Foraging models derived from behavioral ecology have had a dramatic effect on our understanding of variability in archaeological assemblages. Recent reviews of the field demonstrate that over the last three decades zooarchaeologists have, with varying degrees of success and sophistication, increasingly applied the theoretical underpinnings, attendant logic, and predictions of these models (Bird and O’Connell 2006; Lupo 2007; Shennan 2002). Many of these studies address long-standing arguments about the role that hunting mobile prey played in human evolution, including its relationship to constellations of changes in life history, fertility, and health (e.g., Hawkes 2003; Lamb 1993; O’Connell et al. 2002), prestige and sociopolitical complexity (e.g., Bliege Bird et al. 2001; Fitzhugh 2003; Hawkes 2000; Hawkes et al. 1991; Hildebrandt and Jones 1992; Hildebrandt and McGuire 2002; Kennett 2005; Lupo and Schmitt 2002; McGuire and Hildebrandt 2005; Sassaman 2004), tool use and technology (e.g., Bettinger et al. 2006; Bright et al. 2002; Kuhn and Stiner 2001; Ugan et al. 2003), regional colonization and economic intensification.
(e.g., Beaton 1991; Bettinger and Baumhoff 1982; Grayson and Delpech 2002; Jones 1991; O’Connell 2007; Stiner and Munro 2002; Stiner et al. 2000), origins and diffusion of agriculture (e.g., Alvard and Kuznar 2001; Barlow 2002; Hawkes and O’Connell 1992; Layton et al. 1991; Redding 1988; Russell 1988; see contributions to Kennett and Winterhalder 2006), gender and divisions of labor (Kuhn and Stiner 2006; Waguespack 2005; Zeannah 2004; see contributions to Stiner 2005), and resource sustainability and overexploitation (e.g., Barnosky et al. 2004; Broughton 1994a, 1999; Grayson 2001; Jones et al. 2004; Jones et al. 2008a; Jones et al. 2008b; Lyman 2003; Munro 2004; Nagaoka 2002; O’Connell et al. 1982; Porcasi et al. 2000; Simms 1987; Waguespack and Surovell 2003).

The zooarchaeological utility of an approach from behavioral ecology is well illustrated in the development of arguments about “Mesolithic,” “Archaic,” or “broad-spectrum revolutions.” These transitions include long-recognized shifts in terminal Pleistocene and Holocene subsistence strategies around the world, whereby many hunter-gatherers intensified resource use and began to exploit a wider array of prey than did their predecessors (e.g., Clark 1952; Willey and Phillips 1958). Well-known explanations for this change have made reference to increasing familiarity with resource variability, technological innovation or diffusion, intensifying social relations, and declines in the abundance of certain prey, possibly as a result of climate change and/or human population growth (e.g., Binford 1968; Braidwood 1960; Cohen 1977; Flannery 1969; Lourandos 1983). Though all these hypotheses are plausible, and combinations of them are probable, none of them has generated clear predictions or well-defined tests about the nature and direction of intensification.

Early applications of foraging models, especially the encounter-contingent prey choice model (PCM), changed this situation (e.g., Bayham 1979; Beaton 1973; Botkin 1980; O’Connell and Hawkes 1981). One of the principal predictions of the PCM is that the range of resource types exploited will increase with declines in overall foraging efficiency (energetic yield relative to search and handling costs [see the subsequent section and Stephens and Krebs 1986]). In accordance with the PCM, early archaeological applications generated rankings of prey types based on estimates of post-encounter return rate (energetic yield relative to handling costs, e/h) and assumed that the inclusion of highly ranked prey should scale with their local availability. They then demonstrated that, as predicted, most resources added later in time were very low ranked and that their inclusion was a function of fluctuations in the encounter rate with higher-ranked prey, not their own abundance. Much of this work identified climate- or predation-related depression or extirpation of highly ranked prey as a principal determinant of increasing diet breadth and intensification. Many subsequent studies of prehistoric diet change and, to a lesser extent, patterns in patch use have led to similar inferences (e.g., Bagan 1987; Beaton 1991; Bouey 1987; Braje et al. 2007; Broughton 1994a, 1994b, 1997, 1999, 2002; Cannon 2000, 2003; Coddington and Jones 2007; Edwards and O’Connell 1995; Erlandson 1991; Glassow and Wilcoxon 1988; Grayson 1991; Gremillion 1994; Hildebrandt and Jones 1992; Jones 1995; Jones and Richman 1995; Jones et al. 2004; Jones et al. 2008b; Kennett 2005; Klein et al. 2004; Mannino and Thomas 2002; Nagaoka 2002, 2005; O’Connell et al. 1982; Perlman 1980; Porcasi et al. 2000; Raab 1992; Russell 1988; Simms 1987; Szuter and Bayham 1989; Wohlgemuth 1996; Wright 1994; Yesner 1989, 1994; Zeannah and Simms 1999).

This work on changes in resource exploitation has produced important questions about how to establish reliable measures of resource rank (see discussion in Bettinger 1991, 1993; Bird and O’Connell 2006; Broughton and Grayson 1993; Lupo 2007). Some of these problems have been addressed satisfactorily for sessile resources (e.g., plant foods, shellfish) through a combination of ethnographic, ethnohistoric, and actualistic studies (e.g., Barlow and Metcalfe 1996; Bettinger et al. 1997; Bird and Bliege Bird 2000, 2002; Bird et al. 2004b; Cane 1989; de Boer 2000; Jones and Richman 1995; Kelly 1995; Madsen and Schmitt 1998; O’Connell and Hawkes 1981, 1984; Petsuro and Wikens 1984; Raab 1992; Reidhead 1976; Simms 1985, 1987; Simms and Russell 1997; Smith et al. 2001; Talalay et al. 1984; Thomas 2002; Thomas 2008; Thoms 1989; Ugan 2005a). However, the situation for mobile prey has proven less tractable, and thus far, few zooarchaeological analyses have incorporated actual (or actualistic) return rates for
mobile animals (Egeland and Byerly 2005; Lindstrom 1996; Lupo 1998, 2006; Madrigal and Holt 2002; Thomas 2008). This is due in part to (1) the fact that in many cases the opportunity has long passed to record ethnographic return rates for the resources of interest and (2) the presumed difficulty of attempting to evaluate variability in pursuing and capturing mobile prey through replicative experiments (see Thomas 2008 and Simms 1987:43–46 for thorough treatment).

To circumvent such problems analysts have often used proxy measures of post-encounter return rate, the most common being prey body size, assuming that rank scales closely with size and that prey of similar size have similar rank (e.g., Bayham 1979; Broughton 1994a, 1994b, 1997, 1999, 2002; Butler 2000, 2001; Byers and Broughton 2004; Byers and Ugan 2005; Byers et al. 2005; Grayson 1991; M. E. Hill 2008; Janetski 1997; Nagaoka 2001, 2002; Szuter and Bayham 1989; Ugan 2005a, 2005b). A number of researchers have criticized this approach, pointing out that the circumstances and technology associated with collecting resources en masse can make some small prey more profitable than would be predicted by body size (Grayson and Cannon 1999; Madsen and Kirkman 1988; Madsen and Schmitt 1998; Schmitt et al. 2004; Sutton 1995). Ugan (2005a) has addressed this issue with data from a variety of sources, arguing that when compared with individual acquisition, mass collecting offers no substantial increase in the return rates of small animals, except for certain resources such as fish and insects (also see Lupo and Schmitt 2005).

Recently some researchers have incorporated critical components of prey behavior in generating estimates of return rate rankings (Jones et al. 2008b; Lyman 2003; Stiner 2002; Stiner and Munro 2002; Stiner et al. 1999; Stiner et al. 2000; see also Jochim 1976). Most important here are the costs of pursuit and capture, which are highly variable across taxa and at best loosely related to prey size (e.g., O’Connell et al. 1988; Smith 1991:230–231; Winterhalder 1981:95–96). The significance of such has been well illustrated in a number of zooarchaeological studies, including those of Stiner and colleagues (for Middle-to-Upper Paleolithic transitions in the Mediterranean Basin) and Jones et al. (for trans-Holocene variation in central California), both of which demonstrate that while the overall representation of large-bodied prey in the archaeofaunal assemblages shows no significant diachronic decline, the frequency of different taxa of small-bodied prey changes dramatically. Slow-moving, easily captured prey types (tortoises in the Mediterranean; the flightless duck, *Chenodectes lavi*, in California) are common in the early components but decline in relative frequency over time, probably as a result of human overexploitation. In fact, in the California case the relative proportion of large-bodied artiodactyls increased over time, while the flightless duck eventually went extinct by about 2500 B.P. (Jones et al. 2008a). In both cases, as prey with low pursuit costs declined in importance, fast-moving prey (e.g., lagomorphs in the Mediterranean; sea otters in California), presumably lower ranked because they were more difficult to capture, increased proportionally in the assemblages.

The primary problem, well recognized in these studies, remains: we have very little observational data on how post-encounter return rates are determined by the behavior of game relative to hunters (though see Hawkes et al. 1991), leaving analysts little more than their intuition to generate expectations about the effects of such on the ranking of prey in archaeological contexts. This is less likely to be a problem in cases similar to those documented by Stiner and Jones given the extreme differences in the types of prey in those assemblages: the behaviors of tortoises vs. lagomorphs and flightless ducks vs. sea otters are easily, almost iconically, dichotomized. However, as we show in the analysis that follows, under many circumstances more subtle differences in prey behavior and mobility interact in complex ways with prey size and the pursuit and capture success of hunters, which in turn have dramatic effects on return rates and prey ranking.

In this article we examine these effects relative to the foraging practices of contemporary Martu hunter-gatherers in Australia’s Western Desert. Our aim is twofold: (1) to illustrate, by way of quantitative ethnographic observations, some general processes that influence relationships between prey behavior and hunting strategies; and (2) to provide some tools for generating more reliable zooarchaeological measures of prey diversity and rank in a wide array of contexts. We begin with a brief review of foraging models and their problems of application in circumstances where prey are highly
mobility. We then explore the determinants of variability in the post-encounter return rates of Martu prey types across adult foraging bouts and follows recorded between 2000 and 2007, with special attention to the dynamics of prey mobility and a hunter’s investment in pursuit and capture. Results from this work have important implications for commonly applied measures of prey rank and zooarchaeological methods used to analyze relative abundance and diversity of prey types. We highlight the most important of these findings, especially relative to relationships among prey behavior, body size, and handling costs and illustrate how these can be incorporated in future studies of subsistence change in archaeofaunal assemblages.

**Foraging Theory and Prey Mobility**

Foraging theory is a family of models in behavioral ecology used to describe and explain shifts in resource exploitation relative to variability in resource value and availability (Charnov 1976; Charnov and Orians 1973; Emlen 1966; MacArthur and Pianka 1966; Schoener 1971; Stephens and Krebs 1986; see Bird and O’Connell 2006 for archaeological applications). Two of these models, “prey choice” and “marginal value,” are routinely used in zooarchaeology. The components of the models are well known; here we briefly review them relative to problems of application in circumstances where foragers pursue mobile prey.

The prey choice model or PCM (aka diet breadth model, contingency prey model) predicts the suite of resources likely to be handled among an array of options. The model assumes that the goal of foraging is to maximize the efficiency of nutrient intake (usually energy) and that foragers have good working knowledge of prey distribution and exploitation costs and benefits. The PCM is concerned with the trade-offs involved in searching for and handling prey: when a predator encounters an item of a particular prey type, handling it (pursuing to capture and process) costs time that could be spent searching for other prey. Should a forager pursue that item, or pass it over to continue searching? The solution to this trade-off provides the “optimal diet breadth,” the range of prey types that if handled will maximize the average return rate from foraging. The optimal “diet” (not technically what a forager prefers to eat but the range of prey types that will be pursued on encounter) is reached by adding prey types in rank order according to their post-encounter return rate until the marginal gain in overall foraging efficiency is negative; that is, when the post-encounter return rate of a given prey type is less than the overall return rate expected from searching for and handling higher-ranked prey (Stephens and Krebs 1986:17–24). Predictions about diet breadth are generated by comparing the post-encounter return rate for each prey type (\(e/h\), energy per unit handling time) with variability in the overall foraging return rate (\(EIT\), energy per unit foraging time, where foraging consists of searching and handling). An item of the highest-ranked prey type should always be handled on encounter because no opportunity can be lost by its inclusion, and lower-ranked prey are handled independent of their own abundance as a function of the encounter rate with higher-ranked prey. If encounters with higher-ranked prey decline, either through foraging pressure or environmental change, overall foraging efficiency will drop. This will broaden selection to include prey types in rank order as their post-encounter return rate (\(e/h\)) exceeds the declining return rate expected from searching for and handling higher-ranked prey (\(EIT\)). Conversely, as encounter rates for higher-ranked prey increase, diet breadth narrows as low-ranked prey are increasingly dropped from the diet.

One of the most important constraints in the PCM is that encounters with prey are a sequential Poisson process: finding an item of a given type does not change the probability of finding another item of that type. In other words, the PCM assumes that search costs are shared across all prey types while foraging. But where the probability of encountering prey types changes predictably, search should be biased by heterogeneous prey distribution. Under such conditions prey are predictably “patchy,” such that searching for some types of prey involves a loss of opportunity to search for others. After entering a patch, returns may fall over time as a function of resource depression (Charnov 1976), a decrease in the instantaneous gain within a patch. With resource depression in a given patch, at some point an additional unit of gain (the marginal value) in the return rate expected by continuing to search for resources to handle is less than what can be had by traveling to another patch. The marginal value theorem (MVT) predicts...
this point, the rate-maximizing patch residence time (Charnov 1976). According to the MVT, a rate-maximizing predator will choose the residence time in which the marginal rate of gain for a given patch is equal to the average return rate available from the habitat as a whole. If the average overall return rate from the habitat declines faster than the return rate of a given patch, the opportunity costs of traveling to another patch increase, and patch residence times are predicted to be longer, increasing the possibility of overexploitation or extirpation of high-ranked prey. Conversely, the probability of sustainable resource use increases with escalating opportunity costs of continuing to harvest in a given patch. This can occur with increasing overall foraging efficiency or counterintuitively, when in-patch resource depression causes returns from a given patch to fall faster than those expected from the habitat as a whole.

In combination, the PCM and MVT predict that increasing residence time in patches characterized by resource depression increases the reliance on low-ranked resources—resources that are typified by high handling costs relative to their yield. Thus, investments in improving handling efficiency will have a larger effect in situations where handling is the dominant component of foraging time, that is, where exploitation practices have already broadened to include low-ranked resources (see Hawkes and O’Connell 1992). As demonstrated above, archaeologists routinely use evidence of such investment to identify and define economic intensification and broad-spectrum transitions.

When Do Foraging Models Fail?

Despite obvious successes, tests of predictions derived from the PCM and MVT have met with mixed results. The mixed results are instructive; we suggest that patterns in the lack of agreement between predictions and observed foraging behavior actually demonstrate the importance and utility of the approach and should be of special concern to zooarchaeologists.

Common to both ethnographic and nonhuman applications are the ways in which the models often fail to predict the decisions of foragers when hunting for mobile prey. Most important is the differential effect of pursuit in calculating the handling costs of different kinds of prey. As opposed to sessile prey, the decision to stop search in order to handle mobile prey carries an inherent probability of pursuit failure; such failures are rarely included in prey ranking schemes. The problem is well illustrated in Sih and Christensen’s (2001) meta-analysis of 134 nonhuman foraging studies. They evaluated the degree to which foraging models predicted observed resource exploitation as influenced by a wide range of factors, including the type of study (field or lab, experimental or naturalistic), the degree to which the models’ assumptions are met (e.g., for the PCM, encounters are a sequential Poisson process), the type of forager (invertebrate, ectothermic vertebrate, or endothermic vertebrate), and the type of prey (type of plant or animal, degree of mobility from sessile to highly mobile). Of these, only prey mobility consistently explained mismatches between the models’ predictions and observed foraging responses. The PCM, MVT, and related models have generally done an excellent job explaining patterns of resource exploitation for foragers that feed on sessile to slightly mobile prey, regardless of the type of forager: 74 percent of these studies had a close fit between predictions and observations. Conversely, only 37 percent of the studies that focused on predators exploiting mobile prey were consistent with the models’ predictions, and none of the studies that included predators of highly mobile prey corroborated expectations.

Similar results are common in studies of human foraging strategies and are often associated with gender differences in occupation (see Bliege Bird 1999; Hawkes and Bliege Bird 2002; Smith 2004; Winterhalder and Smith 2000). Where they actively hunt game, women often focus on resources and patches with more reliable return rates and less mobile prey, and the range of prey types they exploit varies closely with foraging opportunities and their respective costs and benefits (e.g., Bliege Bird and Bird 2008). Where foraging models fail, they often do so relative to predicting men’s decisions to exploit highly mobile prey. The Meriam of Australia’s Torres Strait offer an illustrative example (Bird and Bliege Bird 2002; Bird et al. 2004b; Bliege Bird 2007; Bliege Bird and Bird 1997, 2002; Bliege Bird et al. 2001; Smith et al. 2003). Meriam women and children focus most of their foraging effort on reef shellfishing and hand-line fishing for small benthic omnivores in the nearshore. Their decisions about switching between patches in these habitats
and prey choice within them are highly sensitive to temporal and spatial variability in foraging returns, consistent with the quantitative predictions of foraging models. Conversely, while hunting for marine turtles offshore, deep-sea fishing for pelagics, or spearfishing on the reef, Meriam men consistently pass over the opportunity to handle encountered prey or switch to other foraging activities that would dramatically increase their overall foraging return rate. Human behavioral ecologists have developed a number of hypotheses for why such patterns are common (see Winterhalder and Smith 2000), including how, for some foragers, the value of pursuing certain kinds of prey is influenced by the way that the costs of acquisition and distribution can guarantee widespread social attention (see Bliege Bird et al. 2008). Here we will consider the direct effect it had on the uncontacted Martu and any implications surrounding Australia’s nuclear missile testing program in Western Desert (Figure 1). The term Martu is now commonly used as self-reference by about 1,000 people from a number of dialect-named groups whose homelands surround Lake Disappointment and the Percival Lakes. The heart of their country lies in the Warnman estates of Karlamilyi, situated in Rudall River National Park, where two of their “outstation” communities, Parnngurr and Punmu, are located. A third outstation, Kunawarritji, is northeast of the park at Well 33 on the Canning Stock Route. Martu established these communities in the 1980s when they returned to their homelands following a mid-twentieth-century exodus into missions and pastoral stations (see Davenport et al. 2005; Tonkinson 1991). The outstation movement provided a foundation for Martu to gain Native Title to much of their homelands in 2002. At any given time each outstation has a population numbering between 50 and 200 people, and about 500 Martu live in the towns of Newman to the west and Port Hedland on the northern coast. While most Martu families keep a permanent “camp” in one of the outstations, they maintain high residential mobility between communities and are often away for extended periods of time traveling throughout the Western Desert and Pilbara regions to fulfill traditional religious and social obligations.

Ethnographic data on Martu social organization and history are available from a variety of sources. Tonkinson (1974, 1978, 1988a, 1988b, 1990, 1991, 2007) provides a comprehensive account of Martu identity, religion, gender, politics, and change with European incursion over the last 50 years. Veth and Walsh have been concerned with Martu prehistory, subsistence ecology, and mobility (Veth 1987, 1989, 1995, 2000, 2005; Veth and Walsh 1988; Walsh 1990). And recently Davenport et al. (2005) have described the events surrounding Australia’s nuclear missile testing program in Western Desert and the direct effect it had on the uncontacted Martu bands that remained on their estates through the 1960s. Elsewhere we have written about Martu subsistence in relation to mosaic burning, seasonality, gender, and age (Bird and Bliege Bird 2005a, 2009; Bird et al. 2004a, 2005; Bliege Bird and Bird 2005, 2008; Bliege Bird et al. 2008). Here we will focus our description and analysis on the nature of contemporary foraging practices among the Manyjilyjarra, Kartujarra, and Warnman Martu who live in the heart of the desert.

The Martu and Data Collection

Martu (aka Mardu, Mardujarra) are the indigenous owners of estates that comprise about 150,000 km² of the northwest section of Australia’s Western Desert (Figure 1). The term Martu is now commonly used as self-reference by about 1,000 people from a number of dialect-named groups whose homelands surround Lake Disappointment and the Percival Lakes. The heart of their country lies in the Warnman estates of Karlamilyi, situated in Rudall River National Park, where two of their “outstation” communities, Parnngurr and Punmu, are located. A third outstation, Kunawarritji, is northeast of the park at Well 33 on the Canning Stock Route. Martu established these communities in the 1980s when they returned to their homelands following a mid-twentieth-century exodus into missions and pastoral stations (see Davenport et al. 2005; Tonkinson 1991). The outstation movement provided a foundation for Martu to gain Native Title to much of their homelands in 2002. At any given time each outstation has a population numbering between 50 and 200 people, and about 500 Martu live in the towns of Newman to the west and Port Hedland on the northern coast. While most Martu families keep a permanent “camp” in one of the outstations, they maintain high residential mobility between communities and are often away for extended periods of time traveling throughout the Western Desert and Pilbara regions to fulfill traditional religious and social obligations.

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Methods and Definitions

We began working with Martu in 2000 in preparation of their Native Title claim (which began in 1992 and was awarded in 2002). Since then we have spent 27 months in residence (consisting of 72 researcher-months across all seasons) in the Martu outstations, based mostly out of Parnngurr (Figure 1). Data reported here were collected in the course of daily foraging trips, usually within a 50-km radius of one of the communities or a temporary residential camp. During foraging trips we recorded the identity of each participant in the foraging party (the group that leaves the community/camp together), the time they spent traveling to foraging locales, route taken, foraging location, and foraging bout details of all party participants. We defined a foraging bout as the time each participant in the party spent searching for, pursuing, capturing, transporting, and processing wild food resources. Following each bout we recorded the number and whole weight of each type of resource that each forager acquired and monitored subsequent food distributions.

On any given day, depending on the season and habitat, Martu can choose from a number of different types of hunting and gathering activities. Here we use Martu definitions for different foraging activities, which correspond to mutually exclusive tasks associated with acquiring particular suites of resources (see Table 1). Martu identify a given foraging activity by the term for its primary resource type and a directional suffix (e.g., parna-jarlpap [sand monitor]-karti [to]). They often group foraging activities into categories differentiated by meat/hunting (kuwiyi/wartilpa) and those focused on plant/collecting (mirrka/mirrka). Hunting includes those activities with active pursuit of mobile prey; collecting focuses on immobile resources. We also use the emic definitions for resource types, which in most cases correspond to a given species (see Table 2). While some of the same resources can be found across different foraging activities, by choosing a particular activity a forager trades off the opportunity to focus search on another suite of resources. Thus, according to the logic of foraging models, different foraging
Table 1. Martu Foraging Activities (83 Adult Foragers, in Order of Percent Foraging Time Allocation).

<table>
<thead>
<tr>
<th>Foraging Activity</th>
<th>Primary Resource Type</th>
<th>Secondary Resource Type(s)</th>
<th>Seasonality</th>
<th>Habitat</th>
<th>n (Bouts)</th>
<th>Return Rate/Bout (kcal/hr)</th>
<th>Foraging Time/Bout (min)</th>
<th>kcal/Bout</th>
<th>% Total Foraging Time</th>
<th>% Total Foraged kcal</th>
<th>Success Rate/ Bout</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sand monitor</td>
<td>Varanus gouldii</td>
<td>Skink, python, cat, larvae, solanum, fruit, nectar</td>
<td>All, peak May–Oct</td>
<td>S</td>
<td>612</td>
<td>641</td>
<td>519</td>
<td>190</td>
<td>77</td>
<td>1,946</td>
<td>1,695</td>
</tr>
<tr>
<td>Kangaroo hunting</td>
<td>Macropus robustus</td>
<td>Sand monitor, hill kangeroo</td>
<td>All</td>
<td>R</td>
<td>91</td>
<td>1,203</td>
<td>3,563</td>
<td>199</td>
<td>87</td>
<td>4,003</td>
<td>12,613</td>
</tr>
<tr>
<td>Perentie hunting</td>
<td>Varanus giganteus</td>
<td>Argus monitor: V. panopter; cat</td>
<td>Nov–April</td>
<td>W</td>
<td>78</td>
<td>697</td>
<td>936</td>
<td>159</td>
<td>83</td>
<td>2,069</td>
<td>2,387</td>
</tr>
<tr>
<td>Cat hunting</td>
<td>Felis silvestris</td>
<td>Sand monitor, skink, python, perentie</td>
<td>All</td>
<td>S, W</td>
<td>25</td>
<td>1,131</td>
<td>1,373</td>
<td>213</td>
<td>59</td>
<td>3,883</td>
<td>4,243</td>
</tr>
<tr>
<td>Bulb collecting</td>
<td>Cyperus bulbosus</td>
<td>Variable, usual peak</td>
<td>W</td>
<td>26</td>
<td>454</td>
<td>186</td>
<td>142</td>
<td>61</td>
<td>1,119</td>
<td>702</td>
<td>.02</td>
</tr>
<tr>
<td>Desert raisin</td>
<td>Solanum centrale</td>
<td>Variable, usual peak</td>
<td>S</td>
<td>41</td>
<td>1,554</td>
<td>834</td>
<td>91</td>
<td>38</td>
<td>2,372</td>
<td>2,113</td>
<td>.019</td>
</tr>
<tr>
<td>Grub collecting</td>
<td>Endoscopha spp.</td>
<td>Variable</td>
<td>S, M, W</td>
<td>51</td>
<td>557</td>
<td>264</td>
<td>76</td>
<td>30</td>
<td>678</td>
<td>364</td>
<td>.018</td>
</tr>
<tr>
<td>Bush tomato</td>
<td>Solanum diversiflorum</td>
<td>Variable, usual peak</td>
<td>S</td>
<td>32</td>
<td>3,842</td>
<td>1,612</td>
<td>50</td>
<td>19</td>
<td>3,096</td>
<td>1,644</td>
<td>.008</td>
</tr>
<tr>
<td>Root collecting</td>
<td>Vigna lanceolata</td>
<td>Variable, usual peak, May–Aug</td>
<td>W</td>
<td>29</td>
<td>418</td>
<td>260</td>
<td>61</td>
<td>39</td>
<td>447</td>
<td>437</td>
<td>.008</td>
</tr>
<tr>
<td>Honey collecting</td>
<td>Apis mellifera</td>
<td>Variable</td>
<td>W</td>
<td>19</td>
<td>5,378</td>
<td>3,081</td>
<td>65</td>
<td>57</td>
<td>5,461</td>
<td>4,739</td>
<td>.006</td>
</tr>
<tr>
<td>Grass seed</td>
<td>Eragrostis etiropoda</td>
<td>Variable, peak</td>
<td>S, M</td>
<td>4</td>
<td>476</td>
<td>27</td>
<td>294</td>
<td>70</td>
<td>2,322</td>
<td>473</td>
<td>.005</td>
</tr>
<tr>
<td>Nectar collecting</td>
<td>Hakea suberea</td>
<td>Flower: Grevillea eristachya</td>
<td>Sept</td>
<td>S</td>
<td>16</td>
<td>8,482</td>
<td>3,350</td>
<td>45</td>
<td>25</td>
<td>6,355</td>
<td>4,881</td>
</tr>
<tr>
<td>Tree seed</td>
<td>Acacia aneura</td>
<td>Tree seeds</td>
<td>M</td>
<td>6</td>
<td>NA</td>
<td>–</td>
<td>119</td>
<td>42</td>
<td>9,351</td>
<td>4,443</td>
<td>.003</td>
</tr>
<tr>
<td>Other</td>
<td>Emu, plains</td>
<td>–</td>
<td>–</td>
<td>28</td>
<td>NA</td>
<td>–</td>
<td>155</td>
<td>93</td>
<td>NA</td>
<td>–</td>
<td>.016</td>
</tr>
</tbody>
</table>


1 Availability of many resource types depends on season, variable rains, and mosaic burning. The Martu calendar is divided into three roughly equal seasons: Yalijarra (hot/wet), January–April; Wontajarra (cool/dry), May–August; and Tulparra (hot/dry), September–December. Most plant resources peak in early Wontajarra following good Yalijarra precipitation, and with scattered rains in Wontajarra many produce again in Tulparra.

2 S = spinifex dune fields, M = mulga woodland, R = rocky range, W = watercourse margin.

3 Feral honey bees first established hives in the region in 2002–2003. Since then honey collecting has become a common activity.

4 Nectar from Hakea flowers is only available for only about a month in Tulparra. In a given patch the flowers will produce nectar only for about a week.

5 Foraging time for acacia seeds includes time spent collecting only. We were not present during processing and, as such, cannot calculate the return rate, but we suspect it would be similar to acacia seed efficiency published elsewhere (500–300 kcal/hr [O’Connell and Hawkes 1981]).
Table 2. Martu Resources (in Order of Percent Contribution of Foraged Calories Across All Follows and Category of Resource Type).

<table>
<thead>
<tr>
<th>Resource Type and Category</th>
<th>n (Follows)</th>
<th>% Total Foraged kcal</th>
<th>Mean Mobility Rank/ Follow</th>
<th>Mean Prey Size/ Individual (g)</th>
<th>Post-Encounter Return Rate/Follow (kcal/hr)</th>
<th>Mean</th>
<th>SD</th>
<th>Post-Encounter Return Rate Without Pursuit Time (kcal/hr)</th>
<th>Mean</th>
<th>SD</th>
<th>Pursuit Success Rate/ Follow</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Kuwiyi</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sand monitor: <em>Varanus gouldii</em></td>
<td>111</td>
<td>.385</td>
<td>3.2</td>
<td>460</td>
<td>4,931</td>
<td>4,781</td>
<td></td>
<td>5,422</td>
<td>5,131</td>
<td></td>
<td>.891</td>
</tr>
<tr>
<td>Bustard: <em>Ardeotis australis</em></td>
<td>128</td>
<td>.34</td>
<td>5</td>
<td>5,491</td>
<td>10,261</td>
<td>21,166</td>
<td></td>
<td>68,333</td>
<td>58,482</td>
<td>.305</td>
<td></td>
</tr>
<tr>
<td>Hill kangaroo: <em>Macropus robustus</em></td>
<td>53</td>
<td>.129</td>
<td>5</td>
<td>21,970</td>
<td>3,844</td>
<td>9,910</td>
<td></td>
<td>58,973</td>
<td>36,321</td>
<td>.302</td>
<td></td>
</tr>
<tr>
<td>Perentie: <em>Varanus giganteus</em></td>
<td>23</td>
<td>.056</td>
<td>3.9</td>
<td>2,304</td>
<td>3,455</td>
<td>4,897</td>
<td></td>
<td>9,754</td>
<td>8,278</td>
<td>.478</td>
<td></td>
</tr>
<tr>
<td>Cat: <em>Felis silvestris</em></td>
<td>18</td>
<td>.034</td>
<td>4</td>
<td>2,536</td>
<td>5,179</td>
<td>12,270</td>
<td></td>
<td>18,642</td>
<td>15,500</td>
<td>.389</td>
<td></td>
</tr>
<tr>
<td>Skink: <em>Tiliqua scincoides</em></td>
<td>27</td>
<td>.03</td>
<td>2.1</td>
<td>301</td>
<td>20,403</td>
<td>12,206</td>
<td></td>
<td>21,188</td>
<td>11,733</td>
<td>.963</td>
<td></td>
</tr>
<tr>
<td>Cossid larvae: <em>Endoxyla spp.</em></td>
<td>64</td>
<td>.011</td>
<td>1</td>
<td>13</td>
<td>887</td>
<td>513</td>
<td></td>
<td>912</td>
<td>552</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Python: <em>Aspidites ramsayi</em></td>
<td>16</td>
<td>.006</td>
<td>3</td>
<td>703</td>
<td>1,491</td>
<td>1,501</td>
<td></td>
<td>2,169</td>
<td>1,327</td>
<td>.688</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>10</td>
<td>.009</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
<tr>
<td><strong>Mirrka</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Desert raisin: <em>Solanum centrale</em></td>
<td>42</td>
<td>.198</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>2,459</td>
<td>1,377</td>
<td>2,459</td>
<td>1,377</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Bush tomato: <em>Solanum diversiflorum</em></td>
<td>35</td>
<td>.192</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>5,006</td>
<td>2,120</td>
<td>5,006</td>
<td>2,120</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Honey: <em>Apis mellifera</em></td>
<td>19</td>
<td>.182</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>5,378</td>
<td>3,081</td>
<td>6,011</td>
<td>2,577</td>
<td>.895</td>
<td></td>
</tr>
<tr>
<td>Corkwood nectar: <em>Hakea suberea</em></td>
<td>16</td>
<td>.181</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>8,482</td>
<td>3,350</td>
<td>8,482</td>
<td>3,350</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Tree seeds: <em>Acacia aneura</em></td>
<td>6</td>
<td>.109</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>4,491</td>
<td>1,472</td>
<td>4,491</td>
<td>1,472</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Bush onion: <em>Cyperus balbosus</em></td>
<td>26</td>
<td>.058</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>454</td>
<td>186</td>
<td>454</td>
<td>186</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Pencil yam: <em>Vigna lanceolata</em></td>
<td>29</td>
<td>.025</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>462</td>
<td>292</td>
<td>462</td>
<td>292</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Grass seeds: <em>Eragrostis eriopoda</em></td>
<td>4</td>
<td>.018</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>476</td>
<td>27</td>
<td>476</td>
<td>27</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Grevillea nectar: <em>G. eriostachya</em></td>
<td>26</td>
<td>.016</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1,462</td>
<td>549</td>
<td>1,462</td>
<td>549</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Other</td>
<td>6</td>
<td>.019</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td></td>
</tr>
</tbody>
</table>

Note: Martu categorize resources as either *kuwiyi* (meat) or *mirrka* (vegetable food). In general these correspond to resources that are hunted vs. collected (see Table 1), with obvious exceptions: Martu usually consider cossid larvae as *kuwiyi* but refer to the foraging activity as *lunki-karti nganyimpa* (grub collecting), and conversely, sometimes *mirrka* is taken on encounter while hunting (see text). Prey mobility is categorized on each follow as 1 = effectively immobile on encounter; 2 = low mobility, always slower than a hunter; 3 = moderate mobility, torpid prey that can still potentially escape a hunter (e.g., burrowed monitors); 4 = high mobility, prey that are faster than a hunter over short distances (e.g., surface monitors); 5 = fast, prey that will always escape a hunter without specialized capture technology. Skink and varanid mobility varies by season and the type of encounter (see text).
activities are analogous to different patches (see Smith 1991).

During each foraging trip, at least one researcher present asked permission to conduct a focal individual foraging follow, where one of us accompanied a forager for the duration of a bout, recording all time allocated to search and the different components of handling: pursuit, capture, and processing. On many follows we also recorded the foraging path using GPS, and as with all bouts, at the end of the follow we weighed and counted each type of resource acquired. Martu most often forage separately, but occasionally people cooperate. During these episodes we divided the returns by the number of individuals that foraged together, although if people were working closely together an experienced observer often could conduct more than one focal follow at a time.

In keeping with the PCM, we considered handling to start when a forager began pursuing a specific item, or collecting multiple items, of a particular resource type, thereby trading off the opportunity to continue searching for other resources. Accordingly, a resource encounter could be either direct or indirect, the latter being when foragers found indications (usually tracks) that caused them to begin following a particular prey item. We thus defined pursuit as time spent in tracking, stalking, or chasing an item (see Winterhalder 1981). These are distinct from the costs of capture, defined as the time foragers spent retrieving, collecting, extracting, and dispatching resources during a follow (e.g., probing for and excavating burrowed game, digging geophytes, picking fruit, extricating cossid larvae). Processing is a substantial proportion of handling for only a few Martu resources, mostly tree and grass seeds. Processing costs, including those in and out of camp (e.g., field preparation of game, in-camp butchery, winnowing of bulbs or seeds), were charged when the focal forager participated in preparing the harvest. This is the case for most plant foods and small game, but larger game (e.g., kangaroo) are often butchered and distributed by someone other than the hunter (see Bird and Bliege Bird 2009). In these cases we did not charge the acquirer with in-camp processing time. Also in keeping with the logic of foraging models, because foragers could usually perform other activities while food cooked, we did not count cooking time as a component of handling cost.

For all types of game except kangaroo, in order to convert whole weight acquired to edible weight, we measured the proportion of refuse to whole weight of specimens \( n = 46 \) representing all small game taxa, as well as four bustards (Ardeotis australis). For hill kangaroo (euro, Macropus robustus), proportional meat and marrow weights for each body part, male and female, were obtained from O’Connell and Marshall 1989: Tables 3 and 4. Edible weights of all resources according to species and body part were then converted to kilocalories using Brand-Miller et al. 1993. These records constitute two primary data sets used in the description and analysis below: 1,347 adult foraging bouts and 649 adult focal individual foraging follows.

Contemporary Martu Hunting

Some of the most vibrant aspects of Martu identity are expressed in their foraging ethos and practice. Martu established the outstations in the 1980s in response to the threat of dispossession wrought by institutionalized racism and processes of assimilation. Living in the outstations allowed Martu to assert ownership over their homelands and maintain their ritual and socioeconomic obligations to the desert. These obligations are manifest in the regular maintenance of their estates through daily hunting, gathering, and mosaic landscape burning. While often unacknowledged or devalued by “mainstream” society and policy, foraging is the dominant occupation of Martu men, women, and children, and many hunt or gather every day. Most families receive government welfare, which is often used for gambling and travel to sustain social and ritual imperatives or to purchase household goods from town or the small shops in the outstations.

Depending on seasonal and individual obligations, foraging provides outstation residents with 25–50 percent of their daily calories per capita and over 80 percent of their meat calories; participants in foraging parties (including all women, men, and children) acquire an average of \( 1,700 \) kcal/capita/day from bush foods (Bliege Bird and Bird 2008). The remainder, mostly in the form of commercial flour and canned goods, is purchased from the shop or during visits to town. Typically a foraging party leaves the community in the late morning, usually...
following household or community business. Vehicles are regularly (although not always) used to access foraging locales, but on arrival much of the hunting and gathering is conducted on foot. Parties average 8.0 ± 3.3 participants (2.3 ± 1.1 men, 3.6 ± 0.8 women, 2.1 ± 1.4 children), although groups of over 20 (in a single vehicle!) are not uncommon.

A given foraging location is decided by consensus among the adults in the party, usually involving discussion about recent returns and intricate ecological and social dynamics. Game animals, especially bustards, are occasionally spotted on route to foraging destinations, and active search often begins as soon as the party leaves camp. Adult men are almost always armed with small-caliber rifles and axes. Women rarely go anywhere outside of camp without their highly prized digging sticks, although they occasionally carry rifles if men are not present, and many of the women are keen shots. On arrival at a foraging locale, the party designates a dinnertime camp: this is the site where all participants will gather after foraging to process, cook, and share resources prior to traveling back to the community. In our sample, dinnertime camps were used on over 90 percent of the foraging trips; this is partly due to firewood constraints around the outstations and, as Martu say, to facilitate sharing (see Bird and Bliege Bird 2009).

Martu country is structured by four foraging habitats: spinifex grass (Triodia spp.) dune fields, low-lying rocky ranges, eucalypt-dominated (Eucalyptus spp.) watercourse margins, and mulga (Acacia anura) woodland. Depending on habitat, season, and expected returns, when foragers arrive at the dinnertime camp, the party splits up, and participants typically engage in one of a number of mutually exclusive foraging activities (see Table 1). Men more often forage alone, while women often forage within earshot of each other, sometimes cooperating in aspects of search, pursuit, and capture (see Bliege Bird and Bird 2008). Typically (though not always) people engage in only one foraging bout per day; adult foraging bouts (not including travel time) across all activities average 159 ± 88 minutes (n = 1,358). Men’s and women’s bouts are similar in length (respectively, x = 158 ± 94 minutes, n = 521, vs. x = 159 ± 83 minutes, n = 835), but women forage more frequently: they make up 62 percent of all adult foraging time and produce 51 percent of all calories from foraged foods. As for other Aboriginal groups (e.g., O’Connell and Hawkes 1981), grass seeds were a traditional staple but have dramatically declined in importance. Today, for both men and women, hunting is far more important than collecting plant resources (Bliege Bird and Bird 2008): 81 percent of all foraged calories and 87 percent of all foraging time are devoted to the four most important hunting activities.

Results I: The Effects of Prey
Mobility on Foraging Decisions

While a description of all Martu foraging activities is beyond the scope of this article (see Table 1 for a summary; for further details, see Bird and Bliege Bird 2005b, 2009; Bliege Bird and Bird 2005, 2008; Bliege Bird et al. 2008), an analysis of the more important hunt types will serve to illustrate the way that prey mobility structures hunting decisions.

Sand Monitor Hunting

The most frequent foraging activity is sand monitor (goanna, Varanus gouldii; parnajarlpa in Martu-wangka) hunting, taking up 54 percent of all foraging time across all seasons, peaking in the cool/dry season (Wantajarra, May–August; Figure 2). Resources from this hunt type account for 35 percent of all foraged calories. Varanids make up the bulk of this, but skink (Tiliqua scincoides; lungkuta) and python (Aspidites ramsayi; kanait) are always pursued on encounter. Although they are usually pursued in other foraging activities, sand monitor hunters sometimes take feral cats (Felis silvestris [see below]), and if encountered they often collect cossid larvae (Endoxyla spp.; lunkti), solanum fruit (Solanum diversiflorum; kampulpaja; and S. centrale; jinyjuwirri), and nectar (wama) from Hakea suberea and Grevillea eriostachya flowers. Sometimes fresh signs of bustard (Ardeotis australis; kipara) or hill kangaroo (euro, Macropus robustus; kirti-kirti) are encountered (especially near the interface of dune fields and mulga woodland or rocky range), but these are rarely pursued during this type of hunting (see below).

Sand monitor hunting is limited to spinifex dune fields and requires an anthropogenic fire regime: lengthy search and pursuit are conducted on foot, and without an established system of burning to
clear the overburden, encounters with tracks and dens are too infrequent to make it worthwhile (see Bird et al. 2005; Bliege Bird et al. 2008). Hunters usually begin their search in a new burn (nyurma), often following along just behind the advancing flames in the clear surface of new ash. This activity usually involves more tracking than the larger game hunting described below; once fresh tracks are found, prey are typically pursued to exhaustion or to a monitor burrow. If the entrance mound of a burrow is fresh and there is no evidence of an exit hole, hunters use their digging sticks to probe in wide concentric circles to locate a terminal chamber, usually found 10–50 cm beneath the surface, although during the hot seasons dens can be significantly deeper. Martu probe and excavate dens with tremendous skill: distinguishing a subsurface chamber den from an entrance shaft or an escape tunnel is very difficult, and care must be taken to not misjudge the occupant, as deadly king brown

Figure 2. Sand monitor (Varanus gouldii) hunting. A view of two Martu women near Punmu outstation walking down a dune to continue hunting in an area prepared by burning off the overburden of overgrown spinifex grass (R. Bliege Bird, photographer).
and taipan snakes often shelter in varanid burrows. All of the varanids are fast, and even when buried, they sometimes escape through a “pop hole” and can outrun a hunter over short distances. Skink, however, are quite slow, and while they may attempt to escape to a monitor burrow, hunters typically capture them in spinifex hummocks after only a short amount of tracking. Success rates from sand monitor hunting are high (Table 1). With an established anthropogenic fire regime, hunts rarely fail outright, and hunters can predictably adjust harvest size with foraging time (Bliege Bird and Bird 2008; Bliege Bird et al. 2008). Return rates from sand monitor hunting across all seasons average 641 ± 519 kcal/hr searching and handling (n = 612 bouts) but drop significantly (an average decrease per foraging bout of 97 kcal/hr; df = 566, t = –2.25, p = .025) during Yalijarra, the hot/wet season that lasts from January to April. This is due to changes in prey mobility: the pursuit and capture costs involved in sand monitor hunting increase in the hot months when all of the herpetofauna are faster and require more tracking/chasing and when probing and excavating the deeper dens become more difficult.

Perentie Hunting

As a consequence of seasonal changes in varanid mobility during the hot/wet season, monitor hunting shifts from the dune fields to the eucalypt-dominated watercourse margins and floodplains, with a focus on very large perentie (Varanus giganteus; yalapara) and Argus monitors (Varanus panoptes; marantu) [see Bliege Bird and Bird 2005]). Average return rates for this hunt type are roughly equivalent to that of sand monitor hunting (Table 1), however, in contrast to sand monitor hunting, efficiency increases in the hotter months (from 507 ± 497 kcal/hr in May–November [n = 22 bouts] to 867 ± 1.068 in December–April [n = 56 bouts]). This is because in the winter perentie nest in impenetrable termite mounds and caves, making capture from a den very difficult. Thus, during the hot/wet season when the large varanids are more accessible (less likely denned) and smaller sand monitors are more difficult to pursue and capture, the average return rate from perentie hunting exceeds that expected from sand monitor hunting by over 200 kcal/hr (df = 286, t = 2.16, p = .031). While perentie hunting is limited mostly to watercourse margins, Martu sometimes pursue the game to other habitats. The hunt type is dominated by tracking/chasing over long distances, with hunters often pursuing the lizards from shelter to shelter until the prey are exhausted. If successful, pursuit usually ends in a tree, with a hunter dispatching the monitor with rocks, a rifle shot, or a quick hit with a digging stick. However, pursuits often fail (over 50 percent of the time/follow; Table 2), and hunters return with nothing on 33 percent of bouts.

Feral Cat Hunting

Feral cats are sometimes pursued during sand monitor and perentie hunting, but they more often make up their own hunt type. Typically cats are hunted on a day following another foraging activity, when a hunter returns to pursue fresh tracks previously encountered. As such, cat hunts have relatively little search time but very long pursuits, effectively limiting the amount of time hunters can search for anything else. As with perentie, cats are tracked/chased from site to site until they capitulate. Most cat hunts occur in the dune fields, and if a pursuit fails (over 60 percent/follow do; Table 2), foragers routinely begin searching for sand monitors/skink/python as described above, increasing the chance that the bout will succeed (Table 1).

Bustard Hunting

As shown in Table 1, women spend as much time, or more, as men in sand monitor, perentie, and cat hunting. Men, however, spend far more time hunting for bustard and hill kangaroo. Bustard (Ardeotis australis; kipara) hunting is the second most common foraging activity after sand monitor hunting, accounting for nearly 20 percent of all foraging time and 30 percent of all foraged calories. Martu report that time allocated to this activity has increased with vehicle and rifle use since they established the outstations. This is because a reasonable encounter rate requires being able to cover a good deal of country: the birds are highly nomadic and thinly dispersed across all arid-zone bioregions, occurring singly, in pairs, or even in small flocks. Whenever in a vehicle, Martu are on the lookout for bustards, especially at the interface of dune fields and mulga scrub or in regions surrounding recent burns. When the birds or fresh tracks are sighted, the hunters make every attempt to pursue them in the vehicle, using it as a mobile blind: if
bustards do not see a human form, they are far less likely to fly and if disturbed by a vehicle, tend to move away slowly in their characteristic stately walk. The mean return rate from bustard hunting is nearly double that of mutually exclusive alternatives such as sand monitor or perentie hunting (Table 1), but choosing it carries a high risk of failure. The coefficient of variation in bustard hunting efficiency is over three times that of sand monitor hunting and double that expected from perentie hunting. This is due to the fact that while they occasionally acquire bonanzas (e.g., six birds in one hunt, equivalent to over 50,000 edible kcal), most of the time bustard hunters return with nothing at all (a failure rate of 56 percent per bout \( n = 289 \)).

**Hill Kangaroo Hunting**

Hill kangaroo (Euro, *Macropus robustus*; kirtikirti) hunting is a common foraging activity for men, accounting for about 20 percent of their foraging time (Table 1, Figure 3). Unlike many other regions across the arid zone, expansive sclerophyll woodlands are quite limited in the Martu homelands, and encounters with plains kangaroo (*Macropus rufus*; marlu) and emu (*Dromiceius novaehollandiae*; karlaya) are rare. As such, except while traveling in far western parts of Martu country or in the Pilbara, large-game hunting is focused on hill kangaroos in the low-lying rocky ranges. Hill kangaroo hunting is conducted on foot with rifles and typically begins with a hunter walking along the base of a range in search of signs of kangaroo resting in acacia shade on the flats and alluvial fans. *Robustus*, especially males, carry a distinctive scent, and stalking often begins when a hunter smells a particular animal. If downwind, the hunter can sometimes stalk the kangaroo to fairly close range (within 30 m). *Robustus* have poor eyesight and if undisturbed by smells or sounds, will often remain prone until after the first shot. If missed or wounded, the kangaroo will bolt for the hillslopes, and if close enough, the hunter will typically continue the pursuit, either tracking or in direct chase. If the hunter is thereafter able to maintain visual contact with the kangaroo, or blood track indicates a good hit, pursuit will continue in an attempt to exhaust the animal. As with bustard hunting, average return rates are higher than that of smaller game hunting (Table 1), but due to the high variance of hill kangaroo hunting, the differences are not significant (e.g., sand monitor vs. hill kangaroo hunting; \( df = 90, t = -1.51, p = .137 \)). The high variance is a product of the low success rate: 79 percent of all hill kangaroo hunts fail \( n = 91 \) bouts. This, in turn, is a function of how mobile kangaroo are relative to the hunter, which proves to be the critical factor in determining their post-encounter return rate.

**Results II: Prey Ranking and the Costs of Handling**

Here we present an analysis of the trade-offs that hunters face in acquiring commonly encountered prey types, directing our attention to the following questions: (1) How are post-encounter return rates affected by the different components of handling, specifically variability in the costs of pursuit and capture relative to prey mobility and size? and (2) How does patterned variability in such costs scale
with commonly used zooarchaeological proxies of prey rank, specifically prey size and yield per unit processing? Figure 4 presents a test of the prey choice model prediction that within a given foraging activity (i.e., patch), only those prey types with post-encounter return rates ($e/h = \text{kcal/hr handling}$) higher than the return rate for the activity overall ($E/T_f = \text{kcal/hr searching + handling}$) should be pursued on encounter. As expected, the only resources that Martu always pass over on encounter
while hunting are those whose mean $e/h$ is lower than the expected $E/T$; these include seeds, pencil yams, and bush onions. However, in violation of PCM predictions, when foragers occasionally encounter fresh signs of bustards or hill kangaroo while sand monitor or perentie monitor hunting, they very rarely stop search to pursue these prey (2 out of 46 bustard pursuits/encounters and 3 out of 16 hill kangaroo pursuits/encounters [$n = 103$ focal follows]). They do not stop even if they are carrying rifles and despite the fact that doing so should increase the mean overall return rate. This is because while monitor hunting, the decision to pursue a bustard or kangaroo will almost always entail trading off the opportunity to reliably acquire more meat: even under the best conditions, pursuits of bustard and hill kangaroo succeed only 30 percent of the time (Table 2). If foraging for daily provisions, Martu find that despite the potential bonanza, the risks from pursuing these larger game are too costly. Elsewhere we have shown that time allocated to bustard and hill kangaroo hunting to the exclusion of more reliable types of hunting is better understood as a political rather than provisioning strategy (Bliege Bird and Bird 2008).

Figure 5 summarizes the distributions of the post-encounter return rates ($e/h = \text{kcal/hr}$ in pursuit, capture, and processing) for each animal prey type, ranked by size. Each point represents, for all items of specific prey type, the sum of all calories acquired during a given foraging follow over the summed time spent pursuing, capturing, and processing on that follow ($n = 440$). Overlying box-and-whisker diagrams show the median (solid bar in box), mean (dash), interquartile range (length of box), and extreme values (whiskers extend to the tenth and ninetieth percentiles) of the post-encounter return rates. Five bustard points lie beyond 60,000 kcal/hr, extending to 113,075 kcal/hr.
type pursued during a given focal follow, ordered from smallest (grubs) to largest (hill kangaroo). The interactive effects of prey size and pursuit failures are well illustrated here; for example, while skink are the second smallest prey type (301 g/specimen), they have the highest average elh (>20,000; see Table 2) with the most normal distribution (median elh = 18,428, skewness = .16). This is a result of the high rate of pursuit success (.963; Table 2). Mean elh values for larger, more mobile prey (kangaroo and bustard) are much lower than we would expect from their size. As Figure 5 shows, this is due to how highly skewed their elh measures are (skewness = 4.03 and 2.73, respectively); kangaroo and bustard have a median elh of 0 but occasional maxima that well exceed 50,000 kcal/hr (in the case of bustard, over 100,000 kcal/hr). Much of this variance in elh is a result of prey mobility.

To measure the effects of prey mobility on elh we use an ordinal index of animal prey types that describes the upper limit of how fast prey can be relative to the hunter: (1) effectively sessile on encounter (cossid larvae); (2) low mobility—always slower than a hunter (skink); (3) moderate mobility—torpid prey that can still potentially escape a hunter over short distances (cool/dry season sand monitor, python; hot season skink); (4) high mobility—prey that are faster than a hunter over short distances (hot season sand monitor, cat, perentie/Argus monitors); (5) fast—prey that will always escape a hunter without technology that allows a hunter to capture prey from a distance (bustard, hill kangaroo). Figure 6 presents a summary of these effects, along with prey size, on post-encounter return rates (elh). As discussed earlier, most archaeological applications of foraging theory have used prey body size or yield and processing costs, without considering pursuit costs, to generate expectations about elh rank and changes in resource use. Figure 6a shows that in the absence of pursuit costs (that is, when we measure elh as kcal/hr spent capturing and processing, by subtracting time spent tracking, stalking, and chasing prey from handling time on follows with successful captures), body size is a reasonable predictor of increasing elh values ($r^2 = .51$ for mean elh of eight animal prey types; $r^2 = .32$ for elh by prey size of animal prey types captured on each follow; $n = 271$, $F = 127.91$, $p < .001$). However, this relationship between size and elh is consistently countered by the effect of relative prey mobility, which is positively correlated with prey size (Figure 6b; $r^2 = .92$, $F = 72.83$, $p < .001$). To control for this covariance and isolate possible consequences of prey size, we regressed elh on mobility and plotted the residual variance in elh against prey size: even if we include only successful pursuits, when we control for the mobility effect, size has no predictive value on elh ($r^2 = .003$, $n = 272$ follows, $F$-ratio = .77, $p = .38$). The mobility effect on elh is a product of the way that predictable prey behavior changes the probability that a given prey type will be captured if pursued (pursuit success rate). While the probability of pursuit success is rarely considered in archaeological prey rankings, it is a critical component of elh and, as shown in Figure 6c, negatively correlated with prey mobility ($r^2 = .87$, $F$-ratio = 38.89, $p < .001$). Thus, when we add the real costs of pursuit in handling time for prey of varying mobility, including pursuits that lead to both successful and unsuccessful captures, there is no relationship between prey size and elh (Figure 6d; $r^2 = .003$ for mean elh of eight animal prey types; $r^2 = .002$ for observed elh by prey size of animal prey types handled on each follow; $n = 439$, $F$-ratio < .01, $p = .98$). These data show that if a hunter stops search while foraging in an attempt to handle an encountered prey item, the probability of failing to capture that item (which is a function of prey mobility) dilutes any predictable effect of prey size on elh.

**Discussion**

Prey mobility has profound effects on Martu hunting decisions. It determines whether or not a pursuit is likely to lead to a capture, which structures post-encounter return rates and prey choice within a given patch (i.e., mutually exclusive foraging activities), patch choice, seasonal shifts in patch residence time, and gender differences in time devoted to different types of hunting. We propose that such results have implications for questions about broad-spectrum transitions and zooarchaeological measures of prey rank and abundance.

**Declining Abundance Indexes and Alternative Goals for Pursuing Larger Game**

The method that is perhaps most commonly used in zooarchaeological investigations of prehistoric
resource depression, especially in North America, posits within-patch prey rankings based on prey size and then calculates an abundance index (AI) of the large-bodied prey relative to the sum of large- and small-bodied prey (Bayham 1979; see Lupo 2007 for discussion). In accordance with foraging models, declines in AI are thus said to imply shifts toward a broader-spectrum economy with intensified investment in handling lower-ranked prey, which results from depression (usually anthropogenic) in the encounter rate with large-bodied prey (e.g., Broughton 1994a, 1994b, 1997, 1999, 2002; Butler 2000, 2001; Byers and Broughton 2004; Byers and Ugan 2005; Byers et al. 2005; Grayson 1991; M. G. Hill 2008; Janetski 1997; Nagaoka 2001, 2002; Szuter and Bayham 1989; Ugan 2005a, 2005b). However, the Martu data show that as a result of predictable differences in the mobility of prey types, there is no relationship between prey size and the ranking of resources by

Figure 6. The counteractive effects of prey size and prey mobility on mean post-encounter return rates (e/h, kcal/hr handling per foraging follow) for animal prey types (linear fit with 95 percent confidence interval curves). (a) Mean e/h regressed by log prey size (see Table 2), where e/h is calculated as kcal/hr spent capturing and processing per follow, subtracting time spent in pursuit from handling during follows with successful captures of a given prey type. (b) The covariance of log prey size and ranked mean prey mobility (see Table 2). (c) The post-encounter pursuit success rate per follow (the probability that attempted pursuits of a given prey type lead to at least one capture on a follow) regressed by prey mobility. (d) Mean e/h regressed by log prey size, where e/h is calculated as kcal/hr spent pursuing, capturing, and processing a given prey type per follow. Results of regressions on actual (nonmean) data points are presented in the text.
Post-encounter return rate (elh, kcal/hr handling). Quantitative evidence from a number of disparate ethnographic and environmental contexts also contradict the postulated prey size and elh correlation (Bliege Bird 2007; Bliege Bird and Bird 1997; Hawkes et al. 1991; O’Connell et al. 1988; Smith 1991:230–231; Winterhalder 1981:95–96). We suspect that under many circumstances, this is caused by differences in prey mobility and its effect on the variance around return rates (that is, the risks of pursuit failure). Larger prey, simply because they are large, do not always have higher return rates. If researchers do not use a more accurate measure of prey rank, declines in AI may not generate predictions about the intensified use of less profitable prey. While a decrease in the frequency of the remains of large game may indicate overexploitation or habitat modification, this does not necessarily reflect the goals assumed in most foraging models (i.e., maximizing foraging efficiency). Where large, highly mobile game are pursued for purposes other than provisioning, such as when the very costs of their pursuit and distribution guarantee honest and widespread advertisement of a hunter’s qualities that are difficult to assess otherwise (e.g., Bliege Bird and Bird 2008; Bliege Bird et al. 2001), standard foraging models are unlikely to provide accurate predictions about variability in the frequency of large game (see Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005). In other words, sometimes we may be right to infer increasing hunting pressure from decreasing AI, but for the wrong reasons (reasons other than those hypothesized in classic foraging models). We now need archaeologically relevant predictions that can differentiate the two broad hypotheses (i.e., foraging for food vs. foraging for prestige, or both) and more sophisticated links between those hypotheses and group dynamics, cooperation, and competition (e.g., Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005). A first step may involve the incorporation of secondary measures of prey abundance (e.g., Cannon 2003; Jones et al. 2008b). Further progress can be made by estimating potential effects of prey mobility on return rates (e.g., O’Connell 2000), which, even when very rough, will provide analysts with tools to more clearly identify violations of foraging models and the determinants of diachronic decreases in abundance indexes.

Increasing Abundance Indexes and Resource Depression

Conversely, in circumstances when AI increases over time, some researchers have treated the pattern as a violation of the prey choice model requiring either appeals to climatic conditions (e.g., Byers and Broughton 2004; Byers et al. 2005) or revisions to the model (e.g., Hildebrandt and McGuire 2002; McGuire and Hildebrandt 2005). Based on the results detailed here, we suggest that the absence of evidence for resource depression of larger prey is not always a pattern that requires a special explanation. That is, in some cases, it may be that a diachronic increase in the proportion of larger-bodied prey in an assemblage is predicted under resource depression. If the elh for larger prey is still higher than the overall return rate for a specific foraging activity in which that prey would be encountered (as with bustards and hill kangaroo in the Martu case; see Figure 4), an increase in the AI of that prey may conform to the model’s predictions, indicating a decrease in less mobile but higher-ranked prey. This does not imply that abundance indices focused on larger prey are meaningless but, rather, that for issues of conservation, overexploitation, and anthropogenic resource depression, there may be smaller, less mobile but higher-ranked prey that are better indicators of intensification (e.g., Jones et al. 2008a; Jones et al. 2008b; Stiner et al. 1999; Stiner et al. 2000). In a concrete example, if we were to assume that the prey ranking (elh) of fauna from the California coastal site of Diablo Canyon (CA-SLO-2; see Jones et al. 2008b) scaled with prey body size, the trans-Holocene increase in artiodactyl remains and concomitant declines in some smaller prey (including the flightless duck, Chendytes lawi) would be consistent with the PCM prediction that diet breadth contracts with increasing abundance of large game. In this case, our interpretation of the ecological dynamics of human predation would be misleading at best: we now know that some of the smaller prey at such sites, the flightless duck in particular, were hunted into extinction (Jones et al. 2008a) and are probably useful markers of long-term subsistence intensification, the exact opposite of the conclusion we would reach if we assumed that larger game are always highly ranked. If, however, relative prey mobility were considered in the prey rankings, the PCM should predict that a relatively immobile flightless
bird would be highly ranked and especially susceptible to overexploitation.

**Seasonal and Technological Effects on Prey Mobility and Rank**

The Martu data also draw our attention to the kinds of local conditions that make prey mobility an important determinant of variability in resource rank and patch choice (see O’Connell 2000 for an illustrative example of similar pursuit costs elsewhere in Australia). Here we highlight two of these: seasonality and technology. The behavior of some game is highly conditioned by season, making a single taxon effectively two different prey types (Smith 1991; Winterhalder 1981). For example, as we show, time allocated to Martu hunting activities shifts dramatically from sand monitor hunting to perentie monitor hunting as the mobility of sand monitors and the costs of pursuing them increase in the hot months. This, in turn, structures gendered differences in foraging, as many Martu men are more inclined to pursue the larger, more mobile perentie. Elsewhere we have argued that this is often more related to concerns about reputations of skill and generosity than foraging efficiency per se (Bliege Bird and Bird 2005, 2008). Similar seasonal differences in prey mobility are common elsewhere, especially for animals that rely on nests or rookeries, and are likely to generate large differences in post-encounter return rate and resource rank (e.g., Bliege Bird et al. 2001; Lyman 2003). Pursuit and capture technology can have similar effects on prey ranking: snares, traps, blinds, and projectile weaponry can dramatically change the effective mobility of prey. For example, hill kangaroo and bustard are too mobile to even be considered as potential prey (let alone be high ranked) without weapons that allow capture from a distance (at the very least boomerangs or spears). As demonstrated here, even with rifles and vehicles, these prey are too mobile to be highly ranked. At contact Martu readily adopted these technologies, which effectively reduced the relative mobility of bustard and hill kangaroo, enhancing the probability of their capture without significantly dampening either the skills/knowledge that can be displayed in ensuring encounters or one’s ability to be generous in their distribution. Likewise, a deer captured by snare is a very different type of prey than one captured by atlatl, and the adoption of either technology would have a predictable impact on post-encounter returns. Both large and small prey with slow life histories whose mobility is predictably constrained by season or technology should be especially susceptible to overexploitation and serve as key indicators of economic intensification. Conversely, prey with high mobility and relatively fast life-history strategies (such as deer acquired by direct pursuit rather than snares) are likely to be lower ranked as subsistence resources, and their populations should be less susceptible to anthropogenic depression or extirpation (Whitaker 2008). Such effects are rarely considered in archaeological resource rankings but could be estimated in actualistic studies designed to evaluate the proportional differences that ethnohistorically known tactics and technologies have on pursuit costs of different prey. This is not a simple solution, but even rough devaluation of the ranking for highly mobile prey relative to variables that are likely to affect pursuit success will significantly improve the predictive power of commonly used foraging models.

**Concluding Remark**

The single most important dimension of zooarchaeological applications of foraging models involves establishing a reliable means for ranking resources based on the post-encounter return rate of different resources. Doing so is essential to many powerful arguments about variability in prehistoric resource use and its implications for understanding phenomena as disparate as the evolution of human life histories, sociopolitical complexity, gender, and sustainable harvesting. The Martu data clearly demonstrate that prey body size and yield relative to processing costs are poor predictors of the post-encounter return rates of highly mobile prey, a pattern that we suggest is common elsewhere. How then should zooarchaeologists measure prey rank? We argue that any proxy measure must incorporate critical components of prey behavior, mobility being one of the most important for predicting handling costs. Future work could focus on measures that consider yield (as body size does) scaled by estimates of pursuit costs that are largely dependent on mobility. This idea is not new (Jochim 1976) but has yet to be applied broadly in analysis of faunal assemblages (Stiner and Munro 2002).
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Notes

1. Some might question whether tracking should be charged to the handling budget or is more appropriately assigned as a search variable. The prey choice model is concerned with the trade-offs entailed in decisions to stop searching for an array of possibilities in order to handle an encountered resource. For mobile prey, handling involves the pursuit of a particular item (or unit of items) of a specific resource type to make capture and processing possible. As such, Martu tracking must be considered as a pursuit cost because this is the point at which a forager decides whether to pursue a particular animal or continue searching for other resources. In this case it is simply wrong to classify tracking as search, because the hunter tracks a specific animal to the exclusion of others. Even for sessile or less mobile prey, Martu pursuits often begin before the resource is directly
sighted (e.g., for cossid larvae, foragers switch from search to pursuit on encounter with fresh droppings and subtle bulges beneath the bark of a eucalyptus or at the base of witchetty acacia and then follow and probe the intraphloem tunnel tracks to extricate the grubs). Elsewhere, similar criteria, including tracking, are identified as crucial for calculating handling costs and post-encounter return rates of mobile prey (e.g., Winterhalder 1981:82, Table 4.4 notes).

2. All errors are given as standard deviation.

3. A woman’s digging stick (wana) is individually owned and highly curated, made for her by her husband, father, or a particularly close male relative. Wana are long (150–220 cm) and thin (2–3 cm in diameter), manufactured from either wooden shafts of *Acacia dictyophleba* or metal rods acquired from spare windmill pump shafts (see Figure 2). They are fire-hardened and sharpened in a spatula shape at one end, specialized to facilitate both probing and digging.

4. Note that these resources are exploited, but only as separate foraging activities, not when encountered during hunting.

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