Interpreting abundance indices: some zooarchaeological implications of Martu foraging

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1. Introduction

In the last few decades, zooarchaeological studies have made important contributions to our understanding of prehistoric human behavior and human-prey dynamics, providing new insights into broad-spectrum revolutions (e.g., Stiner, 2001; Stutz et al., 2009), anthropogenic resource depression (e.g., Broughton, 1994; Cannon, 2003), human caused extinction events (Jones et al., 2008a; Nagaoka, 2002), and variability in gender-divisions of foraging labor (e.g., Kuhn and Stiner, 2006; McGuire and Hildebrandt, 2005). Many of these studies rely on indices of taxonomic abundance to evaluate diachronic variability in prehistoric foraging efficiency and resource choice (see review in Bird and O’Connell, 2006; Lupo, 2007).

Abundance indices (AI) measure the relative profitability of a foraging strategy by calculating the proportion of higher ranking taxa relative to lower ranking taxa in a zooarchaeological assemblage. The initial approach was developed by Bayham (1979) as a means to evaluate predictions of the encounter-contingent prey choice model (PCM) from behavioral ecology (see Charnov and Orians, 1973; MacArthur and Pianka, 1966; Schoener, 1971; Stevens and Krebs, 1986; see also Bettinger, 1991, 2009). The basic PCM assumes that a forager’s main goal is to maximize the rate at which energy is acquired. To achieve this goal, a forager searching for homogenously distributed resources within a patch should always pursue the resource with the highest post-encounter profitability when encountered and should only pursue less profitable resources when the opportunity costs of handling them are less than what could be gained by continuing to search for more profitable prey. Thus, when the encounter rates with the highest ranking prey are frequent enough, foragers should only take that resource. However, when the encounter rates with the highest ranking prey decline, the model predicts that foragers should respond by widening their “diet breadth” to include lower ranked resources, reducing a forager’s overall efficiency. When resources are not distributed homogeneously, this same logic can and has (e.g., Hildebrandt and Jones, 1992; see also Broughton, 1994) been applied to resource patches (see Bettinger, 1991; MacArthur and Pianka, 1966) or foraging activities (Smith, 1991); both of which...
can be thought of as the PCM operating at a larger scale. In such cases, patches or activities are ranked by their energetic return rate and as with the standard PCM, whether or not a forager should enter a patch type or be involved in a foraging activity depends on the abundance of the highest ranking patch in the environment or the abundance of resources within the highest ranking patch. Because neither post-encounter profitability within a patch, nor the profitability of a resource patch or activity type overall can be observed archaeologically, Bayham (1979, 1982) argued that resource rank should scale with prey body size (see Griffiths, 1975) and that the addition of smaller prey is a function of declining encounters with larger prey. Most applications of abundance indices have followed this lead, and as such, the model predictions shift to be specifically about large prey versus small prey (although, see e.g., Stiner et al., 2000; Jones et al., 2008b).

Based on this traditional framework, high proportions of large prey relative to small prey have been used as evidence for high overall foraging return rates and a divergent gender division of labor focused on men’s acquisition of larger prey (e.g., Broughton and Bayham, 2003; Broughton et al., 2008; see also Isaac, 1978). Diachronic declines in the abundance of large prey then suggest declines in overall foraging efficiency (e.g., Nagaoka, 2002), widening diet breadth associated with broad-spectrum revolutions (e.g., Sturtevant et al., 2009) and a gender division of labor in which reductions in large game necessitate the acquisition of smaller game by either men, women or both. However, ethnographic and archaeological work has questioned the assumption that prey body size and prey rank are always positively correlated. Mass capture techniques may increase post-encounter return rates for some types of small prey, particularly fish and insects (Madsen and Kirkman, 1988; Madsen and Schmitt, 1998; Ugan, 2005a,b; Lupo and Schmitt, 2002, 2005). Moreover, under some circumstances, larger prey may be of lower rank than predicted due to the effects of relative prey mobility, which can increase with prey size, and may lead to higher instances of pursuit failure (Bird et al., 2009; see also Hawkes et al., 1991; Jochim, 1976; O’Connell et al., 1988; Smith, 1991:230–231; Stiner et al., 2000; Winterhalder, 1981:95–96). If this is the case, foragers may attain higher overall return rates by pursuing smaller prey that can be acquired more reliably. Because foragers (often men) continue to pursue larger prey despite the acquisition risk, it may be that the actual goals of foraging vary as a function of gender (Jochim, 1988), with men focused on maximizing currencies other than the rate of resource acquisition, such as social capital or prestige (Bliege Bird and Smith, 2005; Hildebrandt and McGuire, 2002). Instances of such behavior represent a clear violation of one of the primary assumptions of the PCM (e.g., Bliege Bird et al., 2001; Hawkes et al., 1991; Hill et al., 1987; see also Lee, 1968).

With this critique, an alternative interpretation of abundance indices has emerged in opposition to the traditional interpretation. This alternative view suggests that high proportions of large prey relative to small prey represent lower overall foraging efficiency (e.g., Hildebrandt and McGuire, 2002; McGuire et al., 2007) and a gender division in foraging labor in which men’s pursuit of large prey is subsidized by women’s labor focused on more reliable resources (Hildebrandt and McGuire, 2002; McGuire and Hildebrandt, 2005). Accordingly, diachronic declines in the abundance of larger prey relative to smaller prey then reflect increases in foraging efficiency and an increase in the overlap between men’s and women’s resource choice, both being focused on small prey (McGuire and Hildebrandt, 1994, 2005; but see also Jarvenpa and Brumbach, 2009; Kuhn and Stiner, 2006; Waguespack, 2005; Zeana, 2004).

That opposite interpretations exist for a single quantitative measure is a problem for zooarchaeological analyses; if both interpretations are taken seriously, competing hypotheses about prehistoric foraging are rendered essentially untestable. However, despite being a static material outcome of complex and dynamic foraging decisions, abundance indices should still provide a relatively straightforward measure of variability in the outcomes of human foraging. That is, where we can control for the effects of differential transport and post-depositional processes, abundance indices should reflect some aspect of the trade-off between hunting larger and smaller prey. As such, actualistic research can provide direct evaluation of the parameters of such trade-offs and the zooarchaeological patterns they produce.

Here we undertake an empirical exercise to examine the meaning of abundance indices. We ask (1) how does foraging behavior predict variation in abundance indices? And (2) how do differences in men’s and women’s foraging decisions explain variation in abundance indices? To answer these questions, we draw on quantitative foraging data collected with Martu, a group of Aboriginal Australians living in arid Western Australia. Specifically, we examine the trade-off between hunting hill kangaroo (Macropus robustus) and sand monitor lizards (Varanus gouldii), two major resources that embody the trade-offs between hunting larger and smaller prey. First, we test predictions derived from the traditional interpretation of abundance indices to examine how the overall rates of energetic return, total foraging time, hunting success and total harvest size for hill kangaroo and sand monitors predict abundance index values. Second, we test predictions derived from the traditional interpretation of abundance indices to examine how gender-differences in foraging strategies are reflected by variability in abundance index values. Following O’Connell (1995), this approach allows predictions derived from general theory of behavior to be tested simultaneously with observations and their archaeological correlates, thus avoiding the problems associated with simple analogy. As such, even though Martu hunting does not represent all variability in prehistoric or even contemporary hunting, the basic links between human foraging decisions, prey size, mobility, foraging returns and their relative impacts on abundance indices should provide a baseline that can help guide future analyses and resolve some of the confusion surrounding their interpretation.

2. Contemporary Martu foraging

Martu, sometimes written as Mardu or Marduarra, is used as a common term of self-reference for a set of Aboriginal Australian dialect groups whose homelands are centered around the Karly-milly (Rudall) River and Pervical Lakes in Western Australia’s Gibson, Little Sandy and Great Sandy Deserts (Fig. 1). Some of these groups came into contact with European Australians in the mid-late 1960s and were subsequently settled onto missions and cattle stations (Davenport et al., 2005; Scezla and Bliege Bird, 2008; Tonkinson, 1991, 1974). After a 20-year hiatus, many Martu returned to their homelands and today have Native Title over their traditional estates. Life in the desert is primarily centered in one of traditional estates. Life in the desert is primarily centered in one of three remote communities or outstations: Parnngurr, Punnmu and Kunawarritji. This work is focused in Parnngurr community, which is home to Martu mainly from the Manjiljarra, Warmman and Kartujarra dialect groups.

Subsistence hunting remains of central importance to Martu in these communities. Hunting parties are sometimes planned in advance, but more frequently emerge ad hoc on a given day. Through open discussion, sometimes occurring partially en route, individuals decide on the motor vehicle they will take, which region they will travel to and the hunting activities they will engage in. On arrival, the party establishes a “dinner-time” camp. Foragers depart on foot from this camp and will later return to process, cook
and share their acquired resources. The time they are away from
this camp we define as a “foraging bout”.

Once at the dinner-time camp, Martu typically choose to engage
in one of a variety of hunting activities including sand monitor
(*parajalpa, Varanus gouldii*), hill kangaroo (*kirti—kirti, Macropus
robustus*), bustard (*kipara, Ardiotis australis*) and perentie monitor
(*yaliparra, Varanus gigiantus*) hunting. As the decision to engage in
one hunting activity is made prior to departure and because people
are essentially technologically and ecologically limited to that
activity after the decision is made, each activity can essentially be
modeled as a resource patch (see Smith, 1991). Bird et al. (2009)
and Bliege Bird and Bird (2008) discuss these hunting activities in
more detail; here, we focus on the trade-offs between two hunt
types: hill kangaroo and sand monitor.

Hill kangaroo hunting occurs in and around the low-lying rocky
ranges that are scattered throughout the desert (see Fig. 1c). Hunters
typically enter a range on foot carrying a 0.22 caliber bolt
action rifle and systematically walk upwind searching the range for
hill kangaroo or signs of their presence. In the suite of game
commonly pursued by Martu hunters, hill kangaroo are relatively
large prey with highly variable returns. Based on a dataset of 125
hill kangaroo foraging bouts recorded from 2000 to 2009 (see data
collection methods below), hill kangaroo hunters return on average
with 3755 ± 12230 total kcal (total harvest size; Table 1), however,
this mean is rarely realized. As reported in Bird et al. (2009), each
encounter has a 30% chance of being successful (pursuit success).
Summing overall encounters during a hunting bout, hunters return
to camp with prey on average only 15% of the time, with a median
chance of success of 0% (see Table 1), however, this mean is rarely realized. As reported in Bird et al. (2009), each
encounter has a 30% chance of being successful (pursuit success).

Sand monitor hunting occurs in the open spinifex (*Triodia sp.*)
sand plains of the desert (see Fig. 1c). While sand monitors are
relatively small (just under half a kilogram per individual), hunters
almost always acquire more than one individual, resulting in
a mean harvest size of 1888 ± 1663 kcal (Table 1). An encounter
with a sand monitor is successful 89% of the time (Bird et al., 2009),
with an equivalent probability of overall hunting bout success
(Table 1). In the wintertime, sand monitors are denned, and Martu
frequently use controlled fire to burn off climax vegetation, which
allows hunters to more easily spot dens resulting in lower search
costs and an increase in the overall return rate (Bird et al., 2005;
Bliege Bird et al., 2008). In the summer, when monitor lizards are
on the surface and encounters result in quick pursuit, overall
hunting returns are lower, but hunting bout success is still reliable
(see Bird et al., 2009). Because hill kangaroo and sand monitor
hunting occur in separate patches, they are mutually exclusive
activities in which search time is not shared.

The decision to hunt one or the other prey-type has serious
consequences for the expected outcome of the hunt. Differences in
the probability of success create greater variability and unpredict-
ability in the expected harvest size and overall return rate for
kangaroo compared to sand monitor hunting. Because of the
stochastic nature of hill kangaroo search and pursuit success, the
amount of time a forager spends hunting hill kangaroo does not
predict total harvest size ($F = 2.865, p = 0.0943$; Fig. 2a). However,
sand monitor hunting time does significantly predict overall
harvest size ($F = 131.3, p < 0.0001$; Fig. 2b). A forager choosing to

<table>
<thead>
<tr>
<th>Variable</th>
<th>Hunt type</th>
<th>N</th>
<th>Median</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total foraging time (min)</td>
<td>Hill kangaroo</td>
<td>125</td>
<td>184.00</td>
<td>182.12</td>
<td>84.76</td>
</tr>
<tr>
<td>Total harvest size (kcal)</td>
<td>Sand monitor</td>
<td>690</td>
<td>191.00</td>
<td>185.83</td>
<td>76.37</td>
</tr>
<tr>
<td>E/T (kcal/min)</td>
<td>Hill kangaroo</td>
<td>125</td>
<td>195.89</td>
<td>188.84</td>
<td>1663.80</td>
</tr>
<tr>
<td>Overall success</td>
<td>Sand monitor</td>
<td>690</td>
<td>8.92</td>
<td>10.59</td>
<td>8.70</td>
</tr>
</tbody>
</table>

* Data from 1516 foraging bouts recorded from 2000 to 2009 (see Section 2).
hunts can more or less control the amount of food they will acquire by adjusting the amount of time they spend foraging, but no such choice or control is possible with hill kangaroo hunting. However, there are potential benefits to hill kangaroo hunting that, despite being realized only rarely, may explain why hunters choose to pursue hill kangaroo at all (Bliege Bird and Bird, 2008; Bliege Bird et al., 2009). As shown in Fig. 3, sand monitor hunters have a 10% chance of returning with nothing, but also have an extremely low probability of achieving a return rate higher than 5000 kcal/h. Hill kangaroo hunters, on the other hand, have an 85% chance of returning empty handed, but may occasionally achieve return rates up to 25,000 kcal/h.

The trade-off between choosing to hunt hill kangaroo or sand monitor is largely one between risk and harvest size. As these differences are driven largely by post-encounter pursuit success probabilities, and given that these are significantly and negatively correlated with prey body size due to the effects of relative prey mobility (Bird et al., 2009), we suggest that these trade-offs may be characteristic of large versus small prey in many (but certainly not all) circumstances.

3. Methods

3.1. Foraging data

We collected quantitative foraging data with a combination of (1) focal follows, where a researcher accompanied a hunter on an entire bout to record all time allocated to search, pursuit, capture and field processing, and (2) continuous dinner-time camp scans, where a researcher stayed at the temporary camp and recorded the departure and return times for all foraging bouts (see Altmann, 1974); in both cases we recorded the number and whole weight of all resources each forager acquired. When two or more hunters cooperated on a hunt, we calculated per-capita returns by dividing total harvest size (whole weight) by the number of cooperators. Whole weights for each resource were converted into edible weights, which were then transformed into caloric values based on published sources (Brand Miller et al., 1993; O’Connell and Marshall, 1989; see Bird et al., 2009; Bliege Bird and Bird, 2008; Bliege Bird et al., 2009 for additional details).

Data used in this analysis includes 1516 adult foraging bouts recorded from 2000 to 2009. These data were aggregated for each camp-day (n = 230), making the unit of analysis the aggregate of all foraging bouts that occurred on a single day at a single dinner-time camp. As we are interested in the archaeological signatures of large and small game hunting, only camp-days in which at least one forager attempted to acquire hill kangaroo were included; days where no foragers acquired any prey (hill kangaroo or otherwise) were excluded as these would have no archaeological signature. A total of 36 days meet both criteria.

To investigate the relative effects of foraging for each hunt type (hill kangaroo and sand monitor), four foraging measures were

Fig. 2. Total harvest size (kcal) as a function of total foraging time (min) for each recorded bout of (a) hill kangaroo and (b) sand monitor hunting.

Fig. 3. A plot of an empirical cumulative density function describing the probability of achieving a given return rate on hill kangaroo and sand monitor hunts.
calculated for each camp day: (1) the overall return rate ($E/T$), measured as total kilocalories acquired per minute (search, pursuit, capture, field processing and transport to the dinner-time camp) for each hunting activity (hill kangaroo and sand monitor) (2) the total foraging time spent (in minutes) for each hunt type, (3) whether or not any foragers were successful (success rate) in either hunt type, and (4) the total harvest size (kilocalories) acquired in each hunting activity which measures the total energetic yield without costs.

Finally, in order to investigate the gender division of labor in terms of the relative effects of men’s and women’s foraging on AI, two relative measures were calculated: men’s contribution to subsistence relative to women’s (i.e., percent of total kilocalories acquired by men) and men’s foraging time relative to women’s (i.e., percent of total foraging time).

An abundance index (AI) was calculated as the total number of hill kangaroo acquired for that day over the sum number of hill kangaroo plus the total number of sand monitors. This can be thought of as a hypothetical measure of the archaeological abundance index for each camp without any transport, depositional or post-depositional biases. Given that this is what zooarchaeologists would choose to measure if it were possible (see Klein and Cruz-Uribe, 1984), we consider this an ideal measure for interpreting abundance indices relative to known foraging variables. As the index is calculated from the number of each prey acquired, it is analogous to an abundance index calculated using the minimum number of individuals (MNI; see e.g., Grayson, 1984; Klein and Cruz-Uribe, 1984).

### 3.2. Statistical methods

As an abundance index value is a ratio constrained to vary between 0 and 1, it cannot be used as a dependent variable in ordinary least squares regression (OLS; see e.g., Faraway, 2006; Kieschnick and McCullough, 2003). Accordingly we used a generalized linear model (GLM) of the binomial family with a logit (logistic) link function. Multivariate models were constructed examining the relative effects of the overall return rate, total foraging time, hunting bout success, and harvest size for each hunt type on the abundance index values per camp-day. The value of each model was judged based on two sets of criteria, the first follows a traditional hypothesis testing approach and the second follows an information-theoretic approach of model selection.

Following a traditional hypothesis testing approach, models are judged to significantly improve the prediction of the dependent variable if the alpha (or $p$) value is $<0.05$. A significant model is judged better than another based on comparing the model’s likelihood ratios ($R^2_L$; Menard, 2000, 2002). Similar to $R^2$ values in OLS, $R^2_L$ values can be interpreted as a reduction in unexplained deviance by the inclusion of the independent variables, thus models with higher values reduce more unexplained deviance than models with lower values. $R^2_L$ values can be calculated easily from the GLM output of most statistical programs (see Menard, 2000, 2002; see also Codding et al., 2010).

Following an information-theoretic approach of model selection, we utilized Akaike’s An Information Criterion (AIC; Akaike, 1974; Burnham and Anderson, 2002) to estimate the relative value of each model. AIC was developed as an estimate of the Kullback–Leibler distance between a particular model and an unknown reality that actually structures the data (Burnham and Anderson, 2002; Venables and Ripley, 2002). As the value represents the estimated distance between the specific model and some “true” model, one model is relatively better than another if that distance is minimized, that is, lower AIC values represent relatively better models.

Statistical analyses were run and accompanying figures produced in R (R Development Core Team, 2010). Wireframe or surface plots were created with the use of R’s Lattice library (Sarkar, 2008).

### 4. Results

Over the 36 camp-days, the return rate for hill kangaroo hunting was highly skewed (median = 0, mean = 35.3 ± 62.2 kcal/min), with a lower median, but higher mean than sand monitor hunting (median = 9.8, mean = 9.6 ± 7.1 kcal/min, see Table 2). More time was spent sand monitor hunting (18,769 min) than hill kangaroo hunting (14,494 min) on these camp-days, resulting in 17 hill kangaroo totaling 437,783 kcal and 217 sand monitors totaling 195,716 kcal. The daily abundance index (AI) values that result from 0 to 1 (median = 0, mean = 0.23 ± 0.40).

#### 4.1. How does foraging behavior predict variation in abundance indices?

Under the traditional interpretation, high abundance index values should be correlated with higher overall return rates from acquiring a greater proportion larger prey and lower index values should represent a lower overall return rate contributed more from acquiring a greater proportion smaller prey (Bayham, 1979). Examining the effect of return rate for hill kangaroo and sand monitor on AI confirms this prediction ($R^2_L = 0.81$, $p < 0.0001$; Fig. 4a); however, the return rate for sand monitor hunting has a greater effect (estimate = −0.49) than the rate for hill kangaroo hunting (estimate = −0.02; see Table 3). This suggests that even if return rates for hill kangaroo are high on a given day, foragers pursuing sand monitors could achieve a lower rate relative to hill kangaroo hunters and the material remains of small prey would swamp out larger prey (see Fig. 4a). Although, this leaves uncertain which component of return rate is driving this trend. Because the

### Table 2

**Summary of the database comprising 36 camp-days.*

<table>
<thead>
<tr>
<th></th>
<th>Sum</th>
<th>Median</th>
<th>Mean</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hill kangaroo mean</td>
<td></td>
<td></td>
<td>35.3</td>
<td>62.20</td>
</tr>
<tr>
<td>Sand monitor mean</td>
<td></td>
<td>9.76</td>
<td>9.58</td>
<td>7.07</td>
</tr>
<tr>
<td>Hill kangaroo total</td>
<td></td>
<td>14,494</td>
<td>402.61</td>
<td>399.72</td>
</tr>
<tr>
<td>Sand monitor total</td>
<td></td>
<td>18,769</td>
<td>521.36</td>
<td>461.77</td>
</tr>
<tr>
<td>Hill kangaroo hunting</td>
<td></td>
<td>13</td>
<td>0.36</td>
<td>0.49</td>
</tr>
<tr>
<td>Sand monitor hunting</td>
<td></td>
<td>29</td>
<td>0.86</td>
<td>0.40</td>
</tr>
<tr>
<td>Hill kangaroo total</td>
<td></td>
<td>437,783</td>
<td>12,160.63</td>
<td>20,923.93</td>
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<tr>
<td>Sand monitor total</td>
<td></td>
<td>195,716</td>
<td>5436.56</td>
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<tr>
<td>% Men’s caloric</td>
<td></td>
<td>0.23</td>
<td>0.39</td>
<td>0.40</td>
</tr>
<tr>
<td>% Men’s foraging</td>
<td></td>
<td>0.49</td>
<td>0.54</td>
<td>0.27</td>
</tr>
<tr>
<td>Hill kangaroo acquired</td>
<td></td>
<td>0.47</td>
<td>0.74</td>
<td>0.74</td>
</tr>
<tr>
<td>Sand monitor acquired</td>
<td></td>
<td>6.03</td>
<td>6.12</td>
<td>6.12</td>
</tr>
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</table>

* The summary data presented here characterizes foraging results for these 36 camp-days, not foraging results for these hunt types overall. For such characterizations, see Table 1, Fig. 2, Fig. 3, Bird et al. (2009), Bliege Bird and Bird (2008) and Bliege Bird et al. (2009).
The rate of caloric return is determined by total foraging time, hunting success (a return rate will be 0 if the bout is unsuccessful) and caloric yield, variability in any of these measures could be driving the effect of overall return rate on AI.

According to the traditional interpretation, the proportion of large prey to small prey should be a function of the proportional foraging time for each resource or in each patch. The model containing the total foraging time for each hunt type significantly predicts the abundance index value ($R^2 = 0.48$, $p = 0.0125$; Table 3). However, sand monitor total foraging time has a greater effect. The model suggests that if foragers spent a large amount of time hunting sand monitors, they would drive the index down regardless of how much time hill kangaroo hunters spent foraging. This is illustrated well in Fig. 4b. No matter how much time hill kangaroo hunters spend foraging, as long as foragers spend time hunting sand monitor, the index will decline rapidly. This is essentially driven by the trend shown in Fig. 2a, which illustrates that there is no significant effect of foraging time on the amount of hill kangaroo kilocalories acquired. This overall model (#2) has a lower $R^2$ and a higher AIC (21.39) value than the previous model (#1, see Table 3), suggesting that total foraging time does not predict variability in the abundance index as well as return rate; but this is a product of the inclusion of hill kangaroo foraging time, which does not predict variability in harvest size (Fig. 2b). These results imply that while the total foraging time for small prey may have a strong effect on AI, the effect of large prey hunting on AI might be affected more by hunting bout success or total harvest size (kcal) than foraging time.

The traditional interpretation of abundance indices does not explicitly consider risk to be a salient variable in understanding archaeofaunal assemblages; however, implicit in this framework is the assumption that high AI values represent successful hunts with larger prey that result in higher overall return rates. If this traditional interpretation is correct, then hunting success with larger prey should positively covary with AI. The alternative interpretation suggests the opposite: that high failure rates with larger prey can lead foragers competing over prestige to focus more on their

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**Table 3**

<table>
<thead>
<tr>
<th>#</th>
<th>Est. DF</th>
<th>AIC</th>
<th>$D_0^a$</th>
<th>$G_0^a$</th>
<th>$R^2$</th>
<th>$p^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Return rate&lt;sup&gt;c&lt;/sup&gt; (whole model)</td>
<td>2</td>
<td>12.74</td>
<td>6.42</td>
<td>27.34</td>
<td>0.81</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td>Hill kangaroo</td>
<td>0.32</td>
<td>-</td>
<td>-</td>
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<tr>
<td></td>
<td>Sand monitor</td>
<td>-0.49</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>2</td>
<td>Total foraging time (whole model)</td>
<td>2</td>
<td>21.39</td>
<td>17.31</td>
<td>16.45</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>Intercept</td>
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<tr>
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<tr>
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<td>-</td>
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<td>-</td>
</tr>
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<td>3</td>
<td>Hunting bout success (whole model)</td>
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<td>1.16</td>
<td>32.60</td>
<td>0.97</td>
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<tr>
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<tr>
<td>4</td>
<td>Total harvest size (whole model)</td>
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<td>11.07</td>
<td>8.05</td>
<td>25.55</td>
<td>0.76</td>
</tr>
<tr>
<td></td>
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<td>-</td>
<td>-</td>
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<tr>
<td></td>
<td>Sand monitor</td>
<td>0.00</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

<sup>a</sup> For definitions, see Menard (2002). The null deviance ($D_0$) for each model is 33.76.

<sup>b</sup> Significant values ($p < 0.05$) are marked with an asterisk.

<sup>c</sup> E/T (kcal/min) = energy acquired over total time spent in search and handling.

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Fig. 4. Surface plots showing the effects of the (a) overall return rate (E/T), (b) total foraging time (TFT), (c) hunting bout success and (d) harvest size (kcal) for hill kangaroo and sand monitor hunting on abundance index values.
acquisition — a process that will lead to higher AI values (e.g., McGuire and Hildebrandt, 2005). If this is true, AI values should negatively covary with hunting success. Our results show that hunting bout success does have a significant and positive effect on AI ($R^2 = 0.97, p < 0.0001$; Table 3), supporting the implicit assumptions of the traditional interpretation. As shown in Fig. 4c, when hill kangaroo hunting bout success is one and sand monitor success is zero, the predicted abundance index value is one; the predicted index is zero in the opposite scenario. When both hill kangaroo and sand monitor hunters are successful, the predicted index value falls between one and zero. While this is intuitive, the tight fit of bout success and AI (a $R^2$ value of 0.97) and the low AIC value (11.6) suggests that AI tracks hunting bout success more than return rate. However, while success rates seem to be accurate in predicting the index value, the resolution is not precise, creating essentially a step-function from 0 to 1. Since total harvest size is a continuous, unbound measure, it may more precisely predict changes in the index value.

If the traditional interpretation of abundance indices is correct, then AI values should increase with hill kangaroo harvest size (total kilocalories acquired) and decrease with sand monitor harvest size. These predictions are upheld: total harvest size has a strong effect on AI ($R^2 = 0.76, p < 0.0001$) and provides the model with the lowest AIC value (11.07; Table 3). As shown in Fig. 4d, AI values are only high when the total hill kangaroo harvest size is high; however, even with a large harvest, the quantity of hill kangaroo remains can still be swamped by a large sand monitor harvest size. As shown above (Section 2), sand monitor harvest size is proportional to the amount of time spent foraging (Fig. 2b), but hill kangaroo hunting is not (Fig. 2a), this implies that the quantity of sand monitor remains deposited at a site is a function of the total amount of foraging time while the quantity of hill kangaroo remains deposited reflects merely hunting bout success. Because sand monitors are smaller than hill kangaroo, even a smaller total harvest will contribute more individuals and disproportionately reduce AI. Moreover, this is accentuated by the fact that successful hill kangaroo hunts only rarely end up with more than a single carcass (23%; Table 2).

Examining Table 3, the effect of hunting bout success on AI provides the best model according to $R^2$ values while the effect of harvest size on AI provides the best model according to AIC values. Taken together, these results imply that the benefits of acquiring large prey are accurately measured by harvest size, but the costs are better measured categorically as hunting success (i.e., success or failure) than continuously as foraging time. Between these two variables, hunting bout success may have the single strongest effect on AI as whether or not any large prey kilocalories will be acquired varies significantly as a function of hunting success (see also Bliege Bird et al., 2009). While the model examining the effect of total foraging time on AI has a low $R^2$ value and high AIC value, this is probably a function of the inclusion of large prey foraging time; an examination of Fig. 4 shows that the effect of total foraging time for small prey has a strong effect on AI. Because harvest size increases linearly with the total foraging time for small prey, and because an increase in harvest size is directly proportional to an increase in the number of individual small prey acquired, the total time spent foraging for time small prey has a dramatic effect on AI. This shows that the effect of small prey hunting on AI is mostly a function of the total foraging time allocated to that activity or patch on a given day because success is nearly guaranteed (so any time at equals success), and because the associated rewards in kilocalories (harvest size) is proportional to the amount of time spent foraging. Thus, the effect of large prey hunting on AI is mostly a function of hunting bout success while the effect of small prey is mostly a function of foraging time.

4.2. How do differences in men’s and women’s foraging decisions explain variation in abundance indices?

The traditional interpretation suggests that high abundance index values represent a gender division of labor focused on men’s acquisition of larger prey. If this is the case, then abundance index values should positively covary with men’s proportional foraging time and men’s caloric contribution relative to women. However, if the alternative interpretation is correct and high index values represent men’s large game hunting that is subsidized by women’s work, then abundance index values should negatively covary with men’s proportional foraging time and their relative caloric contribution (Hildebrandt and McGuire, 2002; McGuire and Hildebrandt, 2005).

The amount of time men spend hunting relative to women on each camp-day has a significantly positive effect on AI ($AIC = 30.36, R^2 = 0.32, p < 0.0066$; see Table 4, Fig. 5a). However, this is primarily a function of women’s foraging time ($AIC = 31.23, R^2 = 0.27, p < 0.0156$), which independently has a much stronger effect on AI than men’s foraging time ($AIC = 41.94; R^2 < 0.0001, p < 0.8168$; see Table 3). This suggests that variability in AI is more a function of women’s time spent hunting for small resources than men’s time spent hunting larger resources. As women differentially target sand monitors over hill kangaroo, when their foraging time increases, AI decreases significantly.

When men contribute larger harvests relative to women, AI is significantly higher ($AIC = 26.04, R^2 = 0.41, p = 0.0033$; Table 4, Fig. 5b). Unlike foraging time, however, when men’s and women’s relative contributions are examined independently of one another, this relationship is more a function of men’s harvest size ($AIC = 38.33, R^2 = 0.27, p < 0.0171$) than women’s ($AIC = 38.33, R^2 = 0.08, p < 0.1380$). As men frequently target larger prey in preference to smaller prey, AI will tend to increase when men’s hunting efforts are successful in acquiring larger prey, leading to a higher caloric contribution.

Comparing the model’s explanatory value based on AIC and $R^2$ values shows that men’s absolute caloric contribution (Model 9; Table 4) is the best gender-specific predictor of AI followed by women’s foraging time (Model 7; Table 4). These results primarily support the traditional interpretation, suggesting that high AI values are best predicted by large harvests contributed by men and little time spent pursuing small prey by women. However, because men’s hill kangaroo hunting success is stochastic, so too is their contribution — this suggests that high AI values cannot be maintained consistently. Our previous work shows that men’s caloric contribution relative to women’s is best predicted by hunting bout success with large prey (Bliege Bird et al., 2009). When combined, these results suggest that consistently high abundance index values, representing men’s reliable acquisition of larger prey, exist only when larger prey is predictably acquired. While this is not typically observed ethnographically (e.g., Hawkes, 1991), it still
possible if the encounter rates with large prey are high enough to mitigate pursuit failures. This is discussed below (Section 5).

5. Summary and discussion

This examination of Martu foraging and its potential material consequences suggest some straightforward interpretations of variability in abundance index values. First, high abundance indices should be a function of both (1a) high frequencies of bout success with larger prey and (1b) little or no time spent pursuing smaller prey; when combined, this should lead to a high caloric contribution by large prey and a high overall return rate. Second, low index values then suggest that foragers either (2a) did not attempt to pursue larger prey at all, (2b) had very low bout success with larger prey, or (2c) spent a disproportional amount of time hunting smaller prey which swamped the contribution of larger prey; any of these would lead to a high caloric contribution of smaller prey, and lower overall return rates than if larger prey were reliably acquired. We discuss and explore these scenarios in greater context and detail below.

5.1. Traditional and alternative interpretations: efficiency and risk

Based on these results, the traditional interpretation of abundance indices appears to be mostly correct. First, high index values do appear to be associated with relatively higher overall return rates, however, this is only because high AI values represent large prey being acquired reliably. When hunting success with larger prey is so high that returning from a bout successfully is nearly guaranteed, large prey will contribute a high proportion of the total harvest and overall return rates will be high. However, if hunting bout success with larger prey is rare, then continuing to hunt larger prey will result in frequent failures and thus frequent return rates of zero. Because large game hunting tends to follow this all-or-nothing structure, the costs and benefits of acquiring large prey are more accurately described by the categorical measure of hunting bout success (i.e., success or failure) than the rate of energy acquired over time. As such, it appears that the link between abundance indices and foraging models has a component of risk that, while modeled elsewhere (e.g., Winterhalder et al., 1999), has yet to be formalized in the traditional interpretation of abundance indices. Here the alternative interpretations of abundance indices are correct to focus on the risk of failure with larger prey, especially because sensitivities (or insensitivities) to such risk may be driving some important foraging decisions, particularly those that vary by gender (Hildebrandt and McGuire, 2002; McGuire and Hildebrandt, 2005).

Contra the traditional interpretation, we have already shown that for Martu, a prey’s post-encounter return rate does not correlate with prey body size (Bird et al., 2009), however, our data also show that when hunting success is certain, larger prey may contribute significantly to overall returns (Bliege Bird et al., 2009; Section 4.1 above). Here we suggest that this is a function of stacking pursuit success probabilities resulting from sequential encounters on a single foraging bout (see also Bliege Bird et al., 2009; Coddington et al., 2010). While pursuing large, highly mobile prey has a higher probability in ending in failure than pursuing smaller, less mobile prey, this probability of failure is a product of low post-encounter pursuit success (Bird et al., 2009; see also Hawkes et al., 1991; Jochim, 1976; Lee, 1968, 1979). Thus, the probability of overall bout success should increase with encounter rates; which may vary depending on season or climate (Bird et al., 2009; Hawkes et al., 1991; O’Connell et al., 1988), changes in hunting methods (e.g., O’Connell et al., 1988), or changes in acquisition technology (e.g., Hill and Hawkes, 1983; O’Connell and Hawkes, 1984; Winterhalder, 1981). In essence, the risk of a failed bout may be overcome if encounter rates with large prey are high enough that the overall probability of bout success nears 100% as a consequence of sequential pursuits. If this is correct, high AI values represent large prey encounter rates high enough to mitigate against the probability of bout failure. What then, does this imply for archaeological evidence of diachronic declines in the proportion of larger prey?

5.2. Declining abundance indices, broad-spectrum revolutions and patch choice

A common archaeological pattern uncovered around the world is a diachronic decline in the proportion of large prey relative to small prey (e.g., Broughton, 1994; Cannon, 2003; Janetski, 1997; Nagaoka, 2002; Stiner, 2001). These trends are interpreted to indicate a broadening of the range of prey or the types of patches exploited as a result of anthropogenic declines in the encounter rates with larger, high-ranked resources or the patches in which they occur.

If large and small prey occur simultaneously in a given hunt type or patch, high AI values may be a function of high encounter rates

Fig. 5. Abundance index values as a function of men’s (a) foraging time and (b) harvest size relative to women’s for each camp-day.
with larger prey, leading to their successful acquisition on a reliable basis (see Section 5.1). When encounter rates with large prey decline to a point where acquisition is no longer guaranteed, foragers would have no choice but to switch to alternative, smaller resources within the same patch, or they would continually return home with nothing. Thus, a decline in AI values may have less to do with foragers evaluating encounter rates with the highest ranking prey and more about repeated failures to acquire larger, highly ranked prey. Under such conditions, diachronic declines in AI may indeed represent prehistoric resource intensification, specifically where foraging shifts from the reliable acquisition of larger prey to the necessary acquisition of smaller prey resulting in lower overall return rates.

In heterogeneous environments where large and small resources are not encountered in the same patch, these trends may be even more pronounced. Declining abundance of patches containing high-ranked prey or declining abundance of high-ranked prey within those patches may lead foragers to cease that activity or cease exploiting that patch completely (Bettinger, 1991:90). If AI values were calculated with large and small prey occurring in two different patches, the archaeological signature of such patch depletion would result in abrupt declines in abundance index values to zero or near zero. Moreover, continued foraging time in the patches containing larger prey will have no discernable effect on AI values as long as some time is spent in the patch containing small prey. This results because any time spent foraging for small prey will result in a contribution of smaller prey remains proportional to the time spent in that patch (e.g., Fig. 2), and consequently a low index value (Fig. 4b).

Responses to such depletions, whether within or between patches, may depend on a forager's degree of risk-sensitivity. While many foragers may want to minimize the risk of acquisition failure, some may want to take the risk of failure for the potential pay-off of a larger overall harvest size -- for Martu, such decisions often vary independent of their effects on mean foraging efficiency (e.g., Bird et al., 2009; Bliege Bird and Bird, 2008). Since foraging decisions, particularly those involving risk, seem to vary for men and women, there may a strong gender component to such a process.

### 5.3. Gender and risk

Our results show that high abundance index values represent low total foraging times by women and high caloric contributions by men's successful acquisition of large prey; low index values indicate the opposite. These findings closely match the traditional interpretation of how gender-differences in foraging are represented by abundance indices. However, we should not expect such patterns to be static. In this regard the alternative interpretation is right in turning attention to the interactive effects of men's and women's foraging strategies and how these articulate with variability in the reliability of large game acquisition.

Recent quantitative ethnographic work suggests that men's foraging behavior is often risk neutral or risk prone while women's is often risk averse (Bliege Bird, 2007; Bliege Bird and Bird, 2008; Bliege Bird et al., 2001, 2009; Hawkes, 1991, 1993; Hill et al., 1987; Sosis, 2000; Smith and Bliege Bird, 2000). From this work, we hypothesize that men are often attempting to maximize harvest size regardless of the risk, while women are often trying to minimize the risk of failure with less attention to harvest size. The way that these goals align or conflict with one another depending on the reliability of large game hunting has serious implications for interpreting abundance indices.

If abundance index values are high, the analysis here suggests that larger prey are being reliably acquired, and thus, both men's and women's goals being met with the same resources even if women are not involved in their acquisition. If men's large game acquisition were stochastic, then we would predict that women would offset this risk by simultaneously foraging for lower risk, alternative resources to provision self and offspring; representing a more divergent division of labor (as with Martu). However, if the reliable acquisition of large prey were habitual with success being nearly guaranteed, we might predict that women would either focus their efforts on hunting larger prey (Kuhn and Stiner, 2006) or the post-acquisition processing of larger prey (Jarvenpaa and Brumbach, 2009); representing a more convergent division of labor. Archaeologically, it should be possible to differentiate these two scenarios. A more convergent division of labor should be identifiable by a ubiquity of larger prey remains with the near exclusion of all else, while a more divergent division of labor should be identifiable by the presence of alternative resources in archaeofaunal or archaeobotanical assemblages and perhaps moderate abundance index values.

A transition from a more convergent, to a more divergent division of labor may occur as a function of declining success rates with large prey. If success rates with larger prey declined and men continued to pursue them, women's foraging goals of risk minimization could only be met by targeting smaller, more reliable prey (Hildebrandt and McGuire, 2002; Zeanah, 2004). This would lead to a diachronic decline in abundance index values as a function of decreased reliability of men's hunting success and an increase in the amount of time women spent hunting smaller prey. In this scenario, a switch from big game to small game, and the corresponding decline in AI, is driven by increased variance in acquisition, not decreased overall foraging efficiency per se. In such cases, evidence for resource intensification may be driven by differences in men's and women's foraging goals. Such a scenario may be identified archaeologically by technology or mobility patterns which suggest a focus on larger prey, but faunal assemblages that are dominated by smaller prey, suggesting the continued attempts to acquire large prey despite high failure rates.

### 6. Conclusion

Abundance indices are valuable zooarchaeological measures that allow researchers to understand variability in prehistoric human behavior. Given recent disagreements regarding their interpretations, the aim of this work is to highlight their value by providing a clearer and more accurate interpretation of the links between such a material measure of human foraging and the actual behavior behind it. We suggest that while abundance indices are static markers of dynamic interactions, they represent a limited set of behaviors: high index values represent the reliable acquisition of larger prey and little or no time spent on smaller prey; low index values represent limited or no hunting success with larger prey and a greater amount of time spent hunting smaller prey. Further, if men's and women's resource choice is determined by the trade-off between acquisition risk and harvest size, then abundance index values may also be a clear marker of gender-differences in foraging strategies.

While the trends shown here may be partially contingent on the particulars of Martu hunting, there are strong reasons to think that these findings will hold elsewhere. Specifically, we suggest that due to the common links between prey size, mobility, utility and risk, and how these factors interact with human foraging decisions, the relative patterns we report here accurately describe variation in abundance index values.

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references


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