archaeologically, changing resource use may, in some cases, be measured by examining the skeletal part representation of large-bodied animals transported back to the site. Initial ethnoarchaeological studies on transport decisions showed that with increasing distance from a central place, human foragers may increase the degree to which large prey are processed in the field (Binford 1978). Recent research has shown that other factors such as the size of the carrying party, the method of transport, and processing time, can influence transport decisions (Bartram 1993; Bird and Bliege-Bird 1997; Metcalfe and Barlowe 1992; O'Connell *et al*.

1988, 1990; O'Connell and Marshall 1989). However, to understand how archaeological models of body part transport relate to patch choice models, it is useful to examine them in their simpler forms. A discussion of other variables that can influence transport decisions is presented later.

Simple models of transport decisions predict that the kind and number of skeletal elements transported back to a central place depend upon the net returns or 'utility' of those elements and the distance to the home base (Binford 1978). In general, the model assumes that foragers will process large animals in the field and discard parts of the carcass in order to create more transportable units (O'Connell *et al*. 1988, 1990), which reduces transport costs while maximizing net returns per load (Bettinger *et al*. 1997; Bird and Bliege-Bird 1997; Metcalfe and Barlowe 1988). Those elements that are transported will tend to be of higher return or utility. For vertebrates, utility is specified for skeletal elements in terms of meat, marrow, and grease (Binford 1978, 1981). Elements are ranked in terms of their utility, and decisions about body part transport are made based on this ranking.

This archaeological model of body part transport is analogous to the MVT or central place patch choice models. But rather than foraging within patches and choosing prey based on net returns, human predators are foraging across an individual carcass, selecting and transporting elements based on the net returns of each element (Bettinger 1991; Grayson 1989). The goal in both cases is to maximize net returns given the costs of returning to a central place.

Since the body part transport model is analogous to patch choice models, we can make similar predictions about the types of resources transported back to the central place. Transport decisions will vary depending on the transport distance involved, and

how that distance changes through time. These changes in transport decisions may be measured by examining the relative abundance of high and low utility elements.

When distance to prey is not changing significantly, then the MVT can be used to make predictions about changing use of prey large enough that field processing must take place. The MVT predicts that when resources, particularly high-ranked resources, are abundant in the environment, time spent within a patch, or foraging across a carcass, will be short, and only the higher return elements should be transported. In a more impoverished environment, time spent foraging across an individual animal will be longer and a broader range of low and high utility elements should be returned to the site. Thus, if distance is not changing significantly, there should be a broadening of the elements transported to the site as foraging efficiency declines.

In cases where distance to prey is increasing, the central place patch model is the more appropriate model to use (Orians and Pearson 1979). When local areas around the central place are being exploited and transport costs are low, a broad range of elements may be transported. As local resources are depleted and foragers are traveling farther to hunt, the range in the utility of the elements they transport back to the central place may constrict to include only higher utility elements.

While transport distance is a significant variable in decisions about body part transport, other variables such as body size, transport mechanisms, and processing time can also influence transport decisions (e.g., Bartram 1993; Metcalfe and Barlowe 1992; O'Connell *et al*. 1988, 1990). For example, research on Hadza butchering and transport patterns show that body size can influence transport decisions in a manner similar to that of distance (O'Connell *et al*. 1988). As the size of the prey increases, fewer elements are transported. Thus, a narrowing in the range of elements may be due to either to

increasing transport distance or increasing size of prey. To minimize the effects of body size on transport analyses, I will only examine changes in the use of single taxa or taxa of similar size.

Transport mechanisms can also affect transport decisions. With the advent of more efficient means of travel, such as horses, boats, or motorized vehicles, the transport costs of central place foraging may decline significantly (e.g., O'Connell and Marshall 1989; Smith 1991; Winterhalder, 1981). If the transport mechanism is so efficient that transport costs become negligible, then body transport decisions may appear to be more in line with predictions of the MVT rather than the central place patch choice model.

More troublesome, Bartram (1993) has shown that bone transport may correlate with the amount of time spent processing. The more time a forager spends processing a given animal, the less of that animal is transported. In the case of Bartram's study, gazelle (*Oryx gazella*) were processed to the point where mostly meat and very few elements were returned to the site. As a result, an archaeological analysis that focuses on skeletal element representation as an index of changing transport has an asymmetrical quality: a lack of change in skeletal element representation may not be meaningful, but patterned change likely will be.

In addition to using patch choice models to examine how individual prey items are being used, these models can be used to determine if element use is changing by treating individual skeletal elements as patches. Since distance is not a factor in this process, the MVT is the appropriate patch choice model to use. When skeletal elements are treated as patches, the prediction from the MVT is that with declining foraging efficiency, time allocation for each element may increase, i.e., each element may be used more intensively (Broughton 1999).

Intensive use of individual skeletal elements may be represented by activities such as the extraction of marrow or grease from bones, which requires that bones be broken to obtain these resources. If marrow and grease extraction increases over time, then there should be a corresponding increase in bone fragmentation. Fragmentation can be measured by comparing the number of bone fragments to the number of elements represented (Lyman 1984, 1994). If other natural taphonomic factors are controlled for, the ratio of the two measures should increase as fragmentation increases.

Summary

Despite the fact that foraging theory models were originally developed to explain observable behavior over relatively short time spans, these models can be and have been used to explain behavioral patterns observable only through the archaeological record. When the assumptions of the models are closely met, significant changes to a resource base (e.g., extinction events) have explicit, predictable consequences. Analysis of archaeological faunal remains provides an excellent opportunity to determine the degree to which human populations respond to these long-term changes.
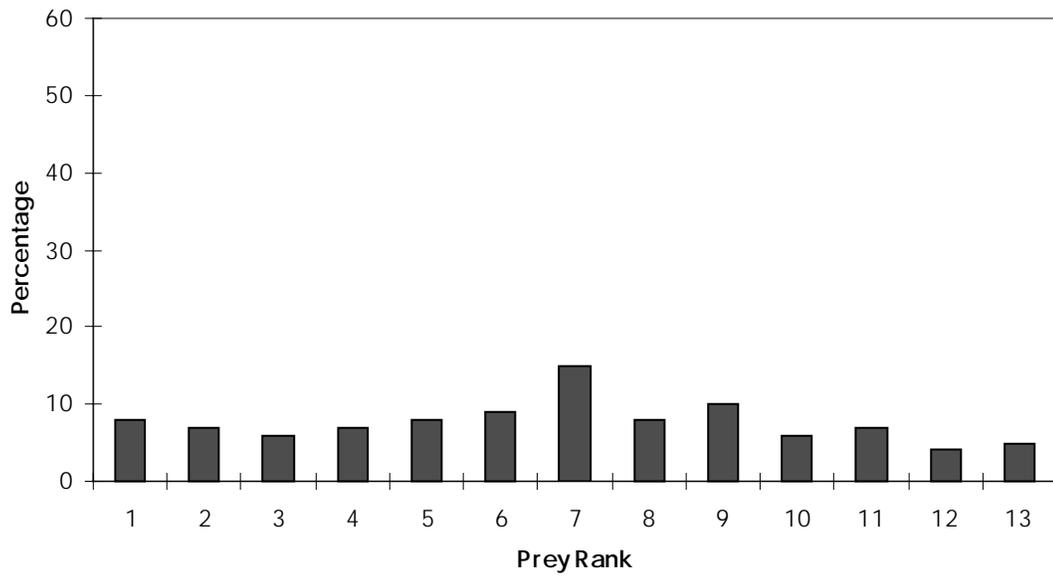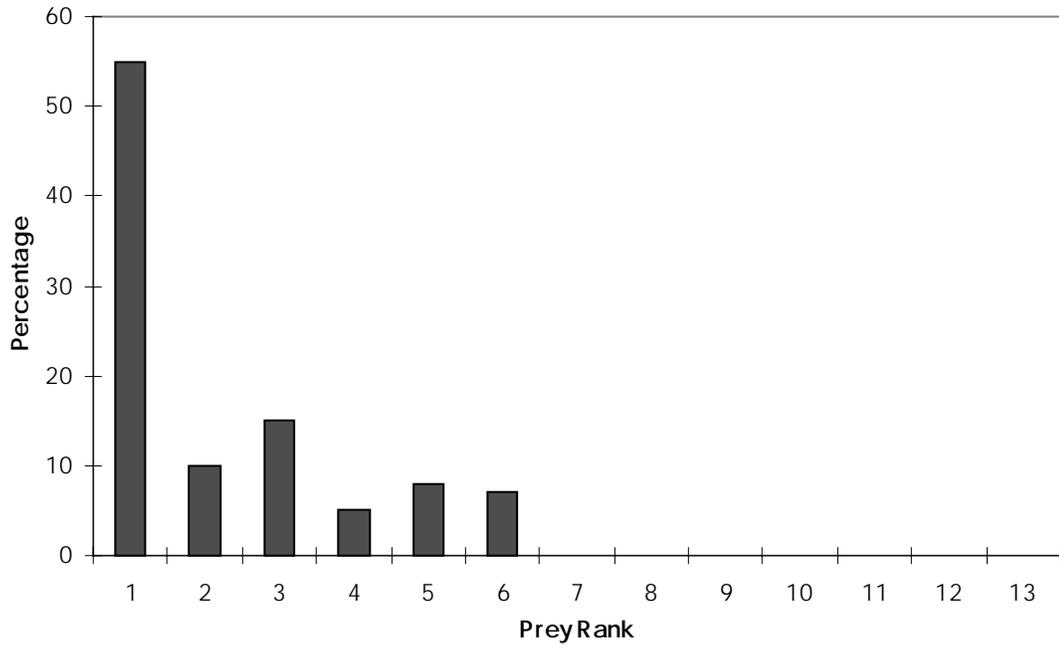
Figure 2.1. The effect of high ranked prey abundance on diet breadth.
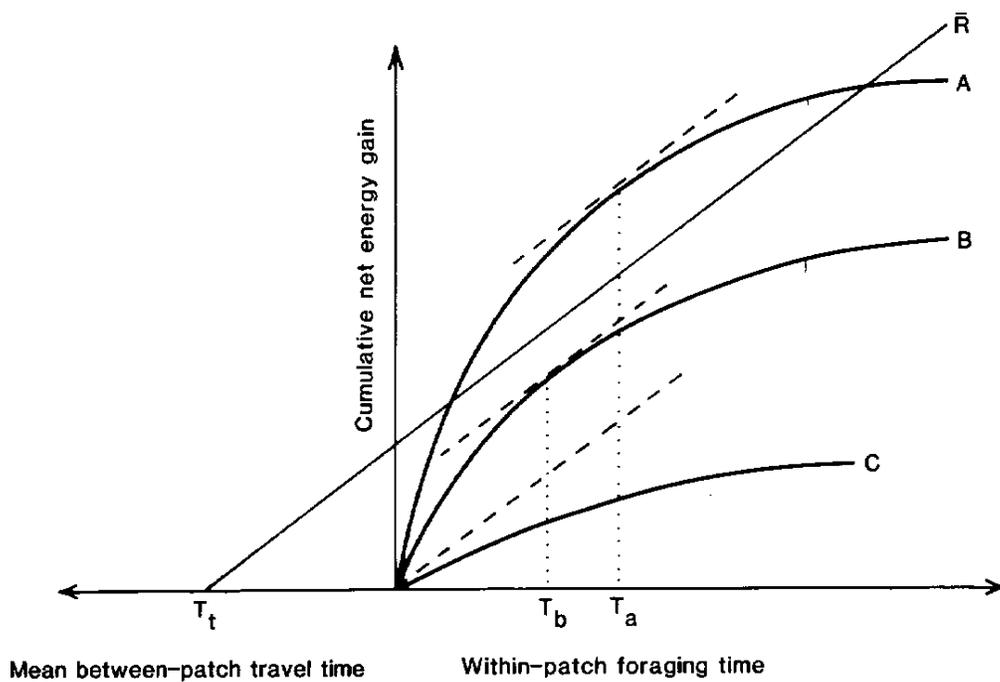
Figure 2.2. Graphical representation of the marginal value theorem (from Smith 1991, after Charnov 1976).
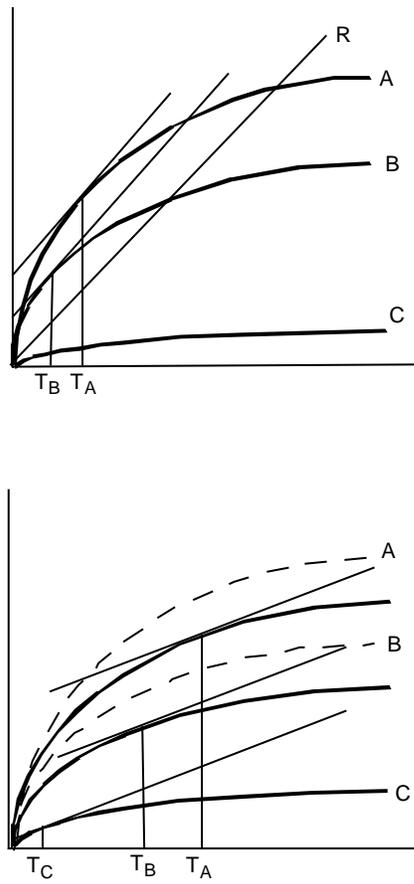
Figure 2.3. The effects of changes in the patch return rates (Curves A, B, C) and average return rates (lines tangent to the curves) on patch choice and time allocation.
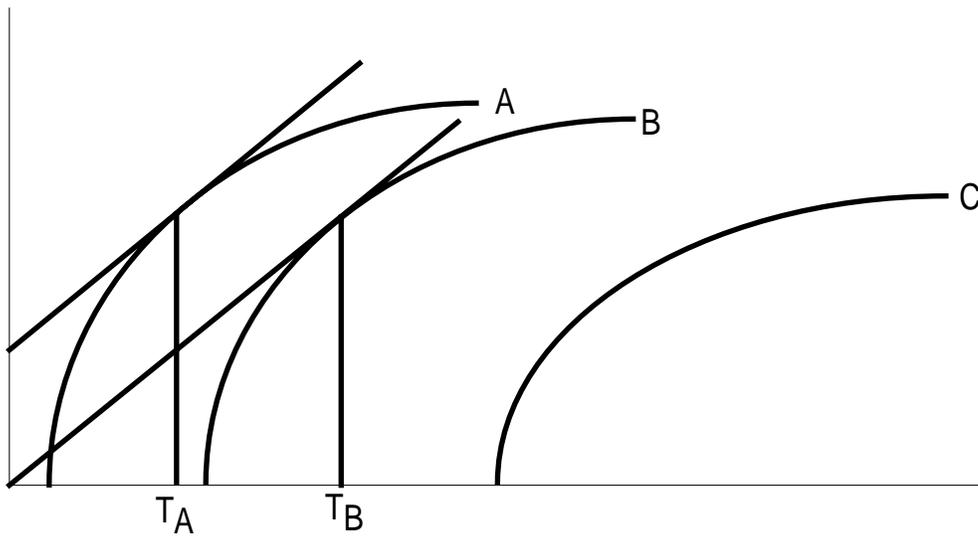
Figure 2.4. Patch choice model with distance for central place foraging (after Orians and Pearson 1979).