

PALEOLITHIC UNGULATE HUNTING: SIMULATION AND MATHEMATICAL  
MODELING FOR ARCHAEOLOGICAL INFERENCE AND EXPLANATION

by

Joseph Edward Beaver

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SIGNED: Joseph Edward Beaver

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## ABSTRACT

Formal models, those which explicitly specify the postulates on which they are based, the development of their 'predictions' from those postulates, and the boundary conditions under which they apply, have the potential to be useful tools in archaeological inference and explanation. Detailed examination of one such model, the mathematical model commonly referred to as the diet breadth or prey choice model, shows that its archaeological application is severely complicated by two factors that are difficult or impossible to specify for prehistoric cases: 1) limits on the amount of meat consumable by a food-sharing group before spoilage or loss to scavengers and 2) hunting failure rates. The former introduce significant uncertainties into the food yield or energetic return term of resource rankings, while the latter affect both resource rankings and the resource encounter rates leading to prey inclusion or exclusion from the diet. Together, these factors make rigorous diet breadth / prey choice model-based inferences from ungulate archaeofaunas impractical, especially in Paleolithic cases. Following success in recent years in making diet breadth model-based inferences about Paleolithic demography from small game analyses that involved computer simulation modeling of prey species' resilience to hunting pressure, the development and employment of a similar model applied to ungulate species reveals that, in general, the differences in the ability of populations of different ungulate species to sustain harvest rates are not sufficient to allow the relative representation of ungulate remains in archaeological sites to be a viable basis for human demographic inferences. However, in cases where ungulate remains allow the determination of both prey age structure and sex ratio, it is possible to distinguish low exploitation rates, high exploitation rates, and overhunting. In some cases, the sex ratio data may also alter relative hunting resilience levels in such a way that it may be possible to infer that one species was capable of supporting a larger human population than another.

## CHAPTER 1

### INTRODUCTION

The epistemology of archaeology may be the most complicated in the sciences. Like historical geology and paleontology, archaeology studies a dynamic past through observation of a more-or-less static present. Like astronomy, it studies its inaccessible subject matter through the by-products thereof. Like sociology, socio-cultural anthropology, and political science, it studies the often intractably complex interactions of human beings. Like all of these disciplines, it is both an intensive and an extensive discipline; that is, it seeks both to discover principles and to elucidate countless unique cases. Unlike each of these other disciplines, however, archaeology must contend with all of these difficulties simultaneously. The archaeologist is faced with uniquely difficult problems. It is therefore unsurprising that a substantial literature has been produced concerning how archaeological reasoning does, can, or should proceed (e.g., Binford 1968a; Clarke 1978; Fritz and Plog 1970; Salmon 1975; Schiffer 1976, 1988; Smith 1977; Spaulding 1968; Watson 1976; Pinsky and Wylie 1989). It is perhaps equally unsurprising that this literature is often contentious and contradictory, describing, prescribing, and even proscribing a variety of approaches to archaeological reasoning.

This dissertation discusses the use of two types of formal models, static mathematical models and computer simulation models, as tools in archaeological reasoning. The specific context of this discussion is the ecological relationship between humans and ungulates during the Paleolithic, with particular reference to the Mediterranean Basin and some adjacent areas. Through scavenging, hunting, and domestication, interaction with ungulates has been an important aspect of the both the physical and social environments of hominin evolution for several million years. For example, competition with carnivores

for portions of scavenged ungulates or for ungulate prey appears to have been an important factor in hominin food acquisition behavior (e.g., Brantingham 1998; Stiner 2002), and sharing of the large food packages represented by ungulates seems likely to have been significant to the evolution of human sociality (e.g., Kuhn and Sarther 2000).

A detailed consideration of the diet breadth / prey choice model (a mathematical model of optimal foraging behavior developed in biology) and its archaeological application—particularly with reference to hominin demography—provides the stimulus for the core research of this study. Variability in and uncertainty about the sizes of hominin food-sharing groups and their food-preservation abilities—and thus of the amount of animal biomass they could consume before loss or spoilage—are shown to seriously complicate diet breadth / prey choice model inferences from Paleolithic ungulate archaeofaunas. Variability in and uncertainty about the ungulate-hunting efficiency of Paleolithic hominins are identified as being similarly problematic. Expanding on the small game simulation research of Stiner et al. (1999, 2000), which had substantial success in making hominin-demographic inferences from archaeofaunal data, a computer simulation model of the effects of human hunting on ungulate prey populations is developed as a potential means of overcoming these difficulties. The simulation model enables examination of both the potential and limitations of archaeofaunal ungulate species representation and age structure in making inferences about hominin population growth and hominin behavior in the Paleolithic.

### **Archaeological Inference and Formal Models**

Archaeological inference is the process of determining, broadly speaking, what happened in the past from the archaeological record as revealed by survey, excavation, laboratory analysis, and so forth. In the terminology of Schiffer (1972, 1976), inferences

are statements describing “systemic context” based on “archaeological context” data. In discussing archaeological inference, it is useful to construct, for heuristic purposes only, a simple hierarchical categorization. *Primary inference* consists of low-level determinations, such as ‘These pieces of flint were modified by people’, ‘These animal bones were brought to this location by humans, not hyenas’ or ‘This charred seed is 10,000 years old’. It should be noted that the low-level nature of the inference does not imply that it is easy to make. Rather, the inference is low-level because it is a straightforward description of some event(s) in the past, without assignment of any significant social or cultural interpretation. *Secondary inferences* require (at least implicit) reference to prior primary inferences, and consist of determinations of more abstract attributes of the past, such as social organization, resource pressure, decision-making, etc. Secondary inference is perhaps best described as applying to the sorts of things that have to be inferred even with extant people (i.e., things that ethnographers, sociologists, etc. cannot directly observe and therefore must *infer*). Secondary inferences can also be considered to include reconstructions of long-term developments (e.g., state formation, domestication, population growth).

In order to see where and how simulation and mathematical models can fit into the process of archaeological inference, a consideration of argument structures is worthwhile. Philosopher C.S. Peirce (Misak 1991:91-92; cf. Walton 1996:256-257) distinguished three types of arguments on structural grounds: *deduction*, *induction*, and *abduction*. Deductive arguments proceed from a rule and a case to a result, whereas inductive arguments proceed from a result and a case to a rule, and abductive arguments proceed from an observed result and a rule to a case. Consider, for example, the following arguments:

- 1) Objects of different weights accelerate at the same rate when dropped (RULE).



Two objects have different weights (CASE). Therefore, when the objects are dropped, they are observed to hit the ground at the same time (RESULT). This is deduction. If the rule is true and the case is accurately described, the result is guaranteed to occur.

2) Two objects have different weights (CASE). When dropped, the two objects are observed to hit the ground at the same time (RESULT). Therefore, objects of different weights accelerate at the same rate when dropped (RULE). This is induction. The truth of the rule is not guaranteed by the accurate description of the case and the result; rather, it is a broad generalization that may be accepted after further testing (see below).

3) Two objects dropped at the same time are observed to hit the ground at the same time (RESULT). Objects of different weights accelerate at the same rate when dropped (RULE). Therefore, the two objects have different weights (CASE). This is abduction. If the result is accurate and the rule is true, the case is guaranteed to be possible; however, a different true rule might lead to a different conclusion about the case. For example, if the rule were 'Objects of the same weight accelerate at the same rate when dropped', the abducted case would be 'the two objects have the same weight'. Both rules can be true (and in this example, assuming that air resistance is ignored, *are* true); thus, both cases can be possible.

Philosophers of science as well as practicing scientists have at times attempted to force all scientific reasoning to fit deductive logic (Couvalis 1997). The attraction is understandable (see Smith 1977 on its attraction for archaeologists), since proper deductive arguments are, by definition, valid. Much of science is, of course, inductive, and the problem of how inductively-achieved conclusions can be considered true has been a major focus of philosophy and especially philosophy of science from Hume to Mill to Popper. Archaeological inference, however, appears to be neither deductive nor inductive, but *abductive*. More specifically, archaeological inference follows an argument

type—referred to by Aristotle as ‘argument from sign’ (cf. Walton 1996:227)—that is a subset of abduction. Though it is often treated as a fallacy (‘affirming the consequent’, which is indeed fallacious if presented as *deduction*), argument from sign is a very normal mode of inference. In argument from sign, an observation that is considered to be associated with some unobserved object or event or state is taken to indicate the presence, possibly in the past, of that unobserved case. For example, water on the ground in the morning is taken as evidence of rain overnight, and a certain pattern of indentations in the ground is taken as evidence that a dog has passed by. The parallel to archaeological inference is obvious. For example, Schiffer’s *correlates* “relate behavioral variables to variables of material objects or spatial relations” (Schiffer 1976:13) and “function in inference justification by allowing the derivation or identification of some aspects of an operating cultural system from knowledge of those aspects, spatial and material, which would be or are present in the archaeological record” (Schiffer 1976:14). Correlates clearly play the role of rules in an abductive, argument from sign, structure.

Abductive arguments in and of themselves are arguments of possibility and plausibility only. Recognition of this problem is evident in archaeological discussions of the problem of equifinality, the situation where different cases (situations or events in the past) might have produced the same observed archaeological result. Clearly, archaeologists intend to do more than simply argue that certain things *may* have occurred in the past, but the necessarily abductive structure of archaeological inference works against this desire. A standard solution is the ‘multiple lines of evidence’ approach. Where independent arguments from sign have the same conclusion, the probability increases that the conclusion is not only possible, but is also likely. Useful as this approach is, its applicability varies. In many archaeological cases, very few potential lines of evidence are available, and it is often the case that only one can yield even a very broad inferential rule

on a given topic. This difficulty is especially apparent in research on the Paleolithic, for which data types are more limited than in many later periods and preservation is often poorer. Narrowing inferential rules, specifically through the process of computer simulation modeling, is explored here as an alternative solution.

### *Inferential Rules and Simulation Modeling*

If the rule in an abductive argument has the form ‘*only* X produces Y’, instead of ‘X produces Y’, then the abductive argument is logically valid. Thus, archaeological inferences are more secure if the specificity of the sign is higher. Cordell (1994:151-152) notes that archaeologists are much more likely to accept arguments that depend on the physical sciences than on the social sciences, a situation that is to be expected since the nature of the data and the ability to conduct repeated experiments has allowed the physical sciences to produce far more narrow associative rules than appears practical in the social sciences. While it may be possible to construct inferential rules of the form ‘only X produces Y’ for some primary inferences (e.g., Lyman 1994; Schiffer 1987), closed inferential rules like this are particularly unlikely to be feasible for secondary inferences, given the complexity of human behavior. It is possible, however, to narrow inferential rules in many cases, thereby increasing the likelihood of a true inference. Furthermore, narrower inferential rules are especially useful to an approach integrating multiple lines of evidence.

Models are simplifications of reality, abstract representations that involve only those variables that are considered relevant to the behavior of the real system under certain boundary conditions. Not all models, especially in archaeology, define the included variables or boundary conditions explicitly. This may be considered the distinction between formal models, which are explicit, and informal models, which are not.

This dissertation focuses on the use of two types of formal models: simulation models and pure mathematical models. Where the behavior of the real system at a given time is dependent on its specific history of events, it is often difficult or impossible to create an analytically tractable model<sup>1</sup> of that system. In such cases, a dynamic model that simulates the relevant behavior of the system by repeatedly carrying out simple operations, here referred to as a simulation model, can often be constructed instead. Simulation models are most appropriate where the relationships between individual pairs of variables are simple, but the emergent system-level behaviors are not readily encapsulated by such variables.

While simulation modeling can be used for a variety of purposes, for example as an intermediate step in hypothesis testing (e.g., Thomas 1972), the form of simulation modeling considered in this dissertation can be categorized as exploratory simulation modeling. The idea behind exploratory simulation modeling is to take well-understood processes that can be easily abstracted and combine them, producing a dynamic model whose behavior can be examined under a wide variety of variable states.

Exploratory simulation modeling can thus play a role in archaeological research similar to that of experimental archaeology. Given certain assumptions (boundary conditions), experiments can increase the specificity of archaeological signs, not only by excluding some potential precursors but also by narrowing the characteristics of the sign associated with a given precursor. Exploratory simulation modeling allows (within appropriate boundary condition assumptions) the extension of experimental archaeology to long-term, dynamic, and stochastic systems.

In this dissertation, simulation modeling is used to help strengthen archaeological inferences about ecological relationships between humans and ungulate prey. The most readily available evidence of the ecological relationships between Paleolithic humans and

ungulate prey is the particular species that are represented in faunal assemblages and the relative abundances of their remains. The feasibility of certain secondary inferences from such data is refined here through the construction of a simulation model of ungulate populations under human hunting pressure. This allows exploration of the impact of different levels and types of hunting pressure on ungulate population size and survival, which in turn affects the sorts of archaeological data which can be regarded as signs of human population levels and hunting strategies. Another useful and frequently available type of data regarding ungulate exploitation by human hunters in the past is the ages at which animals were killed. The simulation model is thus also used to explore the circumstances under which certain types of prey-assemblage age structure are produced, refining the inferential potential of such age-structure patterns.

### **Archaeological Explanation**

The nature of and proper approach to archaeological explanation are not subjects on which archaeologists are in substantial agreement (e.g., Renfrew 1973 and chapters therein; Renfrew et al. 1982 and chapters therein). Common sense, however, makes it clear that an explanation provides an answer to a question of ‘How?’ or ‘Why?’ Furthermore, it is reasonable to view explanations as statements (or series of statements) intended “to take something unfamiliar to [the target of the explanation] and make it make sense...by relating it to something [that is] familiar” (Walton 1996:30). The distinction between inference and explanation (as made in this study), therefore, is that archaeological inferences are claims about the past, while archaeological explanations are attempts to make sense of archaeological data. The distinction may be subtle, but it is argued here to be important. One aspect of this distinction is that inferences can only go so far in explaining the archaeological record; the limitations of archaeological data and the logical

structure of inference (as discussed above) prevent many relationships that are critical to archaeological explanations from being inferred. A second aspect of the distinction between inferences and explanations is that conflicting inferential claims are more problematic than conflicting explanations. For example, an inference that an archaeological site was produced by a year-round occupation and an inference that the site was produced by a summer-only occupation cannot both be true. However, an explanation attributing the year-round nature of the occupation to territorial circumscription and one that attributes it to environmental amelioration could both be correct, though one might well have singled out the more important factor.

As was considered the case above for archaeological inference, a heuristic hierarchical categorization is useful for archaeological explanations. The most basic explanations, here termed *trivial explanations*, are provided by primary inferences. Clearly, statements like those given earlier as examples of primary inferences can sometimes serve to explain concentrations of funny-shaped rocks or piles of bones in the ground. But these explanations only ‘make sense of’ the archaeological record in a fairly inconsequential way. Secondary inferences are more explanatory, and are considered here to constitute *partial explanations*. The inference provides a plausible account of the observed characteristics of the archaeological record. It is only a partial explanation, however, because as explanations even secondary inferences are question-begging. While any inference can be met with the question, “Why?”, in the case of primary inferences/trivial explanations, the answer to this question—when not itself trivial—is often in the form of a secondary inference/partial explanation. Secondary inferences, in contrast, are only partial explanations because something beyond inferences themselves is required to answer (even provisionally) the response “Why?” As put by Trigger (1989:377), “however useful correlations between material culture and human behaviour may be for infer-

ring such behaviour from the archaeological record, these correlations only indicate what happened in the past; they do not provide explanations of why events happened.” Unless and until archaeologists develop methods of inferring causal relationships, truly explanatory accounts in archaeology must go beyond inference.

It is always possible to greet a proffered explanation with a question demanding to know why some component of the explanation is the case; there is thus no natural limit to the number of levels of explanation that could be defined. For practical purposes, however, it can be noted that once beyond the range of inference, any ranking of explanations would be based more on paradigmatic preferences than on inherent characteristics of the explanations. All such explanations are thus lumped together here. This final level in the heuristic hierarchy of archaeological explanations includes (but is not necessarily limited to) *synthetic explanations*, which make sense of secondary inferences (and/or primary inferences and observations of the archaeological record itself) by noting connections between or among inferences and providing reasoning by which this conjunction fits together, and *presumptive explanations*, which differ only in having an uninferred or unferrable, but reasonably presumed, ‘factual’ component. The reasoning that provides links among inferences (and possibly direct observations) can take many forms. Mathematical models and the results of simulation models are only two possible options.

### **Boundary Condition Assumptions**

One of the major epistemological problems in archaeology alluded to at the beginning of this chapter is that the process of reconstructing behaviors, organizational structures, or events and the process of reconstructing the *reasons* for such behaviors, structures, or events are often in conflict (a related point is discussed by Trigger 1989:390-391). Allowing ‘behavior’ to temporarily subsume a whole range of character-

istics of past human societies for simplicity of discussion, the conflict is between the inference of behaviors and the identification of the cultural, social, or biological factors that led to those behaviors.

To illustrate both the distinction being made, and the way in which the two goals conflict, the following example is offered. In the analysis of burial data, generally accepted (indeed often unconsciously assumed) principles are used to associate characteristics of burials (such as grave goods) with social structure (e.g., Binford 1971; but see Carr 1995 for a critical review). Differential representation of grave goods is used to reconstruct differences in social status, occupation, and so forth, based on the assumption that the social group that produced the cemetery being analyzed engaged in status- or role-related differential burial practices. If archaeologists are interested in determining not the social character of the society being investigated, but rather the bases of their cultural behavior, then the inferential process would be reversed: the presence of differences among burials would be seen as evidence that the society had cultural ‘rules’ associating burial practices with social (or other) distinctions. Carrying out both inferential processes simultaneously is logically circular. The difficulty may be more clear if the absence of differences among burials is considered. Does such a case indicate the lack of social differentiation or the lack of cultural ‘rules’ that transfer such differentiation to burial practices? In order to conclude that either option is correct, it is necessary to *assume* that the other is not. To use another example—one more relevant to this dissertation—it is logically impossible to evaluate whether or not Neanderthal hunting practices were in accord with the diet breadth / prey choice model (see chapter 2) while simultaneously using this same model to answer questions about relative population densities in the Middle and Upper Paleolithic.

Ethnoarchaeology and ethnographic analogy do not offer solutions to this prob-



lem. What these types of research do in this context is push the question back one level: instead of asking if the prehistoric people in question did X in situation Y, the question becomes whether the prehistoric people in question were like the ethnoarchaeologically or ethnographically studied people(s)<sup>2</sup>. This, too, is an interesting question, but it is one that needs to be asked and answered (see Kuhn and Stiner 2001) before ethnoarchaeologically derived inferential rules or ethnographic analogies can be applied.

Because of the nature of archaeological data, it is often the case that the evidence needed to determine whether an inferential rule pertains to a given case is the very same evidence to which the archaeologist wants to apply the inferential rule. Standard practice is to simply assume that the inferential rule in question does pertain. The (generally implicit) idea is that if the assumption is incorrect, internal inconsistencies will emerge as research accumulates, eventually requiring that the assumption be revisited and modified or rejected. The alternative suggested in this dissertation is to both formally postulate the inferential rule for reconstruction purposes, and simultaneously question the rule's applicability by explicitly discussing the implications if it is incorrect.

In this dissertation, it is generally postulated that hominins in the Paleolithic behaved in such a way as to maximize the efficiency of food acquisition. While this assumption, which is the core of optimal foraging models such as the diet breadth / prey choice model on which much of this dissertation builds, is not strictly speaking an inferential rule, it is an essential (and hereafter implicit) component of the various inferential rules addressed here. This assumption is therefore a critical boundary assumption for several of the inferential and explanatory models to be discussed; if the assumption is invalid (a topic returned to in chapter 7) in any given case, the results of the modeling efforts presented in the following chapters cannot be presumed to apply. Other boundary conditions involved in this study include uniformitarian assumptions about both inter-

and intraspecific ecological relationships, as well as ungulate species characteristics (especially with regard to life-history).

### **Chapter Organization**

*Chapter 2* introduces the diet breadth / prey choice model and critically evaluates its typical archaeological application, before proceeding to develop an alternative version of the model that is based on the rate of food acquisition rather than on the rate of net energetic return. The mathematical formulation of this alternative version is used to demonstrate sometimes overlooked aspects of the model's predictions. Limits to the quantity of animal flesh that individuals or groups of foragers can consume and/or store affect prey choice decisions through their effects on prey ranking. Variability in the time required to handle resources—especially variability associated with hunting success/failure rates—also affects prey choice decisions by altering both prey ranking systems and the circumstances associated with prey inclusion in the optimal diet. These complicating factors provide the motivation for a simulation model of hominin ungulate hunting as a means of searching for narrower inferential rules associating ungulate exploitation patterns with hominin demography and behavior.

*Chapter 3* describes the basic structure of the hunting pressure simulation model, and the development of species-specific modeling parameters for seven common ungulate species of the Mediterranean Basin and Europe. The model is based on that developed by Stiner et al. (1999, 2000) to examine hunting pressure effects on small game animals. The greater analytical resolution made necessary by the overall similarity of ungulates to one another (in comparison to small game) results in some significant modifications of the model. These include some small changes to the model structure, a different approach to hunting rates, and greater flexibility in data collection. This chapter also pre-

sents detailed discussions of the determination of modeling parameters for the different ungulate species.

*Chapter 4* presents basic hunting pressure tolerance results of the simulation model. Maximum sustainable harvest rates for each species are determined, and the utility of these values as summary measures of hunting-pressure response is discussed. Maximum sustainable harvest rates are, however, heavily influenced by any sex-bias in hunting, as well as the frequency and duration of episodes of exploitation. The effects of variation in both of these areas are examined, and the long-term practicality of sex-biased hunting under random-encounter hunting conditions is dealt with in some detail.

*Chapter 5* uses the hunting pressure simulation model to investigate the relationship between harvest levels and prey-assemblage age structure for ungulates. Many previous investigations of this topic have not made the critical distinction between the effects of hunting pressure on the age structure of the prey population and the way those changes manifest in the archaeofaunal record; making such a distinction raises doubts about the usefulness of some of these previous studies. Even after correcting for this, the basic age structure results of the hunting pressure simulation model employed here differ substantially from those of previous studies. The reasons for these differences are investigated, leading to more refined evidence of the level of hunting pressure needed to produce certain prey age-structure changes, and to a reinforcement of the need to consider hunting strategies in analyzing the age structure of ungulate archaeofaunas. Particularly critical is the need for prey sex-ratio data, as different levels of sex-bias in hunting produce radically different age-structure effects.

*Chapter 6* draws on the results presented in the preceding chapters to investigate the inferential potential in terms of diet breadth / prey choice of changing ungulate species representation in Paleolithic archaeofaunas. Based on a series of factors, including

technological investment costs of hunting, relative food yields sustainable by populations of ecologically equivalent sizes, ambiguity caused by uncertain levels of sex-biased hunting and frequency/duration of exploitation, and others, it is concluded that human-population-growth inferences based on ungulate species representation are much less secure than similar inferences based on small game category representation.

*Chapter 7* summarizes and integrates the models and modeling results described in the preceding chapters. Emphasis is placed on the benefits of using formal mathematical and simulation models to refine hypothesis formation and evaluation in archaeological inference and explanation. Suggestions for future research on each of the topics discussed in the dissertation are made, as is a general call for more formal treatment of inferential and explanatory arguments and explicit discussion of the consequences if postulated elements of such arguments turn out to be incorrect.

#### *Notes*

1. A model is defined to be ‘analytically tractable’ if the mathematical relationships among the variables are such that it is possible to derive a formula for the value of each variable as a function of the remaining variables.

2. This is not to deny the value of ethnoarchaeology and ethnographic analogy as sources of insight into archaeological problems, but rather to emphasize that the fruits of such research cannot be applied directly and indiscriminately to the interpretation of the archaeological record without evidence warranting such applicability.

## CHAPTER 2

### THE DIET BREADTH / PREY CHOICE MODEL: ARCHAEOLOGICAL APPLICATIONS AND MATHEMATICAL COMPLICATIONS

The diet breadth / prey choice model, one of several mathematical ‘optimal foraging’ models developed by ecologists to understand the food-acquisition behaviors of animals (e.g., Charnov 1976; MacArthur and Pianka 1966; Maynard Smith 1974; Orians and Pearson 1979), is perhaps the most commonly invoked mathematical model in the interpretation of prehistoric faunal assemblages. This chapter begins by briefly examining the usual zooarchaeological application of the diet breadth / prey choice model. A simplified version of the model that is argued to be more appropriate to prehistoric—and especially Paleolithic—ungulate hunting is then developed. The chapter concludes with the development and discussion of complicating factors in the application of the model to ungulate hunting in general, and to Paleolithic ungulate hunting in particular.

#### **The Diet Breadth / Prey Choice Model**

The diet breadth model, also referred to as the prey choice model, determines which resources should be included in a forager’s diet on the basis of net energetic return from exploiting each resource, the average time required to exploit each resource once it is encountered, and the frequency at which each resource is encountered, assuming that the goal of the forager is to maximize the net rate of energetic return. The model is based on the assumptions that resources are encountered randomly and that the forager has perfect knowledge of the average encounter rates, average energetic returns, and average handling times for every possible resource. The model states essentially that a resource should be included in the diet if the average energetic return to be expected from pursu-

ing/exploiting it when it is encountered is greater than the average energetic return if the resource is bypassed in favor of searching for other resources with higher return rates. That is, a resource should be included in the diet if the expected energetic return rate of pursuing/exploiting the resource is high enough that the search time required to find a ‘better’ resource would reduce the forager’s overall energetic return rate.

### *Mathematical Formulation*

The diet breadth / prey choice model is defined as follows: a resource  $j$  is included in the optimal diet if and only if (modified from Kaplan and Hill 1992:170):

$$\frac{e_j}{h_j} \geq \frac{\sum_{i < j} T_s \lambda_i e_i - s T_s}{\sum_{i < j} T_s \lambda_i h_i + T_s} \quad (2.1)$$

where  $e_i$  is the net energetic return of resource  $i$  (resources ordered according to their  $e_i/h_i$  ratios),  $h_i$  is the average handling time of resource  $i$ ,  $T_s$  is the time spent searching for resources to exploit,  $\lambda_i$  is the encounter rate with resource  $i$ , and  $s$  is the energetic cost (energy expended per unit time) of search. When quantitative measures of energetic return, exploitation (‘handling’) time, and encounter rate are available, the optimal set of resources can be determined. Strictly speaking, this is the ‘optimal diet’ and the number of resources included therein is the ‘diet breadth’. When, as is more common, such quantitative measures are not available or practical, the qualitative predictions of the model are still available. The model predicts that resources should be either part of the diet or not—that is, a given resource should either always be exploited/pursued when encountered or never exploited/pursued. The model also makes it clear that the frequency with which a resource is encountered is irrelevant to its inclusion in the diet. Rather, the encounter rates of more efficiently exploitable resources (‘higher-ranked’ resources) are

the controlling factor. From this it is clear that when highly ranked resources are abundant, fewer or no lower-ranked resources should be exploited. In contrast, if highly ranked resources are rare, more lower-ranked resources should be exploited (see Kaplan and Hill 1992 or Stephens and Krebs 1986 for further discussion).

### *Archaeological Applications*

Two difficulties are inherent in the archaeological application of the diet breadth / prey choice model. First, it is clear that there are few, if any, archaeological cases to which the diet breadth model *per se* can be applied. While modern experimental or ethnoarchaeological work (e.g., Hawkes and O'Connell 1982) can provide estimates of energetic return rates, these are specific to the technological and behavioral means applied. More obviously, resource encounter rates in a prehistoric environment can rarely be estimated at all, much less with sufficient certainty. Lacking such data, optimal diet predictions cannot be made or tested. Second, the assumptions of the diet breadth model—that resources are encountered at random and that the forager has perfect knowledge, for example—are almost certainly violated in practice (Gremillion 2002; Kelly 2000). Archaeologists examining prey choice deal with the former issue through the use of models inspired by the diet breadth model rather than the diet breadth model itself, though this is not always explicitly acknowledged. The latter issue is rarely given significant consideration. This may be somewhat justified, since it has been suggested that the predictions of the diet breadth / prey choice model remain accurate even if these assumptions are not entirely valid (Sih and Christensen 2001). In general, archaeological analyses that 'apply' the diet breadth model can be divided into two groups. One group looks at different numbers of resources represented in archaeological assemblages or at the relative evenness of the representation of those resources. The other group focuses on

evidence of different exploitation levels of resources in relation to their 'rankings' in terms of presumed energetic efficiency.

Examples of the former type of diet breadth study in the Mediterranean region are those of Edwards (1989) and Neeley and Clark (1993). Being at least partially targeted at the "Broad Spectrum Revolution" suggested by Flannery (1969), it is not surprising that these studies focus on the breadth of diet, rather than on the efficiencies of exploiting the particular resources included therein. Edwards (1989) analyzed faunal assemblages from the Levant with respect to their *evenness*, the extent to which the resources included in the diet are equally represented. This approach utilizes a diet breadth-inspired model that recognizes the time-averaged nature of archaeological assemblages. This (effectively implicit) model recognizes that while the diet breadth model itself is an *instantaneous* model of inclusion versus exclusion of resources, a faunal assemblage is often a *long-term* accumulation of a large number of somewhat independent resource-inclusion events. By looking at the relative frequency of exploitation of different resources, an evenness analysis seeks to distinguish assemblages produced by diets that were consistently dominated by a small number of (presumably high-ranked) resources from assemblages produced by diets that *either* consistently included substantial proportions of many different resources *or* were focused on different resources at different times. The logic is simply that of identifying specialized versus generalized resource exploitation, in line with the general diet breadth model prediction (see above) that an abundance of high-ranked resources leads to specialized exploitation, while a paucity of high-ranked resources leads to generalized exploitation. Edwards' (1989) study did not succeed in identifying an increase in diet breadth. His analysis was hampered by inclusion of non-prey species (cf. Neeley and Clark 1993), which somewhat biased the results, and also by difficulties inherent in a taxonomically-driven approach to the data (see below).



Neeley and Clark (1993), in reaction to Edwards' study, analyzed a similar data set from a *richness* (simple number of resources) perspective. They argued that the evenness approach was inappropriate and had contributed to Edwards' failure to identify the Broad Spectrum Revolution in the archaeological record. Neeley and Clark's study was somewhat more successful on this front, but not tremendously so. While the diet breadth model can in fact be seen as a richness model, and is not and cannot in its true (that is, instantaneous) formulation be an evenness model, Neeley and Clark's (1993) richness analysis suffers from the same basic problem as Edwards' (1989) evenness analysis. This problem has two dimensions. First, these studies rely on biological taxonomy to define what constitutes a resource. On a practical level, this presents substantial methodological issues, due to the nature of zooarchaeological data. For example, at what taxonomic level should resources be defined? If genus or species, what is done with the normally substantial number of specimens that cannot be identified specifically enough? In an evenness analysis, is taxonomic representation calculated using number of identified specimens (NISP) or minimum number of individuals (MNI)? There are theoretical issues as well. Briefly, there is no reason to assume that biological taxonomy is closely related to forager perceptions of resource identity, and thus of exploitation efficiency or encounter rate (see also Stiner and Munro 2002; Stiner et al. 2000). For example, males, females, and juveniles of the same species may be considered different resources (e.g., Mithen 1990)<sup>1</sup>.

The second dimension of the problem is the use of simple numeric summary values that mask the particular resources exploited and *the characteristics thereof that are critical to the diet breadth / prey choice model*. Reducing the composition of a faunal assemblage to a measure of richness or evenness can inappropriately result in treating resource exploitation patterns that are quite different under the model as if they are the same. For example, both the evenness measure used by Edwards (1989) and a richness

measure like that used by Neeley and Clark (1993) will equate the hypothetical assemblages shown in Table 2-1. Both assemblages have a species (or genus) richness of 3. In terms of evenness, both produce Inverse of Simpson's Index (Levins 1968; Simpson 1949) values of 1.68. All else being equal, however, the two hypothetical assemblages indicate drastically different foraging behavior or opportunities. Assemblage A could be interpreted as a relatively specialized diet under circumstances of strong abundance of the highest-ranked resources. Under normal diet breadth / prey choice model-inspired interpretations, Assemblage B represents a case of significant resource depression, possibly due to population growth and possibly indicating population pressure. By conflating such assemblages (though this hypothetical example is admittedly extreme), diversity-index analyses of diet breadth can be misleading or difficult to interpret.

The other common approach to applying the diet breadth model to archaeological data is more appropriate to stratified assemblages from a single site or to small sets of sites in close geographic proximity. Such analyses look at changes in the representation of particular resources, specifically focusing on the presumed energetic efficiency of the exploitation of those resources (e.g., Bayham 1982; Broughton 1999; Nagoaka 2002). These studies typically make use of implicit modifications of the diet breadth model similar to those required by an evenness-measure analysis—specifically, that changes in the relative frequencies of resources in archaeological assemblages can be interpreted in diet breadth terms despite the either/or nature of the formal diet breadth model with

Table 2-1. Hypothetical Faunal Assemblages for Diversity Index Comparisons.

Resource	Percentage of	
	Assemblage A	Assemblage B
Bison	75	0
Deer	15	10
Rabbit	10	15
Field Mouse	0	75

regard to resource inclusion and exclusion.

By focusing more specifically on the prey choice view of the model than on diet breadth *per se*, the approaches in the second group avoid the problems discussed for the first. There are, however, other potential difficulties with these applications of the diet breadth / prey choice model. Specifically, changes or differences in prey choice are virtually always attributed to changes in a single term in the model: resource encounter rates, typically interpreted as indicative of resource density. The addition to the diet (or the increased representation) of prey presumed to have been lower ranked, for example, is interpreted as indicating a decrease in the density of higher-ranked prey. However, there is no *a priori* reason to assume that changes in prey choice relate to the resource-density, rather than resource-ranking, component of the model. It seems likely that such interpretations are due to an assumption, perhaps never made explicit, that resource rankings are static.

This chapter argues for, and develops, a food-yield—rather than energetic return—version of the prey choice / diet breadth model, then discusses the effects of such complicating factors as meat consumption limits and hunting failure rates on the archaeological application of optimal diet models. Both consumption limits and hunting failure rates have direct effects on resource rankings—the latter because of its effect on handling time. Hunting failure rates also affect prey choice / diet breadth by altering the encounter rates necessary for inclusion or exclusion of resources.

### **Food Value, Net Energetic Return, and Diet Optimality**

In the behavioral ecology of ungulate hunting in general—and for the Paleolithic in particular—a case can be made that the diet breadth / prey choice model's reliance on net energetic return is problematic, since certain implicit assumptions of the model do not

appear valid for hominin ungulate hunting. Specifically, it seems clear that individual Paleolithic hunters were not evaluating resources in terms of their *individual* rates of net energetic return directly from the resources in question. Because virtually any adult ungulate (with essentially irrelevant exceptions such as the dik-dik, *Madoqua* sp.) is too large to be consumed by a single hominin forager<sup>2</sup>, the gross energetic return *to the forager* from any hunted ungulate should be effectively the same—equal to the energetic value of the amount he or she could consume. As a result, resource rankings would be determined solely by energy and time *costs* associated with exploiting different ungulates.

Hunted Paleolithic faunal assemblages from a wide variety of regions (e.g., Baryshnikov and Hoffecker 1994; Gaudzinski 1995; Klein and Cruz-Urbe 1994; Stiner 1994, 2005) show a dominance of large ungulates such as aurochs (*Bos primigenius*), bison (*Bison* sp.), horse (*Equus* sp.), and red deer (*Cervus* sp.); smaller ungulates were available to the accumulators of at least the majority of those assemblages, as shown by their presence in low numbers in those same assemblages and in other sites in reasonable geographic proximity and dating to similar times. Under the diet breadth / prey choice model, if there is no cause for a hunter to distinguish among these species on the basis of gross energetic return, then the frequent dominance of larger ungulate species requires either that larger ungulates were consistently more common than smaller ones (producing more frequent encounters) or that exploiting larger ungulates involved *smaller* energy and/or time costs than exploiting smaller ungulates. The former option suggests that not only were environments in much of the Pleistocene different from those of the Holocene, but also that basic ecological processes observed in the modern world were not operative in the past. The latter option could occur in one of two cases. Handling energy and time associated with a successful pursuit could be smaller, which contradicts a variety of modern observations of human hunting (see Mithen 1990:119-122 for a discussion).

Alternatively, the failure rate involved in hunting the larger ungulate could be lower than that for hunting the smaller ungulate; though this is far from impossible, it seems likely that it could only result from specialization in hunting the larger ungulate. Such specialization could occur under a variety of circumstances, but the only such circumstance not associated with greater energetic benefits to be gained is a higher encounter rate (Bright et al. 2002; Ugan et al. 2003). The alternative to these options is to recognize that hominin foragers frequently ranked prey resources based on returns greater than those directly available to them.

The focus on ungulates in Paleolithic hunting, and especially on larger ungulates in many regions and times, is strongly suggestive of food sharing because of the limited food consumption abilities of the individual, as discussed above. This is no surprise to any student of hunter-gatherers, of course, but it provides corroborative evidence of meat sharing by the earliest ungulate hunters, since rather large game were regularly taken by the accumulators of even the earliest definitively hunting-derived faunal assemblages, such as the early Mousterian levels at Hayonim Cave (Stiner 2005). Since meat received through sharing does not come burdened with the same energetic costs as acquiring it through hunting, it seems clear that a significant fraction of the energetic gains from any ungulate kill are obtained by individuals who do not pay any meaningful energetic cost. Furthermore, while some form of reciprocal sharing must be assumed, and therefore the recipients of such largesse can be presumed to have paid similar costs in the past or to expect to do so in the future, this does not eliminate the decoupling of energetic gain and energetic cost. In fact, such sharing fosters this decoupling since reciprocation must be based on transferred food, not on energy gained or expended. That is, a forager may be 'paid back' for the food that he/she shared with another, but is unlikely to be so for the energy he/she expended in the acquisition thereof. This point may perhaps best be made

with a somewhat absurd example. An incompetent hunter who expends as much energy in acquiring a single small deer as another hunter expends in acquiring *ten aurochs* might nonetheless receive a full ‘share’ of the meat from the aurochs, but not because of reciprocity for equal energy expenditure.

Cooperative hunting may somewhat reduce the level of disassociation between costs and benefits, as multiple individuals pay search and pursuit costs—and possibly processing costs as well. However, energetic return and energetic costs remain decoupled so long as meat is shared beyond the specific set of individuals who make the kill (i.e., if the food-sharing group is larger than, or even disjoint with, the hunting party).

This disassociation of energetic gain and cost, and particularly the fact that reciprocal obligations are likely to relate solely to the amount of food transferred<sup>3</sup> and not depend substantially on the energetic cost to the giver, suggests that food yield is a better measure of gain as a decision-making factor than is net energetic return. This view is compatible with both delayed-reciprocity models and social-benefit models (e.g., Hawkes 1991; Winterhalder 1997) of ungulate hunting.

#### *A Food-Yield Model of Optimal Diet*

Converting the diet breadth / prey choice model to a food-yield basis results in rankings based on the rate of food acquisition once resources are encountered ( $y/h$ ), where  $y$  is food yield (kilograms of meat, fat, etc. in the case of ungulate hunting)<sup>4</sup>, and  $h$  is mean handling time on encounter as in the standard diet breadth / prey choice model. A resource  $j$  should be included in the diet if

$$\frac{y_j}{h_j} \geq \frac{\sum_{i < j} T_s \lambda_i y_i}{\sum_{i < j} T_s \lambda_i h_i + T_s} \quad (2.2)$$

where resources  $i$  are ranked in order from highest to lowest ratios of food yield to handling time ( $y/h$ ) so that all resources  $i < j$  are higher-ranked than  $j$ ,  $T_s$  is the amount of time spent foraging, and  $\lambda_i$  is the encounter rate with resource  $i$ . In addition to the change from net energetic return to food yield, this inequality differs from the standard diet breadth / prey choice model formulation (inequality 2.1) in lacking a term for the energy cost of search in the numerator on the right side of the inequality. This lack is in line with *energetic* cost (as opposed to *time* cost) not being a primary factor, as well as the fact that searching can be at least somewhat embedded in other tasks. This version of the diet breadth / prey choice model postulates that hominin ungulate hunters maximize not the energetic efficiency of foraging, but rather the rate of meat acquisition (time efficiency).

Inequality 2.2 can be simplified by canceling the search time ( $T_s$ ) terms. The result shows the specific prey-resource characteristics that determine whether or not a given resource should be included in the diet under this food-yield version of the diet breadth / prey choice model. A given resource  $j$  should be included if and only if:

$$\frac{y_j}{h_j} \geq \frac{\sum_{i < j} \lambda_i y_i}{\sum_{i < j} \lambda_i h_i + 1} \quad (2.3)$$

with variables defined as above. This can be further simplified as:

$$\frac{y_j}{h_j} \geq \frac{\Lambda_j Y_j}{\Lambda_j H_j + 1} \quad (2.4)$$

where  $\Lambda_j$  is the combined encounter rate with all prey resources  $i < j$ :

$$\Lambda_j = \sum_{i < j} \lambda_i \quad (2.5)$$

$Y_j$  is the average food yield, weighted by encounter rate, of prey resources  $i < j$ :

$$Y_j = \sum_{i < j} \frac{\lambda_i}{\Lambda_j} y_i \quad (2.6)$$

and  $H_j$  is the average handling time, weighted by encounter rate, of prey resources  $i < j$ :

$$H_j = \sum_{i < j} \frac{\lambda_i}{\Lambda_j} h_i \quad (2.7)$$

From this point, it is possible to determine how much time must be expected to pass—on average—from the time of an encounter with resource  $j$  to an encounter with a (higher-ranked) resource  $i < j$  in order for resource  $j$  to be included in the optimal diet. Rearranging inequality 2.4 produces:

$$\frac{1}{\Lambda_j} + H_j \geq \frac{Y_j}{y_j} h_j \quad (2.8)$$

Since  $\Lambda_j$  is the combined encounter rate during search with resources ranked higher than resource  $j$ , its inverse ( $1/\Lambda_j$ ) is the average length of search time required before an encounter with one of those resources. Inequality 2.8 puts the food-yield-based diet breadth / prey choice model into the forager's specific decision-making terms. Resource  $j$  is included if and only if the expected amount of time until an encounter with a higher-ranked resource *plus* the average handling time of such a resource is greater than the average handling time of the resource in question multiplied by the ratio of the expected yield of the higher-ranked resource to resource  $j$ 's yield. That is, the expected length of time until a 'better' resource has been both found *and* handled must be greater than the handling time of the encountered resource times the inverse of its relative yield<sup>5</sup>. For example, a prey resource with a yield of 100 kg that requires an average of three hours to handle is higher ranked than a prey resource with a yield of 50 kg and an average handling time of two hours ( $y_1/h_1 = 33.3$  kg/hr;  $y_2/h_2 = 25$  kg/hr). The latter should be included in the diet if and only if the expected length of time before the larger prey resource is both encountered and handled is greater than twice (because of the 100:50 = 2:1 ratio of the yields) the handling time of the smaller resource—in this case, four hours. The



expected time until an encounter with the larger resource must thus be greater than one hour (since it requires an average of three hours to handle)<sup>6</sup>.

This yield-based model of diet breadth / prey choice should be a more appropriate basis for the implicit model generally applied by zooarchaeologists than is the standard diet breadth / prey choice model, at least in relation to the hunting of large mammals. It retains, however, an emphasis on handling time that is frequently dispensed with in archaeological applications, and which is argued later in this chapter to have the potential to dramatically affect hunting decisions. Furthermore, it focuses attention on the quantity of food acquired over a given span of time, rather than the more abstract notion of the rate of net energetic return. This brings the argument full circle to the issue of the ability of a forager to consume a resource, or in light of food-sharing, of a group of foragers to do so.

### **Sharing-Group Consumption Limits and Prey Choice**

The amount of food consumable by a given foraging group can significantly affect the way they rank prey in an optimal diet assessment, and plays an additional role in the on-encounter decision to pursue or not to pursue a resource. These effects seriously complicate diet breadth / prey choice model inferences from ungulate species-representation in the archaeological record in some cases, since data critical to such inferences are rarely if ever available. Hunting failure rates, which also can have major complicating effects, are discussed later in the chapter; thus, while such failure rates are a relevant part of the following treatment of consumption limits and prey choice, consideration of the full import of failure rates is postponed.

Having reached the conclusion that the quantity of food acquired (including both food that is consumed by a forager *and food provided to others*) is a valid and useful currency for understanding hominin ungulate hunting practices in optimal foraging terms

and having developed a version of the diet breadth / prey choice model based on this conclusion, it is worthwhile to expand the consumption-limit idea to the entire food-sharing group. The actual value in food and food-sharing-derived benefits obtained by a forager from an animal is limited not only by the size of the animal, but also by the amount of meat, fat, and so forth that the forager's food-sharing group can consume. This latter amount is determined by the size of the sharing group and their ability to preserve and/or defend the food. At any given time, a food-sharing group will have a maximum quantity of animal mass that is of use to them. Above this quantity, the oft-assumed relationship between body size and ranking of prey is thrown into doubt. All else being equal, two prey animals should be equally ranked despite even large differences in body size if both can provide at least the maximum amount the sharing group can consume. For example, if a group of hominins is not able to fully consume the meat and other tissues it can obtain from a red deer, there is no optimality rationale for ranking aurochs over red deer, assuming for the moment that handling times are equal. The group can fulfill all its needs from either type of animal and thus should not distinguish between them in ranking them as resources.

The amount of meat (from this point forward, the word 'meat' is used to refer to edible animal tissues in general, not simply to muscle tissue) that a group of hominins is capable of consuming depends on several factors. These include the size of the group, how long the meat can be preserved and/or defended, and how much preserved/defended meat is currently on hand. The absolute maximum quantity (or consumption limit) is the product of the group's maximum rate of consumption and the amount of time they can preserve/defend meat. It may thus vary somewhat by season, especially at higher latitudes where seasonal variation in temperatures is greater and freezing may be practical. Additional variation in consumption limits and thus prey rankings derives from the fact

that the maximum usable quantity of meat at a given time is the absolute maximum minus the amount preserved/defended at that time. Thus, though the group's consumption limit is a more or less constant value (with the caveat of seasonality), the operational maximum usable quantity of meat may vary considerably in the short term.

*Choosing among Prey with Similar Effective Yields*

Since all prey animals large enough to satisfy a hominin group's maximum usable quantity of meat are effectively interchangeable in terms of return (i.e., have the same effective yield), differences in handling times are the only distinguishing factor. In the case of Paleolithic ungulate hunting, however, such differences may be small enough for the entire set of sufficiently large prey to always be included within the optimal diet. In order for a resource to be bypassed in favor of continued searching for some other resource with the same return, the processing time of the former must be greater than that of the latter and the added search time *combined*. This is easily seen by setting  $y_j = Y_j$  in inequality 2.8 and rearranging terms, which produces:

$$\frac{1}{\Lambda_j} \geq h_j - H_j \quad (2.9)$$

That is, the difference in handling times must be greater than the anticipated time required to locate a lower-handling-time (and thus higher-ranked) resource. Thus, for generally similar resources such as ungulates, unless the lower-processing-cost resource is so common that an encounter can be anticipated within a relatively short period of time or the handling times differ very substantially (due, for example, to significant differences in hunting failure rates—see below), a resource should be exploited on encounter despite a higher handling time.

Thus, under the above assumptions about failure rates and relative handling times,

an ungulate prey animal must be too small to satisfy the maximum usable quantity of meat in order for it to be excluded from the diet on food-yield-based optimal foraging grounds. The traditional emphasis of optimal-diet analysis on densities or encounter rates is only relevant among such animals. That is, they may be included or not in the diet based on the encounter rate with the set of sufficiently large (and thus higher-ranked) animals, as defined by the food-yield diet breadth / prey choice model. The consumption limit is effectively a boundary condition for the standard application of the diet breadth / prey choice model. Prey animals of such size are referred to here as *potentially excluded*; such prey are included in the diet in one of two cases: the prey animal is the highest-ranked resource available (in which case there are no automatically included prey) or higher-ranked resources are sufficiently rare that inequality 2.8 is satisfied.

A prey animal excluded from the diet can therefore be inferred to be a member of the set of resources actually covered by the encounter-rate aspects of the diet breadth / prey choice model, and indicates that the foraging group's consumption limit is greater than the food yield of that animal (again, assuming that handling times in general, and failure rates in particular, are similar). However, the *inclusion* of an animal in the diet may indicate *either* that the consumption limit is smaller than the yield the animal provides *or* that higher-ranked prey are rare. Therefore, the largest prey animal excluded from the diet represents only a *minimum* value for the group's consumption limit. This minimum bound translates to a minimum value for the product of group size and meat preservation and/or defense capability. As noted above, if meat storage is practiced, the maximum consumable amount of meat will vary depending on the amount currently being preserved/defended. As a result, the mere frequent (as opposed to complete) exclusion of a prey animal from the diet may indicate that the absolute maximum consumable amount of meat is not only greater than that which can be provided by the

animal, but in fact is considerably greater. This is because such frequent exclusion indicates that the immediate consumption limit rarely drops to the point where the prey animal in question can provide it. Standard interpretations of the diet breadth / prey choice model divide resources into two categories: always exploited on encounter and never exploited. Consumption limit considerations can add a third, intermediate, category: resources that are exploited on encounter when the foraging group's current consumption limit is low enough either to be satisfied by the resource or to sufficiently reduce the yield ratio that continued search becomes inefficient, and ignored otherwise.

While any consumption limit value greater than the amount of meat obtainable from a given ungulate prey resource results in that resource being ranked lower than other ungulate prey resources that *can* provide the maximum consumable amount (continuing the assumption that handling times do not differ significantly), this shortfall must often be substantial in order for the difference in ranking to lead to exclusion. Consider a foraging group with a maximum consumable amount of meat of 55 kg. From inequality 2.8, an ungulate prey resource that provides 50 kg of meat will be included unless the expected time to both locate and handle a resource providing more than 55 kg of meat (which counts as only 55 kg because of the consumption limit) is less than 110% ( $55 \text{ kg} / 50 \text{ kg}$ ) of the time required to handle the smaller ungulate. Thus, if handling times are the same, the resource providing 50 kg of meat should only be excluded if the expected time before an encounter with a larger ungulate is less than one-tenth the time required to handle the resource. If the handling time of the smaller ungulate is similar to, but smaller than, the (encounter-rate-weighted) average of the handling times of the larger ungulates (for example, 55 minutes rather than one hour), then the expected time to encounter with a larger ungulate may need to be vanishingly small in order for the smaller ungulate to be excluded (in this example, 30 *seconds*). Thus, in the absence of long or at least very

different handling times, absolute exclusion of an ungulate from the diet is indicative of a consumption limit significantly greater than the food yield of that ungulate.

*Group Sizes, Storage Capability, and Consumption Limits.* While the theoretical relationship (see above) among group size, the ability to preserve or defend meat, and the maximum consumable amount of meat is simple, numerical estimates are more difficult to produce due to uncertainty about maximum consumption rates. Many large carnivores consume very large quantities of meat at a single 'sitting' and then go days without eating. Omnivores like modern humans, and presumably our hominin ancestors, however, are not well-suited to such consumption behavior. Rather, food is consumed on a more regular basis and in smaller amounts. Nonetheless, it is not appropriate to assume that average daily consumption rates by modern humans are the proper basis for calculating how much meat a hominin (and by extension, a food-sharing group of hominins) could consume at one time or over a span of several days. Unfortunately, such average rates are the primary type of data available.

Kelly (1995:Table 3-7) draws meat-consumption-rate data from the ethnographic literature for eleven modern hunting and gathering societies. The highest consumption rate is 1.78 kg (by the Ache, Hill et al. 1985; Hurtado et al. 1985) of meat per person per day. Taking into account the time-averaged nature of this figure, a heuristic estimate of a maximum per-person meat consumption of two to three kilograms per day seems reasonable. The lower value is arguably more likely, representing 'only' four rather large steaks. Considering the possibility that animal tissue might form nearly 100% of the diet (at least in the short term), however, it seems prudent to consider the possibility of somewhat higher consumption rates. As noted above, the Ache appear to consume an average of 1.78 kg of meat daily; given such an average, it is not unreasonable to assume that daily consumption over limited time spans could reach 3 kg/day.

From this estimate of average individual consumption limits, estimates can be made of group consumption limits based on group size and meat preservation/defense capability. The archetypal so-called “minimal band” of 25 individuals without meat preservation and/or defense is thus estimated to have a consumption limit of 50 to 75 kg. With the ability to preserve or defend meat for, say, five days, this estimate rises to 300 to 450 kg. (Note that one day of consumption is treated as ‘free’ in terms of storage capability.)

*Ungulate Inclusion/Exclusion and Group Consumption Limits.* Associating the foregoing means of estimating sharing-group meat-consumption limits with the inclusion or exclusion of ungulate prey animals from the diet (on optimal-foraging grounds) requires estimates of the edible fraction of body mass for the ungulates in question. Though this fraction must vary among species due to physiological differences such as locomotor adaptation and cube-square law issues, as a purely heuristic tool it is considered reasonable to assume that ungulates are similar enough that a single value can be used. However, the usable fraction is also dependent on processing behavior and technology (extent of marrow-cracking, bone-boiling, etc.). Thus, rather than choosing between the most commonly-used values in the literature, 50% (e.g., White 1953) and 60% (e.g., Jochim 1976; Mithen 1990), these values are used here as upper and lower estimates.

With these heuristic values for maximum-individual-meat-consumption rates and for ungulate usable-mass fractions, it is possible to determine the group size and meat preservation/defense capability combinations associated with the inclusion and potential exclusion of ungulates from the optimal diet, under the continuing assumption of minimal handling time effects. Figure 2-1 shows inclusion/potential exclusion zones for the seven ungulate species dealt with in the forthcoming chapters, based on estimated mean adult body mass. Body-size variation within species (intra-population, inter-region, and par-

ticularly over archaeological time spans) should be borne in mind in interpreting these zones. The zone boundary curves are determined by the following inequality (for clarity, only the highest and lowest combinations of consumption rate and consumable fraction are illustrated). The prey resource is *potentially excluded* from the diet if:

$$t_p > \frac{wu}{cg} - 1 \quad (2.10)$$

where  $t_p$  is the length of time meat can be preserved in days,  $w$  is the body mass of the prey animal,  $u$  is the usable percentage (i.e., 50% or 60%) of that body mass,  $c$  is the mean individual maximum-daily-meat-consumption rate (i.e., 2 kg/day or 3 kg/day), and  $g$  is the size of the food-sharing group in question. The subtraction of one day from the dividend of meat weight and daily group consumption converts the number of days required to consume a resource into the number of days it must be preserved/defended in order to be consumed. That is, one day of consumption is presumed to be possible without preservation or defense. It is assumed that the hominins in question are fairly capable of defending meat from other predators or scavengers in the short term, especially while actively involved in consumption; otherwise, it is very difficult to make sense of any ungulate hunting activity. The defense capability time is intended under this assumption to refer to the ability to defend meat without sacrificing the ability for the majority of the group to undertake other tasks; that is, to leave the meat behind and return to it later. Removing this assumption (and thus the subtracted day in inequality 2.10), would shift the zone-boundary curves upward by one day and make them appropriate for consideration of the hominins' ability to defend against confrontational scavengers. However, such a fine-grained approach would also render inappropriate the simplifying assumption (implicit in inequality 2.10 and Figure 2-1) that food consumption occurs continuously rather than in a series of more-or-less discrete episodes<sup>7</sup>.



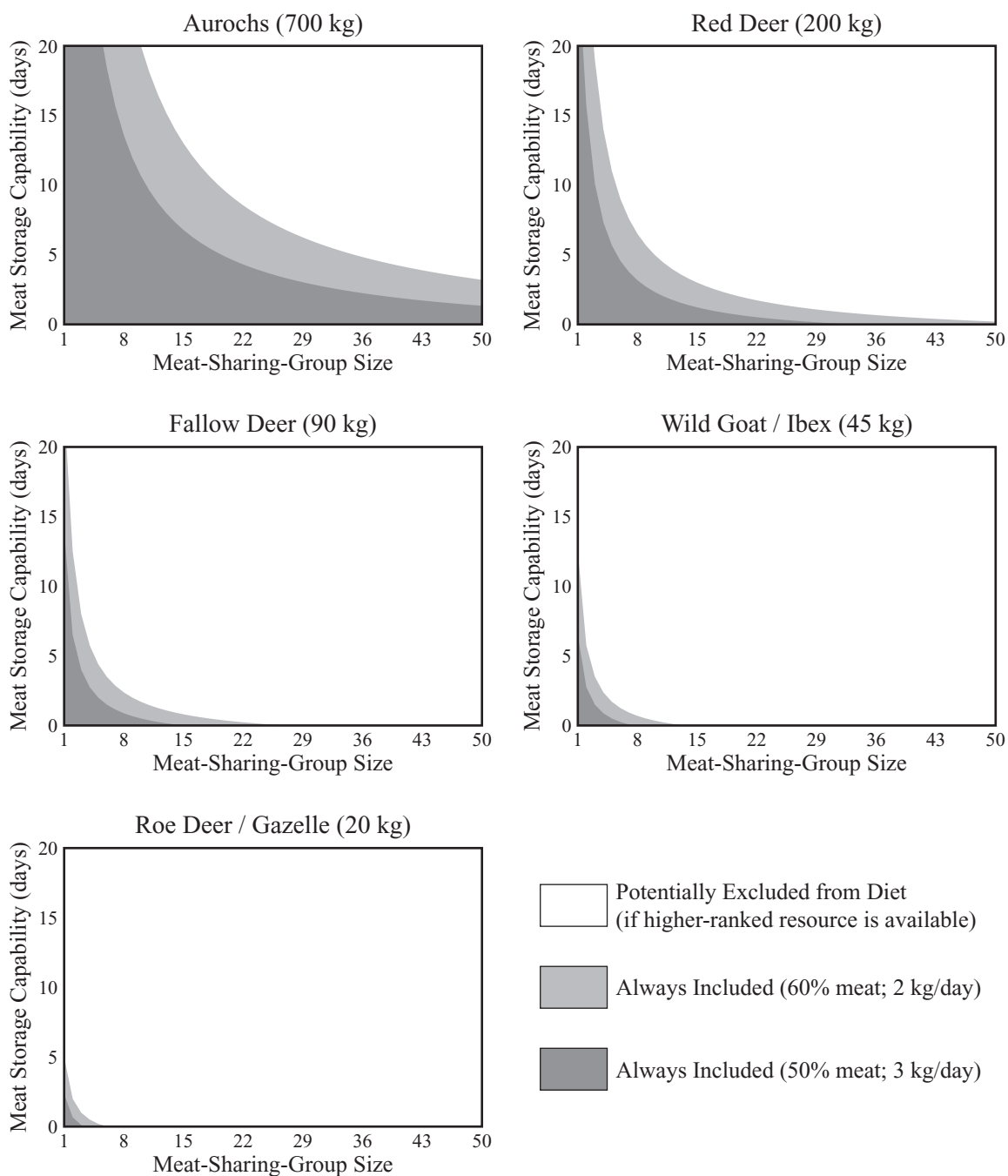


Figure 2-1. Prey animal inclusion in and potential exclusion from the diet based on group size and meat preservation/defense capability, assuming hunting-failure effects are minimal. See text for discussion of meat weight calculations and consumption rates.

### *Implications*

The question of consumption limits raises the possibility that changes in diet breadth can be the result of factors other than environmental changes or hominin-induced resource depression. Shifts in meat-sharing-group size, which do not necessarily correspond to hominin population density changes, can produce both increases and decreases in diet breadth. A decrease in sharing-group size may result in an increase in diet breadth, and *vice versa*. If hominin social organization varies geographically or chronologically, diet breadth may vary geographically or chronologically as well for reasons that have nothing to do with population density or resource availability—though, of course, those factors are almost certainly at play as well.

While it is clear from Figure 2-1 that rather small food-sharing groups (considerably smaller than 25 individuals) and/or a lack of meat preservation/defense capability are necessary for *consumption limits* to significantly affect prey choice decisions, the same cannot be said for *current maximum usable quantities* of meat (see below). Additionally, while there is reason beyond simple ethnographic overgeneralization to provisionally credit the 25-individual minimum group size (Wobst 1974), the day-to-day cohesion of such groups in the Paleolithic (especially the Lower and Middle Paleolithic) should be treated as a fact to be demonstrated, rather than an assumption to be made. If hominin groups occasionally split up for a few days, effective food-sharing-group sizes could easily drop to the point that even ungulates as small as roe deer might enter the always-included range of Figure 2-1.

For a constant meat-sharing-group size, the advent of meat-storage capabilities dramatically increases the size a prey animal must be in order to be exempt from the density-dependence element of the diet-breadth / prey choice model. For example, a

sharing group of 25 individuals should always include both aurochs and red deer (and possibly fallow deer, depending on the actual individual consumption rate and the consumable fraction of body mass) in its optimal diet if it has no meat storage capability, but even a fairly limited storage capability (e.g., two days) reduces the automatically included list of prey to only aurochs. An even greater storage capability (e.g., ten days) places even aurochs in the potentially excluded category, though aurochs would remain included in the diet as the highest-ranked resource available unless mammoth or woolly rhinoceros (for example) are higher-ranked. (The availability of such animals is only expected to result in the exclusion of aurochs if the hunting-failure rates associated with them—see below—are low enough for their on-encounter return *rates* to be higher than that of aurochs.) As a result, there is a definite possibility that a broad tendency toward a reduction in diet breadth (and specifically an increase in the representation of the largest animals) at some point in the Paleolithic might indicate the development—or a significant improvement in—meat-storage capabilities. Evidence from the European Paleolithic may suggest such a reduction in overall diet breadth at some point late in the Lower Paleolithic or early in the Middle Paleolithic. It is an often-noted characteristic (e.g., Gamble 1999:234-237) of many Middle Paleolithic faunal assemblages that they are dominated by a single prey species—often, as noted early in this chapter, a large ungulate. The limited data available for long-term faunal accumulations in the European Lower Paleolithic suggests a stronger reliance on medium-sized ungulates (e.g., Caune de l’Arago, Jourdan and Moigne 1981; cf. Gamble 1999:149). Far more, and better-reported, Lower Paleolithic faunal data would be required, however, to determine if there is any such trend at all. (For example, the dominance of the Caune de l’Arago archaeofauna by mouflon may well be due to environmental availability, and have nothing to do with consumption limits.) Furthermore, consumption-limit change is only one factor that can cause a shift

in diet breadth that is unrelated to resource encounter rates, as will be discussed below.

Yet another complicating factor in diet breadth / prey choice model analyses is the existence of the third diet breadth / prey choice model categorization (see above) of resources—those that are sometimes included due to fluctuations in the currently usable amount of meat. If such resources exist (which should be the case unless the sharing group's absolute maximum consumable amount of meat (consumption limit) is so high relative to the size and frequency of kills that it never drops to the point where there are resources large enough to be automatically included), then the optimal diet (and diet breadth) will vary over short periods of time. The long term average of such diets are expected to be dominated by those resources which are not excluded at any time (whether for consumption-limit or encounter-rate reasons), at rates approximately proportionate to their ecological densities as modified by hunting success rates (see below), with occasionally-included lower-ranked resources forming a smaller portion of the diet (and one not proportionate to density). What would normally be considered lower-ranked resources can thus be included in the diet on optimal-diet grounds in circumstances of low need, in addition to what might be termed 'optimal-survival' grounds in circumstances of high need as suggested by Mithen (1990).

There is also the potential for what would be considered contradictory responses under standard interpretations of the diet breadth / prey choice model. A lower-ranked resource's contribution to the diet could actually grow because of an *increase* in the encounter rate with a *higher-ranked* resource. Consider a foraging group living in an environment with three potential ungulate prey resources: aurochs, red deer, and roe deer. Assume that the group's consumption limit is greater than the meat yield of a red deer (but less than that of an aurochs), and that red deer are included in the optimal diet due to the rarity of aurochs while roe deer are excluded due to the relative commonness of red

deer (standard model interpretation). The foraging group's current maximum usable amount of meat will tend to fluctuate between its absolute consumption limit and the difference between that limit and the amount provided by a red deer, with rare drops to zero caused by the kill of an aurochs. In the aftermath of an aurochs kill, while the current maximum usable amount of meat is near zero, roe deer should be added to the optimal diet on consumption limit grounds. Assuming that the absolute consumption limit is greater than the amount of meat obtained from a red deer plus a roe deer, single red deer kills will not produce this effect. As a result, an increase in the aurochs encounter rate, and the consequent increase in the frequency of aurochs kills, would actually increase the *frequency* (not proportion) of roe deer inclusion in the (consumption-limit interpretation) optimal diet. Whether the *proportionate* representation of roe deer in a hypothetical resulting archaeofauna would increase is dependent on the exact consumption limit, encounter rates, and handling times.

### **Handling Time, Hunting Failure Rates, and Prey Choice**

As noted earlier, archaeological implementations of the diet breadth / prey choice model rarely take explicit notice of the effects of handling time on prey ranking or on resource-exploitation decisions. Handling times affect prey choice in two separate ways. First, they can upset body size-based rankings, as such ranking systems involve an implicit assumption that handling times vary in such a way that rank-ordering resources in terms of returns alone produces the same sequence as does rank-ordering resources by their return-to-handling-time ratios. For example, the ranking of a 200 kg red deer ahead of a 20 kg roe deer is based on the assumption that the red deer takes less than ten times as long to handle. The second way in which handling time affects prey-choice decision-making is by altering the encounter rates (with higher-ranked resources) that lead to the

inclusion or exclusion of a given resource. This effect is well-known (e.g., Winterhalder 1981), particularly when formulated as a causal relationship between high pursuit or processing times and narrow diet breadth. As noted above (inequality 2.8), the time limit before encounter with and handling of a higher-ranked resource (for exclusion of the lower-ranked one) is a linear function of the lower-ranked resource's handling time. As a result, different handling times can produce different optimal diets from the same resource densities (and thus encounter rates).

### *Handling Times and Resource Rankings*

The limited evidence available suggests that (at least for ungulates) field-butchery processing time increases more slowly than does body size (Mithen 1990:121-122). Thus, if butchery (and especially field-butchery) is the primary component of handling time, body-size-based rankings for ungulates are appropriate. If other factors make up a substantially larger fraction of handling time, however, the use of body size alone as a basis for resource ranking can become problematic.

Handling time can be divided into its component elements as follows:

$$h_i = b_i + p_i + q_i f_i \quad (2.11)$$

where  $b_i$  is the average time required to process resource  $i$  once captured,  $p_i$  is the average time required by a successful pursuit<sup>8</sup> and capture of resource  $i$ ,  $q_i$  is the average number of failed pursuits per successful pursuit, and  $f_i$  is the average time involved in a failed pursuit of resource  $i$ . All of these terms are affected by technology and behavior. The efficiency of butchery is dependent on the technology used, but also on the needs of the foragers doing the processing. 'Bulk' *versus* 'gourmet' processing (Binford 1978:81) or grease rendering (e.g., Lupo and Schmitt 1997; Outram 2001), for example, alter the yield from the processed animal but also alter the processing time  $b_i$ . The average time re-

quired by a successful pursuit ( $p_i$ ) of an ungulate is determined by the means used to attack the animal (individual hunting, group hunting, ambushing, stalking, etc.), by the rapidity with which the animal is killed once attacked, and by whether or not a wounded (but not quickly killed) animal is run down or allowed to escape. The same factors that determine the time required by a successful pursuit are involved in determining the time lost to failed pursuits ( $f_i$ ). They can take on even greater importance, however, as factors in total failed-pursuit time due to the multiplication by the average number of failures per successful pursuit ( $q_i$ ).

Hunting techniques and hunting failure rates have the potential to dramatically affect handling times and thereby prey rankings. While the fact that failures affect efficiency is often recognized by Paleolithic archaeologists (e.g., Gamble 1999:234), that it could invalidate common assumptions about rankings does not appear to be. Differences in the hunting techniques applied to different ungulates or differences in the effectiveness of the same technique when so applied may lead to radically different handling times. For example, if a hunter's (or hunting group's) weaponry can kill a 200 kg red deer with a single spear or arrow impact, but can only wound a 700 kg aurochs, which then must be chased to exhaustion, it is not unlikely that the handling time of the aurochs might be more than three-and-a-half times the handling time of the red deer, especially if chases of wounded aurochs fail on a regular basis. In such a case, the red deer should in fact be ranked higher than the aurochs, because its *rate* of yield on encounter is higher than that of the aurochs despite the aurochs' greater ultimate yield.

The rate of hunting failure becomes the critical factor in determining average handling time in cases where animals are stalked for a significant length of time, where the hunter lies in wait<sup>9</sup> for such a time, or where post-attack pursuit may be extended. If the time involved in any such activity approaches that required for butchery, then any

failure rate at all will result in non-processing time (including both successful and unsuccessful exploitation attempts) being a larger component of handling time than processing time. As a result, significant differences among the failure rates associated with hunting different ungulates can potentially result in smaller ungulates being ranked ahead of larger ones.

### *Handling Times and Resource-Inclusion Decisions*

In addition to the potential to upset body-size-based prey rankings, handling time can have significant effects on the breadth of the optimal diet. As noted previously, this is a standard statement about the predictions of the diet breadth / prey choice model (e.g., Winterhalder 1981). Even in cases where the handling times associated with different resources do not overturn body-size-based rankings (i.e., when handling times are similar or increase more slowly than body size—or even decrease with body size), large and small handling times overall—both  $H_j$  and  $h_j$ —can produce very different optimal diets.

Consider a case where two ungulate resources are available, fallow deer with an average body size of 90 kg and roe deer with an average body size of 20 kg (for a 4.5-fold difference in yield). From inequality 2.8, if fallow deer require an average of two hours to handle and roe deer an average of one hour, then roe deer should be included in the diet if the expected length of time before a fallow deer is encountered is more than two-and-a-half hours. If, however, the fallow deer requires an average of ten hours and roe deer an average of five hours—*the same ratio of handling times*—then roe deer should be included in the optimal diet if the expected time to encounter with a fallow deer is greater than twelve-and-a-half hours. Alternatively, if the fallow deer requires ten hours on average and the roe deer nine (in this case, the same difference in handling times as the first example), then the roe deer is included in the diet only if the expected time to en-



counter a fallow deer is greater than 30.5 hours.

Figure 2-2 shows the relationship between overall handling times and relative handling times in terms of their impact on encounter rates necessary for the inclusion or exclusion of a lower-ranked resource. A given encounter rate (expressed as average time until an encounter) represents the inclusion-exclusion border for a wide variety of handling time combinations and yield ratios. For example, an expected time to encounter with a higher-ranked resource of two hours is the minimum for the inclusion of a lower-ranked resource for each of the following sets of resource characteristics: 1) a yield ratio of two-to-one, encounter-rate-weighted average handling time of higher-ranked resources of two hours, and average handling time of lower-ranked resource of two hours; 2) a yield ratio of two-to-one, handling time for higher-ranked resource(s) of eight hours, and a lower-ranked-resource handling time of five hours; 3) a yield ratio of five-to-one, a higher-ranked-resource(s) handling time of three hours, and a lower-ranked-resource handling time of one hour; 4) a yield ratio of five-to-one, an average handling time for higher-ranked resource(s) of five hours, and an average handling time for the lower-ranked resource of 84 minutes.

### *Implications*

Changes in diet breadth / prey choice can result not only from shifts in resource density, but also from alterations in handling times of different resources as a result of changes in hunting technology or behavior. In general terms, the increased (or added) representation in an archaeofauna of smaller ungulates does not necessarily indicate a reduction in the encounter rate with larger ungulates. Rather, such an increase in diet breadth can also result from either across-the-board reductions in handling times (due, for example, to improved hunting technology) or from reductions in the handling time re-

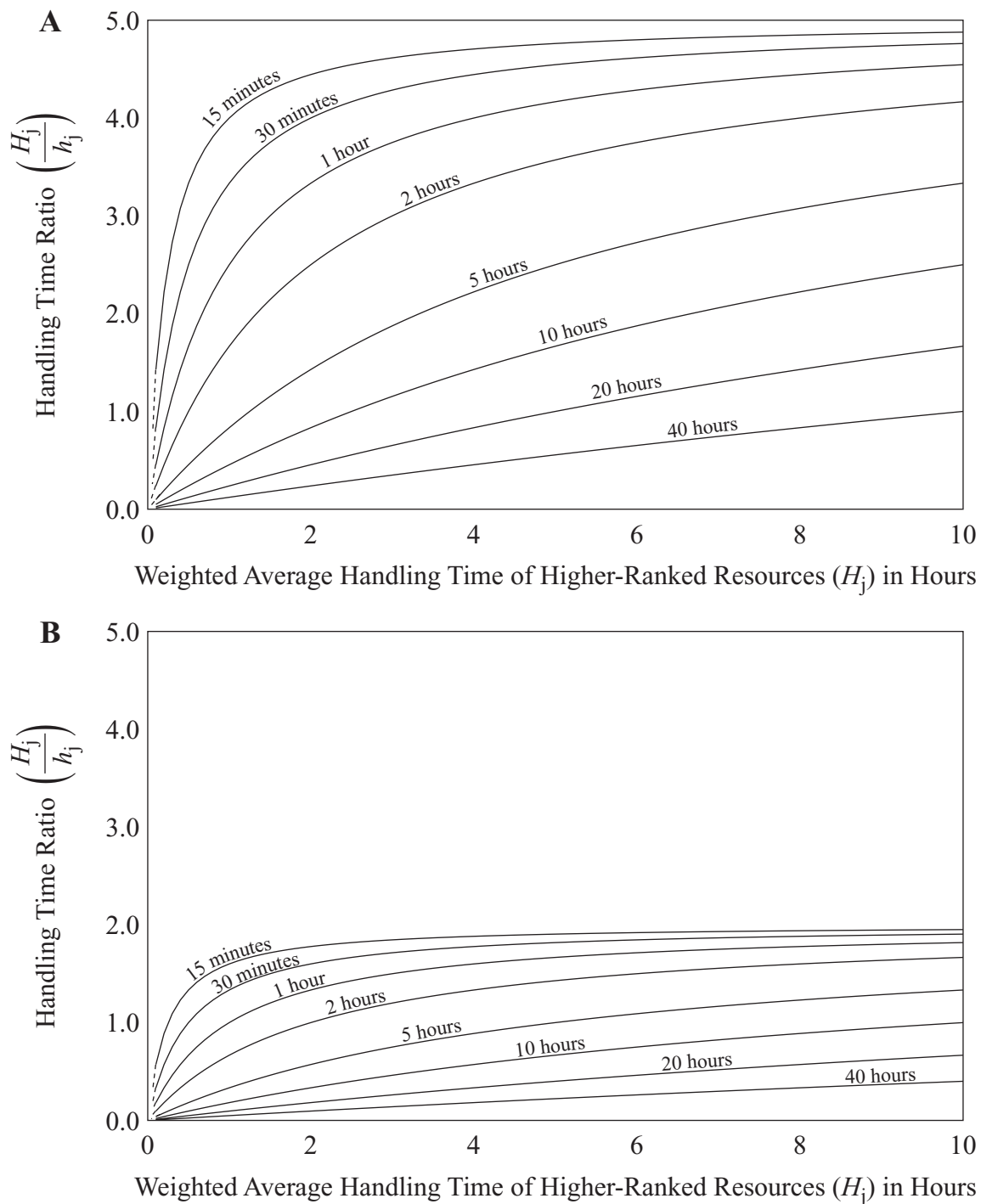


Figure 2-2. Isochrons for minimum expected time before encounter with a higher-ranked resource in order for the lower-ranked resource to be included in the optimal diet, where the encounter-rate-weighted average yield of higher ranked-resources is A) five times and B) twice that of the lower-ranked resource.

quired by the smaller ungulates in question (due, for example, to the development or adoption of hunting technology or techniques specific to those animals).

Nor are such considerations solely applicable to increases in small ungulate utilization. For example, Marean and Assefa (1999) contest Klein's (1994, 1998) argument for lower hunting capabilities in the Middle Stone Age of South Africa compared to the Late Stone Age. Klein's argument is that adult bovids are largely missing from MSA sites because the hominin hunters were not able to kill such animals reliably, but appeared in LSA sites because of an increase in hunting capabilities. Marean and Assefa, arguing in favor of fully competent MSA hunters, suggest that the greater danger involved in hunting the adult buffalo caused them to be ranked lower than other (smaller) resources, and attribute their exclusion in the MSA and inclusion in the LSA to changes in overall diet breadth. What is curious about this argument is that, however relevant danger may be to prey choice decisions, it is not an aspect of the diet breadth / prey choice model, while hunting competence (in the form of failure rates) *is*. Klein's argument for less-adept hunters in the MSA is fully compatible with a diet-breadth interpretation of the changing representation of adult buffalo, as a high failure rate leads to a high average handling time and thus a low yield-to-handling-time ratio—and thus potentially to a low ranking. On diet breadth / prey choice model grounds, the change in adult buffalo representation from the MSA to the LSA could result from *either* changes in hunting competence (reduced failure rates increasing the yield-to-handling-time ratio and thereby raising the ranking of the resource) or the addition of lower-ranked resources to the optimal diet. Moreover, the two options are not mutually exclusive; reduced failure rates could have raised the ranking of adult buffalo at the same time that lower encounter rates with other resources were shifting the efficiency threshold for inclusion downwards.

### **Repercussions for Diet Breadth and Forager Demography**

A common utilization of the diet breadth / prey choice model in archaeology is to look for changes in human population size or density. Forager demography is not formally a part of the diet breadth / prey choice model. In order to connect the model to demography, it is assumed not only that the foragers in question are behaving in accordance with the model, but also that changes in forager population size (or density) cause changes in the densities of exploited resources. If the encounter rate with a resource in the diet drops, the average return rate may decrease enough for an additional resource to be added to the diet. The general expectation is thus produced that, all else being equal, higher forager population densities will result in broader, less specialized diets.

This chapter has shown that there are other factors that can significantly complicate this picture, in addition to the always inherent concern of environmental change. Increases in diet breadth can be produced not only by reductions in encounter rates with high-ranked resources, but also by changes in handling times—particularly as a result of changes in rates of hunting failures—as well as changes in food-sharing group sizes. Furthermore, these alternative causes for changes in diet breadth do not always operate in a simple manner, as in the case (discussed above) where an increase in the density of a large animal could actually lead to increased utilization of a small animal.

This convoluted picture is further complicated by the potential for adaptive changes by the hominin hunters. It has recently been shown that in a diet breadth / prey choice model context, the determination of the resources to which technological investment should be directed is dependent on the encounter rates with all resources, not simply the higher-ranked ones (Bright et al. 2002; Ugan et al. 2003). This would initially appear to strengthen arguments that shifts in resource utilization are the result of changes in encounter rates, as these induce shifts in the specific resources to which technological

investment is directed, resulting in reduced failure rates (for those resources) and thus raising their rankings. However, this potential to raise the rankings of previously lower-ranked resources means that what were previously high-ranked resources may become the low-ranked resources *to which the foragers should turn when their population growth causes a reduction in the density of the newly high-ranked resources*. In combination with possibilities for changes in consumption limits, this is especially bad news for the utilization of prey body size as a proxy measure of ranking. If resources of different sizes have similar effective yields due to consumption limits, these technological investment models suggest that the more common—and thus probably the smaller—of the resources should receive the greatest technological investment, possibly lowering handling times for that resource to the point where the larger resource is excluded from the diet. If sharing-group sizes or meat storage capabilities increase, the newly greater yield of the larger resource could overcome the lower handling time of the smaller resource and be added to the optimal diet.

Without knowing what hunting techniques were used by a given Paleolithic society for hunting which resources and thus being able to estimate time costs of either successful or failed pursuits, without knowing how high or low failure rates might have been, and without knowing what food-sharing group sizes or meat preservation/defense capabilities were, it is essentially impossible to use the diet breadth / prey choice model to investigate forager demography in a rigorous manner. However, this does not necessarily indicate that Paleolithic archaeologists need to await techniques for inferring such data in order to make demographic inferences from resource exploitation decisions.

Stiner et al. (1999, 2000; Stiner and Munro 2002) have had substantial success in making demographic inferences from archaeofaunal data by supplementing the traditional emphasis on body size with additional criteria. They explicitly considered failure rates in

their treatment of fast, hard-to-catch prey *versus* slow, easy-to-catch prey, developed simulation models of prey populations under hunting pressure to examine population resilience and thereby the sustainability of increased exploitation levels, and found independent evidence of hunting pressure on low-ranked prey. These factors allowed them to convincingly argue for the identification of hominin population growth from small-game archaeofaunas from the Mediterranean Basin. The next three chapters of this dissertation develop similar simulation models for ungulates found in and around the Mediterranean Basin as part of an effort to determine if a similar solution can be created that will allow demographic interpretations of ungulate archaeofaunas. The results of these modeling efforts are then synthesized and evaluated in chapter 6.

#### *Notes*

1. For practical reasons, subsequent chapters of this dissertation do not make such distinctions, even though doing so would add some rigor to the arguments being made.

2. Unless consumed over a span of anywhere from several days to months, necessitating preservation and defense, the costs of which are not normally considered to be part of the diet breadth / prey choice model—though they could potentially be included in the net energetic return and handling time terms.

3. The reciprocal obligation in question does not necessarily represent an obligation to provide an equal quantity of food; social support, for example, may be an acceptable or even preferred form of payback.

4. It may be equally or more appropriate to use caloric value of the tissues in question. However, in order to avoid confusion with the *net* energetic return rate (*i.e.*, standard) version of the diet breadth / prey choice model, the mass of edible animal tissue is utilized here. The *gross* energetic return can be substituted with no effect on the math-

ematical formulations presented.

5. This formulation is not dependent on the food-yield approach to resource ranking; a similar, though less precise, result can be obtained for the standard version of the model. The standard, net-energetic-return diet breadth / prey choice model formulation (inequality 2.1) can be simplified to:

$$\frac{e_j}{h_j} \geq \frac{\Lambda_j E_j - s}{\Lambda_j H_j + 1} \quad (2.N5.1)$$

where  $E_j$  is the encounter-rate-weighted average of net energetic return for resources  $i < j$ :

$$E_j = \sum_{i < j} \frac{\lambda_i}{\Lambda_j} e_i \quad (2.N5.2)$$

and all other terms are as defined in the text. Rearranging inequality 2.N5.1 gives:

$$\frac{1}{\Lambda_j} \geq \frac{E_j h_j + H_j e_j}{s h_j + e_j} \quad (2.N5.3)$$

At this point, a simplifying assumption is necessary. Note that since resource  $j$  is included if and only if the expected time to encounter a higher ranked resource is as shown in inequality 2.N5.3, it must also be included if (but *only if* no longer applies):

$$\frac{1}{\Lambda_j} \geq \frac{E_j h_j + H_j e_j}{e_j} \quad (2.N5.4)$$

Because the denominator on the right side of inequality 2.N5.4 is smaller than that in 2.N5.3, the ratio itself is larger; therefore, any value of  $1/\Lambda$  that satisfies 2.N5.4 will also satisfy 2.N5.3, and indicate that the resource should be included. However, a gray area where:

$$\frac{E_j h_j + H_j e_j}{e_j} > \frac{1}{\Lambda_j} \geq \frac{E_j h_j + H_j e_j}{s h_j + e_j} \quad (2.N5.5)$$

has been created in which resource  $j$  should be included but which is not covered by inequality 2.N5.4. With this caveat, inequality 2.N5.4 can be rearranged to yield:

$$\frac{1}{\Lambda_j} + H_j \geq \frac{E_j}{e_j} h_j \quad (2.N5.6)$$

which is clearly analogous to inequality 2.8. The mathematically-inclined reader may be interested to note (in parallel with the yield-based model development in the main text) that the simplifying assumption made in 2.N5.4 is equivalent to the exclusion of the energy costs of continuing to search, which may be particularly justifiable if search is not an all-consuming activity (that is, if it is embedded in other useful activities or *vice versa*).

6. This example assumes that there is only one resource ranked higher than resource two (the 50 kg yield in two hours resource). Alternatively, the values presented for resource one (100 kg yield in three hours) could be considered the encounter-rate-weighted averages of yield and handling time for all higher ranked resources.

7. The ‘one-day-free’ and consumption-continuity assumptions are made because the intent in this section is to deal with general issues raised by consumption limits, rather than specifically investigate hominins’ ability to defend meat from confrontational scavengers.

8. The term ‘pursuit’ is used here in a generic fashion to include all time spent in attempting to kill a particular animal, regardless of whether or not the animal is physically chased.

9. Laying in wait for the purposes of ambushing prey is an aspect of hunting that is not simple to deal with in a diet breadth / prey choice model. If the hunter is attempting to ambush a particular animal (or group of animals) that have been seen approaching, for example, then the time involved is part of pursuit, and thus of handling time. However, if the hunter is instead hiding in a good hunting location hoping that prey will come along, the time involved is properly part of the search time component.



## CHAPTER 3

### SIMULATION OF CYCLICAL PREDATION ON UNGULATE PREY

The simulation model used in this study is descended from that employed by Stiner et al. (1999, 2000) to study population dynamics of small game under human hunting pressure. It attempts to capture the essential population dynamics of each species, while remaining simple enough to avoid model-specific behaviors. The development of this version of the model has involved several incarnations on different software platforms, all of which have produced essentially the same results; this argues for the generality of the model, supporting the contention that the population-size responses to hunting that are presented in chapter 4 reflect the parameters of the various species, and not idiosyncrasies of the model itself.

#### **Model Structure**

Population dynamics are the result of the interplay of fertility and mortality rates, as well as life-history characteristics of the species. The following parameters are used in the model, with values derived from the ecological and wildlife management literature (see below): pregnancy rate, number of offspring per pregnant female, age at first reproduction for females, maximum lifespan, natural adult mortality rate, natural base juvenile mortality rate, and the age at which individuals become subject to adult, rather than juvenile, mortality. Pregnancy rate is defined as the proportion of mature females reproducing in a given year. This parameter and the number of offspring per pregnant female are interrelated values. The computer simulation itself makes use only of the product of these values, since specific parent-offspring relationships are not critical. The parameters are retained as separate values for convenience in discussing their derivation from the

ecological literature.

As in Stiner et al. (1999, 2000), natural mortality effects are simulated differently for adults, who suffer a constant annual mortality rate, and juveniles, whose mortality rate is density-dependent. The restriction of density-dependence in the calculation of natural mortality (that is, mortality from non-human causes) to juveniles reflects the much greater impact of density-dependent causes of mortality on young animals. A base juvenile mortality rate is drawn from the ecological literature that represents the level of juvenile mortality in the absence of density-dependent effects. In practice, this value is never reached in the model (it would occur only when the population size is zero), so it should always be lower than the juvenile mortality rates reported for living populations. Juvenile mortality rates in the model are calculated from this base rate, the current population size, and a carrying capacity value according to the following equation, derived from the logistic model of population growth (Stiner et al. 2000:51):

$$m_a = m_b + \frac{n}{k} (1 - m_b) \quad (3.1)$$

where  $m_a$  is the juvenile mortality rate adjusted for density-dependent effects,  $m_b$  is the base rate of juvenile mortality,  $n$  is the current size of the population, and  $k$  is carrying capacity. This is not true carrying capacity in terms of the maximum supportable population; rather it is an empirically determined value that balances mortality and fertility to hold a population steady at a chosen size. Growing populations stabilize at a level significantly below the carrying capacity value, as some juveniles must survive to replace dying adults. Juvenile mortality in the model therefore varies within a range from the base mortality value to 100%, with lower values when the population is closer to zero and higher values when the population is closer to the carrying capacity value.

The simulation model employs a maximum lifespan parameter to handle the real-world tendency of adult natural mortality rates to increase dramatically in the last few

years of the potential lifespan. This replacement of gradual increases in mortality over a several year span with a single spike to 100% natural mortality is somewhat unrealistic. However, the effects of this modeling decision on the overall behavior of the population are minimal, as the affected age-cohorts form a small fraction of the population, and are outweighed by the benefits to model simplicity.

When human hunting is added to the model, two values are used. First, a minimum age at which individuals are hunted is set. This reflects the tendency of human hunters to focus on mature individuals when possible (Stiner 1994). The second value is the harvest rate itself, which in most cases is simply the number of animals killed by human hunters each year, but in some circumstances is instead a percentage of the extant population size.

The approach of simulating predation by removing a specific number of animals from the population per year, rather than a percentage of the extant population as was used in examining small game (Stiner et al. 1999, 2000), is employed for several reasons. The ungulate species studied here vary in body size up to thirty-five-fold, while the tortoises, hares, and partridges modeled by Stiner et al. (1999, 2000) vary in mean body size by only a factor of four or so. As a result, the actual number of animals exploited (and by analogy, the amount of food acquired thereby) is more critical to comparative analyses of ungulates than of small game. Furthermore, the ungulate species are more similar in their hunting pressure responses than are the small game animals, making simulation of realistic annual exploitation of the population more important. Harvesting a set percentage of the population every year results in widely varying numbers of animals killed over time. For example, if the initial population is 1000 animals and the harvest rate is 10% per year, then approximately 100 animals per year will be killed during the early years of the simulation. Once the population has been subjected to this

harvest rate for a few years, it will have dropped considerably, and the number of animals actually killed per year may drop to ten or fewer (see chapter 5 for additional discussion). The fact that the population is able to sustain this rate is of only limited interest since the *human* population has experienced a tenfold *decrease* in food yield. As noted above, this is not a particular problem if the goal is to compare similar-sized species with very different hunting-pressure resiliencies, as was done by Stiner et al. (1999, 2000); however, it becomes critical when comparing species of very different sizes but with much more similar hunting-pressure tolerances.

It should be noted that this number-per-year harvest simulation approach has the inverse problem in representing reality. While the number of animals killed per year—and thus the amount of food acquired by the hypothetical human population—does not change, the proportion of the extant population which must be killed to achieve that number of killed animals increases—drastically and very unrealistically as the prey population crashes. Therefore, percentage-of-extant-population hunting simulation is utilized under certain circumstances—particularly where the hunting rate needs to be increased gradually. Additionally, a percentage-killed methodology is used at times in order to verify comparability to other studies.

#### *Details of Model Implementation*

The execution of the hunting pressure model is illustrated schematically in Figure 3-1. A simulation model run is distinguished by three factors, the combination of which results in unique model behavior: the stable population to be hunted, the harvest rate, and a random number seed. The first two define the model, the third determines the specific sequence of random numbers used in the course of the simulation, thereby allowing replicability. The simulation model represents a population as two sets of age-cohorts,

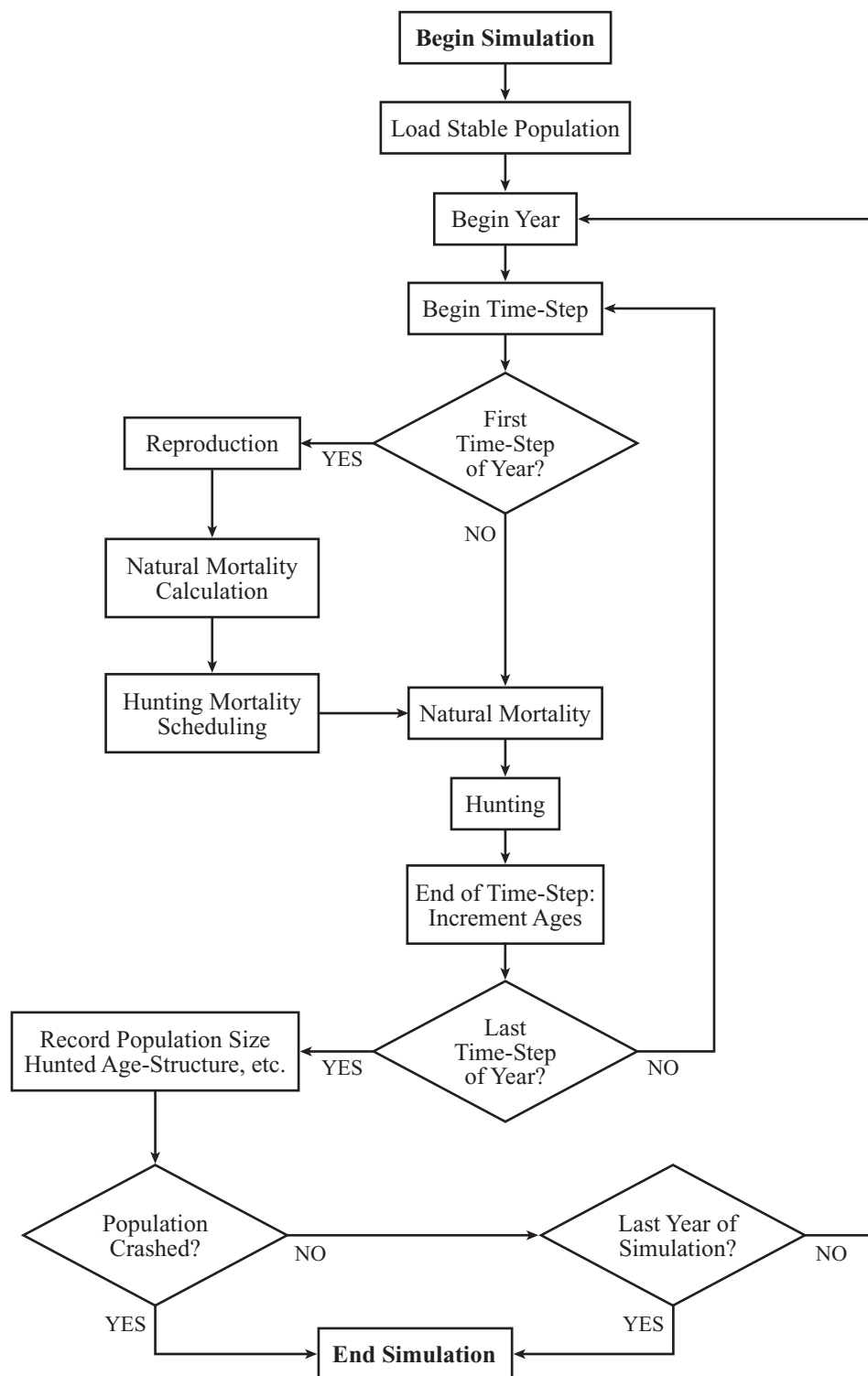


Figure 3-1. Structure of the model simulating predator-prey dynamics.

one female and one male. For each sex, every age (in time-steps—see below) from zero to the maximum allowed has an associated value indicating the number of animals of that age that are found in the population.

*Stable Populations.* Stable populations are created separately using a simplified (*sans* human hunting) version of the model that begins with an arbitrary distribution of animals into age and sex cohorts. The model is run with an arbitrary carrying capacity value until the size of the population stabilizes. The carrying capacity is then adjusted to move the stable population size closer to the target size (e.g., 1000 animals), and the process is repeated. When the population stabilizes at the target size, it is saved for later use in hunting models. This process not only determines the appropriate carrying capacity value for the population, but also allows the population to reach the appropriate equilibrium age-structure (see chapter 5).

*Years.* In the simulation model, years are used primarily for accounting purposes. Though mortality and reproductive rate values are determined in relation to full years, much of their implementation occurs during individual time-steps (see below). Population size and the age-groups of the animals killed are recorded annually for analysis.

*Time-Steps.* The simulation model distributes the effects of the factors impinging on population dynamics among a number of time-steps each year. The primary reason for the utilization of multiple time-steps per year is to minimize the impact of scheduling decisions made in the process of constructing the model. Specifically, in what order should hunting mortality and natural mortality be simulated as taking place? There is no *a priori* answer to this question, but the decision can significantly affect the results of the simulation model. If hunting is implemented *before* natural mortality, an overabundance of juveniles will be available for harvest; if natural mortality is implemented first, the number of juveniles available to be killed will be abnormally low. This dilemma is

resolved through the use of multiple time-steps within each year of the simulation model. By implementing natural mortality and hunting mortality a number of times each year, the specific scheduling of such implementation is made less important (Figure 3-2). As the number of time-steps increases, the results produced by the two scheduling options converge to the same value. For the simulation runs reported in chapters 4 to 6, the number of time-steps per year is set at twelve. This choice represents a compromise between maximum model performance (as the number of time-steps increases, the model takes longer to execute, and less data is recoverable in practical terms) and the greater accuracy afforded by more steps. Twelve time-steps per year produces results that are sufficiently close to those produced by far more steps per year, and has the additional advantage of being convenient for implementation of seasonal hunting in future research.

*Reproduction.* Reproduction occurs during the first time step of each year, an arbitrary simulation choice made for simplicity in recording population sizes. The majority of temperate-zone ungulates reproduce during a short time span each spring; the simulation model year thus effectively runs from spring to spring. Though not all of the ungulate populations modeled here have fully synchronized reproductive periods, all do

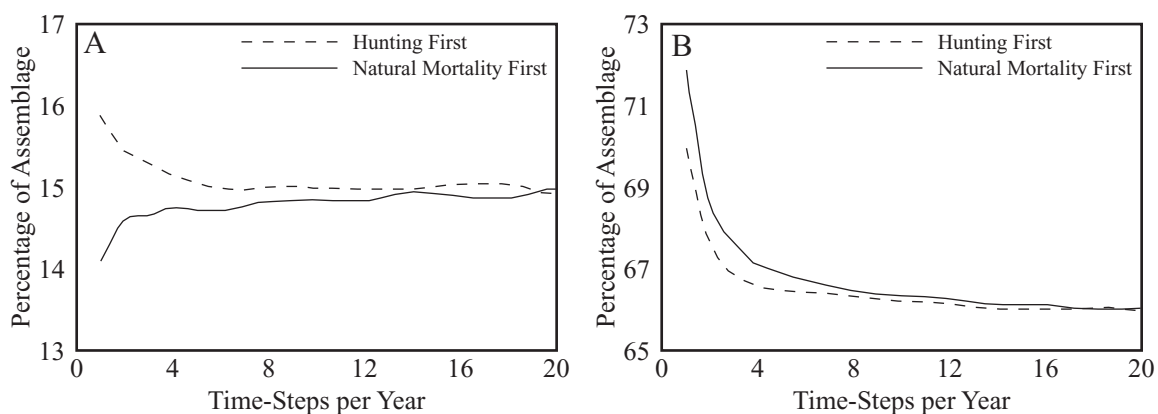


Figure 3-2. Effects of scheduling decisions at various numbers of time-steps per year. Illustrated are the percentages of killed animals falling into A) the juvenile age-group and B) the prime age-group for the red deer low growth model hunted at 1% of the initial population per year.

exhibit a peak in births in late spring.

The number of reproductively mature females in the simulated population is determined by adding together the sizes of the female age-cohorts that are at least as old as the female age of first reproduction. This is then multiplied by the annual reproductive rate (the product of the pregnancy rate and the mean number of offspring per pregnant female). The resulting number of offspring is added to the population, evenly divided between females and males (for simplicity, the model assumes that all species have a one-to-one sex ratio at birth).

*Calculation of Natural Mortality.* During the first time step of each year, immediately following the addition of the neonatal cohorts, the natural mortality that will take place for the entire year is calculated. This calculation has two parts. First, the population-density-adjusted rate of juvenile mortality is determined following equation 3.1 (see above). Second, the adjusted rate of natural juvenile mortality and the constant rate of natural adult mortality are applied to the size of each age-sex cohort, producing a number of individual animals from that cohort that should die of non-hunting causes during the year. This value is divided by the number of time-steps being utilized per year (normally twelve, see above) and stored for later use.

*Hunting Mortality Distribution.* The number of animals to be killed by per year by simulated human hunting is divided as evenly as possible among the time-steps of the year by the following procedure. Each time-step is initially assigned a number of animals to be killed that is determined by dividing the number to be killed for the whole year by the number of time-steps, and rounded *down* to the next whole number. A number of time steps equal to the remainder produced by this division are then selected at random and the number to be killed in each of these time steps is increased by one. For example, if 27 animals are to be killed per year and there are twelve time-steps, each time-step is



initially set to have two animals killed. Three of the time-steps are then chosen at random and their numbers of animals to be killed increased to three animals each.

Where percentage-killed hunting is used, the number of animals to be killed in a given year is determined by multiplying the percentage rate by the population size, which virtually always produces a non-integer value. The fractional part of the value is treated as a probability and compared to a random number. If the random number is smaller than the fraction, the number of animals to be killed is rounded up; if it is larger, the number of animals to be killed is rounded down. Once the final value is determined, it is treated identically to the simple number-killed hunting procedure just discussed.

*Natural Mortality.* During each time step, the size of each age-sex cohort is reduced by the number of individuals calculated for it at the beginning of the year (see above).

*Hunting.* The number of animals to be killed in a given time-step is pre-determined as discussed above. Hunting mortality is carried out by selecting an age-sex cohort at random with the probability of a given cohort being selected determined by its size as a fraction of the total huntable population. The huntable population consists of the age-sex cohorts corresponding to ages greater than or equal to the minimum age hunted. This process is repeated for each of the animals to be killed. Once the age-sex cohort has been selected, its size (that is, the number of animals it includes) is reduced by one. The age and sex of the animal thus killed are retained by the simulation program for data output at the end of the year.

*Age Incrementation.* At the end of each time-step, the value indicating the size of each age-cohort is assigned to the next older age-cohort (recall that cohort ages are kept in time-steps, not years). The oldest allowed cohort (as determined by the maximum age parameter) is thus lost, implementing the death of animals exceeding the maximum age

parameter.

*End of Year.* At the end of each simulation model year, the total size of the population is recorded, as are the age-structure of the living population and the age-structure of the animals that were killed (the latter data are discussed in chapter 5). If the population size has reached zero, or if the total number of years the simulation model was set to run have elapsed, the simulation model ends, and all recorded data are output to data files.

### **Determination of Species Parameters**

There are special difficulties involved in deriving modeling parameters for ungulates from the ecological and wildlife management literature. While human intervention in small game population dynamics (whether direct in the form of hunting, culling, or habitat destruction, or indirect in the form of predator removal) is not uncommon, such intervention is substantially more frequent and consequential with large game. Additionally, supplemental winter feeding is a common aspect of large game management, but virtually unknown for small game. While it would be preferable to restrict data gathering to those populations whose mortality and fertility rates have not been artificially increased or decreased by management efforts, there are simply too few studied ungulate populations that meet such criteria. As a result, it is necessary to take into account the management (and other) impacts to which each population is subject when developing modeling parameters. Fertility and survival rates may be unnaturally high in populations that receive supplemental feeding in the winter. Predator exclusion results in mortality rates that are unnaturally low. Habitat destruction, or exclusion from it, is an even more difficult problem for parameter determination; if a species only exists today in non-optimal environments, determining the 'natural' characteristics of its dynamics is impossible, and the modeling parameters that are derived must be used with this in mind.

As in Stiner et al. (1999, 2000), two sets of parameters are developed, termed the low growth model and the high growth model (abbreviated LGM and HGM) for each species included in this study. These represent extremes of population growth rates, and are used to compensate both for the vagaries of modeling species whose growth behavior cannot be observed in settings equivalent to those that existed prehistorically and for the inability to know how optimal any given area was for any given species in habitat terms. Instead of comparing best estimates of population tolerance of hunting pressure, the resulting comparisons utilize minima and maxima.

Modeling parameters are developed for the following species commonly found in Pleistocene archaeological assemblages in the Mediterranean Basin and Europe: aurochs (*Bos primigenius*), fallow deer (*Dama dama*), gazelle (*Gazella gazella*), goat (*Capra aegagrus*), ibex (*Capra ibex*), red deer (*Cervus elaphus*), and roe deer (*Capreolus capreolus*).

### *Aurochs*

There is, of course, no ecological literature about the extinct aurochs; the literature on modern large wild bovids is used as a proxy. The population characteristics of three species are examined here in order to develop modeling parameters that, while not specific to aurochs, should be more similar to aurochs than to the other species under investigation. North American bison (*Bison bison*) provide the majority of the data, with European bison (*B. bonasus*) and African buffalo (*Syncerus caffer*) providing checks on the American bison data.

*Pregnancy Rate.* Reported pregnancy rates for North American bison vary widely; many studies report values between 28% and 52% (Carbyn et al. 1993:120, 230; Kirkpatrick et al. 1996; Meagher 1973, cf. Calef 1984; Van Camp and Calef 1987; Wolfe

1998; Wolfe et al. 1999). Other studies report higher values—up to 87% (Berger and Cunningham 1994:106; Fuller 1966; Halloran 1968; Haugen 1974, cf. Calef 1984; Meagher 1973, cf. Calef 1984; McHugh 1958; Van Vuren and Bray 1986), but the majority of these higher values are for very low density populations, or populations that are helped through the winter with supplemental feeding. Significant variation is also reported for European bison. Krasinski and Raczynski (1967) report 76.2% and 70.3% pregnancy rates for European bison cows that are human-supported, receiving significant (“intensive”) supplemental feeding in winter. In contrast, they (1967:422) cite several studies from the early twentieth century as describing cows in unsupported populations as calving once every two to three years. Additionally, Krasinski (1978) reports that the pregnancy rate of these populations decreased to an average of 54.1% after the 1967 study, *despite* the bison receiving “almost 100% of the animals’ diet” (Krasinski 1978:13) from hay provided as supplemental feed during the winter. Observed African buffalo values are high as well (69.5%, Sinclair 1977:225; 52.3%, Prins 1996); however, Prins (1996:151) considers this rate to be too high in light of the low juvenile proportion of the population, and concludes that three years is a “more realistic calving interval” (Prins 1996:151). It appears that the higher pregnancy rates reported for all three species are due to exceptionally low population densities and/or supplemental feeding. A reproductive rate approximately equivalent to once per three years (.33) is therefore set for the low growth model. For the high growth model, a rate just less than once per two years (.45) is used.

*Average Number of Offspring.* Twinning is virtually nonexistent in all three species (Berger and Cunningham 1994; Fuller 1966; Krasinski and Raczynski 1967; Prins 1996), so the number of offspring per year is set to one for both models.

*Age at First Reproduction.* North American bison rarely reproduce before age

three (Berger and Cunningham 1994:132; Carbyn et al. 1993:120; Fuller 1966; Haugan 1974, cf. Calef 1984). Krasinski and Raczynski (1967) report that most European bison calve for the first time between 35 and 38 months. African buffalo apparently reproduce for the first time even later. Sinclair (1977:168) reports that only 28% of four-year-olds are pregnant, while Prins (1996:151) reports that the “average cow has her first calf when approximately 6 years.” Given the supplemental feeding and low population densities of the bison populations studied and the later first reproduction of the African buffalo, the age at first reproduction for aurochs is set at four for both the high and low growth models.

*Base Juvenile Mortality Rate.* Juvenile mortality rates for North American bison range from extremely low, such as 2.5% to 4.2% (about half of which is human-caused, Berger and Cunningham 1994), 6% (Van Vuren and Bray 1986), and less than 5% (Calef 1984), to extremely high, such as 70% to 94% (Calef 1984) and 72% (Fuller 1966). The lower rates are for un-predated and fast-growing populations, while the higher rates are for declining or stable populations, usually with significant wolf predation. Krasinski and Raczynski (1967) report a 2.29% mortality rate for European bison calves. However, they cite Wroblewski (1927) for a 49.3% juvenile mortality rate before supplemental feeding began. Krasinski (1978) reports juvenile mortality of approximately 10% for ages 2-3 combined. Prins (1996) reports an African buffalo calf mortality rate of 42.9% in 1983 and 55.3% in 1991, the latter being a drought year. Sinclair (1977) reports calf mortality of 48.5%, and 25% yearling mortality. The absence of predation from the populations whose attributes are probably closest to a base juvenile mortality rate is a significant problem. Van Camp (1987), however, reports that 61% of bison mortality in the Slave River Lowlands population falls into what this model would consider natural. Of the total mortality, 31% for adults and subadults and 27% for calves is attributable to

wolf predation. Thus, with approximately 60% of mortality being natural and approximately 30% of mortality being due to predation, it can be estimated that roughly half of the natural mortality is probably “missing” from the populations that are not subject to predation. Since Van Camp (1987) also suggests that “wolf predation...appeared to be additive rather than compensatory mortality,” the observation that half of mortality may be missing can be used to adjust the low values discussed above. Roughly doubling the low juvenile mortality rates discussed above results in values in the 10-12% range. Data on sex-specific mortality are contradictory. Berger and Cunningham (1994:106) report that male juvenile mortality is about twice that of females. Sinclair’s (1977) data, however, suggest that sex does not significantly impact juvenile mortality in African buffalo. To capture both of these, the base juvenile mortality rates for the high growth model are set to 10% for both males and females, while the low growth model rates are set to 11% for females and slightly higher, 13%, for males.

*Age of Onset of Adult Mortality.* Berger and Cunningham (1994:102) divide adult North American bison from juveniles at ages three (for females) and five (for males); the juvenile mortality rates discussed above relate to these ages. Krasinski (1978) shows a significant drop in European bison mortality rates between age class 2-3 and age class 4-10. Sinclair (1977:210) states that “mortality after two years old was small and relatively constant” in African buffalo. Adult mortality is thus set to begin at age three for both the low and high growth models.

*Adult Mortality Rate.* Berger and Cunningham (1994:106) report adult mortality rates between 0.5% and 3.2% in a non-predated North American bison population. Carbyn et al. (1993:223) use values of 2.5% for summer and 10% for winter mortality in their model. Calef (1984) calculates adult mortality, apparently excluding predation, as no more than 5%. Van Vuren and Bray report adult mortality rates of 4% (females) and

5% (males), again in the absence of predation. Krasinski (1978) provides a graph in which adult mortality of European bison appears to be about 4% for age class 4-10, and reports mortality rates of 2.6% and 2.1% for age classes 11-15 and 16-21, respectively. Prins (1996) reports 4.4% of adult African buffalo females and 12.9% of adult males were killed per year by lions. Lion predation accounted for 89% of total mortality, so adult mortality rates are closer to 5% and 14.5%, respectively. Sinclair (1977) presents lifetables for African buffalo from which adult mortality rates close to 10% can be calculated. For the reasons discussed under juvenile mortality, the North American bison mortality rates are considered to be only about half their 'real' values. In combination with the African buffalo data, this leads to adult mortality rates of 5% (female) and 8% (male) for the low growth model and 4% (female) and 6% (male) for the high growth model. Most of these values are below the African buffalo mortality rates; this is intentional, since predation on aurochs on the eastern and northern edges of the Mediterranean in the Pleistocene (the regions to which the models are primarily applied in subsequent chapters) probably involved fewer lions.

*Maximum Age.* Berger and Cunningham (1994:Figure 3.3) show 18 as a maximum age for North American bison. Similarly, Halloran (1968) reports "very few animals in age classes above 17." Krasinski and Raczynski (1967) report a reserve European bison cow living to age 24, but note that she had her last calf at age 19. They consider two other reserve cows observed with calves at age 17 to be of special interest. Twenty-one is the highest age in the age class system used by Krasinski (1978) for European bison. Sinclair's (1977) lifetables show 18 as the maximum age; however, mortality exceeds 50% at age 16. Based on these data, the low growth model maximum age is set at 16, while the high growth model maximum age is set at 18.

### *Fallow Deer*

The ecological literature on the Persian fallow deer (*D. d. mesopotamica*) is virtually nonexistent, since the subspecies is nearly extinct. Most of the data discussed here therefore refer to the European fallow deer (*D. d. dama*). The majority of fallow deer are park deer—faced with artificially low levels of predation and systematically culled for management purposes.

*Pregnancy Rate.* Pregnancy rates of 95% (Armstrong, et al. 1975) and 91% (Baker 1973) are reported as are fawn per doe rates of 73% (Asher, et al. 1981) and 96% (Chapman and Chapman 1975). Rates of 71% and 78% (Saltz 1996) are reported for world-wide and Hai-Bar Carmel zoo/reserve populations, respectively. A value consistent with the higher set of rates (.9) is assigned to the high growth model, while one consistent with the lower rates (.75) is assigned to the low growth model.

*Average Number of Offspring.* Fallow deer twinning rates are essentially zero (Baker 1973; O'Bryan 1978). The effects of the occasional twin pregnancy should be not only minor but somewhat covered by the use of fawns per doe data in the pregnancy rate.

*Age at First Reproduction.* Fallow deer females occasionally mate at age one and reproduce around their second birthday (Chapman 1974; Chapman and Chapman 1975; Putman 1985). In other cases, the first mating occurs at age two (life-table data in Saltz 1998), giving birth around age three. Because of the rarity of the former case, and its tendency to be associated with park deer, an age of two years is used for both models.

*Base Juvenile Mortality Rate.* The types of studies conducted on fallow deer make it very difficult to determine mortality parameters. In fact, only three studies were found that reported juvenile mortality at all. One, a management modeling effort (Putman 1985) used survivorship rates of 0.6 and 0.8 for the first two years of life. Converting these to a single mortality rate producing the same rate of survivorship through to



the third year produces an annual mortality rate of 30.7%. The second study (Saltz 1998), based on a recently reintroduced population of Persian fallow deer in Israel, reports survivorship rates of 0.66 and 0.93 for the first two years. The same procedure used with Putman's numbers produces an annual mortality rate of 21.7%. The third study reported a survivorship (for the first year only) of 90% (Braza, et al. 1990) in a National Park in Spain. This value was considered surprisingly high even by the authors, and attributed to very mild winters and the effective absence of predators. The equivalent mortality rate has therefore been heuristically increased by 50% and assigned as the base juvenile mortality rate for the high growth model (.15). The lower of the two high values is assigned as the rate for the low growth model (.21). The majority of the data used here represents females only; males were assumed to have the same mortality rates in the absence of data to the contrary, though this is not typical of larger cervids in general.

*Age of Onset of Adult Mortality.* The very limited nature of the data discussed above made it very difficult to determine whether adult mortality should begin at age one (as implied by the data in Saltz 1998, where mortality at age one was the same as at ages two through eight) or at two (the age at which the mortality rate was modeled as dropping to zero in Putman 1985). It is speculated that the effects of predation would increase the likelihood of yearling mortality, resulting in use of an age of two years for both models.

*Adult Mortality Rate.* Saltz (1996) reports a 7% mortality rate for adult females based on world-wide zoo data, and the same figure for mortality from ages two through eight for a reintroduced population in Israel (Saltz 1998). Putman's (1985) mortality rates per two-year age class are somewhat heuristic. He uses a zero mortality rate for ages three through eight, and then increases mortality drastically for the last few years of life. It thus seems better to rely on Saltz's data and use the .07 mortality rate figure for females in the high growth model. Male mortality is set slightly higher (at .08) because of the

more rapid increase in male mortality after age eight shown by Putman (1985). Low growth model values are set higher (.11 and .12 for females and males, respectively) since the reported values are designed to model, or result from observations on, rapidly growing populations.

*Maximum Age.* Mortality begins increasing at age nine in both Putman's (1985) model parameters and in Saltz's (1998) reintroduced population. Putman's (1985) model increases mortality very dramatically in the thirteen and fourteen year-old age class. Saltz (1998) provides a life table that ends with age thirteen, showing a very high mortality rate for that age. Saltz (1996) reports a maximum age of sixteen years for zoo animals, but uses an age of fourteen for modeling his reintroduced population. The high growth model sets the maximum age at fourteen, while the low growth model assumes additional predation effects, and sets the maximum age at twelve.

### *Gazelle*

The ecological literature on mountain gazelle (*Gazella gazella*), the species most likely represented in Levantine Paleolithic sites, has been examined by Munro (2001:227-233) for use in a previous modeling effort. In an effort to avoid some of the difficulties faced by Munro (in particular, having to use the same adult mortality rate for both high and low growth models in order to avoid having the low growth model crash under zero hunting pressure), it was decided to cast a wider net and consider studies of other gazelle species. There are many other species of gazelle, some of which are quite different in size from the mountain gazelle. Most of the supplementary data used here relates to similarly sized gazelle, especially dorcas gazelle (*G. dorcas*) and Cuvier's gazelle (*G. cuvieri*).

*Pregnancy Rate and Average Number of Offspring.* Munro (2001:229-230) set

minimum and maximum values for offspring per female per year at .7 and 1 for the low growth model and 1 and 1.4 for the high growth model. The data collected in broadening the search are similar. Dunham (1997) reports a 100% pregnancy rate and 1.54 offspring per year in a small reintroduced population of mountain gazelle in central Arabia. Martin (2000) reports rates up to 100% in a broader survey of gazelle species than this one. Haque and Smith (1996) report a 27% twinning rate for a *G. subgutturosa* group being released into the wild. Alados and Escós (1991) report 1.31 calves per adult female dorcas gazelle per year (including females that did not reproduce) and 1.56 calves per adult female Cuvier's gazelle (again including females with no calves). Therefore, parameter values are selected here which produce reproductive rates equal to the mean values of Munro's (2001) minimum and maximum values, 1.2 (high growth model) and .85 (low growth model).

*Age at First Reproduction.* Some of the studies consulted here provide data on the age at which females first reproduce that differ somewhat from the values used by Munro (2001). Furley (1986) reports first reproduction at ages one to two in several African gazelle species. Alados and Escós (1991) report first reproduction at age two for both Cuvier's and dorcas gazelle. Martin's (2000) survey of gazelle species notes first reproduction at ages of both one and two. However, none of these data refer specifically to mountain gazelle, and in most cases include some reproduction at age one; therefore, Munro's value of age one year for both the low growth and high growth models is retained.

*Base Juvenile Mortality Rate.* The majority of studies examined here report juvenile mortality rates comparable to those of the studies of Israeli mountain gazelle used by Munro (2001). Alados and Escós (1991) report 17% male and 28% female juvenile mortality during the first month of life for dorcas gazelle and 22.4% mortality

over the first three months for Cuvier's gazelle—though the majority (72%) of this latter figure is attributable to the first month of life. Since mortality should continue to drop over the remainder of the first year of life, these values are likely not too much lower than the actual mortality rates for calves. Although these juvenile mortality rates are not substantially lower than those used by Munro (2001), in order to maintain consistency with the other species models used here, slightly lower values are used as the base juvenile mortality rates to account for the amount of mortality attributable to the population densities at which the study populations are living. Base juvenile mortality is thus set to .4 for the low growth model and .25 for the high growth model. Some additional support for this comes from parameters used by other researchers to model the related (and similarly sized) Mongolian and Przewalski's gazelle (*Procapra guttorosa* and *P. przewalskii*). Li and Jiang (2002) use calf mortality rates of 20-40% for Przewalski's gazelle, and Milner-Gulland and Lhagvasuren (1998) use a base calf mortality rate (a similar system to that used in this study's model) of 22.6%.

*Age of Onset of Adult Mortality and Adult Mortality Rate.* The studies consulted here provide no reason to change Munro's (2001) age at onset of adult mortality values for gazelle. Munro (2001) used a mortality rate of 20% for both the low and high growth models, since the low growth model was unsustainable with a higher rate. The studies examined here suggest that slightly lower mortality rates may be appropriate. Dunham (1997) reports a 22% average mortality rate for all age groups (including juveniles) in a reintroduced mountain gazelle population in Saudi Arabia. Alados et al. (1988) provide lifetables for dorcas and Cuvier's gazelle from which adult mortality rates of 16% and 14%, respectively, can be derived. Although these last two populations are in captivity and are thus provided with food, they have increased mortality due to high population densities (by conspecific aggression in particular). As with the base juvenile mortality

rate, the Mongolian and Przewalski's gazelle data (Li and Jiang 2002; Milner-Gulland and Lhagvasuren 1998) are also suggestive of lower adult mortality rates. The low growth model adult mortality rate used by Munro (2001) is carried over, but the high growth model rate is lowered to .15.

*Maximum Age.* Although some studies report lower maximum ages than that used by Munro (2001)—e.g., 9 for dorcas gazelle and 10 for Cuvier's gazelle (Alados and Escós 1991), this limited amount of data seems insufficient to alter the values, particularly given that the maximum age parameter has a relatively small impact on population dynamics.

#### *Wild Goat*

The ecological literature on wild goats is not comprehensive; as a result, data on closely related taxa such as feral goats (*Capra hircus*), tahr (*Hemitragus* sp.), ibex (*C. ibex*, see below), and markhor (*C. falconeri*) have been consulted for cross-checking purposes.

*Pregnancy Rate and Average Number of Offspring.* In significant contrast to many studies of cervid taxa, reproductive data are actually less available than mortality data. Only two data points were found for wild goat pregnancy rates, 72% in a Himalayan population (Schaller 1977:125) and 42% for one year only in an isolated small population of Cretan agrimi (Husband et al. 1986). Pregnancy rates for tahr populations vary widely, including 38%, 39%, and 43% for three separate populations (Caughley 1977) and 90% for a fourth (Caughley 1971; cf. Schaller 1977:125).

Similarly little data is available regarding the number of offspring produced by wild goats. Korshunov (1994:241) reports that wild goats in Turkmenistan have “usually...two kids.” Husband et al. (1986) report 19 kids born to 11 females, though

less than half the adult females reproduced that year. Aleem (1979) reported an overall reproductive rate (product of pregnancy rate and number of offspring) of 1.025 for markhor in Pakistan. Tahr populations are reported as always producing only a single offspring (Caughley 1970, 1977), but Schaller (1977:127) notes that low altitude arid habitat goats have a high twinning potential compared to high altitude goats (although this does not technically include tahr).

Pregnancy rate parameters were chosen in line with the available pregnancy rate data, while numbers of offspring are lower than the reported cases of significant twinning, but take into account Schaller's statement about the higher twinning rates of low altitude goat populations. The pregnancy rate and number of offspring parameters chosen produce kid:female ratios of  $(0.6 \cdot 1.5 =) 0.9$  for the low growth model and  $(0.7 \cdot 1.7 =) 1.19$  for the high growth model. These are consistent with the limited data available for wild goat total reproductive rate.

*Age at First Reproduction.* Of the studies examined, Korshunov (1994:241) presents the only data for wild goats as to the ages at which females have their first offspring, stating that age two is the minimum while three is more common. Caughley (1971; cf. Schaller 1977:125) reports that 67% of tahr females reproduce for the first time at age two in a good habitat, while only 27% do so in a poor habitat (the remainder reproducing for the first time at age three). Because of concern that the habitats of the referenced populations are less hospitable than the Mediterranean Basin habitats of the populations being simulated, an age of two years is used for both models.

*Base Juvenile Mortality Rate.* The basal rate of juvenile mortality is the most difficult parameter to set, since very few populations can be considered to be under no population pressure. Schaller reports kid mortality in markhor in Kashmir is 50-60% (Schaller 1977:128) and that of a wild goat population in the Himalayas is approximately

three-quarters. Husband and Davis (1984) report 25% and 26% kid mortality rates for female and male agrimi, respectively. Comfort (1957) reports a 36% mortality rate for wild goat kids (over the first ten months, not the full year) in captivity. Aleem (1979) reports a 29% kid mortality rate for markhor in Pakistan. Schaller (1977:129) reports a kid mortality rate of less than 25% for Nilgiri tahr, while Caughley (1977) reports a 37% kid mortality rate in an increasing tahr population and a 53% kid mortality rate in a stable tahr population. In significant contrast to all of these, Korshunov (1994) reports a mortality rate of 0.5%; this is presumably indicative of sampling and visibility problems, but also suggests that mortality can be considerably lower than the other reported rates.

The lowest mortality rates should be close to the base mortality rate, but are by definition (if we assume that our model of juvenile mortality is actually in effect) higher than the base rate, which would only occur at a population size of zero. Therefore a value similar to the lowest reported rates is set as the base juvenile mortality rate for the low growth model (.25) and a lower rate (.15) is set for the high growth model.

*Age of Onset of Adult Mortality.* Several of the studies cited above in the discussion of juvenile mortality report both kid and yearling mortality rates or discuss yearling mortality in general terms. In most cases, the yearling mortality rate is significantly lower than that for kids. For example, 13% instead of 29% for Pakistani markhor (Aleem 1979) and 5% instead of 25-26% for agrimi (Husband and Davis 1984). Adult mortality is thus considered to take effect at the age of one year for both the low and high growth models.

*Adult Mortality Rate.* Wild goat in Turkmenistan provide the highest adult mortality rate at 23% (calculated from Korshunov 1994:Table 5). Estimated lifetables provided for agrimi by Husband and Davis (1984) suggest mortality rates of 15.4% for females and 16.6% for males. Schaller (1977) reports 8-20% adult mortality for Karchat wild goats. Comfort's (1957) lifetable data on animals in captivity indicate a 10% mor-

tality rate. Adult mortality for feral goats on the island of Rhum, Scotland is 16.3% (calculated from life table in Boyd 1981). Tahr adult mortality rates of 11% and 15.4% are reported by Caughley (1977), while Schaller (1977) reports a 19% mortality rate for Nilgiri tahr. The low growth and high growth model adult mortality rates are set to 15% and 10%, respectively.

*Maximum Age.* Korshunov (1994) reports a maximum age of 11 for wild goats in Turkmenistan, Husband and Davis (1984) report a maximum age of 12 for agrimi, and Schaller reports a maximum age of 15 (Schaller 1977:131) for wild goats. As fifteen seems excessive when compared to other similarly-sized ungulate species, the maximum age parameter is set to 12 for both models.

### *Ibex*

The ecological literature on ibex is extremely sparse. All ibex data are therefore evaluated in light of wild goat data (see above)—though with the recognition that ibex tend to live in less productive environments and at lower population densities and are thus expected to have lower reproductive and mortality rates.

*Pregnancy Rate and Average Number of Offspring.* There is considerable variability in the few reports of ibex pregnancy rates that were located. Habibi (1994:94) reports that all mature females were followed by kids, suggesting a 100% pregnancy rate. Loisan et al. (2002) report a pregnancy rate of 87% in a very rapidly growing recently introduced population. Toïgo et al. (1997) report an 80% pregnancy rate after age two. Escós and Alados (1991) report kid/female ratios for three populations, with mean values for the two populations with multi-year data of 50.5% and 77.1%. Most authors seem to assume only one kid per pregnancy, though Habibi (1994:94) reports an approximately 30% twinning rate and Fandos (1989) reports a 20% twinning rate for animals in semi-



captivity. However, Fandos (1989) also reports a lack of twins in a free-roaming population. The 100% pregnancy rate reported by Habibi is not the result of systematic quantitative study and is therefore not given significant weight—furthermore, this is a desert, rather than mountain, ibex population. The remaining values are spread primarily around 80%, with one outlier near 50%. The former value is accepted for the high growth model. The 50.5% value suggests that the low growth model rate should be lower, but the consistency of the 80%-plus values suggests that it should not be this much lower; it is therefore set at 70%. The number of offspring for the low growth model is set at one. Though there are two reports of higher twinning rates, the high growth model number of offspring is set to only 1.1 since twinning does not seem to be particularly common in ibex.

*Age at First Reproduction.* Fandos (1989) reports observing no free-roaming two-year-old ibex with kids, but Loisan et al. (2002) report age two as the normal age of first reproduction in their rapidly growing introduced population. Toïgo et al. (1997) report that many two-year-old females are followed by kids, but “many” here apparently means something less than 80%, since they go on to report that over 80% of females over the age of two are followed by kids; this suggests that reproduction at age two occurs, but is not common in their study population. Age two does, however, appear to be the most common age of first reproduction, and is therefore used for both low and high growth models.

*Base Juvenile Mortality Rate.* Virtually no data are available regarding juvenile mortality rates in ibex. Kid to female and yearling to female ratios reported for consecutive years by Escós and Alados (1991) suggest kid mortality rates on the order of 50-60%. The lowest single year apparent rate is 33%. In the absence of sufficient information on ibex, the parameters assigned for the related wild goat (*Capra aegagrus*) are considered. The base juvenile mortality rates for the ibex low and high growth models are arbitrarily

set one-fifth lower than the respective rates for wild goat.

*Age of Onset of Adult Mortality.* No useful data have been found for ibex populations regarding the shift to adult mortality. There is suggestion, however, of a longer period of development, so the age at onset of adult mortality is set to two, rather than one.

*Adult Mortality Rate.* As with juvenile mortality rates, very little information has been found for ibex adult mortality rates. Loisan et al. (2002) report adult mortality of about 6% in a very rapidly growing, recently introduced population, and Toïgo et al. (1997) report 3% mortality rates for both males and females in a growing reserve population. Since both populations are relatively protected, these values are likely slightly low. With this caveat, the values are not too far out of line of the results of applying the same one-fifth reduction to the wild goat high growth model adult mortality rate as was applied to the wild goat base juvenile mortality rates. Similarly, an 11% adult mortality rate for ibex reported by Schaller (1977) is close to one-fifth less than the wild goat low growth model adult mortality rate. As a result, this procedure is followed here as well.

*Maximum Age.* No useful ibex-specific data could be located regarding lifespan. The values for the wild goat low and high growth models are carried over by default.

### *Red Deer*

The ecological literature on red deer includes no pristine populations. Rather, all studied populations are protected for scientific study, sport hunting, or are farmed.

*Pregnancy Rate.* Pregnancy rates of 82.3% for two-and-a-half year old hinds and 90.0% for three-and-a-half year-old hinds are reported by Bunnell (1987). An overall pregnancy rate of 71% is reported for a farmed population by Hamilton and Blaxter (1980). Calf-per-hind rates of 30.7% (Mitchell 1967), 34.6% (Mitchell 1967; Mitchell et al. 1977), 38.1% (Clutton-Brock et al. 1982), 39.2% (Mitchell and Crisp 1981), 41.5%

(Mitchell 1967), and 45.8% (Staines 1978) are reported for populations in Scotland. The difference between the high rates reported by Bunnell (1987) and the lower calf-per-hind rates are probably attributable to neonatal mortality, which is unlikely to appear in juvenile mortality data, and therefore should be considered here. Thus, pregnancy rates of 45% (low growth model) and 65% (high growth model) are used.

*Average Number of Offspring.* Reported percentages of pregnancies with twins are low enough that a case was published as the first known in Britain (Guinness and Fletcher 1971). Brna (1969) reports a 2.0% twinning rate. Clutton-Brock and Albon (1989) report a 0.7% twinning rate. With such low rates, and any twins likely covered through the use of calf-to-hind ratios rather than pregnancy counts above, the number of offspring per year is set to one for both models.

*Age at First Reproduction.* Though there are several reports (e.g., 32.2% for one-and-a-half year old hinds, Bunnell 1987) of yearling pregnancies, these appear to occur only in extremely favorable conditions. At the other end of the spectrum, hinds breeding for the first time in their fourth year are not uncommon (Albon et al. 1987). Age at first reproduction is thus set at three for both models.

*Base Juvenile Mortality Rate.* All available juvenile mortality data derive from studies on the island of Rhum, Scotland. Albon et al. (1987:Table 1) report a range of juvenile mortality rates for separate cohorts of females from which the following mean values are derived: 22.7% for calves, 9.8% for yearlings, and 17.3% combined calf and yearling. Clutton-Brock et al. (1982:Figure 5.5) report calf mortality rates of 24 to 27% (for females) and 16 to 36% (for males), as well as yearling mortality rates of 9% (for females) and 6 to 23% (for males). They also separately report (Clutton-Brock et al. 1982:Table 12.1) calf mortality rates of 13.6% (for females) and 16.2% (for males), and yearling mortality rates of 7.4% (for females) and 15.4% (for males). Weighted (by

cohort size) averages of these values are 11.9% for females and 15.4% for males. Albon et al. (1987) report a juvenile mortality rate of zero for an extremely low population density. Given the non-predated nature of these populations, high growth model rates are set roughly equivalent to these sets of values, while low growth model rates are set somewhat higher.

*Age of Onset of Adult Mortality.* There is a significant reduction in mortality from yearlings to two-year-olds, where mortality is very close to its lowest point (Albon et al. 1987; Clutton-Brock et al. 1982). Adult mortality is therefore set to begin at age two in both models.

*Adult Mortality Rate.* As with juvenile mortality rates, sufficiently detailed data regarding adult mortality rates are also restricted to the Rhum studies. Albon et al. (1987:Table 1) report annual mortality rates for females of 0-8.6% (mean 4.4%). Clutton-Brock et al. (1982:Table 12.1) show mortality rates ranging from 1.1-8.7% (mean 3.4%) and from 1.8-37% (mean 6.7%) for males. Since this is a non-predated population, the effects of the increased mortality at old ages are not excluded in the hope that this will cancel out the lack of predation. High growth model values are set in accordance with these typical values, and again the low growth model values are determined by increasing the high growth model values slightly.

*Maximum Age.* Though the un hunted populations from which most of these data are derived often have individuals surviving to ages in the high teens (and individuals living into their 20s are occasionally reported), there is a dramatic increase in mortality in the early teens. Maximum age is set at 14 years old for both males and females in both models.

### *Roe Deer*

The ecological literature on roe deer is relatively abundant, since modern populations remain common. Roe deer have adapted quite well to the modern world, and are extremely common in Europe—sufficiently so that a half-million can be killed annually in Germany (mostly by automobiles) without endangering the population (Nowak 1999:1132).

*Pregnancy Rate.* Pregnancy rates in roe deer vary considerably. Fruzinski and Labudzki (1982) and Vincent et al. (1995) report low pregnancy rates of 55% and 50%, respectively. The latter figure however, is the rate for that study during high population density years. During low population density years, Vincent et al. (1995) report a pregnancy rate of 80%. Furthermore, Vincent et al. (1995) determined their figures from observations of does with fawns, and they therefore argue that the high population density figure may represent increased fawn mortality rather than a decreased pregnancy rate. Their low population density figure is more in line with the pregnancy rate of 81% reported by Hewison (1996). Two other studies report significantly higher pregnancy rates of 93% (Kaluzinski 1982) and 96% (Prusaite et al. 1976; cf. Sadleir 1987). Since the 50%-range figures likely represent population density effects (either directly on pregnancy rates or on juvenile survival rates), and this model accounts for population effects only through juvenile mortality, these figures are generally discounted here. The pregnancy rate parameter is therefore set at 80% for the low growth model and 90% for the high growth model.

*Average Number of Offspring.* Vincent et al. (1995) report twinning rates of 78% (during low population density years) and 85% (during high population density years). Several other studies report similar values: 82% (Fruzinski and Labudzki 1982), 87.5% (Aanes and Andersen 1996), and 95% (Gaillard et al. 1998). However, fully three studies

report mean litter sizes of two or more (Kaluzinski 1982; Prusaite et al. 1976, cf. Sadleir 1987; Borg 1970, cf. Sadleir 1987). These cases are due to rates of triplet/quadruplet pregnancies higher than the rate of single-fetus pregnancies. Since most of these data are derived from autopsy data (either numbers of fetuses or numbers of *corpora lutea*), it is likely that they slightly overstate the numbers of offspring which are both born and escape perinatal mortality. Therefore, the high growth model number of offspring per year is set at only 2. The low growth model number of offspring is set to 1.8 to reflect the lower twinning rates.

*Age at First Reproduction.* While female roe deer do not appear to produce as many offspring as yearlings as they do later in life, yearling females do mate regularly and reproduce the following year (Borg 1970; cf. Sadleir 1987). Thus, the female age at first reproduction is set at two years.

*Base Juvenile Mortality Rate.* Two sets of data are drawn from the literature for the determination of basal juvenile mortality. First, average juvenile mortality rates for each study (which are most commonly reported) are used to determine typical rates of juvenile mortality. Second, the minimum value of juvenile mortality (usually the year with the lowest mortality rate) in each study is used to help determine where to set the base juvenile mortality rate, since we are interested in the theoretical minimum rate in the absence of any population pressure. Average rates of juvenile mortality vary widely, from Pielowski and Bresinski's (1982) 23.8% to Focardi et al.'s (2002) 62%. Other values cluster around 30% to 40% (37.6%, Fruzinski and Labudzki 1982; 33%, Gaillard et al. 1997, 1998; 35.2%, Pielowski 1984; 42%, Gaillard et al. 1997) and around 50% (50%, Aanes and Andersen 1996; 56%, Kaluzinski 1982). Some of these figures are good examples of population density effects. For example, Focardi et al.'s (2002) extremely high value of 62% is derived from a population in Italy which had been un hunted for fully

fifty years prior to the study (and also facing little predation)—furthermore, the population experienced an outbreak of *E. coli* during the study, which increased mortality rates even further (juvenile mortality had ranged from 31% to 50% prior to the *E. coli* outbreak).

Minimum values for annual juvenile mortality in each study are also rather variable, ranging from 10% at Trois Fontaines, France (Gaillard et al. 1997) to 33.7% at Zielonka, Poland (Fruzinski and Labudzki 1982). Other minima include 17% at Chize, France (Gaillard et al. 1997), 21% at Czempin, Poland (Kaluzinski 1982), and 31% (as mentioned above) at Tredozio, Italy (Focardi et al. 2002).

Basal juvenile mortality is set around the lower of the minimum values for the high growth model at 20% and in the upper range of the minima (which is also the lower range of the averages) for the low growth model at 30%. As with adult mortality (see below), there is insufficient data presented in the literature to differentiate male and female mortality; however, this is not unreasonable given the low sexual dimorphism of roe deer.

*Age of Onset of Adult Mortality.* Yearling mortality is not much different from that of adults (Gaillard et al. 1993); as a result, adult mortality rates are applied to individuals one year old or older in both the low and high growth models.

*Adult Mortality Rate.* Mortality rates for adults also vary considerably, and as with juvenile mortality rates, only very limited amounts of information are available for sex-specific mortality rates. Adult mortality figures range from 7% (Cederlund and Lindstrom 1983) to 32.3% (Fruzinski and Labudzki 1982). However, it is clear from several sources (Fruzinski and Labudzki 1982; Gaillard et al. 1993; Kaluzinski 1982) that adult mortality is generally low, except in instances of severe winters. In Fruzinski and Labudzki's (1982) study, adult mortality jumped from 9.8% in normal winters to 30.7%

and 32.3% in two unusually harsh winters. Gaillard et al. (1993) report a similar situation where mortality in mild to intermediate winter years is 16% for males and 10% for females, but 29% for males and 26% for females in severe winters. In these severe winters, it appears that abnormally thick and long-lasting snow cover is the primary factor in this increased mortality. Using the more typical mortality rates, adult mortality for the high growth model is set at 10%, the highest of the mortality rate figures (7%, Cederlund and Lindstrom 1983; 10%, Focardi et al. 2002; 9.8%, Fruzinski and Labudzki 1982) for non-severe winter conditions. Adult mortality for the low growth model is set at 15%, a compromise figure somewhat lower than several of the higher overall mortality rates (21%, Kałuzinski 1982; 25.2%, Pielowski 1984), which are raised by unusually severe winters, including one described as “catastrophic” (Kaluzinski 1982).

*Maximum Age.* Survival past age ten is rare for roe deer, and only a few have been documented past age 12. As a result, maximum age is set to 10 for the low growth model and 12 for the high growth model.

### **Summary of Species Model Parameters**

As the discussions above should make clear, all parameter sets cannot be attributed equal levels of confidence. The development of the aurochs and gazelle models is hampered by difficulties inherent in the need to work solely (in the case of aurochs) or substantially (in the case of gazelle) with ecological studies of other species. In general, the procedures followed may be expected to result in high and low growth models that are further from a ‘true’ average than is the case for other species. Thus, the high growth models are likely to excessively overstate growth rates, while the low growth models may understate them. The latter is particularly likely to be true for gazelle, where the studied populations of the target species, *Gazella gazella*, are found only in unusually marginal



environments. Similar concerns apply to ibex, for which a number of parameters can only be considered educated guesses.

Table 3-1 lists all of the simulation modeling parameters for the seven ungulate species included in this study. From the parameters alone, it is apparent that despite the much greater range of body sizes represented among the ungulates in comparison to the small game modeled by Stiner et al. (1999, 2000), the modeled ungulate species are relatively similar. The majority of the parameters vary less than three-fold among the ungulate species. Stiner et al. (2000) note that maturation rate is significantly more important than reproductive rate in determining predation resilience in small game. The parameters determined above suggest that these two factors are more closely linked among ungulate species and have more similar impacts on resilience. If the pregnancy rate and mean number of offspring parameters are combined into mean offspring per female per year, the resulting values are significantly variable, ranging from .33 to 1.8, or better than five-fold. Female age of first reproduction values vary four-fold and in relatively direct opposition to reproductive rate.

Some other specific contrasts between the ungulate parameters and those developed for small game by Stiner et al. (2000) are of interest. As is not unexpected on simple r- versus K-selection grounds, ungulate and small game base juvenile mortality rates are substantially different, individual ungulates—regardless of species—being significantly more likely to survive to maturity. This is, of course, counteracted by the categorical differences in the numbers of offspring produced per year, where ungulates produce no more than one or two offspring and the small game animals consistently produce a half-dozen or more. Of greater interest in understanding the differences between the resilience patterns within the ungulate (see chapter 4) and small game animal groups is the substantially greater similarity in adult mortality rates to be found among the

Table 3-1. Simulation Model Parameters for Ungulate Species.

Species	Model	Pregnancy Rate	Mean Number of Offspring	Female Age of First Reproduction	Age of Onset of Adult Mortality		Base Rate of Natural Juvenile Mortality		Adult Natural Mortality Rate	
					Female Mortality	Maximum Age	Female	Male	Female	Male
Aurochs	LGM	.33	1	4	3	16	.11	.13	.05	.08
	HGM	.45	1	4	3	18	.1	.1	.04	.06
Fallow Deer	LGM	.75	1	2	2	12	.21	.21	.11	.12
	HGM	.9	1	2	2	14	.15	.15	.07	.08
Gazelle	LGM	.85	1	1	1	12	.4	.4	.2	.2
	HGM	1.0	1.2	1	1	12	.25	.25	.15	.15
Goat	LGM	.6	1.5	2	1	12	.25	.25	.15	.15
	HGM	.7	1.7	2	1	12	.15	.15	.1	.1
Ibex	LGM	.7	1	2	2	12	.2	.2	.12	.12
	HGM	.8	1.1	2	2	12	.12	.12	.08	.08
Red Deer	LGM	.45	1	3	2	14	.15	.19	.06	.11
	HGM	.65	1	3	2	14	.12	.15	.04	.07
Roe Deer	LGM	.8	1.8	2	1	10	.3	.3	.15	.15
	HGM	.9	2	2	1	12	.2	.2	.1	.1

ungulates. Ungulate adult mortality rates determined above vary from .04 to .15 *per annum*; in contrast, Stiner et al.'s (2000) small game adult mortality rates vary from .053 to .6—there is three times as much variability in adult mortality rates in the small game models. In general, the within-group variability of the ungulate parameters is patterned in substantially different ways than that found in Stiner et al.'s (2000) small game parameters. The ungulates are more variable in reproductive rate and juvenile mortality, but less variable in maturation rate, lifespan, and adult mortality rate.

## CHAPTER 4

### UNGULATE POPULATION DYNAMICS UNDER CYCLICAL PREDATION

This chapter covers the basic results of simulation modeling of the impact of human hunting on ungulate prey populations. Three different approaches to the human-ungulate predation relationship are examined: simple perennial hunting of randomly encountered animals (the baseline), hunting in which males are targeted preferentially, and intermittent hunting where periods of human predation are separated by periods in which the ungulate population is left 'fallow'.

#### **Perennial Unselective Hunting**

Simulation results for a single set of simulation runs for each ungulate species model are shown in Figure 4-1. In each case, an initial stable population of 1000 individuals is hunted for 1000 years with the listed number of animals being harvested each year. For clarity, only selected harvest rates are illustrated: the rate that crashed the population in that set of runs, the highest sustained harvest rate, and rates approximately two-thirds and one-third the maximum sustainable rate. Population sizes of 1000 are used in order to allow easy conversion to percentages of initial population, while the 1000-year time frame represents an empirically determined stabilization time. If a given harvest rate is sustainable, the population typically stabilizes at a reduced size in less than 500 years, allowing the remaining 500 years to be used for the determination of mean (stabilized) population size. Additionally, harvest rates that are not sustainable generally crash the population in less than 1000 years.

The effect of a given fractional or percentage harvest rate scales directly with the size of the initial stable population. For example, the maximum number of animals that

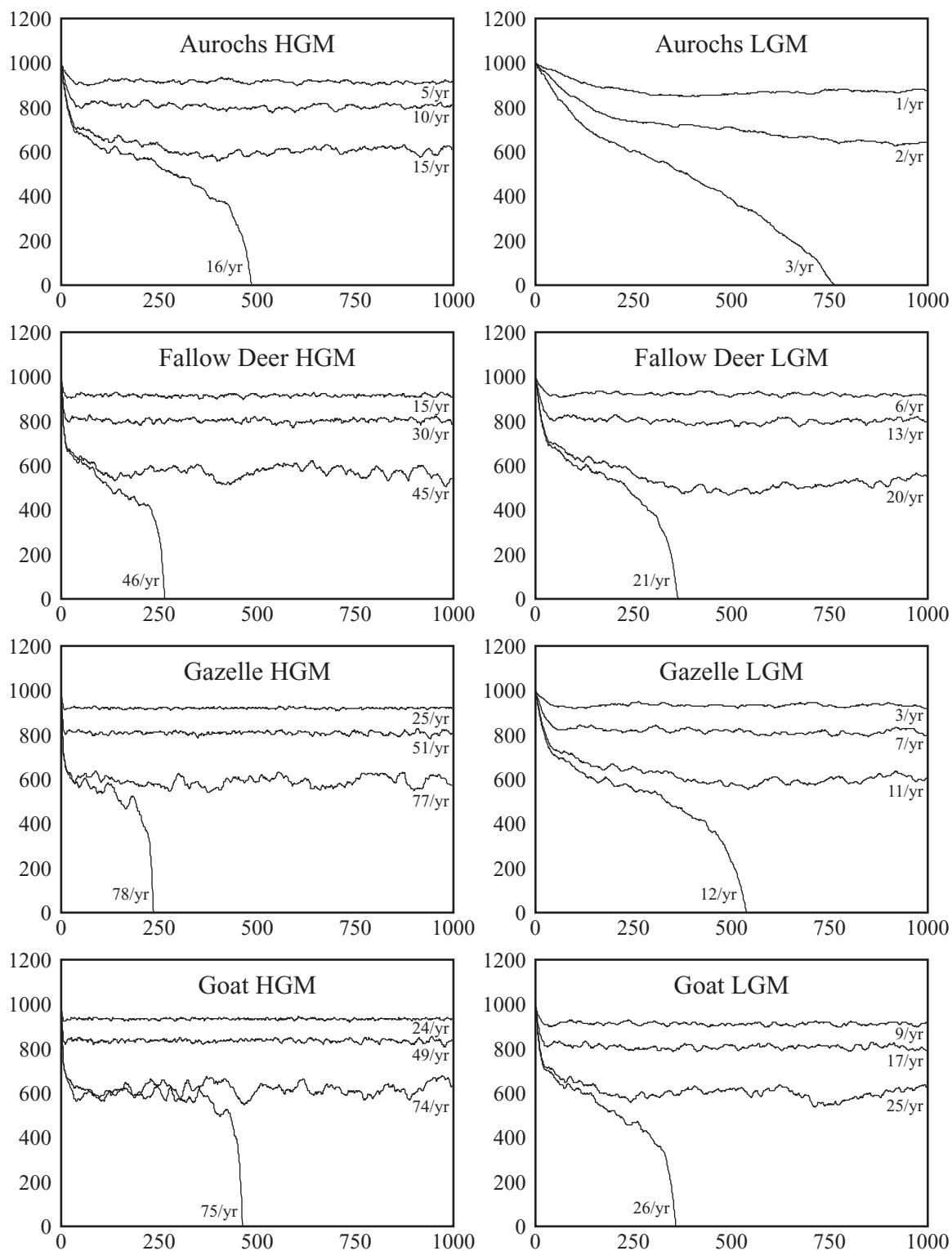


Figure 4-1. Ungulate species model population responses to human harvesting of a given number of animals per year. The x-axes are time in years, the y-axes are population size.

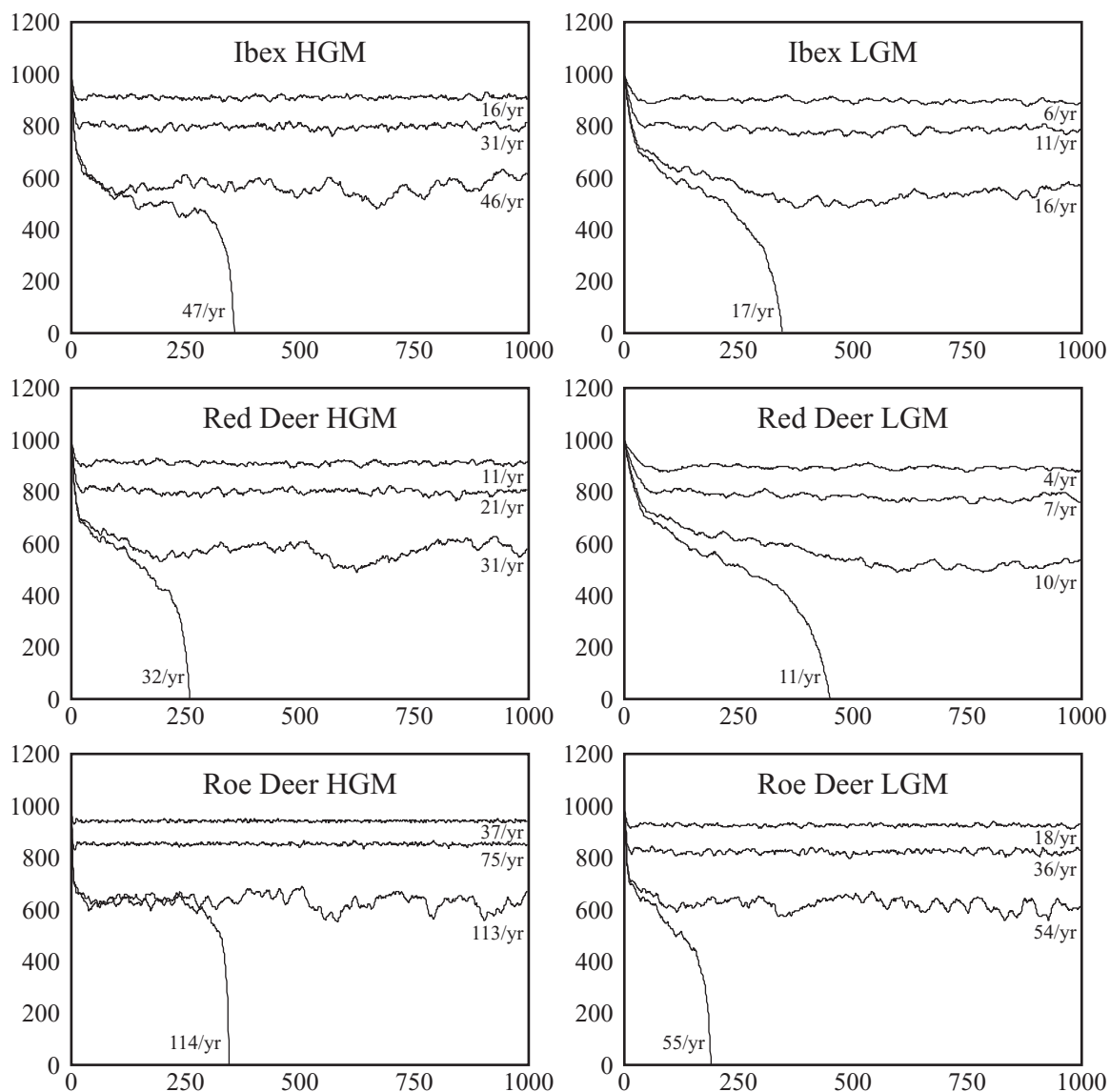


Figure 4-1 continued. The x-axes are time in years, the y-axes are population size.

can be harvested sustainably per year from a 1000-animal aurochs-high-growth-model population is 15 (occasionally 16—see below); a 2000-animal aurochs high growth model population can sustain a maximum of 30 (occasionally 31 to 32) animals killed per year. Results for perennial hunting of size-1000 populations can therefore be used to generalize to populations of varying sizes (see chapter 6).

### *Maximum Sustainable Harvest Rate*

Because there are inherent stochastic processes involved in population-dynamics simulation modeling (as well as in the real world), harvest rates that are normally sustainable sometimes crash the population, and *vice versa*. The random application (to animals at least the minimum age that is hunted) of hunting mortality is the most important of these stochastic processes. Random deviations toward higher or lower numbers of females (see below for more detailed consideration of the effects of sex-biased hunting), or toward younger or older females, being killed by human hunters affect the impact of predation on the prey population. In the former cases, the population will decrease at a faster rate and to a greater extent, because the population-wide reproductive rate will be lower. The opposite will, of course, occur for the latter cases. As a result, no single set of simulation model runs can be considered definitive, especially with regard to the maximum sustainable harvest rate. A mean maximum sustainable harvest rate is therefore determined for each species model.

The average maximum harvest level that a population can survive can be determined from the proportions of runs at each harvest levels in which the population survives, using the following equation:

$$r_{\max} = \sum_i r_i v_i (v_{i-1} - v_{i+1}) \quad (4.1)$$

where  $r_{\max}$  is the mean maximum sustainable harvest rate,  $r_i$  is the  $i$ -th harvest rate, and  $v_i$  is the fraction of runs that survive at harvest rate  $r_i$ . For the vast majority of harvest levels, either all runs survive or all runs crash. As a result, a good estimate of the mean maximum sustainable harvest rate can be determined using only the subset of harvest rates that immediately surround the mean maximum sustainable rate.

To determine estimated mean maximum sustainable harvest rates, 100 runs are carried out for each species model at the maximum sustainable rate from the initial run data illustrated in Figure 4-1, followed by 100 runs at incrementally higher and lower harvest rates until 100% crashing and 100% survival are reached. Figure 4-2 illustrates the results for one example of this process. With harvest of whole numbers of animals from initial populations of 1000 animals, the average range from highest rate with 100% survival to lowest rate with 0% survival for the fourteen species models is 2.43 animals per year, equating to less than a quarter percentage point when scaled against the initial population size.

This procedure was utilized with populations of an initial 1000 animals to produce the mean maximum sustainable harvest rates listed in Table 4-1, with one exception. An initial population size of 10,000 was used for the aurochs low growth model, as its maximum sustainable harvest rate is so low that a population of 1000 animals does not produce sufficiently fine-grained results.

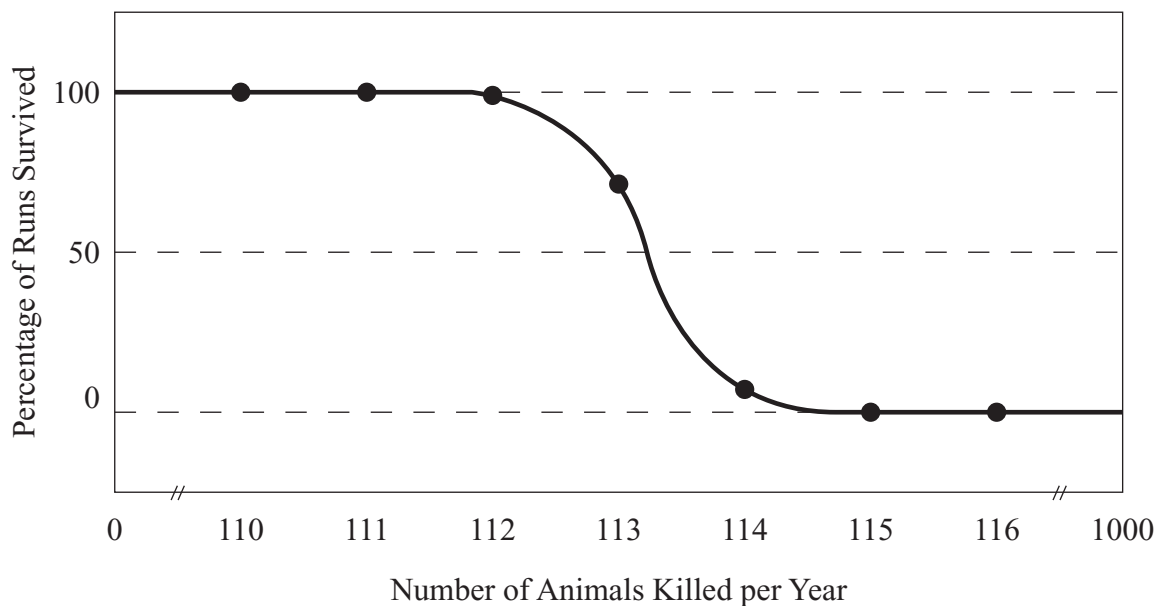


Figure 4-2. Survival rates of roe deer high growth model populations at various harvest levels (initial population of 1000 animals). The solid circles represent points where actual rates have been determined by the methods described in the text.



Table 4-1. Mean Maximum Harvest Rates Sustainable by Modeled Populations.

Species	Sustainable Percentage	
	LGM	HGM
Aurochs ( <i>Bos primigenius</i> )	0.260	1.513
Red Deer ( <i>Cervus elaphus</i> )	0.999	3.102
Fallow Deer ( <i>Dama dama</i> )	1.989	4.529
Goat ( <i>Capra aegagrus</i> )	2.524	7.393
Ibex ( <i>Capra ibex</i> )	1.598	4.584
Gazelle ( <i>Gazella gazella</i> )	1.102	7.727
Roe Deer ( <i>Capreolus capreolus</i> )	5.397	11.277

#### *Population Depression under Human Hunting*

Ungulate prey population responses to hunting pressure short of that required to crash the population are non-linear. The extent to which the prey population is depressed by hunting pressure is shown in Figure 4-3A. The data on which this figure are based are derived from ten runs, each lasting 1500 years, of size-1000 populations of each species model at each whole-number harvest rate from one animal per year to the rate crashing the population<sup>1</sup>. The population sizes over the last 500 years of each of the ten runs are then averaged, allowing a full millennium for the population to stabilize. As is clear from this figure, as well as the runs illustrated in Figure 4-1, the effect of a given increase in the harvest rate is greater at higher levels of exploitation than at lower ones. This progression culminates when the harvest rate reaches the maximum sustainable by the prey population, at which point the population is depressed by around 40%.

Figure 4-3B shows the population-depression effects of harvest rates as fractions of the mean maximum-sustainable rate for each species model (*i.e.*, the values listed in Table 4-1). It is clear that the ungulate population models respond to hunting pressure in essentially the same way.

The strong similarity of the curves in Figure 4-3B, as well as visual examination

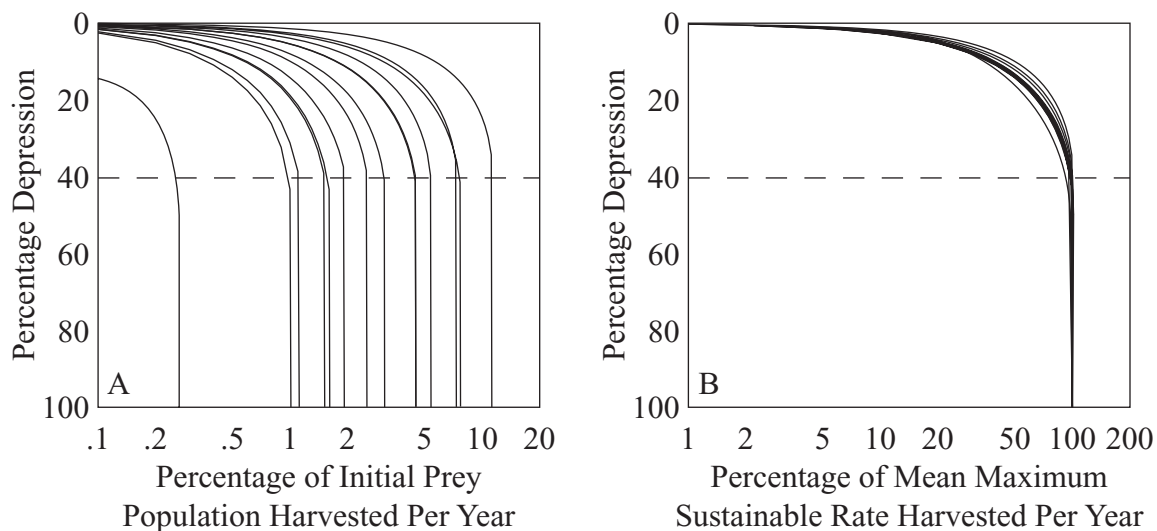


Figure 4-3. Extent of ungulate population depression caused by human predation: A) Population depression versus absolute harvest rate for each of the fourteen species models; B) population depression versus harvest rate as a percentage of the maximum sustainable by the species model. Dashed lines indicate approximate maximum level of depression that can be sustained without population crash. X-axes are log-transformed for clarity.

of the overall responses shown in Figure 4-1, makes it clear that these responses—and thus the predator-prey population dynamics of the various ungulate species models—can be treated as a single general type, with each specific model distinguished simply by its maximum sustainable harvest rate (Table 4-1). This value is sufficient in and of itself to characterize the hunting pressure resilience of each species model.

### Perennial Male-Biased Hunting

The preceding discussion assumes that human hunting of ungulates is targeted randomly, except for the exclusion of young juvenile animals (see chapter 5 for a full discussion of age-structure patterns; for this chapter, it is sufficient to note that the random targeting produces age-group frequencies on the border between living-structure and prime-dominant patterns [*sensu* Stiner 1994]). This section discusses the effects of a bias toward the hunting of males preferentially over females.

It is relatively obvious that killing females at a lower rate than males will increase the overall harvest rate sustainable by a population of a species in which only a fraction of the male population is required to impregnate all fertile females. Since the proximate determinant of population survival is the extent to which reproduction compensates for mortality, minimizing female mortality (and thereby maximizing the population's reproductive rate) maximizes resilience. In order to investigate the effects of a bias toward the hunting of males, a modification of the population dynamics simulation model is required. Male-biased hunting is implemented by setting a probability that otherwise-acceptable female prey (i.e., those of at least the minimum hunted age) will be bypassed when encountered. When the randomly selected prey animal is female, the simulation model will reject the selection with this probability. If the female is rejected as prey, another prey animal is selected normally and the process repeats until either the selected prey animal is male or a female that is not rejected. The male-bias rate is therefore *not* the percentage of animals hunted that are male; the latter value is dependent on both the male-bias rate and the population sex ratio<sup>2</sup>. For example, at a male-bias rate of 50% and a population sex ratio of 60:40 (female to male), on average 57% of the prey killed are male and 43% female, while at a sex ratio of 50:50, on average 67% are male and 33% female. These are instantaneous proportions from a hypothetical infinite population—in reality, the percentages of males killed would be slightly higher due to the further increase in the female to male ratio that occurs during the hunting process as a result of the higher rate of predation on males.

#### *Effects of Male Bias on Maximum Sustainable Harvest Rate*

As the maximum sustainable harvest rates listed in Table 4-1 are based on nonselective hunting with regard to the sex of the prey, they are invalid if prehistoric hunters

significantly targeted males over females. For most archaeological purposes, however, it is the *relative* resiliencies of different prey species that are relevant. Figure 4-4 illustrates the relative increases in maximum harvest rates sustainable by ungulate populations at three different levels of male-bias. When female prey are rejected at relatively low rates, there is little change in the relative resiliency of the ungulate species models. At a 25% male-bias rate, species-model maximum sustainable harvest rates are increased by an average of 31.6% with a standard deviation of only 1.8%. The spread of values increases slightly at a 50% male-bias, and substantially at a 75% male-bias. This increased spread among the maximum sustainable harvest rates of the species models is not due to an increase in separation among the *species* themselves; rather, it is due to a decrease in the relative separation between the rates sustainable by high and low growth model populations of each species. The maximum sustainable harvest rates of the low growth model populations generally increase more with higher male-bias rates than do those of high growth model populations. This somewhat reduces the overlaps in the sustainable hunting rates of the different species. The smaller increase in sustainable harvest rates experi-

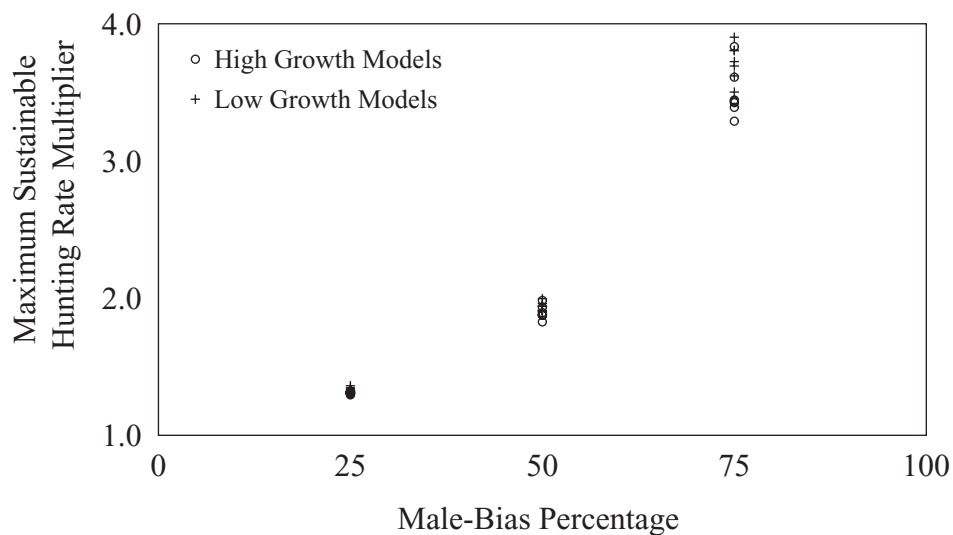


Figure 4-4. Effects of bias toward harvest of males on prey population resilience for all fourteen ungulate species models (low and high growth) included in this study.

enced by the high growth models appears to be the result of the sheer magnitude of the fraction of the population that is hunted each year.

At the 75% male-bias rate illustrated in Figure 4-4, the species models showing lower increases in sustainable hunting rates are those whose sustainable harvest rates are the greatest in absolute terms. Dividing the set of species models in half is instructive: The lower half in terms of relative increase (over the rates in Table 4-1) all have maximum sustainable harvest rates (at zero male-bias) greater than 3%, while the same rates for the upper half in terms of relative increase are all less than 2%. The high growth model *versus* low growth model distinction noted above is actually the product of *this* pattern, which is itself caused by the way the probability-of-bypassing-a-female approach to male bias operates at high bias *and* high harvest rates. As the fraction of the population hunted each year gets close to the fraction of the population comprised by adult males, the hunters' encounter rate with females increases dramatically. This is due to the near-exponential increase in the female-to-male ratio that occurs as the male population declines toward zero. The fraction of the total number of animals killed that is made up by females therefore increases. The higher the maximum harvest rate sustainable by a population, the greater this effect; as a result, species model populations with higher maximum sustainable harvest rates at zero male-bias exhibit smaller proportionate increases in sustainable harvest rates with high male-bias levels than do those populations with lower maximum sustainable harvest rates at zero male-bias.

#### *(In)efficiency of Male-Biased Hunting*

The foregoing suggests that substantial biases toward the hunting of males can radically alter the overall harvest rates sustainable by the various species models, significantly reducing the utility of the basic maximum-sustainability rates determined for

unselective hunting (Table 4-1). However, the simple fact that the modeled maximum sustainable harvest rates under substantial male-bias are much higher than without a bias toward the hunting of males does not necessarily mean that such practices would have been utilized by prehistoric hunters. The efficiency of different hunting options is presumed (under the boundary condition of efficiency-maximization postulated in chapter 1) to have been the most critical factor in the hunters' decision-making process. (Risk is also an important factor, in some cases a more important one; in the following, however, the two are not in conflict.)

The actual efficiency of ungulate hunting is a combination of a number of factors (see chapter 2, equation 2.11); for the purposes of this discussion, a simpler value, termed 'encounter efficiency' is used. Encounter efficiency is defined as the ratio of yield (in metric tons of biomass acquired per year from a population initially of 1000 animals) to the proportion of the population that must be killed or encountered-and-bypassed (in percent) in order to acquire that biomass<sup>3</sup>. Under the simulation model's assumption of random individual encounters between hunters and prey, encounter efficiency thus reflects only search among hunting costs. Encounter efficiency rates can be compared validly, however, as long as the biomass acquired and processing costs per animal killed are held constant (accomplished here by dealing with only one species).

The fallow deer low growth model population is selected to examine the effects of male-biased hunting on encounter efficiency, as its relative increase in maximum sustainable harvest rate is closest to the mean of all the ungulate species model populations at each of the male-bias levels (25%, 50%, and 75%) for which maximum sustainable hunting rates have been determined for every model. At each male-bias rate from 1% to 99% (at 1% intervals), a 1000-animal fallow deer low growth model is run at hunting rates starting at one animal per year, increasing the hunting rate by one animal per year

until the population crashes. For each run, the average population and the numbers of male prey killed and female prey encountered (whether killed or not) are recorded for the second half of the run (500 years), providing the necessary data to calculate encounter efficiency. Figure 4-5A shows the optimum male-bias rate (i.e., the rate that produced the highest encounter-efficiency value) for each harvest rate from 0.1% to 10%. Above the latter value, the curve continues to slowly increase toward a 100% male-bias rate, a value it would reach at a harvest rate of approximately 38.7% (these higher harvest rates are excluded from both Figures 4-5A and B in order to better illustrate transitions at lower harvest rates). The optimum male-bias rate is essentially zero—either 0% or 1%—until the harvest rate approaches the maximum sustainable by an unselective hunting model, at which point it increases rapidly before beginning to level off. This substantial shift in the shape of the curve marks the transition between two different efficiency regimes. In the first, at harvest rates low enough to be sustainable regardless of the level of male bias, the dominant factor in determining efficiency is the number of animals that must be encountered before the desired number are killed. Since the prey population is not significantly depressed, regardless of the relative numbers of females and males that are killed, efficiency is maximized by minimizing the rate at which females are bypassed and thereby the number of encounters required. This effort-minimizing regime gives way to a sustainability-maximizing regime shortly before the harvest rate reaches the maximum sustainable under unselective hunting (in the fallow deer low growth model example, the division is between 1.7% and 1.8%, while the mean maximum sustainable rate for unselective hunting is 1.989%). As unselective (or very low male-bias rate) hunting begins to depress the population significantly, maintenance of prey population size (and subsequently its simple survival) becomes more important. In this regime, male-biased hunting is more efficient simply because it allows substantially higher harvest rates. In

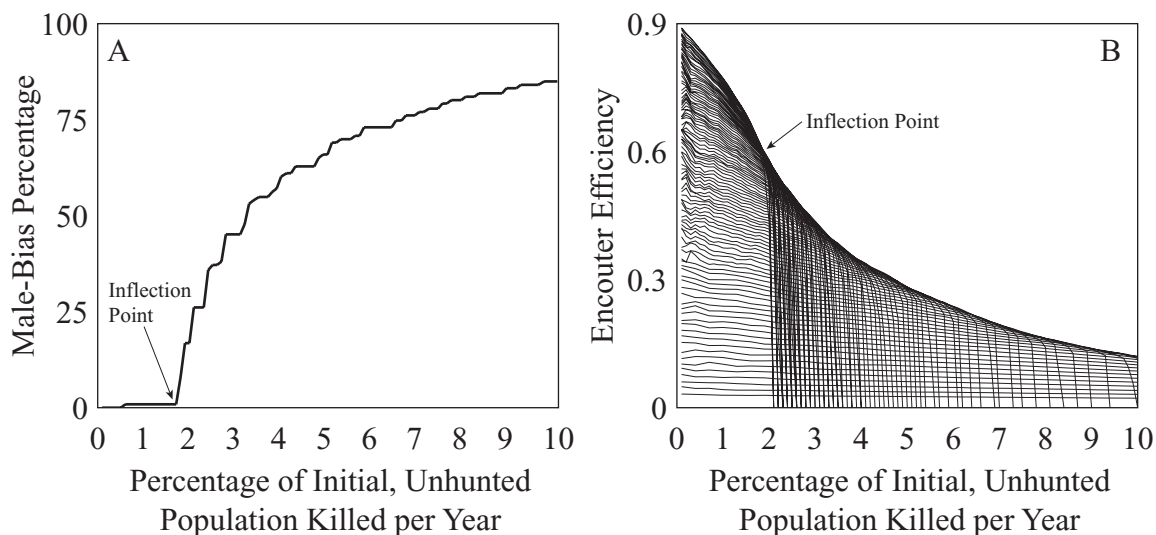


Figure 4-5. Effects of bias toward males on encounter efficiency of hunting the fallow deer low growth model: A) The optimum rate (in terms of encounter efficiency) at which females should be bypassed (male-bias rate) relative to the overall percentage of the initial population killed each year. B) Encounter efficiency *versus* overall percentage harvest rate for male bias rates from 0 to 99% at 1% intervals. The inflection point marking the transition between the effort-minimizing and sustainability-maximizing regimes is indicated in both graphs.

Figure 4-5B, this transition can be seen where the lowest male-bias-rate efficiency curves drop rapidly as they approach population crash, crossing below the efficiency curves of higher male-bias rates that extend population survival. After this point, the most efficient male-bias rate increases rapidly with harvest rate, as lower rates fail to prolong population survival. At any given harvest level, the most efficient male-bias rate is generally the *lowest* that allows the prey population to survive that hunting rate.

*Adaptive Hunting.* The foregoing treatment of efficiency, however, treats the male-bias rate as a characteristic of the human hunters' hunting behavior that is 'chosen' before the population is hunted at all and remains fixed thereafter; it also considers efficiency only over open-ended time spans. Treating the male-bias rate as a flexible strategic or tactical decision yields rather different results, especially where the time span is limited to a human timescale. There are two basic options for approaching conscious



human decision-making in an adaptive computer model. First, the simulated human decision-makers can utilize their ‘experience’, applying different behavioral options to some span of the recent past, in a “what if we had...” sense, and choosing an option for the future that would have resulted in better circumstances than those actually realized. Second, the decision-makers can forecast, applying different behavioral options to existing circumstances and choosing an option that seems to be likely to produce the best future results. The accuracy of the simulated decision-makers’ knowledge of actual past and present circumstances and of their ability to determine the effects of alternative behaviors is a separate facet of such models, and is extremely difficult to model. Useful boundary condition data can be developed, however, by assuming ‘perfect’ knowledge.

In order to examine the circumstances under which human hunters might choose to employ male-biased hunting tactics in a random encounter environment, the simulation model is modified to use the second decision-making approach discussed above: forecasting. This is implemented by running simultaneous simulation models at male-bias rates from 0% to 99% for a given length of time (‘planning depth’), again using the fallow deer low growth model. At the conclusion of these runs, the encounter-efficiency levels enjoyed by the simulated hunters are compared, and the most efficient run deemed to be the one to have actually been used for that time period. In effect, the human hunters are running thought experiments with perfect knowledge and foresight for the upcoming 20 or 50 or 100 years, and then implementing the most efficient male-bias rate. The results are unequivocal: at low harvest rates (up to the 2.0% maximum sustainable harvest rate for unselective hunting), as expected from Figure 4-5, the chosen male-bias rate never deviates from 0% (had planning depth times of 1000 years been included, 1% would have occurred at the 2.0% harvest rate). At a 2.1% harvest rate, the male-bias rate deviates from 0% under a 20-year look-ahead capability only in a desperate, and doomed, attempt

to prevent the final crash of the prey population (Figure 4-6A). Much longer look-ahead/ planning-depth periods are required to produce significant utilization of male-biased hunting and thereby extension of prey population survival (Figure 4-6B). At higher harvest rates, though theoretically easily sustainable with moderate male-bias rates, the prey population inevitably crashes. For example, a 3.0% harvest rate of a fallow deer low growth model population is sustainable given a male-bias rate of at least 34% (see Figure 4-5). However, at this harvest rate, even a 100-year look-ahead capability is insufficient (Figure 4-7). As noted previously, the most efficient male-bias rate is the minimum that prevents the population from crashing. Thus, with 100-year look-ahead, the most efficient male-bias rate is 15%, well short of the 34% required for indefinite sustainability, with the result that the population crashes after 101 years.

A more computationally intensive approach allows the simulated hunters to forecast for a given period (such as 20 years), but change their male-bias rate annually. That is, the simulation determines the most efficient male-bias rate over the look-ahead period, but that rate is only utilized for one year, after which the entire process repeats. This precludes the situation shown in Figure 4-7B, where the prey population crashes

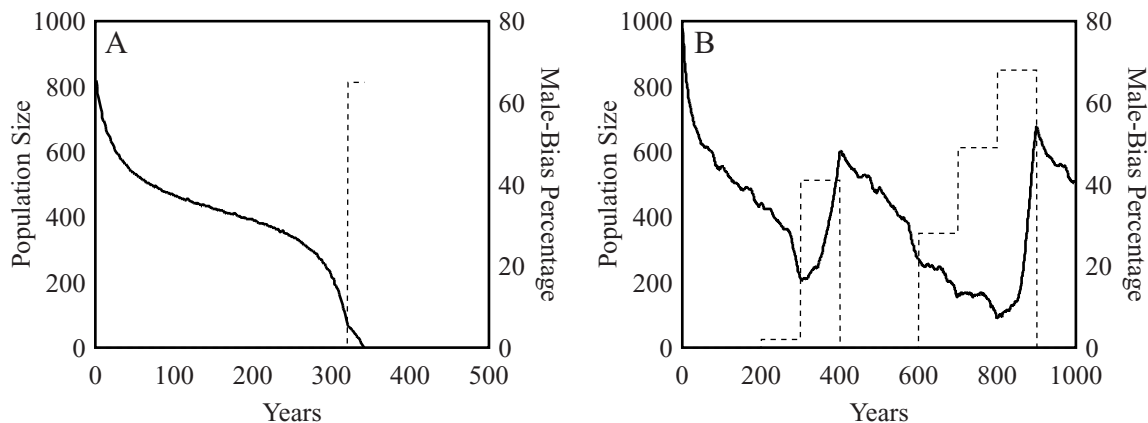


Figure 4-6. Fallow deer low growth model population size and male-bias rate utilized by 'perfect forward knowledge' adaptive human hunters (see text) at 2.1% harvest rate with A) 20-year look-ahead and B) 100-year look-ahead. Solid line is prey population size; dashed line is male-bias rate.

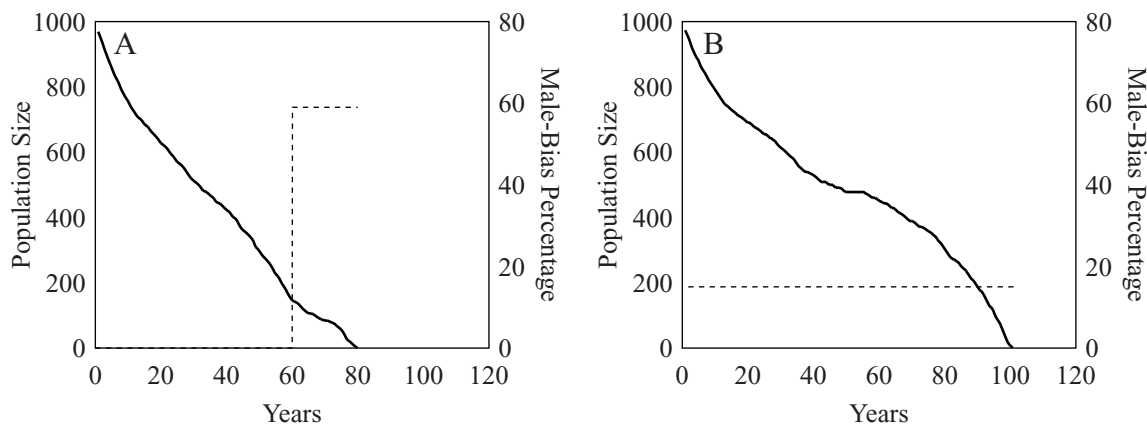


Figure 4-7. Fallow deer low growth model population size and male-bias rate utilized by 'perfect forward knowledge' adaptive human hunters at 3.0% harvest rate with A) 20-year look-ahead and B) 100-year look-ahead. Solid line is prey population size; dashed line is male-bias rate.

immediately following the end of the first look-ahead period. However, even with this greater flexibility, super-generational look-ahead periods are required, as shown in Figure 4-8. In the 50-year look-ahead case (Figure 4-8B), where the prey population survives, the encounter-efficiency level is extremely low. At such high male-bias levels, virtually all adult males in the prey population are killed each year and virtually all adult females are encountered, many of them repeatedly.

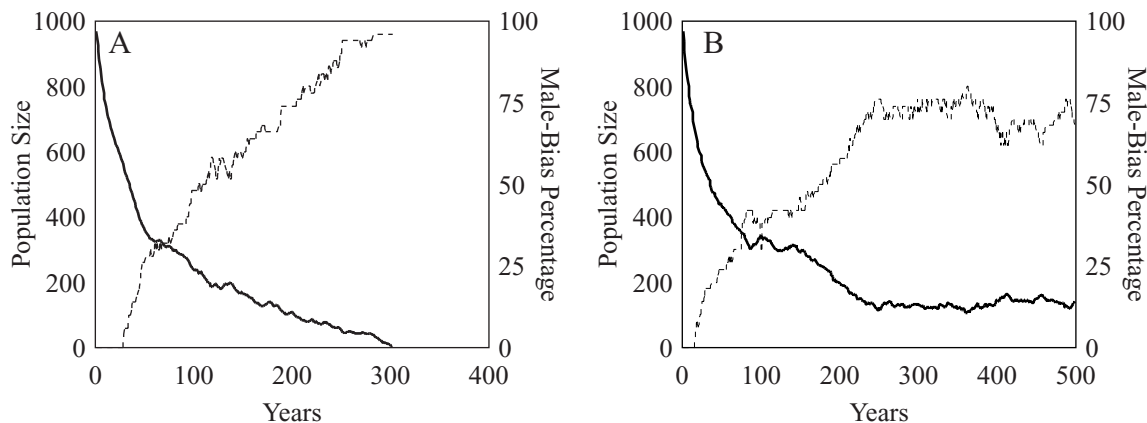


Figure 4-8. Fallow deer low growth model population size and male-bias rate utilized by 'perfect forward knowledge' adaptive human hunters changing their male-bias rate annually at 3.0% harvest rate with A) 40-year look-ahead and B) 50-year look-ahead. Solid line is prey population size; dashed line is male-bias rate.

*Implications.* In circumstances of random-encounter hunting, two conditions are required for male-biased hunting to be selected by hunters based on efficiency. First, the harvest rate must be greater than the maximum sustainable with no male-bias, but not too much greater. Second, the time period over which the human hunters project the effects of their male-bias rate options must be substantially longer than one human generation. The willingness of human groups to consider the effects of contemporary policies on future generations is beyond the scope of this dissertation; however, it can very reasonably be argued that regardless of willingness, the capability to accurately foresee such effects is unlikely to extend beyond one or two generations, assuming it exists at all.

Yet archaeofaunal assemblages are not uncommonly found to exhibit biases toward the hunting of males (e.g., D’Errico and Vanhaeren 2002; Horwitz et al. 1991; Tchernov and Bar-Yosef 1982). In general, the simplest explanation for the dominance of males in an archaeological assemblage is that in the real world, ungulate hunting does not occur only in the form of random *single-animal* encounters. Where ungulate prey sexually segregate by habitat (a seasonal phenomenon for some species), the hunters’ search areas can be targeted to those preferred by male prey without any loss of efficiency. Similarly, many ungulate species are somewhat gregarious—hunters will frequently encounter groups of prey including both males and females. When this happens, targeting the male prey preferentially also involves little or no reduction in encounter efficiency. In sexually dimorphic species, targeting the male in such circumstances will in fact increase efficiency somewhat, even in the absence of long-term male-bias effects.

Since the social behaviors of ungulates vary not only among species, but also seasonally and for some species with population density (e.g., gazelle [Baharav 1976; Mendelsohn 1971]), the ability of human hunters to exploit an ungulate population efficiently through bias toward the hunting of males is likely to vary in ways for which it

is almost certainly impossible to control in the archaeological record. In order to determine *population* sex ratios, unbiased hunting must be assumed; the ungulate behavior thus construed from the sex ratios obviously cannot then be used to determine the likelihood or efficiency of male-biased hunting. As a result, the relative abilities of any two ungulate species to withstand human hunting pressure cannot be assumed to follow the values listed in Table 4-1, unless bias toward the hunting of males can be shown to be absent or low.

### **Unselective Intermittent Hunting**

To this point, it has been assumed that prey populations are exploited continuously, or at least effectively so (i.e., are hunted during every year). Hominid populations have not always filled all available territory, however. In order to examine the effects of intermittent occupation and thus prey population exploitation, two new variables are incorporated into the simulation model. First, the overall percentage of years in which the prey population is hunted is a proxy measure of the extent to which the total human population of a large region is filling the environment in that it maps to the fraction of ungulate populations being exploited at any given time. Second, the number of consecutive years the population is hunted during periods of exploitation is a proxy measure of how often human groups move to new territories. Figure 4-9 shows the relative resiliencies of the modeled ungulate populations under various lengths and intervals of exploitation. These can vary considerably from the rates determined for annual hunting, which are most similar to the sub-graph at the top right of Figure 4-9.

Two patterns are discernable in these results. The more obvious pattern is variability in the relative breadth or narrowness of the confidence ranges for maximum sustainable harvest rates among the species, visible as the height, rather than the location,

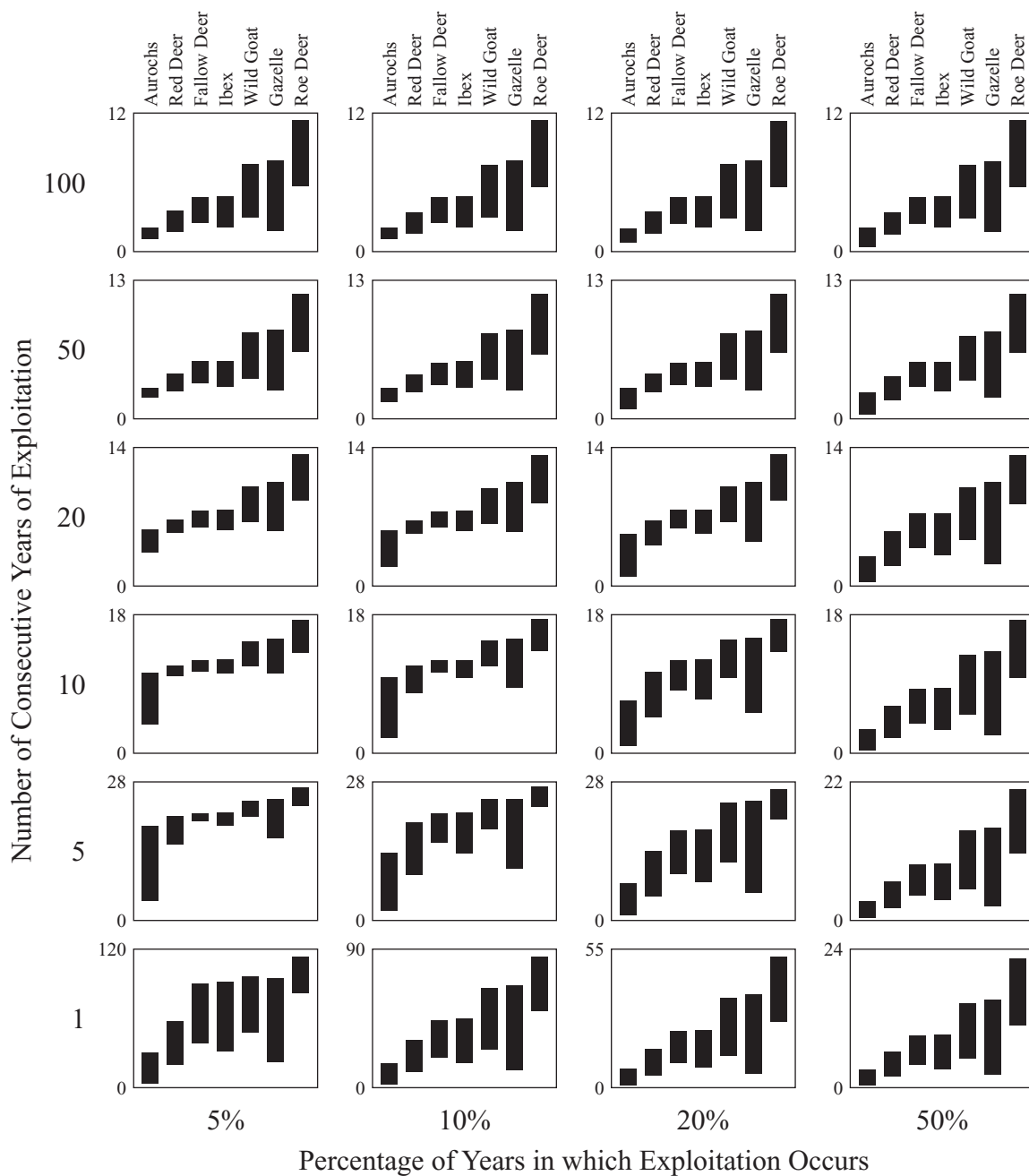


Figure 4-9. Comparison of harvest rates sustainable by modeled ungulate populations at varying durations and intervals of exploitation. Y-axes of graphs are percentage of base unharmed population size killed per year during periods of exploitation. Bars represent confidence ranges for maximum sustainable harvest rate from low growth to high growth model values. NOTE: The roe deer high growth model maximum sustainable rate exceeds 100% in the bottom left graph through the harvest of substantial numbers of juveniles born at the beginning of the year, and thus not counted in the stable population size.

of the bars in Figure 4-9. At the extreme case where the ungulate population is hunted only one year at a time and in only 5% of years, the greatest uncertainty in maximum sustainable harvest rates is to be found in the species of medium to medium-high resilience (fallow deer, ibex, goat, and gazelle). Remaining at an exploitation duration of only a single year, but increasing the frequency of exploitation shifts the largest uncertainties toward the higher-resilience species (goat, gazelle, and roe deer). At exploitation durations shorter than ungulate life-spans, the least resilient species (aurochs, and to a lesser extent red deer) show high relative uncertainty in maximum sustainable harvest rate at low exploitation frequency, while at higher exploitation frequencies, uncertainties shift toward the more resilient species. At long durations of exploitation (multiple ungulate generations), the effect of exploitation frequency on relative uncertainty decreases.

More subtly, the relative differences in sustainable hunting rates are shaped differently, depending on duration and frequency of exploitation. Considering the mean of the high and low growth model maximum sustainable harvest rates for each species, this can be seen as variation in where along the resilience spectrum the greatest changes occur. In general, short durations of exploitation at long intervals (low re-exploitation rates) are associated with more substantial differences among the lower-resilience species. More substantial differences in maximum sustainable harvest rates are found among the high-resilience species with longer durations of exploitation, especially at low overall exploitation frequencies, and also at high exploitation frequencies and low exploitation durations.

Both of the foregoing pattern descriptions are overly general, overstating some trends and certainly overlooking unusual particular cases. That the data in Figure 4-9 do not lend themselves to simple description is an important point in itself, and one which will be discussed in more detail in chapter 6, with specific reference to sustainable yields.

### **Summary of Simulation Modeling Results**

Under circumstances where ungulate populations are hunted continuously, the maximum harvest rate sustainable with no bias toward the hunting of males is a good measure of the relative resiliency to hunting pressure for the modeled ungulate species populations. The responses of modeled populations to human harvest rates expressed as a fraction of the maximum sustainable rate are virtually indistinguishable. The utility of the perennial-unselective-hunting maximum sustainable harvest rate as a general measure of resilience extends to moderate levels of male-biased hunting (through about a 50% bias rate). At higher levels of male-biased hunting (which are expected to occur only where species-specific—and potentially population-density-specific) characteristics of the prey population permit), or where there is reason to suspect—as there usually will be—that different prey species were exploited in different ways or had different behaviors, these values become less useful.

Where it is possible to determine prey sex ratios in archaeological assemblages, it may be practical to make more detailed use of the male-biased hunting model results. Model results (not presented here) that specify the simulated ratio of male to female prey could be used to estimate the increase in the prey population's maximum sustainable harvest rate over the unselective-hunting values in Table 4-1 (but see Note 2 for a caveat), and thus evaluate the relative utilization of different species in light of the resiliencies to be expected given the male-bias levels at which they appear to have been hunted.

One potential avenue of future research on male-biased hunting is to test the hypotheses that male-biases should be targeted primarily at species that have greater tendencies to segregate sexually by habitat or to live routinely in groups combining males and females. This would require not only thorough examination of behavioral literature



for each ungulate species, but likely also improvements in the determination of sex ratios in archaeofaunal assemblages. Existing research of this kind has been substantially targeted at the domestication process (*e.g.*, Cope 1991a, 1991b; Dayan and Simberloff 1995; Hesse 1984); a greater focus on this question in the Paleolithic might help refine models of relative resilience of different ungulate species, and thereby improve models attempting to relate species choice to such matters as demography.

Intermittency of hunting also affects the relative resilience of ungulate species, in ways that cannot be reduced to just one or two trends. The effects seen here in maximum sustainable hunting rates lead to even greater complexity in maximum sustainable yields, a focus of much of chapter 6.

#### *Notes*

1. As previously, a population size of 10,000 is used for the aurochs low growth model in order to allow for sufficiently fine-grained results.
2. While it is possible, and potentially very useful (see chapters 5 and 7) to create a simulation model in which the ratio of male to female kills is predefined, the concept of a maximum sustainable harvest rate becomes problematic in such a simulation. As populations are substantially depressed, the number of males that must be killed in order to maintain the modeled sex ratio can reach and even exceed the number of huntable-age males in the prey population. The highest harvest rate at which this does not occur is the maximum possible at that sex ratio, but since the population is not crashed *per se* at higher rates it does not seem appropriate to consider it a maximum sustainable harvest rate.
3. Hunting failure rates (see chapter 2) are presumed here to be zero; this affects the details of the analysis, but not the general picture.

## CHAPTER 5

### HUMAN HUNTING AND UNGULATE POPULATION AGE STRUCTURE

Along with the proportionate representation of animal species and the differential representation of particular bones from those animals, prey age structure is one of the major types of data that can be developed from archaeofaunas. Between tooth eruption-and-wear data (e.g., Grant 1982; Payne 1973; Severinghaus 1949) and bone-fusion data (e.g., Moran and O'Connor 1994; Silver 1970), it is often possible to determine the approximate ages of mammals—especially ungulates—represented in archaeofaunas. As noted by Lyman (1987), many early archaeological analyses of ungulate age structure in archaeofaunas, being heavily influenced by paleontology, focused on determining if the prey assemblage's age structure fit a pattern of catastrophic or attritional mortality. This trend of interpreting prey mortality patterns in terms of human hunting practices has become more sophisticated over the last two decades (e.g., Stiner 1990, 1994), recognizing that human hunting practices do not necessarily fit paleontological expectations. Furthermore, interest in utilizing prey mortality patterns as proxy measures of living population structure, and thus potentially of human impacts on ungulate populations, has become a significant focus of research (Koike and Ohtaishi 1987; Lyman 1987; Munro 2001, 2004; Stiner 2005; Wolverson 2001). These attempts to analyze ungulate prey age structure patterns in terms of hunting pressure have been based on real-world wildlife management data (e.g., Koike and Ohtaishi 1987) and on models of population response to human hunting (e.g., Lyman 1987; Munro 2001; Wolverson 2001), normally derived from ecological or wildlife-management research. This chapter expands upon the latter, looking at how certain archaeofaunal ungulate age-structure patterns are produced by human hunting, with reference to the level of hunting pressure and hunting practices. The

goal is to delimit the circumstances under which prey assemblage characteristics that have been interpreted as signs of hunting pressure can be generated.

While the motivation behind the chapter is a general inquiry into hunting pressure and prey population (or archaeofaunal assemblage) age structure, particular attention is paid to the interpretation of gazelle age-structure patterns in Natufian archaeofaunas. Small game analyses (Stiner et al. 1999, 2000; Stiner and Munro 2002) have shown strong evidence for higher human population densities in the Natufian than in preceding time periods, and gazelle remains exhibit intriguingly high proportions of juvenile animals (Munro 2001, 2004) in these assemblages. The reasons for this emphasis on the Natufian gazelle question are twofold. First, it is one of the few cases where simulation-modeling efforts have been previously brought to bear; and, second, both age-structure and sex-ratio data are available for the assemblages in question. The importance of the convergence of these two types of data for inferring hunting pressure is a key conclusion of this investigation.

### **Ungulate Population Structure and Analysis**

A stable, un hunted ungulate population has an age structure determined by age-specific rates of mortality. In this structure, as shown in Figure 5-1, the fraction of the population formed by animals of a given age is always less than that formed by animals of younger ages, with the largest changes occurring at the youngest ages, since juvenile mortality rates are higher than those of adults. Any mortality inflicted on the population in addition to the 'natural' mortality, such as human hunting, results in compression of the age structure toward the left side of the graph. This compression is the result of two related effects. First, since fewer animals survive from one age class to the next, this effect is compounded in older age classes (e.g., a 1% increase in mortality for all age

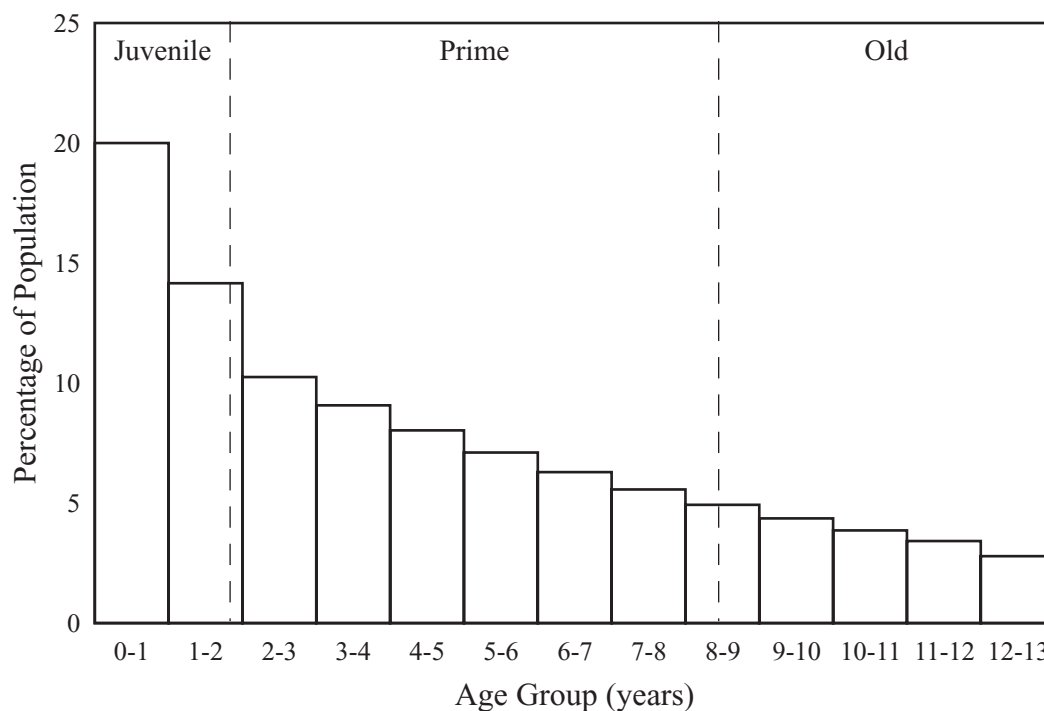


Figure 5-1. Sample age structure of a stable, un hunted model ungulate population, with corresponding three-age system groups indicated (see Figure 5-2 and text). Data from fallow deer low growth model pre-hunting stable population.

classes will reduce the size of the one-year-old age class by 1%, but will reduce the size of the ten-year-old age class by about 9.5%). Second, a reduction in overall population lowers the level of intraspecific competition, which reduces juvenile mortality rates more than it does adult mortality rates. (In the simulation model used here, only juvenile mortality rates decline.) The extent of compression depends on the amount of additional mortality.

Because of limitations on the level of resolution achievable and the frequent limitations of sample size in archaeological analyses, it is often worthwhile to use broad age categories rather than estimates of specific ages in years or months. This study follows Stiner (1990, 1994:288-289) in using a three-age system, dividing the lifespan of ungulates into juvenile, prime, and old age categories. In archaeological terms, the

division between the juvenile and prime age categories is the replacement of deciduous with permanent dentition (see Table 5-1 for the ages used in the simulation model). The division between the prime and old age categories archaeologically is the point at which half the tooth crown has been lost to wear (normally of the fourth premolar, Stiner 1994:290-291). This generally occurs at between 61% and 65% of the total potential lifespan (Stiner 1994:292); 65% of the maximum attainable age is used here as the division for modeled ungulates.

Archaeofaunal assemblage data or population data divided in this manner can be graphed on a ternary diagram (Figure 5-2). Stiner (1990, 1994) defined regions within the diagram that correspond to general mortality patterns in archaeofaunas. The juvenile,

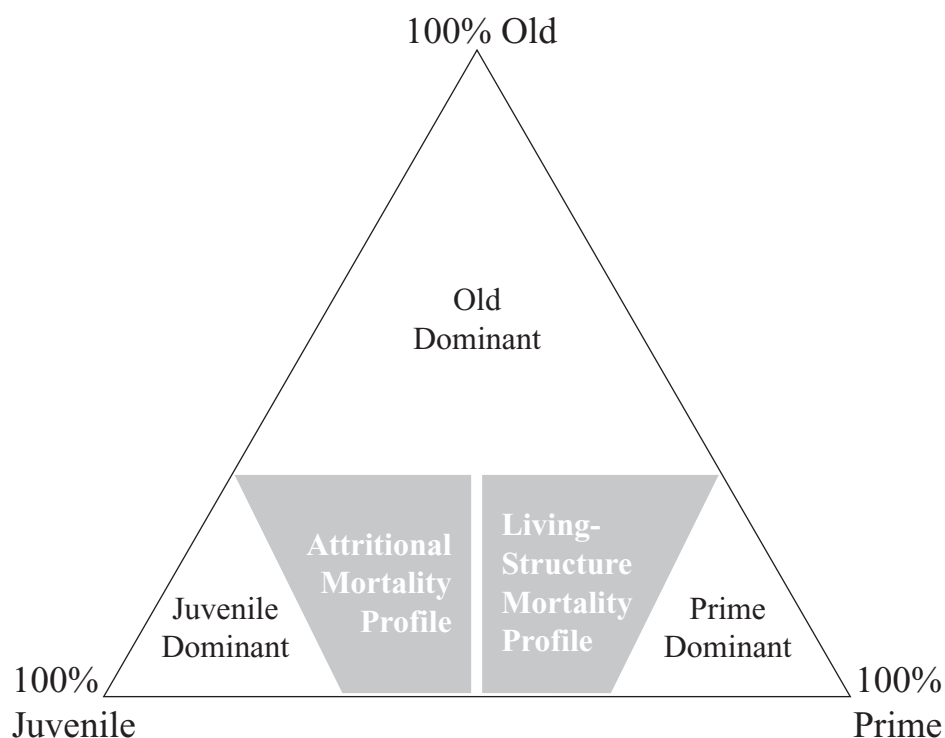


Figure 5-2. Ternary diagram used to illustrate ungulate mortality patterns in terms of age structure (after Stiner 1994:Figure 11.3). See text for definitions of Juvenile, Prime, and Old.

prime, and old-dominant regions are self-explanatory; the old-dominant region is significantly larger than any other region because old animals should always be the minority in a living population, and thus any mortality pattern that includes more than about one-third old animals may be considered to be dominated by them. The attritional mortality region is that area of the graph where an assemblage created by natural deaths or processes that affect the population in similar ways would fall. A living structure mortality profile is produced by *any* process that adds animals to the assemblage in a non-selective or random manner; catastrophic mortality is simply the best-known example.

In a broad examination of both archaeological and modern cases of both human and carnivore hunting, Stiner (1990, 1994) found that attritional mortality profiles are commonly produced by cursorial, or long-chase, hunters, while living-structure mortality patterns are typically produced by ambush hunters, including humans. Furthermore, mortality patterns produced by human hunters tend to be closer to, or within, the prime-dominant region of the ternary plot. This suggests at least a slight level of selectivity in human hunting, probably best explained as a tendency not to hunt young or very young animals. (The simulation model is constructed to apply this form of selectivity.)

### **Modeled Age Structure Results from Numerical Hunting**

The-age structure changes produced by hunting (using the default non-selective except for exclusion of very young animals hunting strategy—see Table 5-1) the ungulate species models discussed in the preceding chapters are illustrated in Figures 5-3 (high growth model populations) and 5-4 (low growth model populations), with age structures based on averages over the last 500 years of ten 1500-year simulation-model runs at each harvest rate. An important distinction is made in these figures between the age structure of the living population being hunted and the age structure of the animals killed by

Table 5-1. Minimum Ages Hunted and Juvenile-Prime Cutoffs for Modeled Ungulates.

Taxon	Minimum Age Hunted (months)	Juvenile-Prime Division (months)
Aurochs ( <i>Bos primigenius</i> )	12	36
Red Deer ( <i>Cervus elaphus</i> )	12	27
Fallow Deer ( <i>Dama dama</i> )	12	22
Ibex ( <i>Capra ibex</i> )	12	35
Goat ( <i>Capra aegagrus</i> )	6	35
Roe Deer ( <i>Capreolus capreolus</i> )	6	8
Gazelle ( <i>Gazella gazella</i> )	6	18

human hunters (and thus of human-created archaeofaunas). The age structures of the exploited populations remain generally within the living-structure region of the ternary graphs (roe deer populations move into the prime-dominant region of the graph). Killed-assemblage age structures, produced by the filter of human hunting practices, are generally closer to, or within, the prime-dominant region. The exact positions in the diagrams where the age structure of populations or killed assemblages of particular species appear should not be given too much weight, as they are heavily dependent on specific characteristics of the modeling process. For example, the age structures produced by the model for roe deer are consistently more prime-dominated than other species because the juvenile-prime division (Table 5-1; cutoff data are estimates drawn from Hillson 1986, except for gazelle, where Munro's [2001] value is used) occurs much earlier, leading to a larger prime-age segment of the population.

The low growth models show smaller changes under hunting pressure than do the high growth models because they can sustain smaller ranges of harvest. For example, while the red deer high growth model age structure curve represents an increase in hunting rate from 0.1% to 3.1% of the initial unharvested population, the red deer low growth model age structure curve only represents an increase from 0.1% to 1.0%. The high

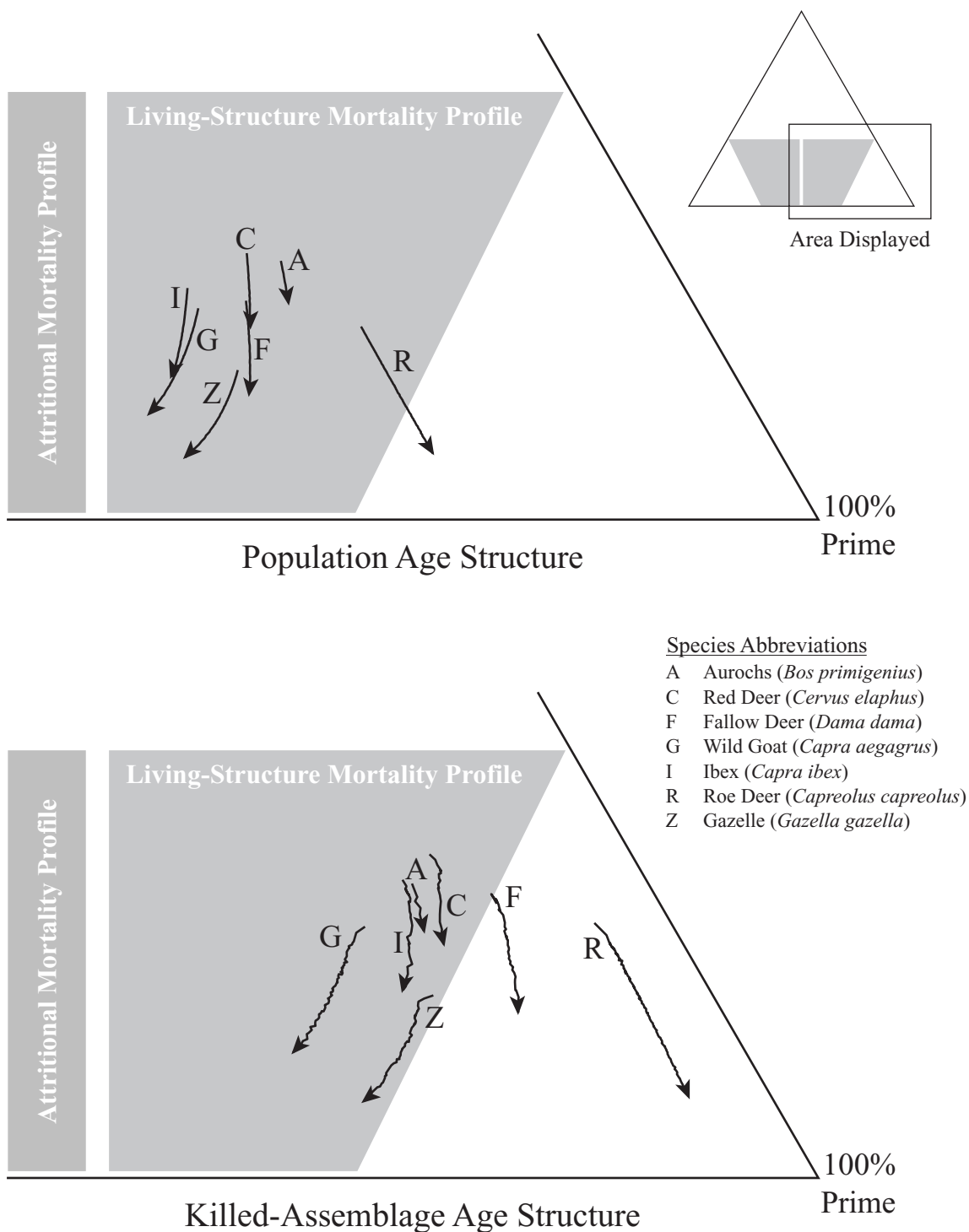


Figure 5-3. Effect of increasing absolute harvest rate on age structure of ungulate high growth model populations and of the group of animals killed in the process. Age structure at the maximum sustainable harvest rate for each species model is indicated by the tip of the arrowhead.



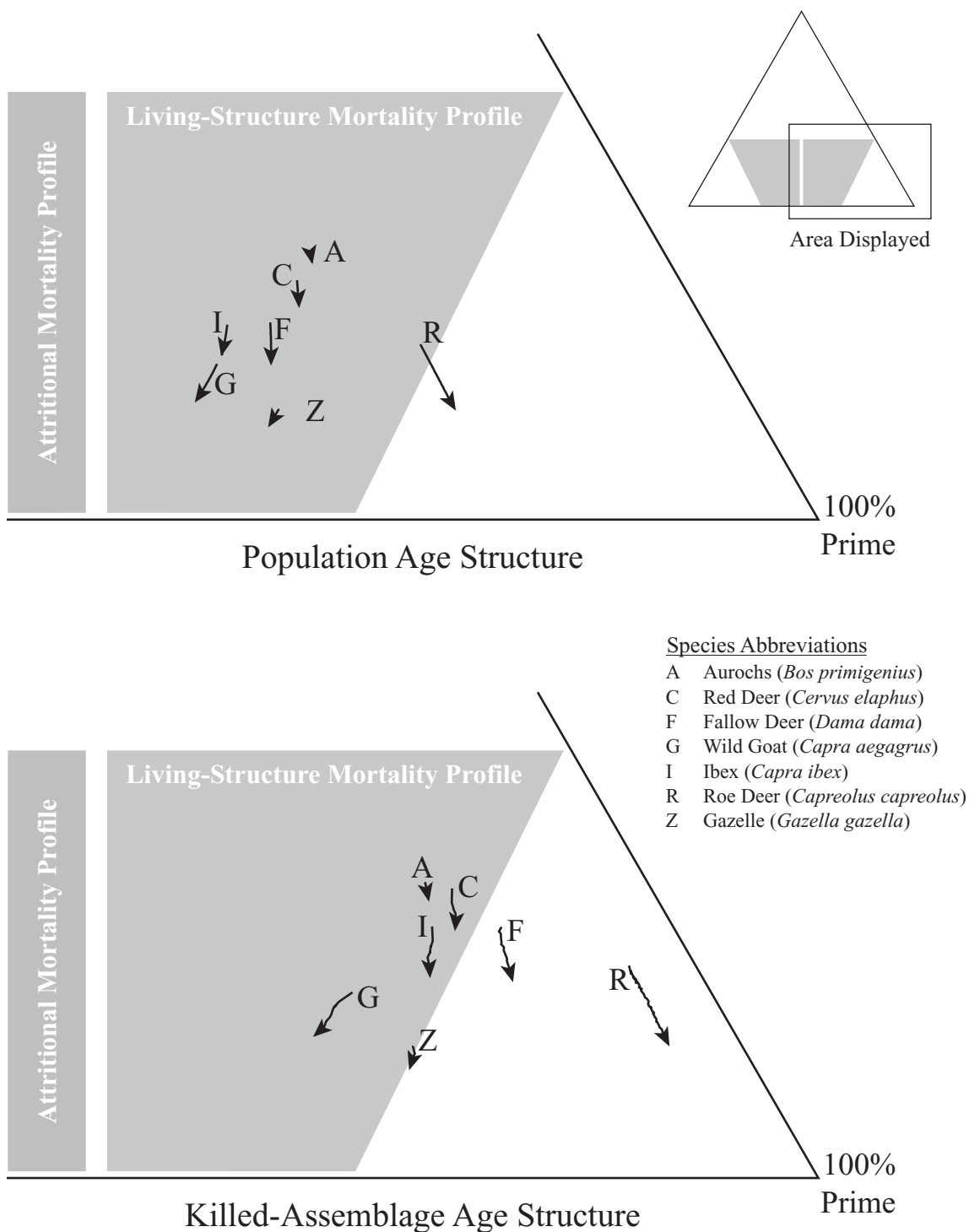


Figure 5-4. Effect of increasing absolute harvest rate on age structure of ungulate low growth model populations and of the group of animals killed in the process. Age structure at the maximum sustainable harvest rate for each species model is indicated by the tip of the arrowhead.

growth model results cover three times as large an increase in hunting pressure. If hunting rates below 0.1% were added, each low growth model curve would be longer, though the end points and general trends would be unchanged.

The dominant effect of increased culling of ungulate populations, as seen in Figures 5-3 and 5-4, is a distinct reduction in the fraction of the population in the old age category. Age structures of killed assemblages generally change more than do those of the populations from which they derive, because the exclusion of some juveniles from the former means that the absolute drop in the number of old animals in the population results in a larger relative drop in the number of old animals killed. The magnitude of the change in the proportion of old animals is largest for those species that can sustain the highest hunting rates; this appears to be largely due to the same relative change in hunting discussed above in relation to high versus low growth models. In most cases, the 'lost' old animals are 'replaced' fairly evenly by juvenile and prime adult animals. That is, while the fraction of the population in the juvenile age group increases, the prime adult fraction increases as well, such that the general trend for both population and killed-assemblage age structures is straight down in the ternary diagrams. The species-specific variation seen in Figures 5-3 and 5-4 is closely related to the relationship between the juvenile-prime age group transition and the minimum huntable age (as discussed above). Thus, roe deer models show a significant trend toward prime animals because the prime-age segment of the population includes those animals that benefited from reduced natural juvenile mortality rates (due to reduced population overall) the preceding year. In contrast, the wild goat and gazelle model age structures tend to shift somewhat toward juveniles; in these cases, the later juvenile-prime cutoffs allow cohorts benefiting from reduced natural juvenile mortality in the previous year (or years in the case of wild goats) to remain in the juvenile age group. This effect is more clear for these species than for

the remaining ungulates because they are modeled with a minimum age hunted of six months, rather than one year. In any case, these shifts toward juveniles are not large enough to even approach juvenile-dominated populations or assemblages.

This reduction in old animals, with little significant shift toward juveniles at the expense of prime adults, accords well with the conclusions of Lyman (1987:139-140) that hunting pressure tends to deplete or remove animals in the latter third or so of their life expectancies. It also matches the shift in age structure associated by Wolverton (2001:35, Figure 3.8) with lower levels of hunting pressure. However, the model results presented here differ significantly from model results of Wolverton (2001) for higher levels of hunting pressure and of Munro (2001:233-235; Figure 6.7), who both find significant increases in the proportion of juveniles, not simply as a result of a reduction in the proportion of old animals but in fact relative to the proportion of prime age animals, as well.

### **Modeled Age-Structure Results from Percentage Hunting**

A major difference between the ungulate hunting simulation model utilized in this dissertation and the model used by Munro (2001), as well as the model data of Taber et al. (1982) used by Wolverton (2001), is the definition of the harvest rate as an absolute numerical value described as a percentage of the *initial, un hunted* population size, rather than a variable rate defined as a percentage of the *current* population size. The following discussion relates primarily to Munro's (2001) simulation, since there are additional issues with the data used by Wolverton (2001), which are dealt with later.

In order to make justifiable comparisons between the results of absolute hunting rates and percentage hunting rates, the percentage-of-extant-population hunting option described in Chapter 3 is used to match the basic structure of the model used by Munro (2001). The primary difference in the simulation model itself is the provision for a

hunting rate that is dependent on the current population size.

In order to take into account the effects of human hunting practices, the simulation models discussed here use a range of minimum ages at which gazelle are hunted, from 3 months to the 18-month juvenile-adult cutoff. This acts to both allow for potential variation in the effects of hunting on the prey population and to control for the human hunting 'filter' in the creation of archaeofaunal assemblages. Figure 5-5 shows the age-structure effects on the gazelle high growth model of increasing harvest rates (from 0.1% to the maximum sustainable rate at each minimum age hunted: 25% or 26%). Though the actual maximum-sustainable-percentage-harvest rates found here differ somewhat from those found by Munro, probably due to differences in model structure, the increase in the proportion of juveniles in the population is very similar, increasing from 34% to 46-52%

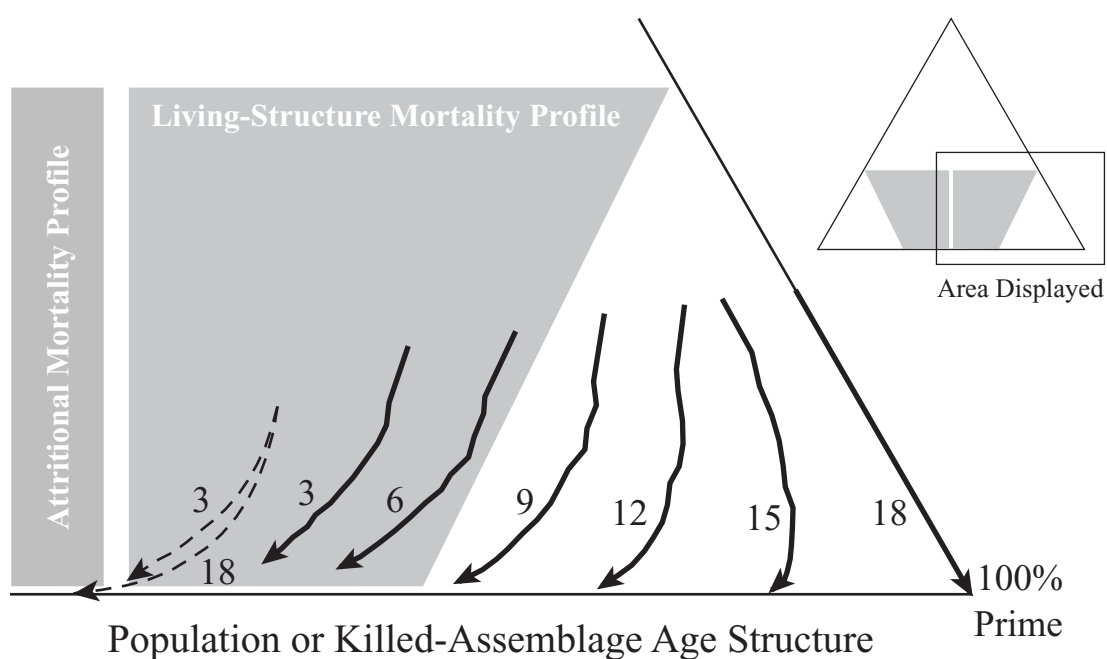


Figure 5-5. Effects of increasing percentage-of-extant-population harvest rates on age structure of gazelle high growth model populations and of the animals hunted from those populations at different minimum ages hunted. Solid lines are hunted assemblage age structure; dashed lines are population age structure. Labels indicate the minimum ages hunted in months.

(depending on minimum age hunted). The age-structure effects on low growth model populations (shown in Figure 5-6; harvest rates range from 0.1% to the maximum sustainable rate of 3.7%) are also very similar. In this case, the population age-structure effects at different minimum ages hunted are effectively indistinguishable. The changes in the juvenile percentage of the population are not quite as similar for the low growth model, rising from 33% to 36%, only about half the magnitude found by Munro (2001), though with a similar upper limit. Since the maximum sustainable percentage of hunting found here for the low growth model is smaller than produced by Munro's model, the smaller increase is not surprising. As noted in chapters 3 and 4, the gazelle low growth model may be erroneously low; since it is the high growth model that produces the major increase in juvenile animals, discussion for the remainder of the chapter is limited to the

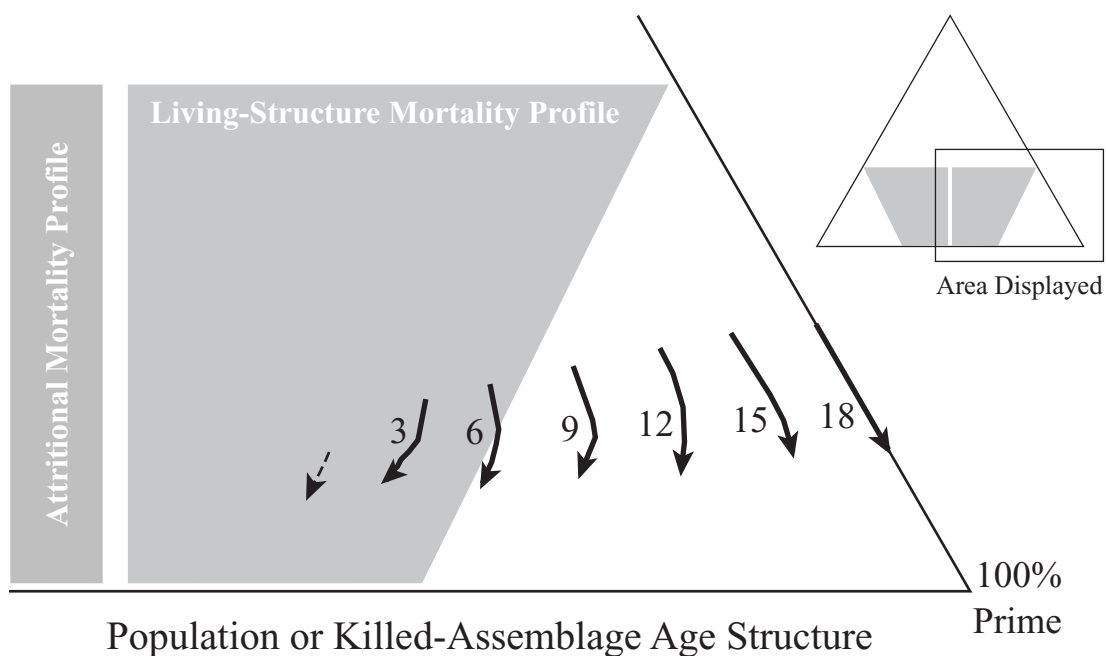


Figure 5-6. Effects of increasing percentage-of-extant-population harvest rates on age structure of gazelle low growth model populations and of the animals hunted from those populations at different minimum ages hunted. Solid lines are hunted assemblage age structure; dashed line is population age structure. Labels indicate the minimum ages hunted in months.

high growth model. It is important, however, to bear in mind the limited increase in juveniles in gazelle low growth model populations, as it suggests the possibility that age structure changes limited primarily to decreases in old animals will be produced even by maximal levels of percentage hunting pressure.

The killed-assemblage age structure results shown in Figures 5-5 and 5-6 indicate the importance of the hunting strategies or practices employed by human hunters. These practices (along with transport and processing decisions, preservation, and recovery, of course) are the critical filter through which changes in population age structure reach the archaeological record. The more random or non-selective the hunting practices employed, the more representative the hunted animals, and thus the archaeological assemblage, will be of the source population. In the gazelle case, under a percentage-of-extant-population harvest regime, the hunting of animals as young as one year is necessary to carry population changes in the fraction of juveniles through to the killed assemblage.

Truly substantial increases in the percentage of juvenile animals, such as those seen in the Natufian (e.g., Munro 2004), require even lower minimum-age-hunted values. Even in such cases, the percentage of juveniles in the killed assemblage remains significantly lower than that of the living population. For example, at a minimum-age-hunted value of six months, the percentage of juveniles increases from 34% to 48% in the gazelle high growth model population, but only from 18% to 36% in the killed assemblage. With low minimum-age-hunted values, the magnitude of the increase in juveniles in the killed assemblage can be larger than in the population, but the absolute representation of juveniles is necessarily smaller (unless the minimum age is zero). Having established that a substantial fraction of the juvenile age range must be subjected to hunting in order for percentage hunting to produce substantial increases in the representation of juveniles in the killed assemblage, after this point all simulation model data are derived from runs

with the minimum age hunted set at six months. Even though archaeological data (Munro 2004) suggest the inclusion of animals younger than six months in at least some Natufian assemblages, it is considered preferable to use a higher value due to the presumed unlikelihood that such young animals would be targeted at levels equal to adult animals.

### *Percentage Hunting and 'Hunting Pressure'*

Hunting higher percentages of an ungulate population annually can produce substantial increases in the juvenile fraction of both the population and the killed assemblage. However, it is unclear that this permits the conclusion that *hunting pressure* in particular produces such increases. While the percentage of the population that is killed annually seems to be a reasonable measure of hunting pressure, it is problematic if the term hunting pressure is intended to have connotations of higher harvest levels and perhaps of elevated human population size or reliance on a hunted resource. As shown in

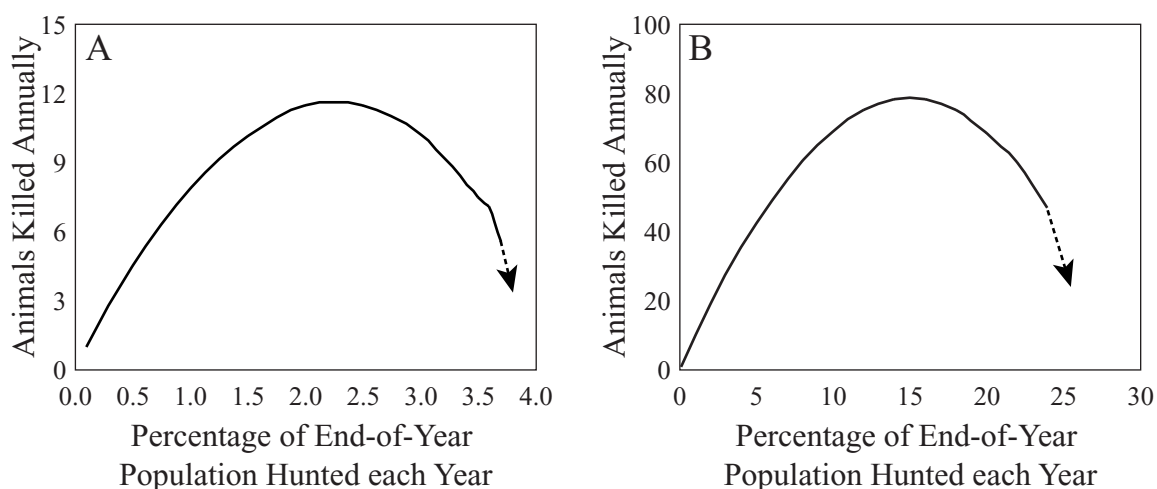


Figure 5-7. Annual offtake rates in the percentage-of-annual population hunting regime for gazelle low growth model (A) and high growth model (B), based on mean number of animals killed per year over the last 500 years of 1000 year model runs from populations composed initially of 1000 animals. Dashed line and arrow indicate population crash. Minimum age hunted: 6 months.

Figure 5-7, the number of animals killed annually once the prey population has stabilized does not increase uniformly with an increased percentage-of-extant-population harvest rate. In fact, at the highest such rates, the absolute number of animals killed is substantially lower than at moderate harvest rates. While a gazelle high growth model population may reasonably be considered to be under more hunting pressure at a 24% harvest rate than a 15% harvest rate (for example), the human population would acquire approximately the same amount of food (after population stabilization) with a 6% harvest rate as at that 24% rate. Furthermore, as shown in Figure 5-8, a human population harvesting an ungulate population at a given percentage-of-extant-population rate experiences a substantial decrease in its food acquisition from that prey population over the course of a single human generation or so (in the case of the gazelle high growth model; there is

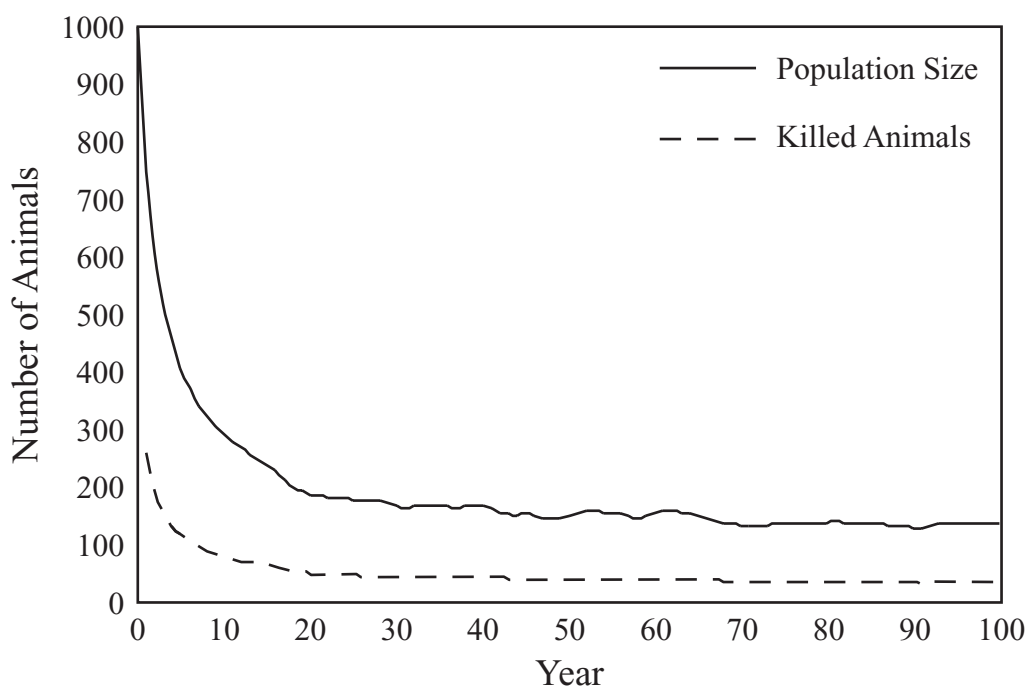


Figure 5-8. Population size and number of animals killed by year for a gazelle high growth model population with 24% of the population killed annually by human hunters, and a minimum hunted age of 6 months. Note that the general pattern holds for any species and any hunting-age cutoff.



some minor variation among species), as a result of the large drop in prey population caused by the initially high absolute hunting levels; this effect is particularly large if the percentage harvest rate is high (relative to the maximum sustainable by the prey population). Indeed, it is this high initial level of harvest, relative to the level once the prey population has stabilized, that produces the oddity of having two different harvest rates produce the same yield. There is thus a trade-off between initial yields and the percentage of the population that must be hunted to attain a given yield in the long term.

#### *Percentage Hunting and Juvenile Abundance*

This history-dependent relationship between hunting rate and the number of animals killed has important implications for the interpretation of age-structure changes in ungulate populations and archaeofaunas. The fraction of juveniles in a population is inversely related to the population size to carrying capacity ratio, because juvenile survival is determined by this ratio (see chapter 3). Thus, the smaller the population size, the larger the proportion of juveniles in the population will be. As a result, in a situation where a previously (or at least recently—several decades or so) unhunted ungulate population is subjected to a significant percentage-of-extant-population harvest rate, the population size will initially drop rapidly, but show very limited changes in population age structure. As the population size decreases, the total number of animals killed drops as well, but the population's age structure exhibits larger changes. To this point, most of the change in age structure is in the form of reduction of old animals, without a significant shift toward juveniles over prime adults. When the population and the absolute number of animals killed annually subsequently stabilize at their lowest levels, the maximum changes in the population age structure and the killed-assemblage age structure are produced. This pattern is summarized in Figure 5-9.

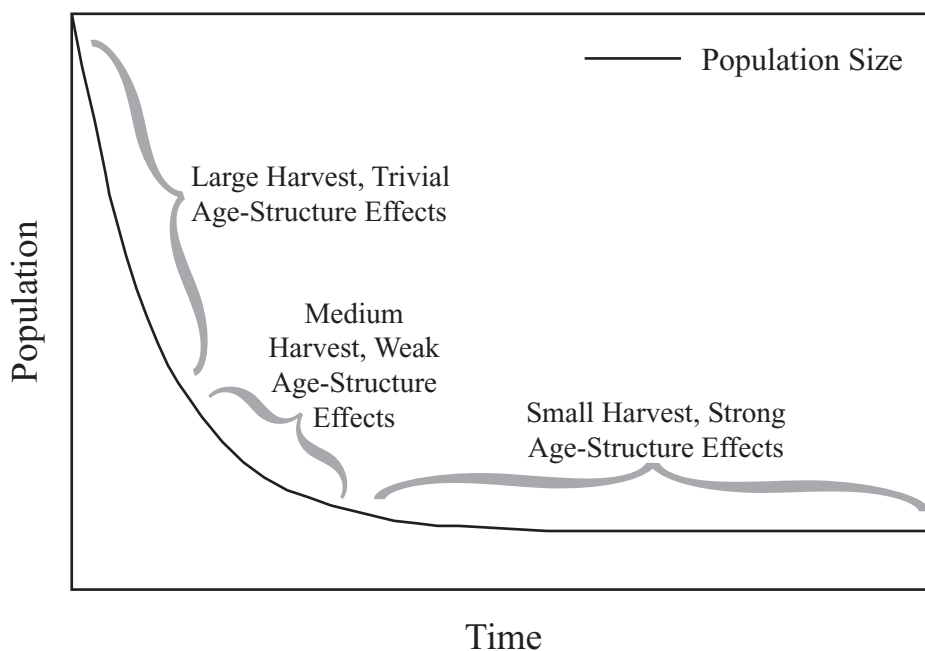


Figure 5-9. Schematic illustration of prey population response to simple percentage-of-extant-population culling showing harvest and age-structure effect regions.

A high percentage of juvenile animals in an ungulate archaeological assemblage is thus produced by simple percentage-of-extant-population hunting only when the number of animals being killed has declined dramatically. A significant increase in the percentage of juveniles, especially one not produced simply by reduction in old animals, therefore indicates that the number of animals being killed annually has in fact dropped dramatically. It is indicative not of a *contemporaneous* high absolute level of exploitation, but rather of such a level of exploitation *prior* to the accumulation of the assemblage. A population held at a low population size relative to its carrying capacity by a low absolute (though high percentage-of-extant-population) level of harvest will have a significantly increased juvenile fraction. A population that is declining due to a high absolute harvest level will not. If a human population is assumed to be maintaining (much less increasing) its overall level of food acquisition, the presence of a strongly juvenile-biased ungulate

prey assemblage indicates that the human population has already been forced to find substitute sources of food. The juvenile-bias in the killed assemblage does not so much indicate heavy exploitation of the prey population as it does *previous overhunting*.

While the discussion here is based on models in which various rates of harvest are applied to pristine ungulate populations, this potentially unrealistic modeling simplification is not responsible for the resulting patterns in the (percentage-of-extant-population) harvest-rate-to-yield relationship and the association of significant increases in juvenile representation with overhunting. Model runs in which the harvest rate increases gradually over time produce closely related overall results, and specifically replicate the connection between age-structure effects and historical stage of hunting.

Figure 5-10 illustrates the effects on gazelle high-growth-model-population size and hunting yield of gradual increases in the percentage of the prey population killed each year. Two approaches to increasing the harvest rate are shown (both begin at 1%): a steady increase of 1% every 25 years, and an exponential rate of increase at 1% (of the existing rate) per year. Though the overall shapes of the resulting yield curves (and, to a lesser extent, the population-size curves) are different, they follow the same general pattern. Initially, the growing harvest rate produces increasing yield, though it should be noted that this is always a process of diminishing returns. That is, a given proportionate increase in the harvest rate always produces a smaller proportionate increase in the number of animals killed, since the population decreases under the additional culling. As the harvest rate nears its optimum in terms of yield (the top of the curve in Figure 5-10), the population-decreasing and the relative yield-increasing effects of the rising percentage-of-extant-population harvest rate come into rough equilibrium. At these harvest levels, increases in the percentage of the prey population that is killed each year are balanced almost perfectly by decreases in the population size. Consequently, the number

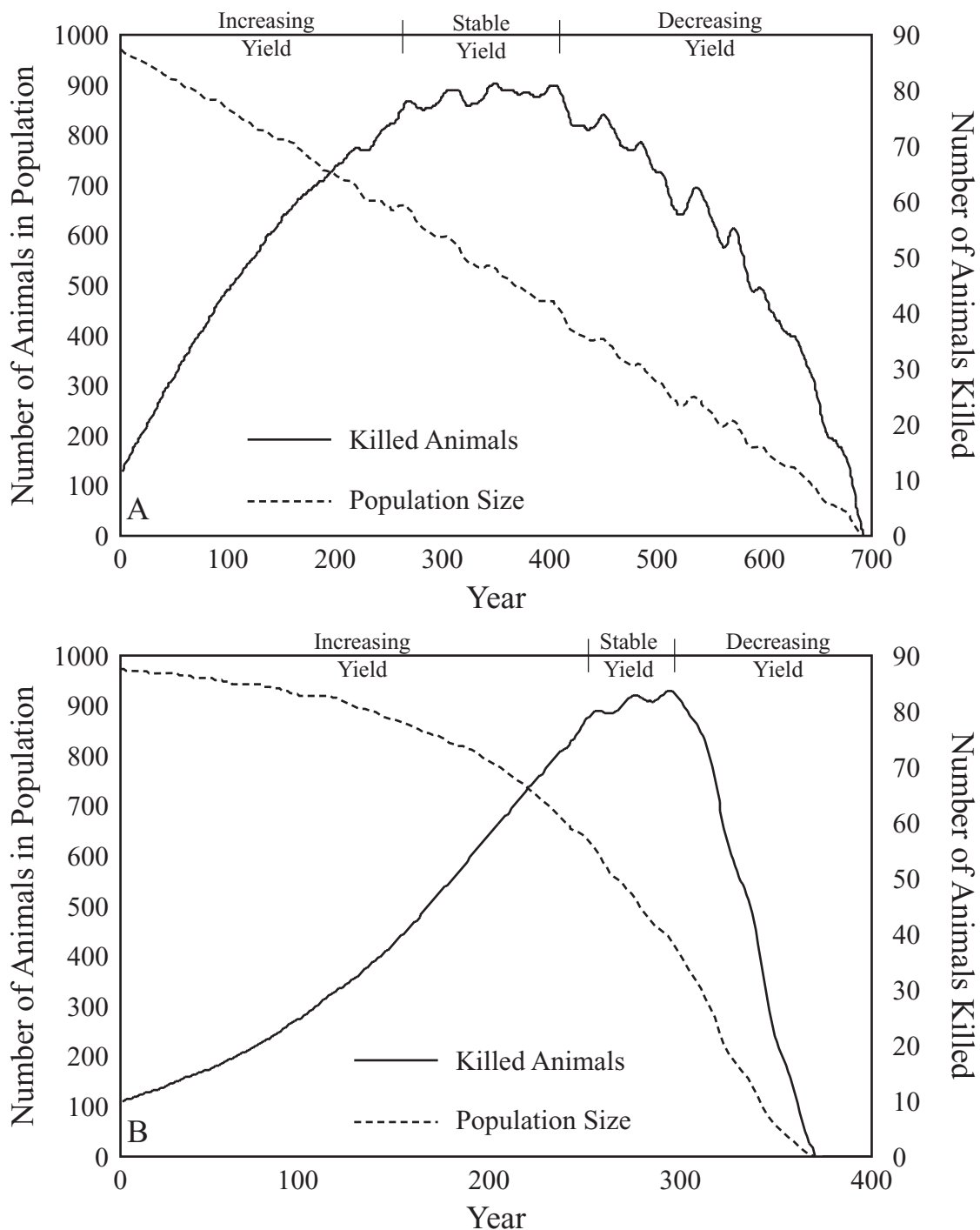


Figure 5-10. Population size and number of animals killed annually for gazelle high growth model populations hunted at gradually increasing percentage rates with A) constant increase (.04% added to hunting rate each year), and B) exponential rate of increase (hunting rate increasing by 1% of its value each year). Yield stages are defined across the tops of the graphs (see text and Figure 5-11). Minimum hunted age: 6 months.

of animals killed each year remains relatively stable. Eventually, however, the continuing increase in the hunting rate causes this near-equilibrium situation to reach a tipping point, and further increases in the percentage harvest rate begin to result in *decreases* in the number of animals killed per year. Note that the ungulate population decreases throughout the entire process; it is only the yield which temporarily stabilizes. The continued reduction in prey population size eventually, and rather abruptly, becomes more important than the increased rate of harvest.

This pattern in the hunting-rate-to-yield relationship has interesting implications for the pressures placed on any human group faced with it. During the increasing-yield stage, there is only moderate adaptive pressure, since increasing investment in hunting continuously produces higher yields, though of course other resources might be added in accordance with optimal foraging models (see chapter 2). In the stable-yield stage, adaptive pressure builds as 'attempts' to increase yield by killing a higher fraction of the prey population are often futile, and where successful (due to stochastic factors) are only so for a few years. The hunters may begin to look at other resources to make up the inevitable shortfalls (or, if other resources are already part of the diet, to increase the use thereof). When the decreasing-yield stage begins, adaptive pressure becomes extreme. The prey population has been reduced to the point where the only way to increase yields is to *reduce* the harvest rate for some years until the population has recovered somewhat. Thus, there is a constant pressure to replace some of the food previously acquired from the ungulate species in question with some other resource (or to move elsewhere).

The population and killed-assemblage age structures associated with these yield stages are shown in Figure 5-11 for the gazelle high growth model population and yield histories illustrated in Figure 5-10. The illustrated points are averages over the entirety of each yield stage. The overall change in age structure during the course of each model run

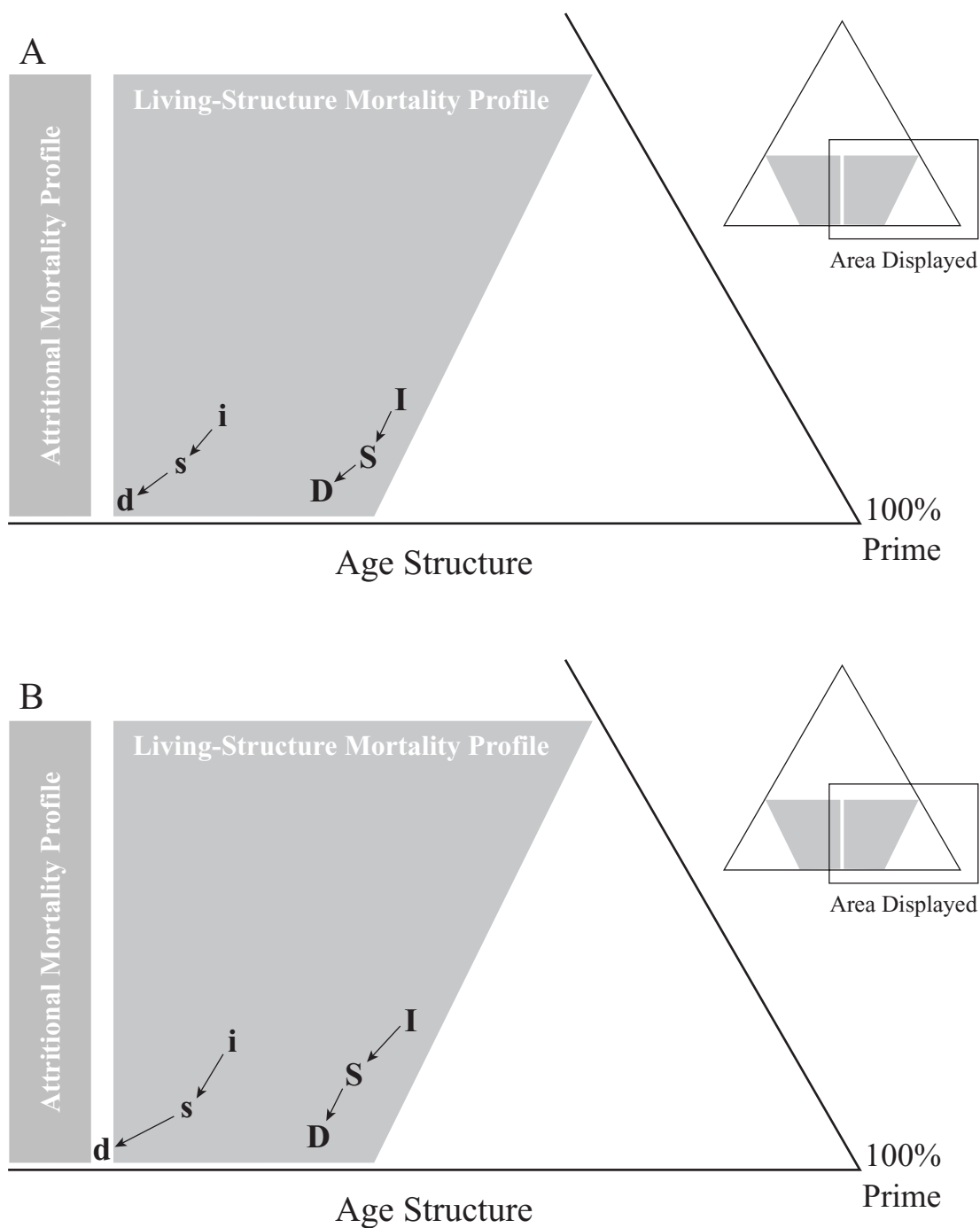


Figure 5-11. Age structures of gazelle high growth model populations hunted at gradually increasing percentage rates with A) constant rate of increase (.04% added to hunting rate each year), and B) exponential rate of increase (hunting rate increasing by 1% of its value each year). Displayed letters indicate yield stage (see text and Figure 5-J): I = increasing, S = stable, D = decreasing. Lower case letters indicate population age structure; upper case letters indicate hunted assemblage age structure. Minimum hunted age: 6 months.

is thus larger than that shown. This is particularly the case for the killed-assemblage age structures, since these values are calculated based on total animals killed, which has the effect of giving greater weight to the portions of the increasing-yield and decreasing-yield stages with the highest yields (that is, the latter part of the increasing-yield stage and the early part of the decreasing-yield stage).

The general pattern, however, is clear. Age structures in the increasing-yield stage are compressed relative to an un hunted population, but not as extensively as those associated with the stable-yield stage. The most extensive compression of population and killed-assemblage age structures occurs when the prey population is being overhunted in the decreasing yield stage. The extreme increases in the juvenile fraction of the population, such as where the percentage of juveniles reaches or exceeds 50% for the gazelle high growth model (as in Figure 5-5 above), represent even greater age-structure compression than the mean for the decreasing-yield stage. Such values occur only when the prey population has not only been overhunted, but has very nearly been crashed. Most importantly, prey populations exhibiting such age structures as a result of non-selective hunting (except for the possible exclusion of particularly young animals) do not and cannot produce substantial hunting yields. Such populations must have been almost completely replaced by some other resource in the human diet.

#### *Age-Structure Effects of Sex-Biased Hunting*

If the foregoing analysis of ungulate archaeofaunal age structures were universally applicable, it would imply that inferences of both substantial hunting pressure and substantial human reliance on the species, based on high proportions of juveniles in ungulate archaeofaunas, are not well-founded. However, a critical factor has not yet been included in the simulation-model analysis of age-structure effects: sex-biased hunting.

As discussed in chapter 4, simulation modeling results suggest that sex-biases in ungulate hunting (generally, preferential hunting of males) should reflect behavioral characteristics of the prey species. The data from the Wadi Meged, Israel (i.e., Hayonim Cave and Meged Rockshelter), support this contention in that sex ratios of gazelle are consistently in the 60% to 65%-male range throughout the sequence (Stiner 2005:213-217), even though both environmental and level-of-exploitation changes are believed to have occurred over the large time span represented by the sequence.

That sex-biased hunting might produce very large age-structure changes in ungulate populations is hinted by Wolverton's (2001) conversion of Taber et al.'s (1982) Leslie-matrix modeling of elk-management strategies. Wolverton used the simulated life-table data presented by Taber et al. (1982:Tables 40-42) for different cull levels to examine the intensity of population age-structure compression associated with various harvest rates. From these data, Wolverton (2001:35) concluded that "(p)rogressively greater harvest pressure results in progressively steeper survivorship, which results in juvenile-biased population age structures." However, the major increases in the juvenile fraction of the simulated populations on which Wolverton based this conclusion cannot be validly attributed simply to high harvest pressure. Because Taber et al. (1982) were interested in the intentional management of a modern ungulate population, their cull simulations are directed primarily at the effects of different levels of culling of males. As a result, the Taber et al. model looks at *four different levels of male-biased hunting* at four different levels of hunting pressure.

Taber et al. (1982:296-298) constructed a simple model of the female cohort of an elk population based on field research, and produced both a life table for this cohort in the absence of hunting and a life table for the cohort with 10% of the population removed annually by hunting. Assuming that males have the same population dynamic character-



istics (not technically likely, but reasonable for heuristic purposes), the age-structure effects of this 10% hunting rate can be generalized to a full population hunted at a 10% rate: an approximately 34% drop in the percentage of old animals, with 6.4% and 2.5% increases in juvenile and prime adult animals<sup>1</sup>, respectively. After this point, however, Taber et al.'s model results and/or presentation thereof become problematic. They present (Taber et al. 1982:Table 42) a male cohort life table copied from the 10% harvest-rate female life table as "0 percent" harvest rate. Their assumption that the first two age classes of such a life table should match the female life table is reasonable, since they are assuming the 10% female harvest rate, the number of animals born each year and natural juvenile mortality rates can be assumed to be the same for males and females, and the 'female' hunting rate is explicitly defined as the "unantlered" hunting rate. However, the remaining age classes should not experience the same total mortality (natural and hunting combined) for males and females if females are hunted and males are not.

In addition to the 'unhunted' male cohort, Taber et al. (1982) purport to subject the male cohort to harvest rates of 25%, 40%, and 80% (while maintaining the 10% harvest rate of unantlered animals, that is, all juveniles and adult females). The life table results for these harvest rates show considerable age structure compression, with juvenile fractions of the male cohorts of 51.6%, 68.1%, and 92.7%, respectively<sup>2</sup>. The harvest rates listed as producing these patterns are erroneous<sup>3</sup>; however, the general trend of producing higher percentages of juvenile animals than those described earlier for non-sex-biased hunting when the male cohort is culled at higher rates than the female cohort is not affected by these errors.

Wolverton's (2001) association of such substantial increases in the juvenile fraction of the population with harvest pressure in general, rather than male-biased harvest pressure specifically, reflects a common problem in using modern wildlife data to

interpret archaeofaunal age-structure patterns. Koike and Ohtaishi (1987), for example, use age-structure data for a population of sika deer in which only males are hunted to estimate the harvest rates to which prehistoric deer populations were subjected, even in cases where the archaeological assemblages are biased toward females. Such uses of modern data ignore the fact that a male bias in hunting or culling skews the population dramatically from its 'natural' state. When hunting focuses primarily (or even solely) on males, as is normally the case in modern managed or restricted hunting, the recruitment of males into the population is only affected slightly, and may in fact increase as a result of reduced intraspecific competition; juvenile males are also typically protected from hunting. Since there is always a fresh supply of juvenile males, the adult male component of the population can be hunted at levels producing male-population-size reduction and age-structure compression that the population as a whole could not sustain.

Such population reduction brings up the question of the filtering effect of hunting. For example, in Taber et al.'s (1982) model, 112 females are hunted annually regardless of the male hunting rate. Since the female cohort is only slightly compressed<sup>4</sup> by this hunting (see above), this would provide a substantial counterweight to the heavy compression of the male cohort in the age structure of the combined killed assemblage. Unfortunately (see note 3), it is not possible to determine the actual numbers and ages of males hunted in Taber et al.'s model as would be necessary to calculate a killed-assemblage age structure. Without such data, application of Taber et al.'s male-cohort age structures to archaeological data that combines males and females is unwarranted.

To examine the effects of sex-biased hunting on the associations between population age structure, killed-assemblage age structure, and harvest rates, the simulation models of gazelle high growth model populations conducted above for gradually rising harvest rates are repeated with hunting biased toward males such that 65% of the animals

killed are male, in accordance with the ratio found by Stiner (2005:213-217) for the Wadi Meged, Israel series. Population size and number of animals killed per year are shown in Figure 5-12. The male-bias is implemented differently here than in chapter 4. In this case, the number of animals to be killed is calculated from the harvest rate and the pre-reproduction beginning-of-year population size as described for non-male-biased percentage-of-extant-population hunting in chapter 3. The resulting value is then split between males and females at the 65:35 ratio, with the inevitable fractional animal assigned probabilistically to either the male or female kills.

The overall patterns of population decline and yield growth are initially very similar to those seen with the non-sex-biased models; however, the truly stable-yield and declining-yield stages are never reached. Before the yield can stabilize, much less drop, the male segment of the population is reduced to the point where there are not enough males of huntable age to maintain the male-bias rate. In reality, this point itself would never be reached, since it requires that effectively all males of huntable age be killed every year, a practical impossibility.

Importantly, the age-structure effects of increasing percentage-of-extant-population harvest rates with a 65:35 male bias differ significantly from those found without the male bias. In the unbiased case discussed earlier, major shifts toward juvenile-dominance of the gazelle population occur only during the decreasing-yield stage, and while the percentage of juveniles in the killed assemblage increases, it does not approach the 50-52% level found by Munro (2001, 2004) in the Hayonim Cave and Terrace Natufian gazelle assemblages. In the male-biased case, there are no clear yield or other stages for which to determine associated age structures. Therefore, the simulation model run is arbitrarily divided into three equal time stages, and the population and killed-assemblage age structures for each are illustrated in Figure 5-13. With a male bias such as that seen

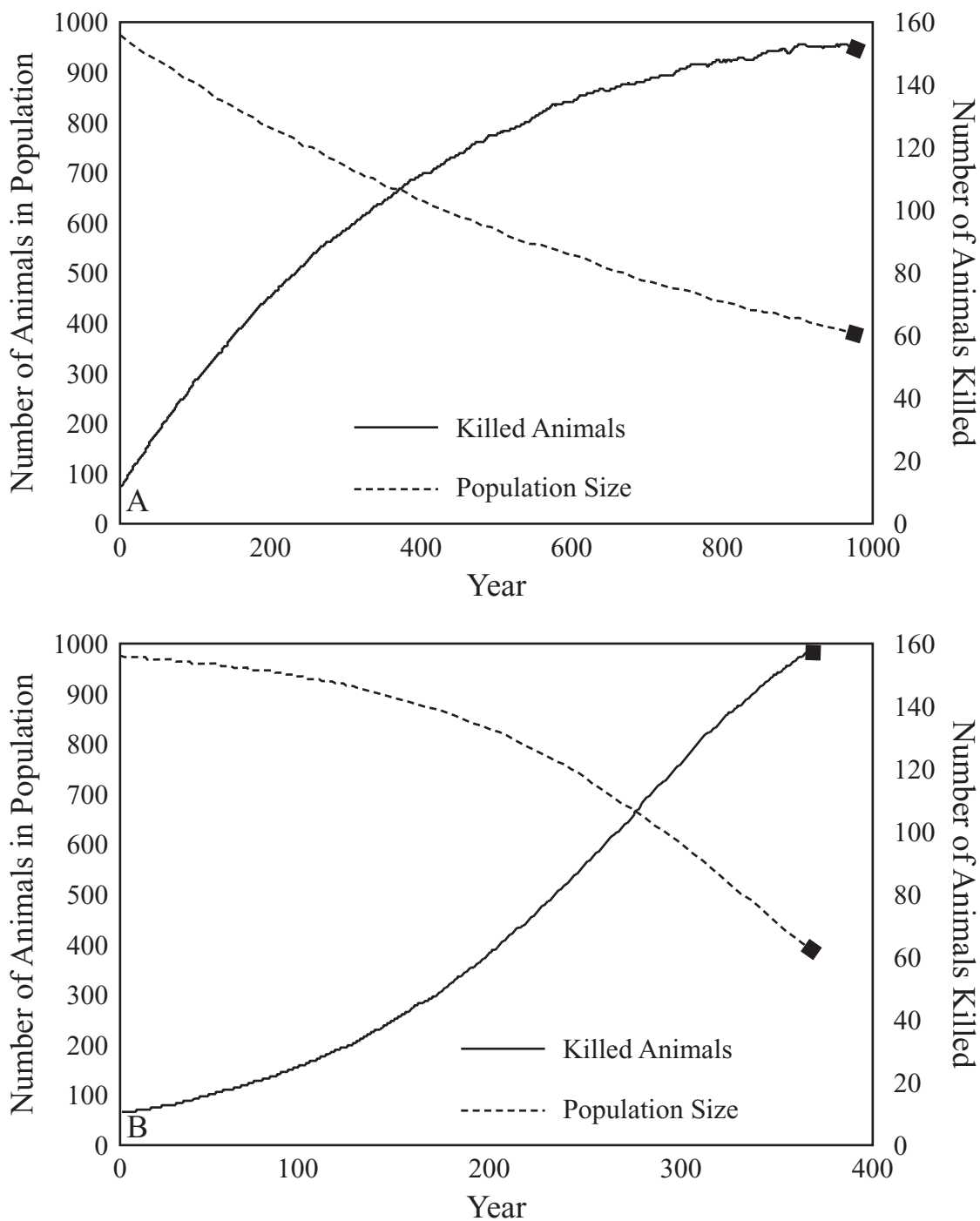


Figure 5-12. Population size and number of animals killed yearly for gazelle high growth model populations hunted at gradually increasing percentage rates and a male bias: A) constant rate of increase (.04% added to hunting rate each year), and B) exponential rate of increase (hunting rate increasing by 1% of its value each year). Minimum hunted age: 6 months. Boxes indicate that male-bias level can no longer be maintained (see text).

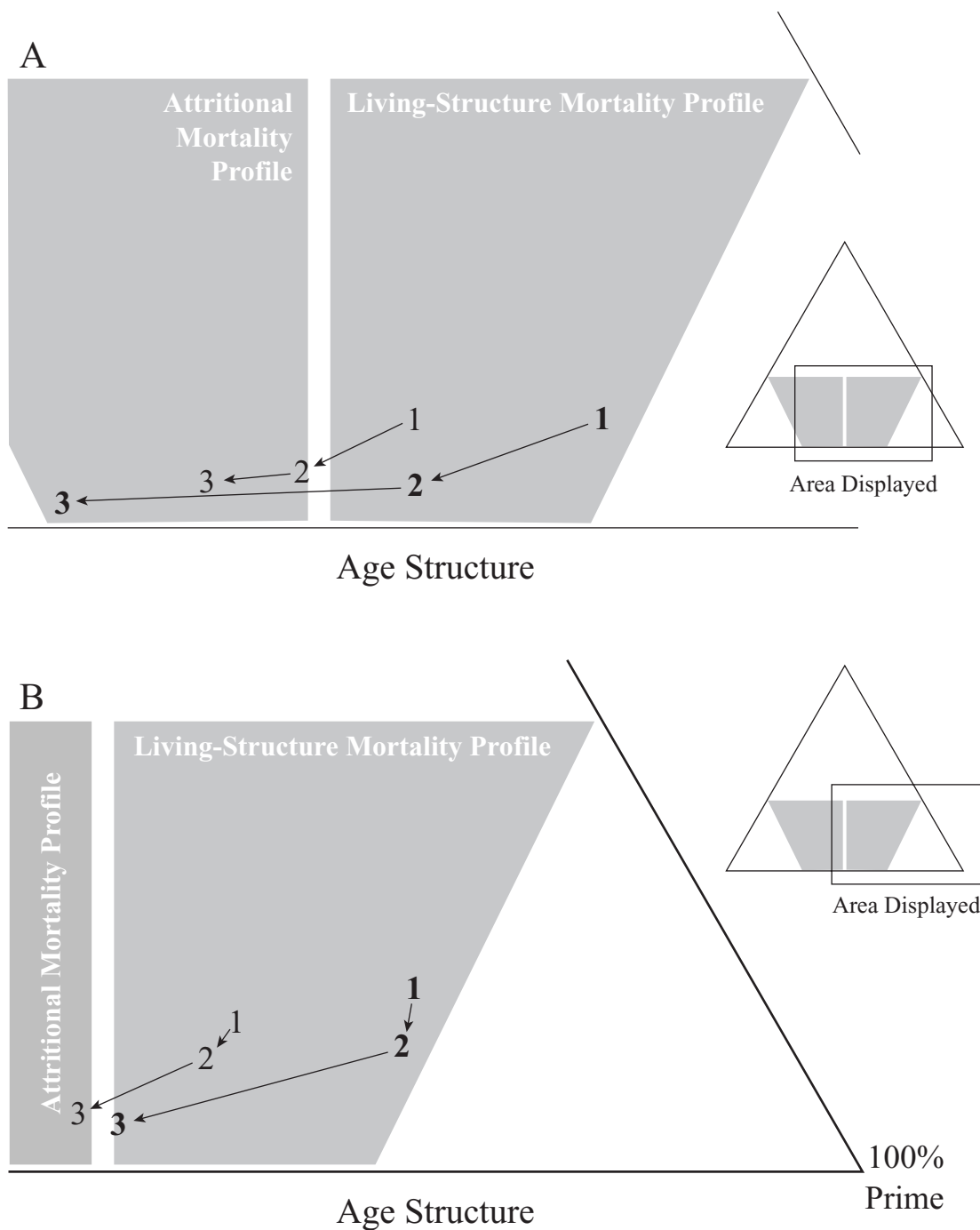


Figure 5-13. Age structures of gazelle high growth model populations hunted at gradually increasing percentage rates and a male bias with A) constant rate of increase (.02% added to hunting rate each year), and B) exponential rate of increase (hunting rate increasing by 1% of its value each year). Displayed numbers indicate arbitrary time divisions (see text). Boldface numbers are hunted assemblage age structure; normal-type numbers are population age structure. Minimum hunted age: 6 months.

in the Hayonim Cave gazelle, population age structure is compressed as much as or more than in the non-sex-biased case, *without the shift to a stable or declining yield*. Even more importantly, major compression of the killed-assemblage age structure occurs, with juvenile percentages theoretically capable of reaching 70 to 75%. Note that the differences between the age-structure effects illustrated in Figure 5-13A and 5-13B, in particular the smaller and later increase in juveniles in the exponential-growth case, are primarily the result of the decision to employ arbitrary time, rather than yield, divisions. Yield-based divisions would leave the constant-growth case unchanged; the exponential-growth case would become very similar to it.

### **Discussion**

Hunting pressure plainly causes age structure compression in ungulate populations. However, the relationship is not a simple one, particularly from the viewpoint of the archaeologist seeking to infer human demographic conditions or resource stresses. The hunting strategies or practices employed by the accumulators of an archaeological ungulate assemblage play a critical role in determining the age structure of the archaeological assemblage that results. The decisions about which animals to hunt not only act as a filter through which the ungulate population's age structure is transformed into the archaeofaunal assemblage's age structure, but also are a prominent factor in the production of the population's age structure in the first place.

Two aspects of the hunting strategy are particularly important, age preferences and sex biases. Age preferences appear to operate primarily as a filter, having relatively little effect on the ungulate population's age structure response, which is determined primarily by the level of harvest. However, caution should be used in applying this conclusion, because all of the modeled hunting strategies considered in this chapter are based on the

non-selective to prime-dominant hunting strategy associated with most human hunting (Stiner 1994). Hunting strategies that target substantially different sets of age classes are unlikely to produce the same pattern. However, the filtering effects of such strategies are likely to overwhelm any differences in effects on population age structure, making the exact nature of the latter unimportant. For example, hunting that is restricted to juvenile animals will produce a juvenile-only archaeological assemblage, regardless of the structure of the prey population. The exception to this is hunting strategies that produce age structures mimicking attritional mortality. It is unclear what population age-structure effects such a strategy would have, and this issue is not readily resolved through modeling, since a critical factor in such a model is the extent to which such hunting is compensatory (that is, removes animals that would have died anyway of non-human causes).

Additionally, it is important to recall Lyman's (1987) caution that age structure should not be used in isolation in drawing conclusions about hunting practices. Lyman was referring specifically to the identification of catastrophic kills, but the principle is also important for inferences about hunting pressure. For example, in the Italian Middle Paleolithic sequence studied by Stiner (1994), the significant local decrease in the old adult fraction of cervid assemblages seen around 55 kya might be interpreted as the result of higher harvest rates, if skeletal-element-representation patterns in these cases did not strongly suggest that it instead represents a shift in the importance of scavenging and hunting.

A bias toward the hunting of males has both filtering and population-age-structure-producing effects. It is clear from the treatment of sex-biased hunting above that sex-ratio data are absolutely critical to the interpretation of age structures in ungulate assemblages. In the example of the Natufian gazelle from Hayonim Cave and Terrace (Munro 2001, 2004), if the gazelle assemblage did not show a strong male bias, the

dramatic increase in the proportion of juvenile gazelle relative to preceding time periods would not indicate a high level of hunting pressure on the gazelle population during the Natufian. Rather, it would indicate the overhunting of that population *prior* to (or at the very beginning of) the Natufian, and if human population (or population density) were constant or higher, that the food previously supplied by gazelle in the human diet was supplied during the Natufian by other resources. This is because the percentages of juveniles seen in the Hayonim Natufian assemblages appear to be produced only in populations that have been overhunted to the point where they produce small fractions of their previous yields. Such an interpretation would not be well supported by the fact that gazelle seem to have been the primary protein source during the Natufian (Stiner 2005:Figure 9.7), despite the significant contemporaneous increase in small game use (Munro 2001, 2004; Stiner et al. 2000). The bias toward males in the Hayonim Natufian gazelle assemblages, however, means that the high percentage of juveniles could have been produced by harvest levels that placed the gazelle population under pressure, but that did not involve overhunting (in the sense discussed above) and reduced yields. The particular ages of juveniles hunted are important here as well, since such percentages of juveniles should only be produced—even with male-biased hunting—if not simply some (older) juveniles, but in fact much of the juvenile age group, is subjected to hunting. Figure 5-14 shows the age-structure effects of male-biased hunting of the gazelle high growth model for different minimum ages hunted. Killed assemblages with as high percentages of juveniles as are found in the population are produced even at high harvest rates only where the minimum age hunted is nine months or less. Since there are individuals less than six months old in the Hayonim Natufian gazelle assemblages (Munro 2004), it is clearly possible that the high percentage of juveniles is the product of a particularly high level of reliance on gazelle.



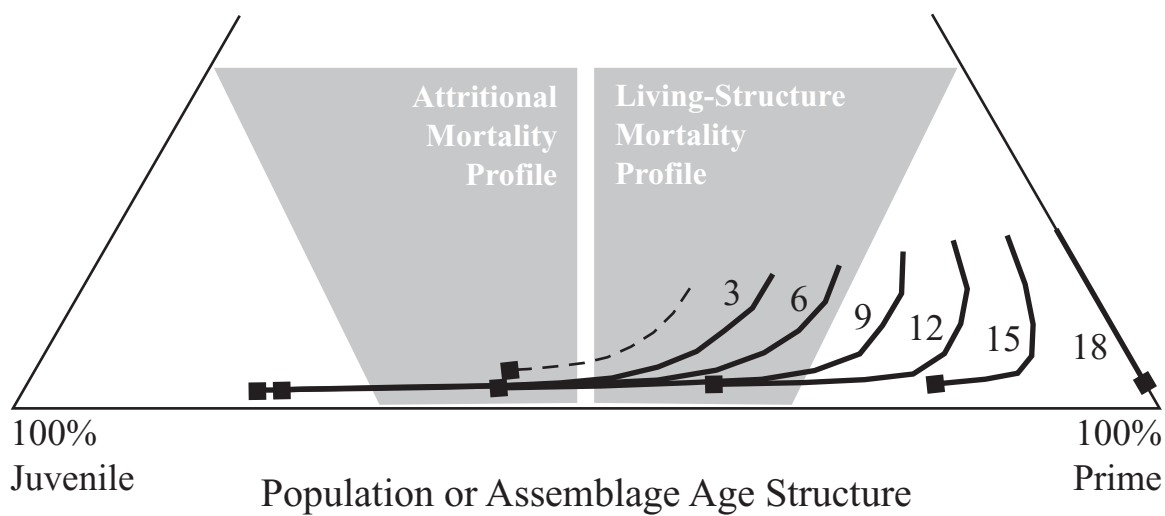


Figure 5-14. Effects of increasing percentage hunting rate with a male bias on age structure of gazelle high growth model populations and of the animals hunted from those populations at different minimum ages hunted, based on mean age structure over the last 500 years of a 1000 year model run. Solid lines are hunted assemblage age structure; dashed line is population age structure. Labels indicate the minimum ages hunted in months. Hunting rates range from 0.1% to the maximum rate at which male bias can be sustained (indicated by boxes; from 24% to 46%, depending on minimum age hunted). Population results for all minimum hunted ages between 3 and 18 months are effectively identical and are thus represented by a single line. For hunted assemblage results, note that 18 months is the juvenile-adult cutoff age (following Munro 2001).

However, there is a characteristic of the Hayonim Natufian gazelle assemblages that is not readily explicable by reference to the hunting pressure models reported here. Munro (2001:Figure 8.10) places the age structures of the Hayonim Cave and Terrace Natufian gazelle assemblages near the center of the attritional-mortality-profile region, with an apparent representation of old adults of about 17%. There are at least two alternative explanations for this value. First, the assemblages may in fact represent a significant change in gazelle-hunting practices in the Natufian relative to earlier time periods, with a non-selective (except for the possible exclusion of young juveniles) ambush-style strategy being replaced by a cursorial-style one. In this case, it is not practical (for the reasons noted above) to make hunting-pressure assessments. Second, there may be

discrepancies between the simulation model 'real age' definitions of old animals and the tooth wear definitions used in archaeological analysis. In particular, if the rate of tooth wear for Terminal Pleistocene gazelle in northern Israel is greater than that implicitly assumed by the simulation model (in its maximum age parameter), animals considered to be of later prime adult age by the simulation model may be identified as old in the archaeological assemblage. The sex-biased nature of the Natufian gazelle-hunting provides a potential means of discriminating between these possibilities. If the high proportion of juveniles is due to hunting pressure, then the male and female sub-assemblages should show different age structure patterns. Specifically, the male portion of the assemblage should be substantially more biased toward juveniles. The practicality of such an analysis is beyond the scope of this dissertation.

### **Summary**

The basic, invariant effect of increasing harvest rates following hunting strategies that are non-selective to prime dominant is to reduce the fraction of the ungulate prey population that is comprised of old adults, and thereby reduce the percentage of such animals in the produced archaeological assemblages. Significant compression of population age structures can also be produced by hunting pressure; however, the nature of the hunting practices employed by the human hunters are of vital importance in this process. Clearly, no level of hunting pressure will produce juvenile-biased archaeological assemblages if hunting tactics preclude the killing of too large a fraction of the juvenile age group. Even more importantly, sizeable increases in the juvenile fraction of the prey population correspond to very different human hunting situations in different sex-bias regimes. Where there is little or no bias toward the hunting of males, higher percentages of juvenile animals in archaeological assemblages indicate low overall yields relative to

those obtained at some point previously<sup>5</sup>. The actual juvenile-biased assemblage in such a case represents a situation where human population density was lower than it had been in the past, or the ungulate species was no longer an important food resource. In contrast, where there is substantial bias (e.g., the 65:35 male:female ratio seen in the Wadi Meged gazelle) toward the hunting of males, higher percentages of juveniles indicate contemporaneous hunting pressure, and indeed near maximal utilization of the ungulate species as a food resource. As a result, it is very important that considerable caution be exercised in interpreting age-structure compression in ungulate archaeofaunas. In many cases in the Paleolithic, the sex-ratio data that are required for the proper interpretation of the representation of juveniles will not be obtainable, or will be of limited reliability because of small sample sizes.

### *Notes*

1. These values are based on the following division of Taber et al.'s (1982) age classes: juveniles, age classes 0-1 and 1-2; prime adults, age classes 2-3 through 9-10; old adults, age classes 10-11 through 14-15.
2. Taber et al. (1982) do not increase juvenile survival of either males or females as a result of the decrease in total population associated with these hunting rates, despite doing so while calculating their 10%-hunted female cohort. The juvenile percentages of the male cohorts are thus possibly understated.
3. While the 10%-hunted female cohort is explicitly described as stabilizing at 1120 animals with an annual offtake of 112 animals, the cull rates for the male cohorts are inexplicably based on the assumption that the number of antlered males harvested must equal the number added to the antlered cohort annually (146 animals surviving into the 1-2 age class) since the population has stabilized (Taber et al. 1982:297-298). This value is

divided by the total size of the male cohort to produce the 25%, 40%, and 80% 'harvest' rate values. In effect, Taber et al.'s presentation assumes that all adult male mortality is due to hunting. The actual models must have been different, because if 146 animals were culled from a cohort stabilized at a size of 913 animals (the '25% harvest rate'), it is not clear how the population could reach a stable size of 692 animals (the '40% harvest rate') with the same absolute number (146) of animals killed per year.

4. In fact, the female cohort should show some increase in juveniles, because of the reduction in intraspecific competition caused by the reduction in males.

5. Since the overhunting process by definition yields far more animals per year, an assemblage with a high-enough percentage of juveniles to place it outside the living-structure mortality region of the ternary graph must either entirely post-date overhunting or have accumulated over a length of time many times longer than that involved in the overhunting process.

CHAPTER 6  
HUMAN POPULATION GROWTH AND PREY REPRESENTATION:  
POTENTIAL AND LIMITATIONS OF UNGULATES VERSUS SMALL GAME

The role of population pressure and/or population growth in human social, economic, and technological evolution has long been subject to debate in archaeology (e.g., Binford 1968b; Cohen 1977; Cowgill 1975a, 1975b; Keeley 1988; Redding 1988; White 1959). Nonetheless, it has become clear that, even if population growth or pressure is not a 'prime mover', the size and density of human populations are relevant factors in such evolution (e.g., Fletcher 1995; Gamble 1999; Harpending and Bertram 1975; Winterhalder et al. 1988).

While numbers and sizes of archaeological sites are the most commonly used archaeological proxy measures of population size in most times and regions (e.g., Adams 1965, 1981; Bocquet-Appel et al. 2005; Hill et al. 2004; Kramer 1980, 1982), for hunter-gatherer populations in particular a major approach has involved the application of the diet breadth / prey choice model from behavioral ecology (e.g., Edwards 1989; Grayson and Delpech 1998; Neeley and Clark 1993; Stiner 2001; Stiner and Munro 2002). Generally speaking, the model (Pulliam 1974; Stephens and Krebs 1986; chapter 2 of this volume) is used to argue that larger populations will exploit either a broader range of resources, resources that are not as economical, or both. As discussed in chapter 2, however, the diet breadth / prey choice model is more complicated than its usual archaeological applications make it appear, particularly with regard to the hunting of large-bodied prey in deep time. The preceding three chapters have developed computer simulation models of ungulate populations exposed to human hunting as part of an attempt to determine if data from such models can help overcome the limitations of diet breadth / prey

choice models as tools for inferring changes in human population densities from ungulate species representation in Paleolithic archaeofaunas.

Figure 6-1 shows changing ungulate-species exploitation in three areas of the Mediterranean Basin. During the Middle Paleolithic, the largest available ungulate species (aurochs and red deer) represent a much larger portion of the human diet than do smaller ungulates. During the Upper Paleolithic (and Epipaleolithic), there is a clear shift to the smaller ungulates. Since larger game animals are normally argued to be more economical to exploit and thus higher-ranked in diet breadth analyses (see chapter 2), it is very tempting to interpret this shift as evidence of human population growth.

This chapter examines the simulation model results presented in chapters 4 and 5 for their implications with regard to such an inference, arguing that these results do not generally provide strong enough evidence to surmount the difficulties involved in making hominin demographic inferences from ungulate prey 'choices' discussed in chapter 2. To briefly recap, under diet breadth / prey choice models of ungulate hunting (whether based on net energetic return or food yield), increases in diet breadth can occur in multiple circumstances, only some of which can be associated with predator (i.e., hominin) population growth. Decreases in hunting-failure rates, changes in hunting techniques, and changes in the number of individuals with whom meat is shared can all produce increases in the utilization of smaller ungulates, in addition to the decreases in population density of larger ungulates to which a simple reading of the diet breadth / prey choice model might attribute such increases.

As with so many things in archaeology, it is difficult to make such an argument in absolute terms; thus, much of this argument is couched in terms of comparing the diet breadth / prey choice model use of ungulates to the proven effectiveness of parallel analyses using small game (Stiner et al. 1999, 2000). Here, the use of ungulate species

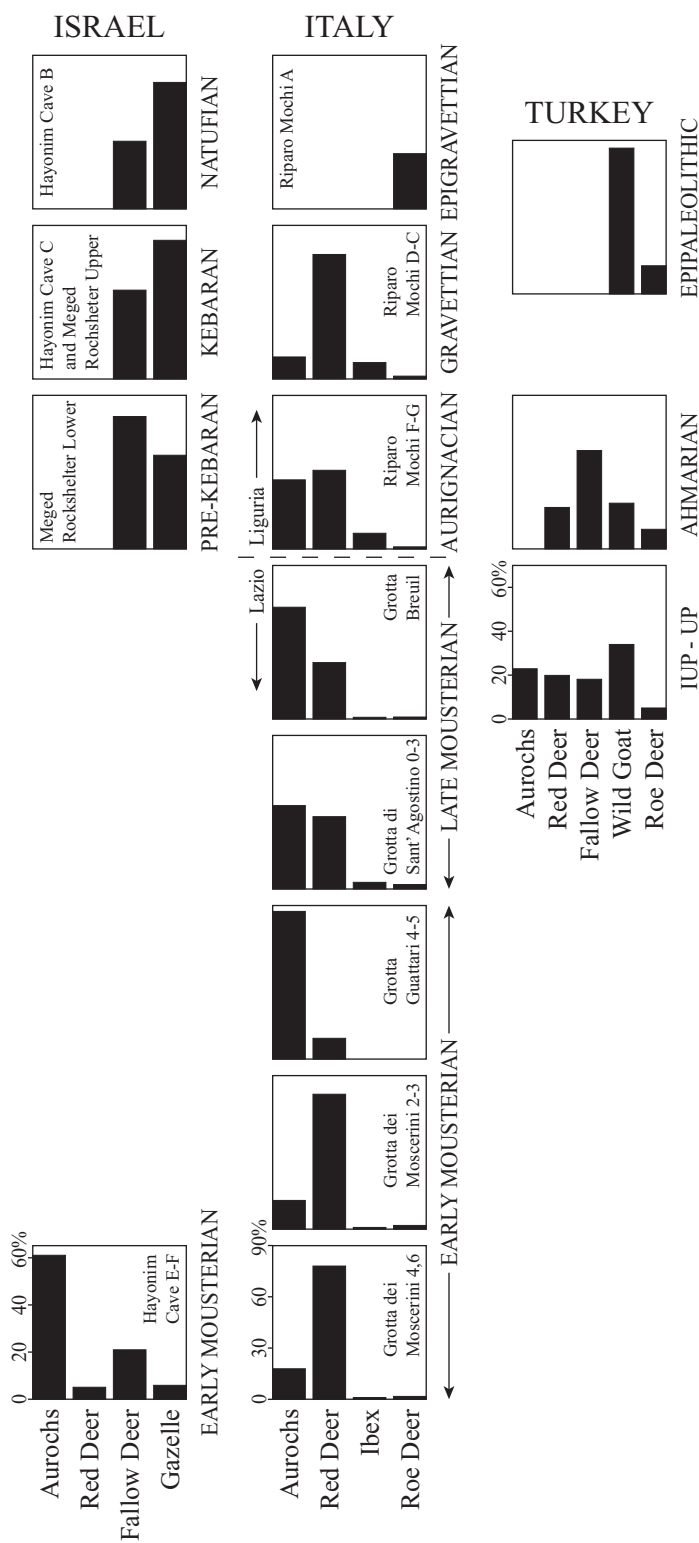


Figure 6-1. Percentages of biomass attributable to size-ordered ungulate taxa in three Mediterranean data sets (modified from Stiner 2005:Figure 9.7); assemblages are approximately time-ordered. Scales are invariant within data sets. Note that the Italian sequence has chronological gaps not shown in this figure.

exploitation is compared to small game exploitation in a hunter-demography context on seven fronts: technological investment, magnitude of sustainability differentials, covariation of payoff and sustainability, availability of independent evidence of hunting pressure, sex biases in exploitation, source-sink dynamics, and the impact of different patterns of human population growth.

### **Inferring Demography from Archaeofaunal Resource Representation**

The most obvious issue complicating the demographic interpretation of changes in resource representation is environmental change. Non-anthropogenic causes of resource-availability changes clearly undermine demographic interpretations, since the latter are predicated on human-induced resource depression. Evidence for environmental stability or countervailing change is therefore useful, if not absolutely necessary, for demographic interpretations of resource-exploitation patterns. Additionally, arguments for human population growth are substantially strengthened by independent evidence that the higher-ranked resource(s) whose relative representation is decreasing is under some form of exploitation stress (in the case of animal prey, hunting pressure). The magnitude of the efficiency differentials between high-ranked and low-ranked resources also affects the strength of demographic arguments. If resource representation shifts toward a much less efficiently-exploited resource, the argument that this represents resource depression is much stronger than if the lower-ranked resource is only marginally less efficient to exploit. Most archaeological applications of diet breadth principles rely on body size as a measure of energetic return, only implicitly including the handling time that is key to the conversion of return into efficiency. In such cases, large shifts in body size are more convincing than small ones, though this may be complicated by parallel reductions in processing costs. Though the diet breadth / prey choice model, as strictly defined, does



not include pre-encounter costs, explicit consideration of the relative technological costs of exploiting different resources can be an alternative to reliance on energetic return. For example, Stiner et al. (2000; Stiner and Munro 2002) divide small game animals between slow, collectable prey (low to zero technological investment) and fast, difficult-to-catch prey (requiring significant technological investment). Where these technological costs relate directly to the difficulty of exploiting a resource, they are highly relevant to the relative failure rates involved in such exploitation, a key factor in handling time and therefore efficiency (see chapter 2).

Evidence that the new or newly important resources are able to withstand higher exploitation rates than the resources being replaced is also an important factor in demographic arguments (e.g., Stiner et al. 1999, 2000; Stiner and Munro 2002). Since the basic argument is that human population growth has resulted in increased exploitation of the higher-ranked resource(s), lowering their population densities and thus human encounter rates with them, which in turn leads to increased exploitation of the lower-ranked resource(s), the lower-ranked resource(s) must be able to replace the food 'lost' due to the reduction in the exploitation rate of the higher-ranked resource(s). If significant human population growth is argued for, the lower-ranked resource(s) should, in fact, be able not only to replace the 'lost' food, but to do so without as significant levels of population depression (thus retaining the ability to provide additional food).

### **Demographic Potential of the Exploitation of Ungulates versus Small Game**

While ungulates consistently dominate faunal assemblages in the Paleolithic in most areas, recent research has suggested that small game animals are more sensitive, or at least easier to use, indicators of human demography (Stiner et al. 1999, 2000). The following discussion makes use of the simulation model results presented in the previous

chapters, as well as a variety of other comparisons between ungulates and small game, to demonstrate why this is often the case.

### *Acquisition Techniques*

One of the largest differences between ungulates and small game in terms of diet-breadth analyses is the radically different basis for the determination of rankings. The seven ungulate species considered in this dissertation vary up to thirty-five-fold in body size. The energetic or food-yield returns from exploiting these species are thus tremendously different. In contrast, the body-size differences among the small game taxa examined by Stiner et al. (1999, 2000)—tortoises, hares, and small game birds like partridges—are only on the order of four-fold (see Table 6-1). On yield alone, it would appear that the ungulate group has greater potential for recognizing demographic change through changing species representation. However, the ungulates fit well into a standard diet breadth approach that only considers post-encounter handling costs, because the technological investment necessary to hunt different ungulate species is very similar. While technological and behavioral specialization to particular ungulate prey may occur,

Table 6-1. Estimated Mean Adult Body Masses for Ungulate and Small Game Taxa.

Taxon	Mass (kg)
Aurochs ( <i>Bos primigenius</i> )	700
Red Deer ( <i>Cervus elaphus</i> )	200
Fallow Deer ( <i>Dama dama</i> )	90
Goat ( <i>Capra aegagrus</i> )	50
Ibex ( <i>Capra ibex</i> )	50
Gazelle ( <i>Gazella gazella</i> )	20
Roe Deer ( <i>Capreolus capreolus</i> )	20
Hare ( <i>Lepus</i> sp.)	2
Tortoise ( <i>Testudo</i> sp.)	1.5
Partridge, etc. ( <i>Alectoris chukar</i> , <i>Perdix perdix</i> , <i>Coturnix coturnix</i> )	0.5

the general process of hunting and butchering can be extremely similar whether the targeted animal is a roe deer or a red deer<sup>1</sup>. As discussed by Stiner et al. (2000), this is very far from being the case with the small game group. Tortoise exploitation entails no pre-encounter preparation and peri-encounter costs are extremely low; even small children can simply pick up an encountered tortoise and carry it away. The exploitation of hares or game birds, however, requires substantial pre-encounter investment. If such prey are to be hunted on encounter, technology that allows rapid, accurate delivery of a projectile is extremely helpful, though not strictly necessary. Alternatively, the construction and setting of snares enables non-encounter 'hunting' of such game (placing it completely outside the bounds of the diet breadth / prey choice model), but requires substantial preparation as well as potentially fruitless search time afterward in order to check previously set snares.

Clearly, then, there is a much greater difference in the amount of investment required to exploit different prey within the small game group than within the large game group. As a result, for the small game group, decisions about prey exploitation and targeting may need to be made well before the point of encounter.

As noted above, the technological investment involved in hunting can be expected to parallel hunting failure/success rates, which can have a significant impact on both resource rankings and resource-inclusion decisions. Because the techniques used in hunting different ungulates (particular in the independent-encounter regime specified by the diet breadth / prey choice model) are in general more similar than those involved in acquiring different types of small game, there is more concern that the specific failure rates experienced by ungulate hunters will affect resource-inclusion decisions, potentially undermining body-size-based resource rankings.

### *Sustainable Hunting Pressure*

As noted previously, arguments relating resource exploitation changes to demography are substantially strengthened if the lower-ranked resource can be shown to be able to withstand higher levels of harvest pressure than the higher-ranked resource. This is the major methodological innovation of Stiner et al.'s (1999, 2000) small game study, along with the just-discussed focus on acquisition techniques and technological investment. In that study, it was demonstrated that tortoises, which are the higher-ranked prey due to their much lower technological investment and handling costs, are able to maintain viable populations only at very low exploitation rates. The low-ranked prey, such as hares and partridges, in contrast, are able to withstand exploitation rates that are many times greater.

The pattern is rather different in the ungulate group. While lower-ranked (in this case based on return rate rather than acquisition technique—see above) species are able to survive greater harvest rates, the differential is not nearly as strong. Figure 6-2 compares the hunting rates sustainable by each ungulate species (data from Table 4-1). The species are shown in groups appropriate for comparison to the three geographic regions presented in Figure 6-1. In comparison to the small game group (see Stiner et al. 2000:Figure 9), there is very little definitive separation among the confidence ranges (low growth model to high growth model) for maximum sustainable harvest rates. With the exception of roe deer in the Italian species set, adjacent species in the body size / presumed diet-breadth rankings do not differ definitively in their abilities to withstand having fractions of their populations removed regularly by hominin hunting. Substantial shifts down the body-size spectrum (e.g., from aurochs to roe deer) are therefore necessary to even approach the differences in sustainable hunting rates seen in the small game group.

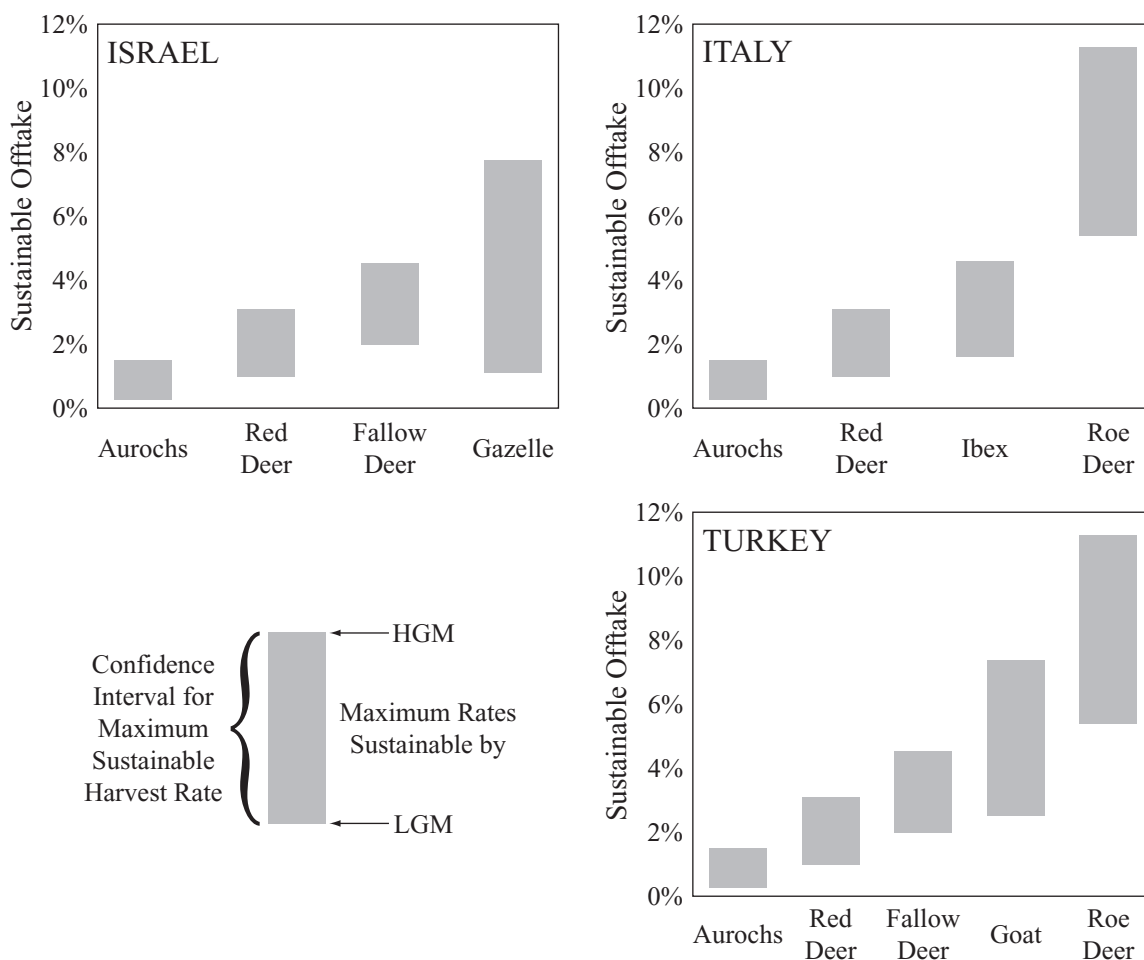


Figure 6-2. Comparison of sustainable annual offtake rates for ungulate species in each Mediterranean data set as percentages of initial, unharvested population.

### *Sex-Biased Hunting*

The sustainable harvest rates shown in Figure 6-2 are based on the assumption of sex-neutral hunting. However, as shown in chapter 4, the potential for biases toward males in ungulate hunting can radically alter maximum sustainable harvest rates. Substantial male biases can double the maximum harvest rate sustainable by a population, and potentially increase it even more. Because the practicality of ungulate hunting with a substantial male bias is heavily dependent on the social behavior of the hunted species, and especially since ungulate social behavior can vary not only seasonally but also with

population density (see discussion in Chapter 4), the possibility must be confronted that some species in a regional species set may be substantially more open to male-biased hunting than others. Furthermore, which species are more susceptible may not be predictable. If sex ratios can be determined for the various species represented in a series of assemblages, it should be possible to use the simulation model to determine sex-ratio-specific maximum sustainable hunting rates. In the absence of comprehensive sex-ratio data, however, the possibility of male-focused hunting dramatically reduces the utility of the simulation results.

While male-focused hunting of small game animals would certainly produce similar difficulties, it is much less likely to occur. While it may be relatively easy to discriminate males and females at a distance for some game birds, this is not the case for hares. Additionally, 'hunting' of these animals may be undertaken through the use of snares, which are not well-known for their ability to distinguish the sex of animals that are trapped. Moreover, any sex bias that is managed in spite of these handicaps is likely to be toward males, increasing the maximum sustainable harvest rates of these taxa. Sex biases in human hunting (or collection) of tortoises, in contrast, are likely to be in the direction of females (Stiner et al. 2000), as the females are generally larger than the males. This bias is a significant factor in the much lower maximum sustainable harvest rates of tortoises in comparison to hares and partridges.

The possibility of sex-biased hunting therefore favors demographic analyses of small-game exploitation, since it increases the difference between the harvest rates sustainable by high- and low-ranked prey. In contrast, the same possibility in the ungulate group works against such analyses by increasing uncertainty about the relationships among maximum sustainable harvest rates of the various species.

### *Independent Evidence of Hunting Pressure*

Stiner et al. (2000) were able to argue that size reduction in tortoise remains in the Wadi Meged, Israel data set was the result of hunting pressure, bolstering their argument that increasing exploitation of lower-ranked prey (hares and small game birds) was a response to a demographically-driven reduction in tortoise populations. Demographic-focused analyses of ungulate data could be similarly strengthened if similar independent evidence of hunting pressure were available. Hunting pressure on ungulates, however, commonly results in *increased* adult body size, since the reduction in local population results in increased resource availability (e.g., Jacobson 1992; Keyser et al. 2005). Any size diminution in archaeological assemblages of ungulates under hunting pressure is likely to be due to increased representation of juveniles among the hunted animals.

Age-structure depression is the obvious candidate for independent evidence of hunting pressure on a high-ranked ungulate prey species. As is seen in Chapter 5, however, juvenile biases in ungulate archaeofaunas are not necessarily indicative of high coeval levels of exploitation. The sex bias (if any) involved in hunting an ungulate population has a strong effect on the level of age-structure compression produced by a given harvest rate. Without sex-ratio data for the ungulate species in an archaeological assemblage, different human-ungulate interaction histories cannot be distinguished.

Additionally, the hunting techniques used can affect the components of the prey population that end up in archaeological assemblages. While all simulation models in this dissertation have assumed that ungulate hunting is non-selective except for the exclusion of younger juveniles, archaeological analyses must always consider the possibility that an assemblage was accumulated through some form of selective hunting.

### *Relationship between Payoff and Sustainable Harvest Rate*

Not only are the maximum exploitation rates sustainable by different types of small game very different, those rates are also independent of body size (Figure 6-3). This is not the case for the ungulate group (Figure 6-4). Maximum sustainable harvest rates produced by the simulation model (data from Tables 4-2 and 6-1) are very strongly correlated with body size. The relationships between maximum sustainable harvest rate and body size illustrated in Figures 6-3 and 6-4 are quantified in Table 6-2. For the ungulates, maximum sustainable harvest rate is strongly predicted by body mass, following a power-law relationship, but body mass is a very poor predictor of maximum sustainable exploitation rate in the small game group.

The strong negative relationship between ungulate maximum sustainable harvest rates and body size (a more-or-less direct measure of food-yield return and a proxy measure of energetic return) has substantial implications for the use of ungulates in demographic analyses of archaeological species representation. It calls into question the ability of the lower-ranked species to replace food no longer being obtained from the

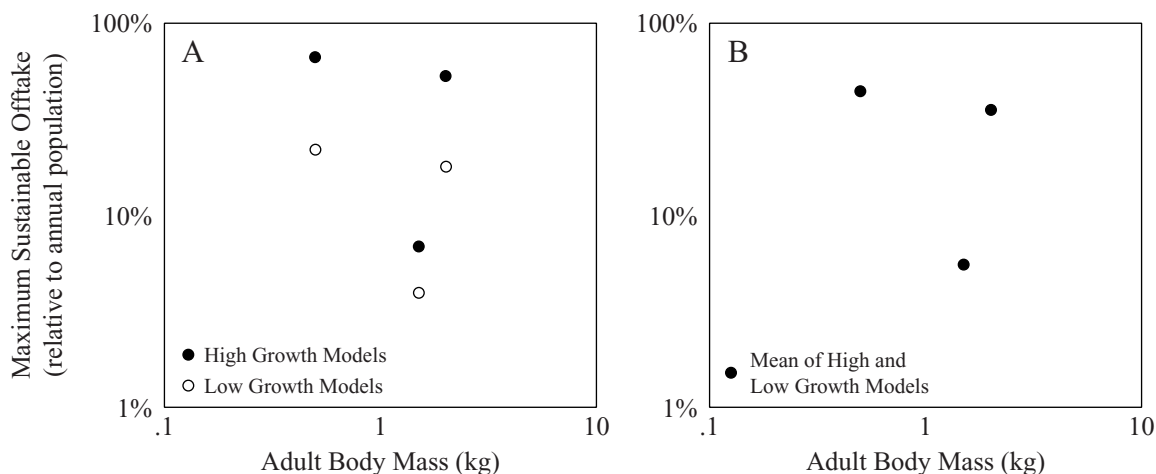


Figure 6-3. Log-log plots of sustainable offtake rate vs. body size for small game taxa modeled by Stiner et al. (1999, 2000), showing lack of significant relationship: A) High and low growth models treated separately; B) Mean of high and low growth model maximum sustainable harvest rates.



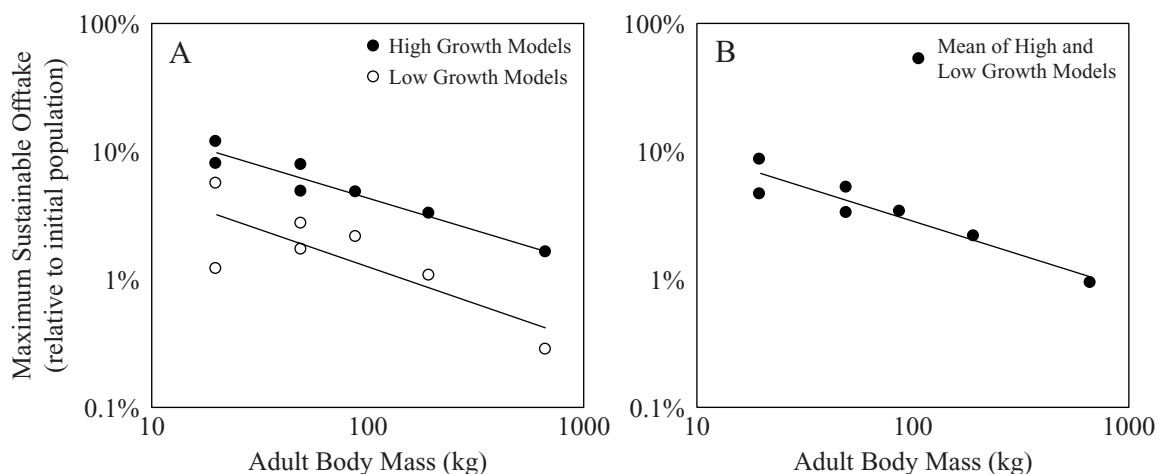


Figure 6-4. Log-log plots of sustainable offtake rate vs. body size for ungulate species modeled in this study, showing power-law relationship: A) High and low growth models treated separately; B) Mean of high and low growth model maximum sustainable harvest rates. Note that offtake rates are percentages of initial population, not annual population as in Figure 6-3. See Table 6-2 for regression equations and statistics.

Table 6-2. Relationships Between Body Size and Sustainable Harvest Rates.

Comparison of Body Mass with	Best-Fit Regression Curve			Rank-Order	
	Equation	$r^2$	$p$	$r_s$	$p$
<b>Ungulates</b> (Chapters 3 and 4)					
HGM Max Sustainable	$r_{max} = .4232w^{-.503}$	.928	<.001	-.982	<.001
LGM Max Sustainable	$r_{max} = .1821w^{-.590}$	.643*	.03*	-.655*	.111*
Mean Max Sustainable	$r_{max} = .3070w^{-.526}$	.886	.002	-.855	.014
<b>Small Game</b> (Stiner et al. 2000)					
HGM Max Sustainable	$r_{max} = -.2167 \ln w + .4493$	.262	.658	-.5**	.667**
LGM Max Sustainable	$r_{max} = -.0663 \ln w + .1556$	.263	.657	-.5**	.667**
Mean Max Sustainable	$r_{max} = -.1415 \ln w + .3025$	.262	.658	-.5**	.667**

NOTE: In the regression equations,  $r_{max}$  is sustainable harvest rate (as a fraction of initial, unharvested population for ungulates and as a fraction of annual population for small game);  $w$  is estimated mean adult body mass in both sets of equations.

\*If the potentially inaccurate Gazelle Low Growth Model is omitted, regression equation is  $r_{max} = .5424w^{-.794}$  ( $r^2 = .939$ ,  $p = .001$ ) and rank-order  $r_s = -.899$  ( $p = .015$ ).

\*\* With only three cases,  $|r_s| = .5$  is the weakest possible rank-order correlation in a data set with no tie values. As the only other option is  $|r_s| = 1$ , this is essentially a distinction between perfect correspondence and none.

exploitation of higher-ranked species. Thus, while roe deer, for example, can sustain significantly higher harvest rates than can red deer, human hunters must kill significantly more roe deer to obtain the same quantity of meat. Figure 6-4 and Table 6-2 show that this is the case for any group of ungulate species. It is therefore worthwhile to attempt to estimate relative sustainable *yield* from a population in addition to sustainable harvest rates. Sustainable harvest rates can be converted to sustainable yields by multiplying by body mass and population. It is not, of course, possible to determine actual prey population sizes for prehistoric human groups. However, sustainable yields of ungulate species can be compared through the use of heuristic estimates of comparable population sizes based on relative population densities.

*The Relationship between Body Size and Population Density.* Quite a few macroecological studies over the past quarter century have dealt with the question of body-size scaling of population density among animals. Damuth (1981) initiated this research by noting that among mammalian herbivores, published population densities for different species were closely related to the mean adult body size for that species. The relationship is described by the following power-law equation:

$$d = Cw^{-.75} \quad (6.1)$$

where  $d$  is the population density,  $w$  is the mean adult body mass, and  $C$  is a proportionality constant. When plotted on a log-log graph, such a power-law relationship is linear, with a slope equal to the exponent. As a result, the exponent is often referred to as the ‘slope’ of the power-law. Damuth (1981) noted that this relationship exactly inverts the well-known relationship between body size and metabolic rate, and from this concluded that in a given habitat each species captures the same amount of energy. Nee et al. (1991) subsequently coined the term “energetic equivalence rule” to describe this relationship, though the energetic basis of the relationship between body size and population density

has since been questioned (e.g., Blackburn et al. 1993).

The (log-log) linear nature of the body size-population density relationship has also been questioned. Some studies (e.g., Brown et al. 1993; Marquet et al. 1995) have found a positive-slope relationship for animals smaller than about 100 g. While this clearly suggests some additional difficulties for the relationship as a universal ecological law, it is not relevant to the ungulates discussed in this study. Similarly, radically non-linear (log-log) body size-population density relationships have been found by some researchers (e.g., Brown and Maurer 1987; Currie 1993). In general, such studies use raw, or regional, densities. That is, they use population densities for species in a specific region or study area, while the studies finding a (log-log) linear relationship are based on what are referred to as ecological densities, population densities for species in their preferred habitats. Here, too, this study need not be concerned with the contradictory findings, since it is specifically the relative population densities of animals *in environments where they can be relied upon by human hunters* that are of interest.

The scope of the (log-log) linear relationship has been extended to a variety of animal types, including insects, amphibians, reptiles, birds, and mammals in general (e.g., Damuth 1987, 1991; Juanes 1986; Marquet et al. 1990). In the process, it has become clear that while the  $-0.75$  slope holds generally for this very wide range of taxa and body sizes, it does not always accurately describe relationships within taxonomic groupings and feeding guilds. In particular, the slopes of the body size to population density relationship can vary significantly depending on the included taxa. As a result, it is advisable for the purposes of this study to determine an appropriate relationship for the included ungulate species.

Body size versus population density studies of herbivorous mammals have found a variety of slopes. Damuth (1987) reports a slope of  $-0.73$  for mammalian primary con-

sumers in general, and (1993) a variety of slopes between -.85 and -.94 for herbivores in non-tropical Eurasian and North American environments. However, it is clear that these values are substantially affected by the range of body sizes included. The slope to be used in this study is therefore determined empirically from available data (drawn from Damuth 1987), with a heuristic focus on relevant taxa. In doing so, two separate approaches are taken. First, population density versus body size data points for species closely related to those examined in this study are included. Damuth's (1987) data include values for *Bison bison*, *B. bonasus*, and *Bos guarus* (averaged to substitute for *Bos primigenius*), *Capra hircus* and *C. waalie* (averaged to substitute for *C. aegagrus* and *C. ibex*), *Capreolus capreolus*, *Cervus elaphus*, and *Gazella thomsonii* (used as a substitute for the very similarly-sized *G. gazella*). No appropriate substitute taxa are available in this data set for fallow deer or true ibex. These five data points produce a power law relationship between body size and population density with a slope (exponent) of -.618. A second, broader data set including all artiodactyls between 20 and 700 kg mean adult body mass is also drawn from Damuth's (1987) data. The sixty species meeting these criteria produce a power-law slope of -.604. Given this level of agreement between both highly restricted and much more general data sets, this study postulates the following proportionality between body size and population density for the seven modeled ungulate species:

$$d = Cw^{-.6} \quad (6.2)$$

The relative population densities and heuristic population sizes that are calculated using this relationship (Table 6-3) are referred to here as 'ecologically equivalent' populations and represent estimates of the sizes that are expected for populations of different species occupying the same geographic range under good habitat circumstances for each species. The calculated populations are based on a population of 1000 red deer. This choice is

Table 6-3. 'Ecologically Equivalent' Populations and Biomasses for Ungulate Species Based on Mean Adult Body Mass.

Species	Estimated Mean Adult Body Mass (kg)	'Ecologically Equivalent' Population Size	'Ecologically Equivalent' Standing Biomass (metric tons)
Aurochs ( <i>Bos primigenius</i> )	700	472	330.1
Red Deer ( <i>Cervus elaphus</i> )	200	1000	200.0
Fallow Deer ( <i>Dama dama</i> )	90	1615	145.3
Goat ( <i>Capra aegagrus</i> )	50	2297	114.9
Ibex ( <i>Capra ibex</i> )	50	2297	114.9
Gazelle ( <i>Gazella gazella</i> )	20	3981	79.6
Roe Deer ( <i>Capreolus capreolus</i> )	20	3981	79.6

solely a matter of convenience and the effects discussed below are independent of the particular 'base' species and population size.

*Sustainable Yields from Ecologically Equivalent Populations.* As noted above, given heuristic population sizes, it is possible to calculate comparable maximum sustainable yields. The ecologically equivalent standing biomass values in Table 6-3 are multiplied by the maximum sustainable hunting rates in Table 4-2. Figure 6-5 shows the resulting transformation of Figure 6-2, comparing confidence ranges for maximum sustainable biomass yields for the regional ungulate species sets. Since yield is proportionate to the product of harvest rate, prey population density, and body size, the following relationship emerges:

$$y_{\text{pop}} = wr_{\text{max}}da = (w)(.3070w^{-.526})(Cw^{-.6})(a) = C_1w^{-.126} \quad (6.3)$$

where  $y_{\text{pop}}$  is maximum yield sustainable by the prey population,  $r_{\text{max}}$ ,  $d$ ,  $m$ , and  $C$  are as defined previously, and the regression equation for the mean maximum sustainable harvest rate from Table 6-2 is used for  $r_{\text{max}}$  ( $C_1$  is a new proportionality constant, equal to  $.3070C$ ). Thus, while sustainable yield decreases with increasing body size for the seven

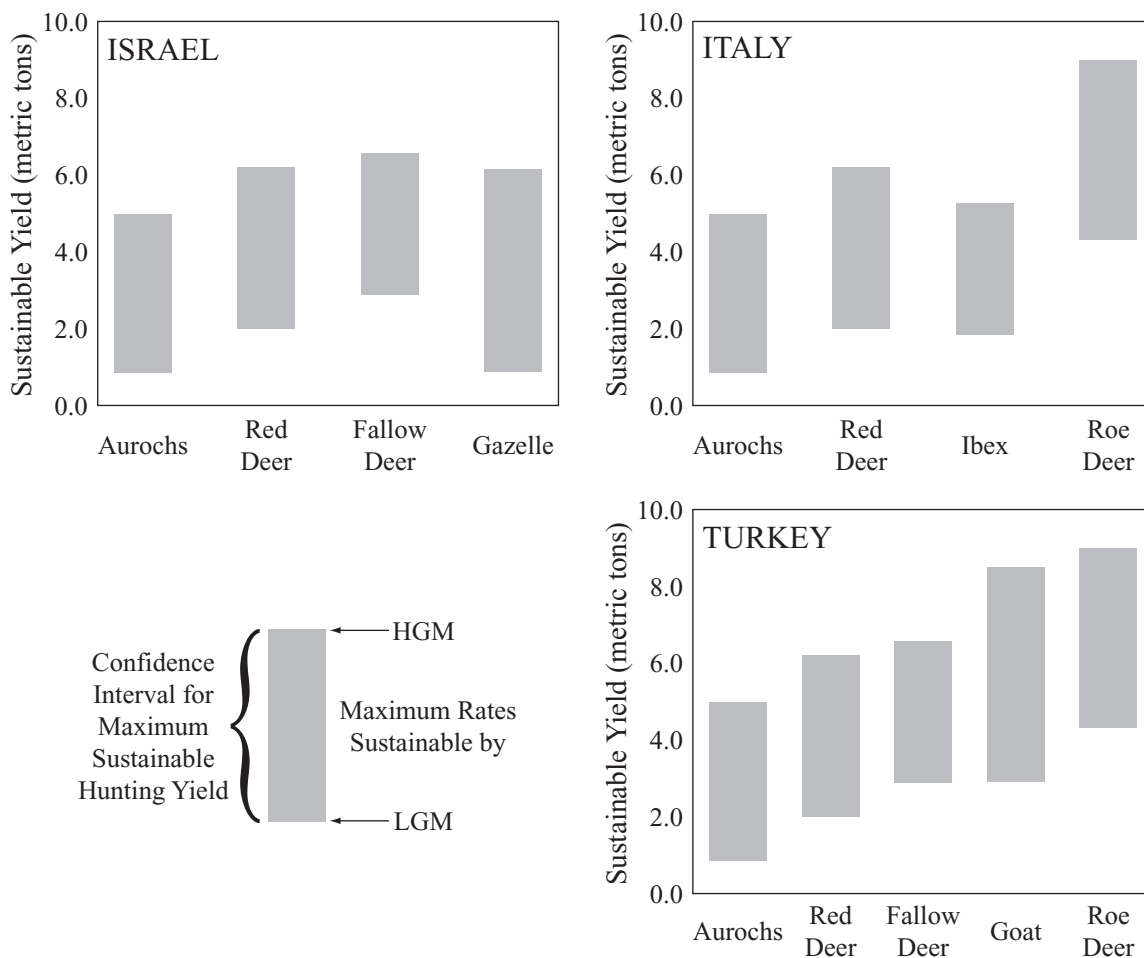


Figure 6-5. Comparison of sustainable annual biomass yields for ungulate species in each Mediterranean data set. Hunted populations are 'ecologically equivalent' (see text) to a population of 1000 red deer.

ungulate species, the decrease is relatively slight, and is consistently well within the range of possible values as determined by the high and low growth models. While it may very well be the case that transitions to smaller ungulate prey represent increases in the total amount of food potentially harvestable by a hunter-gatherer population, the basic simulation model results of this study do not provide strong support to such a conclusion in any particular case.

The diet breadth / prey choice model *per se* does not require that resources added

to a diet as it 'broadens' be able to sustain higher yields than those of the 'narrower' diet. However, such an ability substantially strengthens arguments for demographic growth as a cause of increasing diet breadth. The results presented here therefore indicate that the utility of changing ungulate species exploitation patterns as indicators of demographic change is limited by the relatively low increases in maximum sustainable yields associated with lower-ranked species, particularly in light of the wide confidence intervals produced by the high and low growth models for each species.

### *Source-Sink Dynamics*

The foregoing treatment of food yields sustainable by ungulate populations assumes that prey populations are discrete. In the real world, there is always some movement of animals into and out of any given habitat (with the exception of terrestrial animals in island habitats, of course). When habitats vary in their suitability for the animals in question, source-sink dynamics can arise. A source is a habitat in which reproduction outstrips mortality, leading to an outflow of animals. A sink, in contrast, is an area that absorbs such outflow because reproduction cannot keep up with mortality. Normally in ecology and biogeography, this nomenclature is used to describe situations in which source areas are good habitats, while sinks are poor habitats where reproductive success is low. However, source-sink dynamics should be particularly strong in circumstances where the sink area is a good habitat—except for high harvest rates by human populations.

Consider two adjacent habitats, equally suitable for a given prey species. If one has a lower population density than the other, then there will be a tendency for animals to move from the higher-density habitat to the lower one. In the process, the population density of the higher-density habitat will drop, reducing population pressure and thus

resulting in a higher total population growth rate. Under normal circumstances, the population densities of the two habitats will quickly reach equilibrium. However, if one habitat's population density is 'artificially' kept low by human hunting, a flow of some animals from the higher- to the lower-density habitat will be maintained. If the flow rate is high enough, the human population is effectively exploiting both populations, and a substantially higher yield should be sustainable. However, at lower population-flow rates, the effective size of the prey population is not increased as substantially.

The extent to which source-sink dynamics affect sustainable yields is therefore dependent on the mobility of the prey species. Among mammals, home range increases with body size (Harestad and Bunnell 1979), suggesting that larger—and thus presumably higher-ranked—ungulates are likely to move into ecological space opened up by the hunting of their neighboring conspecifics at a higher rate than smaller ungulates. Source-sink dynamics thus have the potential to further even up the sustainable yields shown in Figure 6-5. More importantly, source-sink dynamics can be expected to have substantially higher effects in the opposite direction relative to resource-ranking within the small game group. Fast, and especially flight-capable, prey species are clearly more capable of moving into an exploited territory and replacing harvested conspecifics than are slow prey species. Like sex-biased exploitation, the possibility of source-sink effects strengthens demographic arguments for changing small-game assemblage patterning, while weakening similar arguments for ungulate assemblage patterning.

#### *Variation in Demographic Growth Patterns*

As discussed in Chapter 4, maximum sustainable harvest rates for ungulate species are also strongly affected by the duration and frequency of exploitation. Since changes in one or both of these are likely to be involved in human population growth, the



consequent impacts on maximum sustainable food yields are relevant to demographic interpretations of prey-species exploitation rates. Figure 6-6 illustrates confidence ranges for maximum sustainable yield for 'ecologically equivalent' populations of each of the seven modeled ungulate species under durations of exploitation ranging from one year to one century and frequencies of exploitation ranging from 5% to 50%. The latter is a proxy measure—presuming constant *local* human population densities—of regional human population. Population growth under a given duration of prey-population exploitation would result in 'movement' from left to right across the appropriate row of the figure.

The sustainable yield for each ungulate species at a given combination of exploitation duration and frequency results from a complex combination of sustainable harvest rate, population density, potential growth rate, and maturation rate. The standing biomass represented by un hunted, stable populations of the larger ungulate species are significantly higher than those of the smaller species (see Table 6-3). In the short term, they are thus able to provide higher yields. However, these species also have lower potential growth rates and longer generation times, resulting in slower recovery from exploitation and thus lower yields when exploited frequently.

These effects introduce substantial additional uncertainty to the issue of sustainable yields associated with exploited species. While the smallest ungulate species can sustain higher yields under some occupation/reoccupation patterns, under other patterns it is the largest species that can do so—under yet other conditions, the species capable of supporting the highest yield is of intermediate size. Furthermore, the sizes of the confidence ranges for sustainable yield for the various species also vary substantially depending on exploitation circumstances. In particular, low exploitation frequencies and moderate exploitation durations have substantially different effects on high and low growth

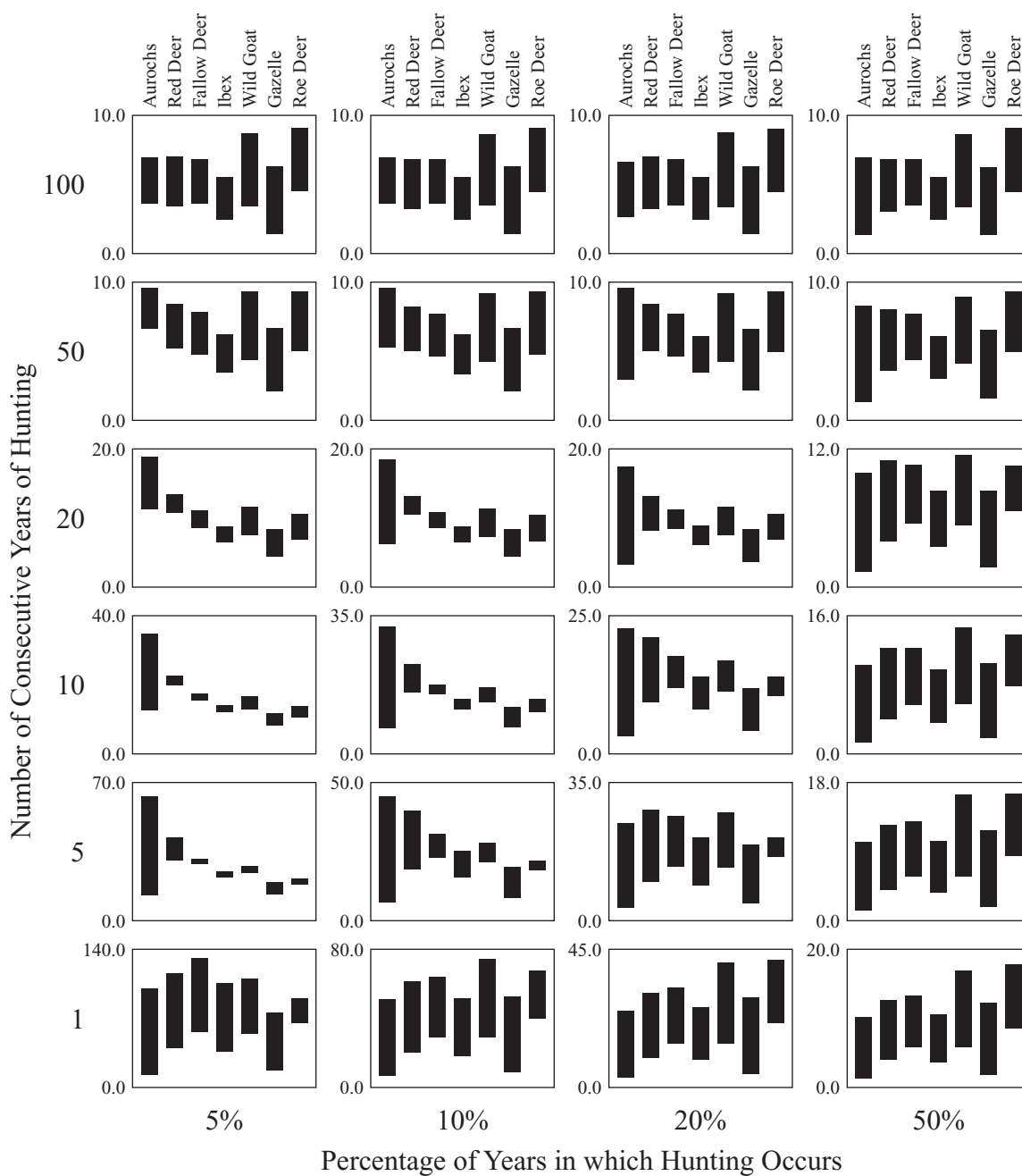


Figure 6-6. Comparison of biomass yields sustainable by modeled ungulate populations at varying durations and intervals of exploitation. Y-axes of graphs are biomass yield in metric tons per year during periods of exploitation. Bars represent confidence range for maximum sustainable yield from low growth to high growth model values. This figure represents a biomass yield conversion of Figure 4-9 much as Figure 6-5 is a biomass yield conversion of Figure 6-2. Note that individual graphs have different scales.

models of large ungulates, resulting in extremely broad ranges within which the actual expected sustainable yield may fall.

In contrast, these effects are not likely to be as pronounced in the small game group. Much of the disorder in Figure 6-6 is produced by the relative similarity of generation lengths and the related population recovery rates. Fairly small changes in duration or frequency of exploitation result in significant changes in relative species performance because the optimum exploitation patterns for each species are somewhat similar. The much larger differences in generation lengths and growth rates of the different categories within the small-game group should result in much simpler patterning. Low-turnover animals like tortoises should exhibit dramatically increased sustainable yields only in circumstances of very short durations and low frequencies of exploitation, while high-turnover animals like partridges and hares should exhibit very consistent sustainable yields across a much wider variety of exploitation durations and frequencies.

### **Summary of Ungulate versus Small Game Demographic Potential**

Ungulate species exploitation patterns are substantially less definitive indicators of human demography than are similar patterns in small game exploitation. Shifts from high- to low-ranked resources are by definition shifts to less efficiently exploited resources, but the relationship of such shifts to hunter demography is dependent on a variety of other factors. Ungulate assemblages are less viable bases for demographic inferences for a variety of reasons. The ability to hunt ungulates with relatively similar technology means changing species foci do not necessarily indicate substantial changes in pre-encounter, and indeed pre-search, investment. The wide disparity in sustainable hunting rates found by Stiner et al. (1999, 2000) for groups of small game is not found among the ungulates, a situation exacerbated by the potential for different biases toward

the hunting of males to occur for different ungulate species. Furthermore, ungulates are not as readily shown to be under hunting pressure as are high-ranked small game such as tortoises. The significant negative correlation in the ungulate group between the maximum sustainable harvest rates produced by the simulation model and body size further limits the demographic utility of ungulates, since confidence ranges of sustainable biomass yields for the various species overlap to a large extent. Source-sink dynamics may further reduce the already shallow trend toward higher sustainable yields with smaller body sizes, and relatively similar patterns of human population growth can result in widely different patterns of sustainable yields. The use of small game for demographic reconstruction is not substantially affected by some of these issues, while others actually increase the utility of small game to the analyst.

#### *Notes*

1. Mass kill techniques are the rather substantial exception to this; as a result, it is important to always consider the particular species involved in any given analysis.

## CHAPTER 7

### CONCLUSIONS

This dissertation has sought to illustrate the utility and the limitations of certain types of formal models—mathematical models and simulation models—as tools in archaeological inference and explanation. This objective has been addressed in the specific context of Paleolithic ungulate hunting, seeking to clarify, if not always strengthen, archaeological inferences and explanations based on ungulate archaeofaunas accumulated by Pleistocene hunter-gatherers. Archaeological data from the Mediterranean basin have been used in several cases as either motivation or illustration, but in general, specific inferences from those data have been avoided because the additional evidence required is beyond the scope of this dissertation’s focus on mathematical and simulation models. Instead, the focus has been on inferential ‘rules’—or aspects thereof—associated with both the diet breadth / prey choice model and a simulation model of ungulate population dynamics under human hunting pressure.

As discussed in the introductory chapter, a distinction is made here between archaeological inference and explanation, even though it is recognized that these concepts are not fully independent, with inferences serving as partial explanations for archaeological phenomena and being critical elements of higher-level explanations. In short, inferences are considered to be statements about occurrences or conditions in the past. Inferences are derived from (often implicit) statements—‘rules’—attributing a class of archaeological observations (or lower-level inferences) to a particular type of occurrence or condition in the past; these are combined with observations of the archaeological record (that fall within the class of observations to which the inferential rule pertains) to yield inferences about the humans/hominins whose actions produced the piece of the archaeo-

logical record in question. Inferences are thus statements specific to a body of archaeological data, while inferential rules are universal (within their boundary conditions). Archaeological explanation, in contrast, involves statements about why the archaeological record, or the past as understood through archaeological inferences, is the way it is. Explanations are considered to always be specific to archaeological cases—universal explanations may be possible, but it is epistemologically unwise to *assume* that they exist.

This chapter discusses what has been learned about the general use of mathematical and simulation models in archaeological inference and explanation, the specific inferential and explanatory refinements that have been developed regarding Paleolithic ungulate hunting, and possibilities for future research suggested by these refinements.

### **Utility and Limits of Mathematical and Simulation Models**

The primary value of mathematical and simulation modeling efforts in archaeological inference lies in their power to produce specific ‘predictions’ of the value of any one variable given the specification of all others. Though mathematical and simulation models have much in common—both being ‘formal’ models explicitly connecting their postulates to their conclusions—they also have some significant differences. The most important of these is that mathematical models of the level of mathematical complexity used by archaeologists tend to be more or less static—they do not include random elements and, if time-transgressive, cannot deal with discontinuous change in their constituent variables. Simulation models, in contrast, are almost by definition dynamic and deal easily with discontinuities. Additionally, simulation models are significantly more reliant on details of the real-world cases they are designed to simulate. For example, the diet breadth / prey choice model, which has formed the backdrop for much of this dissertation, produces qualitative predictions even in the absence of any quantitative input data, while

the simulation model developed and employed here cannot function at all without such data. Even though simulation models are constructed from mathematical models, their utilization differs substantially, with the result that different lessons have been learned about the use of each in the course of this dissertation.

### *Mathematical Models*

In general, the outstanding characteristic of mathematical models is their mathematical rigor. If the basal postulates of the model are valid and the boundary conditions are satisfied—and, of course, if there are no mathematical errors in the derivation from the postulates—then the resulting model must be correct. In principle, this should make the application of such models to archaeological inference very strong. However, in practice there are a series of complications. Despite occasional attempts to the contrary, virtually all models (whether mathematical or not) developed for secondary archaeological inference and non-trivial explanation are models of phenomena on a human scale in both time and space. Because this problem is general to all of archaeology, it has received relatively short shrift in this dissertation—it is expected that the reader has automatically taken such issues into account just as he/she would if reading a discussion of stone tool manufacture. One aspect that is particularly important here, however, is the caution that there is a temptation to ignore this problem when dealing with mathematical models because they appear to be so definitive. Some aspects of the way this needs to be dealt with were discussed early in chapter 2.

A second issue is the importance of keeping in mind the basal postulates and boundary conditions of mathematical models when applying them. Furthermore, though the boundary conditions and basal postulates of formal models are explicit, their abstract nature can sometimes lead to their details being overlooked. The diet breadth / prey

choice model, for example, postulates that the forager whose behavior is being modeled maximizes his/her rate of net energetic return and thus evaluates each resource on those specific grounds. However, as noted in chapter 2, when the model is applied, it is common for the energetic value of resources to be evaluated instead. Focusing on the fact that it is the energetic return, not the energetic value, of a resource that is a term in the model leads to the conclusion that the diet breadth / prey choice model *per se* does not predict ungulate hunting in preference to small game hunting or the hunting of large ungulates in preference to small ungulates, because the energetic *return* to the forager is only partially dependent on the energetic *value* of the resource—it is also affected by the ability of the forager to extract energy from the resource. Since a single forager is unlikely to have the capability to extract the full energetic value of large game animals, this leads to the conclusion that, if Paleolithic foragers hunted ungulates—and especially large ungulates—in preference to small game, then the diet breadth / prey choice model is invalid in such cases. A (partially-related) example discussed in this dissertation is the tendency to view resource rankings in a diet breadth / prey choice model as inherent characteristics of the resources, when in fact they are dependent on circumstances, technology, and resource-acquisition strategies. A variable-by-variable examination of a mathematical model, asking what factors can influence the value of each variable, can lead to both new inferential possibilities (e.g., consumption-limit-derived predictions regarding sharing-group size and/or storage technology) and increased awareness of the inferential uncertainty of a model (e.g., the influence of hunting failure rates and handling times on resource rankings and resource-inclusion decisions).

A closely related issue in the application of mathematical models to archaeological inference is the very reasonable tendency to bring knowledge extraneous to the model to bear informally on the process. The knowledge that human foragers share food—



especially meat—is almost certainly a key factor in the tendency to treat the diet breadth / prey choice model as if it were based on energetic value not energetic return. It is certainly important to bring multiple sources of knowledge to bear on archaeological data, but the conscious examination of the full implications of a mathematical model *in isolation* can lead to new approaches and deeper understandings, which can later be combined with other ideas. It is for this reason that, except for a few general statements, this dissertation has ignored the idea of risk-minimization as a factor in hominin decision-making with regard to ungulate hunting, even though it is clearly an important factor. Furthermore, as noted by Kuhn (2004:563), many models are most informative when they are demonstrated not to apply to a given case. Such case-specific falsification requires that the predictions of the model be drawn directly from the postulates and boundary conditions; if instead the predictions are affected by outside knowledge, non-fulfillment of the predictions cannot be validly used to deduce that one or more of the postulates or boundary conditions does not hold in the case in question.

### *Simulation Models*

Computer simulation models allow the concatenation and iteration of easily definable (if not necessarily perfectly realistic) ‘local’ interactions—expressed mathematically—to form large-scale dynamic systems allowing the examination of effects of different variable values, including those estimating real-world behavior. They thereby enable the exploration of the behavior of complex, interrelated processes and the performance of ‘experiments’. While many uses of simulation modeling are possible, this dissertation has generally been restricted to exploratory simulation modeling, looking at the outcomes of a wide variety of variable combinations in order to establish which sets of combinations are associated with what outcomes. The smaller the range of inputs that

lead to a given outcome, the narrower and thus stronger an inference based on the archaeological observation of that outcome is. A variety of issues in the use of such models can be illustrated from the simulation work in the preceding chapters.

A major issue is the inevitability of incompleteness. In general, with any simulation model of even moderate complexity, it is not practical to examine all possible, or even reasonable, combinations of variable values. For example, in chapter 4, simulation model results are presented for perennial unbiased hunting, perennial male-biased hunting, and intermittent unbiased hunting of ungulates. These categories logically imply the existence of a further category of intermittent male-biased hunting. Since one of the lessons of mathematical and computer modeling in general is that results obtained through varying the value of one element while holding another constant cannot be generalized to situations with different values of the latter, the results of the perennial male-biased hunting and the intermittent unbiased hunting analyses cannot simply be combined. (With systems that are at all complicated, non-linearity must be presumed until and unless linearity can be proven.) Practical limitations, such as the necessary computer time and the multidimensionality of the data that would have been produced prevented an analysis of intermittent male-biased hunting from being considered worthwhile, even though this limits the confidence that can be placed in any narrowing of inferential rules based on the results of the simulation model.

Because it is never possible to examine all conceivable combinations of variables in a simulation model, it is very important to demonstrate general applicability of results wherever possible. Thus, for example, the basic perennial unbiased hunting analyses reported in chapter 4 required that simulation models be run at a wide variety of population sizes in order to ensure that the maximum sustainable harvest rates determined for each species model scale to any population size. Another approach to such generalization

is the use of targeted extensions of the basic simulation model, such as the examination of the efficiency of male-biased hunting in chapter 4. This null-model approach, showing that with the assumption of random-encounter hunting, male biases are unlikely (given the dissertation-wide efficiency-maximization assumption), allows the conclusion that non-random-encounter hunting is probably necessary for male-biased hunting. With this basis, the ways in which hunting encounters can be non-random can be examined, leading to the conclusion that male-bias levels are likely related to attributes of the prey species as much or more than to hominin hunting decisions. While the resultant ambiguity in fact broadens (and thus weakens) inferential rules based on the general simulation model results, it also clarifies the type of research needed to eventually narrow those rules.

More intensive simulation modeling analyses like these, which also include examination of the age-structure correlations of varying harvest types and rates in chapter 5, are limited for practical reasons to a single species model. In both cases, however, the general patterns were confirmed by less-detailed subsets of the simulation model runs based on other species models. These confirmational simulation model runs support (but do not prove) the qualitative results of these analyses, but in the absence of specific quantitative results, they can only be applied tentatively to other species.

These particular analyses also illustrate the importance of approaching the definitions of simulation model elements (just as with mathematical model variables) in a very broad and detailed manner in order to minimize the risk of oversimplification. Hunting is treated not simply as the killing of a given number of animals per year, but rather as a complex pattern of sex biases, age biases, and year-to-year variation. While (as just discussed) it is impractical to examine the full range of values for all aspects of such variables, conscious awareness of the unanalyzed parts of the property space (the multidimensional space defining all possible combinations of variable values) minimizes the risk

that results will be considered more general than they in fact are.

The foregoing issues encountered in simulation modeling relate primarily to the process of exploration; other critically important issues relate to the process of constructing the simulation itself. It is regarded here as axiomatic that the avoidance of type I errors (reaching false conclusions) is more important than the avoidance of type II errors (failing to reach true conclusions). When real-world parameters are processed by the model, the impact of any errors in the estimation of those parameters becomes lost in the non-linearity of the results. A 5% error in a natural mortality rate, for example, could conceivably produce a 1% error in maximum sustainable harvest rate with one set of variable values, but a 50% error with a different set of values. As a result, though a single 'best' estimate of real-world parameters would yield more easily comparable results, there is good reason for the use of upper and lower bounds for each parameter. Here, again, the issue of practicality arises. Simulation model runs at all possible combinations of these upper- and lower-bound parameter values would provide a better sense of the potential variability and tendencies of the output variables (such as sustainable harvest rates); however, with the five parameters involved in modeling each ungulate species that differ between the low and high growth models (for example), such an approach would increase the amount of computer time required (and the amount of data to be analyzed) by a factor of  $2^5 = 32$  (though in some cases other variable values are shared between the LGM and HGM, as well, reducing this to a factor of 16 or even eight for some species).

### **Paleolithic Ungulate Hunting: Inference and Explanation**

As with lessons learned from the development and exploration of mathematical and simulation models, the inferential and explanatory potential of these different types of models follow different patterns. The diet breadth / prey choice model is a ready source

of inferential and explanatory possibilities, but these tend to be broad and difficult to apply, particularly because of the complexity of converting human-scale predictions to archaeological results. The simulation model of ungulate population dynamics under hominin hunting, being more narrowly tailored to specific questions and requiring the utilization of specific real-world data, produces fewer inferential and explanatory possibilities, but ones that are more specific and better-suited to archaeological cases.

#### *Diet Breadth / Prey Choice Models*

In chapter 2, it is inferred that Paleolithic hunters in Europe and the Mediterranean Basin did not behave in accordance with the standard diet-breadth / prey choice model, based on a prediction of the model, the observation that the prediction does not hold archaeologically, and a uniformitarian assumption that general ecological relationships in the Pleistocene did not differ from those of today. As mentioned above, the standard diet breadth / prey choice model (based on net energetic return) indicates that an individual forager should not preferentially exploit large ungulates over small ungulates, because there is little or no difference (with some caveats—see chapter 2) among the energetic returns obtainable therefrom. Because this is a falsification-of-the-model-style inference (learning from the failure of the model), casting it as an inferential rule is slightly awkward: ‘If hunters preferentially exploited large ungulates whose energetic return to them individually was no greater than that available from smaller ungulates, then they were not behaving in accordance with the diet breadth / prey choice model.’<sup>1</sup> Combined with archaeological evidence of higher exploitation rates of large ungulates than of small ungulates (note the glossed-over primary inferences) and the aforementioned uniformitarian assumptions about relative population densities of different-sized mammals, this results in the inference of non-conformance with the diet breadth / prey choice model.

This inference prompts the creation of a new version of the diet breadth / prey choice model—one explicitly based on the idea of food-sharing, and thus based on the efficiency of food acquisition by quantity rather than net energetic return. While this model explains the ungulate-hunting behavior seen in the European and Mediterranean Paleolithic, this is not at all meaningful since the model was specifically developed in order to do so. However, postulating the new model's appropriateness and considering details of its formulation allows the development of a new inferential rule.

Although food sharing makes it appropriate to consider the food yield of an ungulate resource beyond the amount that could be consumed by a single forager, any limit to the ability of the entire food-sharing group to consume animal tissue remains relevant. Between group size and meat storage/defense capability, a given food-sharing group has a maximum amount of meat—or consumption limit—that is of use to them. Because low-enough consumption-limit values lead to different resources having the same yield to the food-sharing group, the following inferential rule can be put forward: 'Food-sharing groups of foragers of a given size, ability (in terms of length of time) to preserve/defend meat, and average ability (in quantity of meat per unit time) of the individuals in the group to consume meat produce archaeological assemblages whose largest regularly excluded ungulate provides less meat than the product of those three characteristics.' There are two points that must be emphasized here: First, there are some specific boundary assumptions involved regarding similarity and absolute magnitude of handling times (see chapter 2). Second, this is not the only possible inferential rule whose archaeological sign would be satisfied by such an exclusion; that is, there is a significant equifinality issue. In fact, the very same model produces a competing inferential rule, the well-known association of high encounter rates with higher-ranked resources. From a traditional approach to diet breadth / prey choice models, then, the consumption-limit-

derived inferential rule reduces the strength of the encounter-rate inferential rule.

Another aspect of the diet breadth / prey choice model (in this case, the different versions of the model produce quantitatively different predictions, but have similar implications for archaeological inference) that reduces the strength of the encounter-rate inferential rule is the importance of handling time variation in determining both resource rankings and resource-inclusion decisions. If handling times differ substantially for different resources, and particularly if these differences correlate positively (as they are likely to do) with yield or energetic return (as appropriate), then resource rankings may not follow the same order as do yield or energetic return. Yield or energetic return can be estimated far more securely for archaeological cases than can handling times; the possibility that resource rankings might not track with body size—or could change over time—is therefore a serious potential obstacle to inferences based on a diet breadth / prey choice model. Because high hunting failure rates have the potential to cause the time lost to failed pursuits to be a large factor in mean handling time, uncertainty about failure rates (both relative and absolute) further reduces confidence in inferences based on a diet breadth / prey choice model.

### *Simulation Models of Ungulate Hunting*

The foregoing conclusions help to show why Stiner et al. (1999, 2000) are successful in making prey-choice-related inferences from small game in archaeological assemblages. The small maximum size of the prey considered (on the order of 2 kg) eliminates any concern with consumption limits. The similar sizes of the prey and their division into groups based on the difficulty of capture allow relative hunting success/failure rates to be the major factor in reconstructing prey rankings, rather than an obstacle thereto. Stiner et al. back this up with analyses showing hunting pressure on high-ranked

small game resources and simulation models demonstrating that these resources are far more vulnerable to overhunting than the lower-ranked resources, making an archaeofaunal transition from the former to the latter a stronger sign of higher hominin population density.

The core chapters of this dissertation are devoted to determining if parallel analyses and simulation models applied to ungulates can overcome the complications of uncertain consumption limits and hunting failure rates. The simulations and analyses are aimed at two different processes of inference from ungulate archaeofaunas: inferences about the overall level of hominin exploitation of ungulates based on relative representation of different species in archaeofaunas and inferences of hunting pressure on individual prey species based on archaeological assemblage characteristics.

In the case of inferences from relative species representation, the aspiration is to augment the diet breadth / prey choice model (which is somewhat weak in regard to ungulate hunting in the Paleolithic for the reasons discussed above) with data about the relative ability of populations of different ungulate species to survive when subjected to varying levels of predation by humans. The most basic results are favorable to such inferences, showing that different ungulate species respond in qualitatively similar ways to the regular removal by hunting of some fraction of their initial population size. When harvest rates are expressed as a fraction of the maximum harvest rate sustainable by each species, the modeled populations respond in quantitatively similar ways, as well. Furthermore, the relative ability of simulated populations of each species to sustain human hunting places the species in the same order as their presumed diet breadth / prey choice model rankings (based on body size). The lower-ranked ungulate taxa are able to withstand having higher fractions of their populations killed by human hunters, though some overlap in the confidence intervals (from low growth model results to high growth model



results) for maximum sustainable harvest rates of body-size-adjacent species makes it clear that this pattern is not nearly as definitive as in the small game case.

Further explorations using the simulation model are not as supportive of inferences from relative species representation. High levels of male-bias in hunting ungulates reduce the strength of the relationship between resilience (ability to withstand high harvest rate) and body-size-based ranking, and the possibility of different levels of male bias being involved in the hunting of different species introduces a level of uncertainty that would make inferences on this basis unfeasible. Furthermore, specifically targeted simulation-modeling analyses (discussed above) of the efficiency to be expected in male-biased hunting strongly suggest that male biases in ungulate hunting are likely to relate to characteristics of the various species.

Geographic and chronological variation in regional human population density and inter-annual mobility is shown (through proxy measures of percentage of years a prey population is continuously exploited and number of consecutive years of such exploitation, respectively) to have a significant effect on the ordering and confidence range overlaps of the maximum sustainable harvest rates of the various ungulate species (see Figures 4-9 and 6-6). In the Paleolithic, where the extent to which hominins fill available ranges and the rate at which such ranges are abandoned is difficult, if not impossible, to determine, this variability in relative resilience patterns is a substantial obstacle to making inferences that depend on consistent relationships among the resiliencies of the various species. It is particularly problematic for inferences that work on the assumption that resilience to hunting pressure increases uniformly with decreasing body size.

Additional difficulties appear when the target of such inferences is hominin demography. In addition to the harvest rates sustainable by different ungulate species, the yields obtainable by hunting those species become relevant. The basic maximum sustain-

able harvest rates for the modeled ungulate species (that is, those determined under assumptions of constant hunting with no male-bias) are very strongly related to the mean body masses of those species. This relationship forms a power-law (linear when both axes are log-transformed) with a slope (exponent) that is substantially offset by that of the empirically-derived power-law relationship between body size and population density. As a result, there is a much more limited correspondence between sustainable yields and body-size rankings. When the uncertainty captured by the high and low growth models for each species is factored in, the inference of even the possibility of higher overall yields from hunting of lower-ranked ungulates becomes questionable. Uncertainty as to Paleolithic mobility levels and regional demographic saturation weakens any such inference even further, as does any uncertainty regarding sex biases in hunting.

The second inferential domain examined is the identification of hunting pressure on an individual ungulate species. The prime candidate for such inferences is the age structure shown in the archaeological assemblage and its implications for the age structure of the prey population from which it derived. Simulation-modeling results show that hunting at constant or increasing hunting rates (up to those which crash the prey population), without a bias toward the hunting of males, produces age-structure compression in the form of a reduction in the proportion of old adults in both the prey population and the animals culled therefrom. In order for substantial increases in the proportion of juveniles, and especially in the relative proportions of juveniles to prime-age adults, to appear, prey population-size reductions unattainable (without crashing the population) by hunting at constant or increasing harvest rates are required. Such reductions are produced by high harvest levels that drop off as the prey population gets smaller. The high proportion of juveniles is associated with the small prey population size and the concomitant low harvest rate. While it may thus be reasonably considered an indicator of hunting pressure,

it does not indicate a high level of hominin reliance on the species in question. In fact, it indicates that the level of hominin reliance on that species was substantially higher at some point in the past. With a sufficient level of male bias in hunting, however, higher harvest rates produce higher proportions of juveniles in both prey populations and archaeological assemblages (assuming at least some fraction of the juvenile cohort is hunted). Age structures found in ungulate archaeofaunas are thus associated with different hominin exploitation levels and histories at different rates of male bias, producing a significant equifinality problem for archaeological inference if the level of male bias is unknown. However, where the sex ratio of animals forming the archaeological assemblage can be determined, simulation models of the appropriate species applying kills at the appropriate sex ratio can produce data leading to strong inferences about hominin exploitation and hunting pressure.

Because of the difference between inference and explanation, models and model results that yield only weak inferential rules can be useful as elements of proposed explanations for archaeological phenomena. Though the diet breadth / prey choice model and the simulation model of ungulate population dynamics under human hunting are not sufficient for shifts down the body-size spectrum in ungulate archaeofaunas to form the basis of a strong inference of hominin population growth in the absence of sex ratio data (see chapter 6), the models do provide the potential connections between hominin population growth as inferred from other data (such as small game) and ungulate exploitation patterns that make the former a plausible explanation of the latter.

### **Future Research**

Several avenues of additional research are suggested by the modeling studies in this dissertation; a few of the more salient are addressed here. The importance of food-

sharing group sizes and storage capabilities for ungulate-hunting decisions may have social implications in certain archaeological cases. This is a particularly good example of the often two-way nature of mathematical models when it comes to archaeological inference. As suggested in chapter 2, there may be evidence of a reduction in diet breadth in the later Lower Paleolithic or early Middle Paleolithic of Europe, from which it may be possible to infer an increase in either food-sharing-group sizes or in meat storage capabilities. Because of the way consumption limits work within the diet breadth / prey choice model context (not to mention environmental issues), individual cases of archaeofaunas skewed toward smaller ungulates preceding archaeofaunas skewed toward larger ungulates are not convincing. (Hunting success/failure rates are also relevant here.) Regional-scale analyses involving multiple assemblages, however, may provide at least a basis to consider the possibility. One critical element of such research must, of course, be the demonstration that the assemblages are produced predominantly by hunting rather than scavenging, because consumption-limit analyses require consistent estimates of meat yield. A potentially critical line of evidence that might disentangle the problem of equifinality in the diet breadth / prey choice model is evidence of processing intensity. If smaller ungulates are included in the diet because larger ungulates are sufficiently rare—not because the larger ungulates exceed the group's consumption limit, then both large and small ungulates should be thoroughly processed. However, if smaller ungulates are included in the diet on consumption-limit grounds, they should be more thoroughly processed than larger ungulates, because the latter cannot be fully consumed.

It is equally plausible to suggest an association between increased diet breadth (specifically the inclusion of smaller ungulates and potentially even small game) and reductions in the scale at which meat is shared. Social changes that involve family-level food-sharing only, for example, could produce consumption limits low enough to place

small ungulates in the always-included category. Then again, a reduction in the size of typical prey for non-consumption-limit reasons, such as environmental change or resource depression, could provide an environment in which food-sharing at the family, rather than forager-group, level is selectively advantageous. Could such a process, and even a feedback loop where the smaller sizes of food-sharing groups made possible by smaller prey then discouraged investment in hunting larger prey even if their availability rebounded, have been involved in the apparent increase in social complexity seen in the late Upper Paleolithic/ Epipaleolithic/Mesolithic in many parts of the world? Detailed (and probably large-scale) examination of covariation in prey body size and archaeological indicators of social differentiation might allow such an explanation to be put forward.

Research aimed at quantifying the relative advantages of different hunting techniques (including stalk/chase times) and/or technologies relative to different ungulate species is likely to be difficult. Ethnoarchaeological research has some potential along these lines, but the differences between modern ecological circumstances and those of the Paleolithic, as well as potential cognitive differences between modern humans and Paleolithic hominins, must be carefully considered in the application of any such research. Ethnoarchaeological and experimental research may be on stronger ground in examining processing times, however. Any improvement in the ability of the archaeologist to control for hunting failure rates would strengthen inferences based on the diet breadth / prey choice model, and strong awareness of the problem alone should produce more careful and nuanced interpretations.

In terms of the computer simulation model of ungulate population dynamics under hominin hunting, the most important avenue of further research relates to sex-biased hunting. There are two avenues of research that could further our understanding of hunting *vis-à-vis* sex structure of ungulate archaeofaunas and its critical impacts on both

sustainable harvest levels and hunting pressure interpretations of age-structure patterns. The more immediately practical, but inferentially weaker, is the use of modern ecological and wildlife-management research in an attempt to associate sex-segregation and/or grouping patterns of various ungulate prey species with estimates of the sorts of sex ratios that should be expected and comparing these results with those archaeological cases where sex-ratio estimates can be developed. Are the species that appear from modern studies to be more susceptible to male-biased hunting the same ones that show male biases in the archaeological record?

The second approach is to emphasize the determination of sex ratios in ungulate archaeofaunas where sample sizes make it practical, and to look for means of determining such ratios where sample sizes are smaller. DNA extraction techniques may someday allow such determinations, but there are other potential options now. For example, zooarchaeologists might consider amalgamating geographically and chronologically close sets of assemblages for the purpose of measurement-based estimation of sex ratios. Since Paleolithic archaeofaunas deposited over multiple millennia are routinely treated as being derived from a single prey population, it does not seem unreasonable to pull together assemblages of similar age across ranges of several kilometers, particularly for the more sexually dimorphic ungulate species. Simulation models run with such estimates provide much stronger evidence of hominin exploitation levels (through age-structure analyses) and of relative sustainable yields, which could (depending on specific results) allow inference of transition to resources with the potential to support higher (or lower) hominin population densities. Sex-ratio data are absolutely essential to the use of the simulation model of ungulate population dynamics developed in this dissertation; such data dramatically narrow the archaeological signs associated with past human behaviors.

### **Closing Caveat**

As discussed in chapter 1, it is commonly the case in archaeology—especially in Paleolithic archaeology—that in order to answer one question it is necessary to assume the answer to another. In this dissertation, most models and arguments have been based on a core assumption that hominin ungulate-hunting behavior is rooted in economic rationality and efficiency. In a sense, all of the inferences made or avoided, and all of the explanations suggested or dismissed, are part of a null model in which hominins are presumed to have behaved as meat-eating automatons. It is certainly possible, even likely, that motivations other than efficiency drove hominin ungulate hunting behavior in the Paleolithic. Variance-minimization-style risk management and the minimization of physical danger are obvious candidates for other motivations, but not the only ones. While it is hoped that this dissertation has illuminated both the utility and the limitations—both theoretical and practical—of formal models in archaeology, and especially in the archaeology of the Paleolithic, it must be emphasized that the core assumption made here should also be considered a topic worthy of independent research; presupposing its truth allows the provisional inference of certain past hominin behaviors, but archaeologists should also be interested in the causes of those behaviors—a topic whose investigation requires questioning the very same assumption.

#### *Notes*

1. Alternatively, the following (standard structure—see chapter 1) inferential rule could be stated: ‘Foragers behaving in accordance with the diet breadth / prey choice model produce archaeological assemblages that are not dominated by large ungulates (whose energetic return to them individually was no greater than that available from smaller ungulates).’ Since this is equivalent to an ‘If A then B’ structure, by the basic rules of logic, it is also equivalent to ‘If not B, then not A’.

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