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Mosaics of fire and water: the co-emergence of anthropogenic landscapes and intensive seed exploitation in the Australian arid zone

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ABSTRACT

In arid Australia, the antiquity, role and ecological contexts of ‘firestick’ farming in seed-based foraging economies remain unclear. We use Landsat imagery to analyse effects of contemporary Martu hunting fires on seed-bearing grasses and forbs. Today, Martu rarely harvest wild seeds but inadvertently foster patches of grass when they burn to hunt burrowing monitor lizards. Therefore, anthropogenic seed patches need only be by-products of fires set to achieve other goals rather than the intended crop of firestick farming. Nonetheless, sustained burning over the long-term creates and maintains closely juxtaposed mosaics of seed and small game patches. We use the marginal value theorem (MVT) to model how pre-contact foragers may have used seed patches within such mosaics in response to climate change and population growth. We show that seeds would have been reliably available to foragers in anthropogenic patches whenever small game hunting returns were low and travel distances to new hunting patches long. Such circumstances probably occurred during the middle to late Holocene when population growth filled better-watered habitats of arid Australia, and climatic variability associated with the El Niño/Southern Oscillation (ENSO) reduced the number of water sources that could support foraging. Prolonged occupation around the water sources that remained triggered the emergence of fine-grained, anthropogenic fire mosaics. If so, the late Holocene proliferation of formalised seed milling equipment closely followed the emergence of firestick farming and signalled the consequent development of seed-based foraging economies, further fuelling population growth and social complexity when more mesic climatic conditions returned. Earlier milling technology during the Pleistocene and early Holocene probably accommodated seed distributions created in fire regimes other than the mosaic burning conducted by Martu today.

Introduction

Two unusual aspects of subsistence ecology in arid Australia relative to historically known hunter-gatherers elsewhere were the practice of landscape burning for various subsistence and social purposes (Gammage 2013; Gould 1971; Jones 1969; Kimber 1984; Walsh 1990) and the reliance on small-grained, grass seeds as staple foods (Allen 1974; Gould 1969; Meggitt 1957; O’Connell et al. 1983; Tindale 1977; Veth and Walsh 1988). Jones (1969) argued that the two were intrinsically linked, in that anthropogenic burning should properly be considered ‘firestick farming’ because it enhanced the long-term productivity of such economically useful plants. But if Australian foragers farmed with fire, they never domesticated their cereal crops, as did broad-spectrum foragers elsewhere in the world (Lewis 1972). The reason, as Gould (1971) pointed out, may be that the beneficial effects of burning on plants were inadvertent consequences of fires set to achieve shorter-term hunting and social goals in a foraging, not farming, economy.

These long-standing, but contending perspectives of the intent and consequences of firestick farming foreshadow recent considerations of collective action and future discounting dilemmas in foraging economies (Bowles and Choi 2013; Gallagher et al. 2015; Mattison et al. 2016). Without centralised institutions to manage private property, in the interim between setting the fire and harvesting the seeds, a forager who burns to foster future seed crops risks losing the crop to those that do not pay the costs of burning. This may stimulate development of territoriality and ownership in a foraging society if the costs of burning are relatively high. But if seed crops are by-products of fires set to achieve immediate goals there are fewer payoffs for social sanctions that exclude free riders. Obviously, links between burning and seed use in Australia offer profound insight into both the emergence of agriculture and of social complexity worldwide (Bird et al. 2016a).
Most archaeologists treat the origins of anthropogenic burning and seed-based foraging economies as temporally separate, and causally independent phenomena (Denham et al. 2009). In Pleistocene contexts, they have sought evidence for the impact of intentionally set fires on Australian ecosystems in pollen and charcoal profiles as a signature of human occupation of Sahul (Kershaw et al. 2006; Mooney et al. 2011), and a potential cause of megafaunal extinctions (Bird et al. 2013; Flannery 1990; Miller et al. 2005, 2016), under the assumption that humans began burning soon after their arrival on the continent. In contrast, although archaeologists broadly agree that incidental use of small-grained grass seeds may have begun in the Pleistocene (Balme 1991; Edwards and O’Connell 1995; Fullagar and Field 1997; Fullagar et al. 2015; Gorecki et al. 1997; Hayes 2015; Veth 2005), many see little evidence for intensive use of seeds, as practised by historic arid zone populations, until the late Holocene when formalised wet milling technology became common (David 2002; Smith 1986, 1988, 1989, 2010, 2013). These arguments situate seed-based economies as a critical component of both population growth and expansion into the most arid habitats (Smith and Ross 2008), and of social complexity, achieved by using seeds to provision large gatherings (David 2002; Lourandos 1997; McDonald and Veth 2012; Veth 2006). None of these accounts consider any contribution of anthropogenic burning to late Holocene population growth or social complexity (cf. Smith 2013).

That fire and intensive seed exploitation might be linked are suggested by ecological studies showing that fire promotes the productivity of some Australian grasslands. Areas burned one to four years previously grow more diverse seed grasses, produce larger and more predictable seed crops and retain richer seed banks than unburned areas (Letnic et al. 2004; Pastro et al. 2006; Walsh 1990; Zeanah et al. 2015). Arid zone grasses that increase in density after a burn include bunch panic grass (Yakirra australiense), button grass (Dactyloctenium radulans), armgrass millet (Brachiaria subquadripara), fringe rush (Fimbristylis oxystachya), pigweed (Portulaca oleracea) and woolybunt (Eragrostis eriopoda) (Bolton and Latz 1978; Letnic et al. 2005; Southgate and Carthew 2006, 2007), all traditional seed resources of Aboriginal foragers (O’Connell et al. 1983; Veth and Walsh 1988) as well as important forage for small marsupials (Clayton et al. 2015; Gibson 2001; Pearson 1989; Southgate and Carthew 2006). Although burning has beneficial effects on seed productivity regardless of its origin, some ecologists argue that the cessation of Aboriginal burning in the twentieth century directly led to local extinctions of small marsupials that depended on human-set fires to rescale the landscape into a tight mosaic of vegetative regrowth and promote the growth of the seed grasses small fauna consumed (Bolton and Latz 1978; Letnic and Dickman 2005; Letnic et al. 2004, 2005; Lundie-Jenkins 1993; Murphy and Bowman 2007; Southgate and Carthew 2006, 2007), as well as protect them from catastrophic wildfires (Bliege Bird et al. 2012, 2013).

Contemporary Martu foragers in Western Australia offer a unique opportunity to investigate the ecological relationships between anthropogenic burning and traditional seed use. Martu are among the last remaining hunter gatherers who still forage for a significant portion of their diet, and use fire regularly to manipulate their environment. Although Martu rarely harvest seeds today, small-grained wild cereals were staple foods merely a few decades ago (Veth and Walsh 1988; Walsh 1990; Zeanah et al. 2015). Martu elders are expert in the application and ecological consequences of fire, and were trained as children in techniques for harvesting and processing seeds. Understanding why contemporary Martu foragers usually bypass seeds, and the subsequent effects that their burning practices nonetheless have on seed ecology offers key insight into the role that anthropogenic burning played in the development of pre-contact seed-based foraging economies.

In this paper, we investigate linkages between fire and seed exploitation by analysing the effects of contemporary Martu burning practices on seed ecology and foraging patch distributions, and analysing seed handling costs relative to the scale of habitat patchiness. We concentrate on the fire ecology and foraging economy of grasses and forbs that bear small-grained edible seeds in the cool season, ignoring summer-ripening acacia pods. Although both resources are affected by fire and were important components of traditional Aboriginal subsistence, the links between fire ecology and grass seeds are more easily tracked with remote sensing data and foraging observations. We also downplay, for the moment, archaeological evidence for the milling of spinifex (Triodia spp.) seeds as food (Fullagar and Wallis 2012; Hayes et al. in press), since spinifex makes-up the climax communities that Martu target for burning (Bliege Bird et al. 2013, 2016a). Nonetheless, our findings bear implications for the temporal and ecological contexts in which consumption of spinifex seeds should occur. We predict that sustained hunting fires inadvertently create juxtaposed mosaics of lizard hunting and seed gathering patches. Such fine-scale anthropogenic landscapes would have proven crucial for pre-contact hunters, because they would have allowed seeds to serve as reliable low return resources whenever hunting returns were poor. This relationship has implications
for the roles that population growth and climate change played in driving seed use intensification, firestick farming, and social complexity in arid Australia.

Martu background

People who today call themselves Martu lived relatively recently as full-time hunter-gatherers in the Great Sandy and Little Sandy Deserts with little extensive contact with Euro-Australian society. Throughout the first half of the twentieth century, many Martu gradually migrated westward to settle around cattle stations and missions in the Pilbara, but many traditionally oriented families remained in the heart of the desert until Australian authorities compelled most to move to the Apostolic Church mission at Jigalong in the mid-1960s (Davenport et al. 2005; Tonkinson 1974, 1991). Final holdouts joined their relatives at Jigalong over the next few years, temporarily abandoning their vast home estates.

The exodus of Aboriginal foragers interrupted traditional burning practices (Burrows et al. 2006) and the widespread sand plains on Martu estates reverted to relatively homogenous spinifex (Triodia schinzii and T. basedowii) grasslands disturbed only sporadically by catastrophic lightning fires. Martu report that this had detrimental effects on the abundance and distribution of early-mid successional, seed bearing grasses. The absence of intentionally set and managed fires probably restricted seed grasses to the dead core of mature spinifex clumps (Southgate and Carthew 2007), along stream channels and clay pans (Walsh 1990), and the expansive burn scars of lightning fires (Bliege Bird et al. 2012).

Martu living at Jigalong Mission found it difficult to forage for many of the bush foods they valued, and grew dependent on Western clothing, tools, and food, especially flour. It was during this exodus that their contemporary cultural identity coalesced from pre-contact traditions (Tonkinson 1974) as speakers of several closely related dialect groups came to call themselves ‘Martu’ (aka Mardu, Mardujarra). Members of these groups assumed authority of the modern Jigalong community in 1974, and began to reassert ownership over their customary estates in the 1980s by re-establishing permanent occupation of the desert in the communities of Punmu, Parnngurr, and Kunawarritji. They gained native title of 136,000 sq. km of their original homelands surrounding Karlamilyi (Rudall River) National Park in 2002.

Foraging resumed a preeminent role in the subsistence economy of these communities, initially including the harvest of wild seeds (Veth and Walsh 1988; Walsh 1990). Martu also resumed traditional burning practices, but it took years to re-establish the fine-grained anthropogenic mosaic of vegetation communities that existed previously (Bliege Bird et al. 2012, 2016b). Martu saw foraging and burning as key to maintaining their social and religious ties to their homelands, as well as economic necessities for living in remote communities (Bird et al. 2016b).

Today, most Martu families are highly mobile and frequently shift residences among the three remote communities and Jigalong, as well as the Western Australian towns of Newman, Port Hedland, and Broome. While many Martu are employed in local conservation work for Kanyirrinpa Jukurrpa (a Martu-based NGO) or produce commercial artwork through Martumili Artists cooperative, foraging remains an important component of a complex hybrid economy (Codding et al. 2016a). Martu foragers now use 4-WD motor vehicles, firearms, and many other technologies to assist their hunting and gathering efforts.

Today when Martu hunt and gather, on average each individual forager acquires 1700 calories per day, which in some seasons accounts for nearly half of all calories and the bulk of protein that residents in the remote communities consume (Bird et al. 2016b, Bliege Bird et al. 2008, Scelza et al. 2014). Contemporary foraging parties drive up to 50 km from the communities to establish short-term, logistic camps. They then typically forage on-foot within 3 km of the ‘dinnertime camp’. Although they collect a variety of plants and animals, sand monitor lizards (Varanus gouldii) make up about 45% of all bush foods the Martu acquire by weight, and women devote over 70% of their foraging time to monitor lizard hunting. In addition to monitor lizards, Martu hunters also frequently encounter bustard (Ardeotis australis), skink (Tiliqua scincoides), python (Aspidites ramsayi), and signs of feral cat (Felis silvestris) in a freshly burned tract (nyurnma, see below). Men hunt monitor lizards as well, but often prefer to hunt larger hill kangaroo and bustard, even though these contribute only about 10% of total foraged food (Bliege Bird and Bird 2008).

Contemporary Martu hunting fires

Today Martu burn for various economic and social purposes, but hunting for monitor lizards accounts for most fires set by Martu. From April to September hunters regularly burn off large patches of old growth spinifex on sand plains to expose monitor lizard tracks and burrows. This dramatically increases encounter rates and significantly improves both the yield and reliability of monitor lizard hunting, immediately rewarding the hunter who set the fire (Bird et al. 2016a; Bliege Bird and Bird 2008).

Martu recognise five ethnecological stages of succession following a fire (Bird et al. 2016b), referring to a newly burned area as nyurnma, the first
stage in which most visible regrowth has been reset immediately following the application of fire. While new growth can emerge within days or weeks depending on moisture, burn scars sometimes remain sparsely vegetated for a year or two following the fire, until rains spark the emergence of herbaceous growth, marking the *waru-waru* stage. The diversity and density of plant resources peak in the third successional stage, *nyukura*, usually one to three years after the rain. Early *nyukura* communities include fruit from bush tomatoes (*Solanum diversiflorum*) and desert raisins (*S. centrale*), as well as grasses and forbs. Nectar may be harvested from cork tree (*Hakea subarea*) and honey grevillea (*G. eriostachya*) as the *nyukura* patch matures. Spinifex usually begins to squeeze out herbaceous plants five to seven years following rain, but cossid moth larvae (*Endoxyla spp.*) may be extracted from the roots of young acacia trees. It is during this *manguu* phase that spinifex hummocks have grown sufficiently to carry a fire from the crest of one tussock to another. On tracts of *manguu* that escape burning, expanding spinifex dies out in the centre of the hummock marking the final *kunarka* stage. Both *manguu* and *kunarka* patches provide important shelter for small to medium sized reptiles and mammals (Bliege Bird et al. 2013; Lundie-Jenkins 1993). Martu target patches of *manguu* and *kunarka* for burning because by these stages of development sand monitor dens are once again common, and burning the spinifex during the cool, dry season exposes burrows when the monitor lizards are denned beneath the spinifex hummocks (Bird et al. 2005).

Contemporary Martu hunting fires have a profound impact on the structure and diversity of resources (Bird et al. 2016b; Bliege Bird et al. 2008, 2012, 2013, 2016a; Kauhanen 2011). Analysis of a 10-year sequence of remote Landsat imagery (Bliege Bird et al. 2012) demonstrates that areas regularly foraged by Martu have significantly more, but smaller, fire scars than do more remote regions where summer lightning strikes are the predominant cause of ignition. The result is that regions regularly burned by Martu have significantly higher richness, diversity, and evenness of fire ages than areas burned by wildfires alone. The creation of small-scale mosaics of closely juxtaposed burn scars buffers the size of wildfires, because the successional vegetation of earlier burns breaks the spread of newly set fires. A result of this buffering effect is that more long-unburned tracts occur in areas regularly burned by Martu than in lightning regimes (Bliege Bird et al. 2012). Similar landscape level effects of indigenous fire management have been documented elsewhere in arid Australia (Bowman et al. 2004, 2008; Vigilante et al. 2004; Yibarbuk et al. 2001).

In Martu country, burning to hunt sand monitors fosters biodiversity because it replaces spinifex-dominated grasslands with a fine scale mosaic of more varied and productive early- to mid-successional biotic communities. Paradoxically, sand monitor lizards benefit from successional edges that result from hunting fires, so at a landscape scale population densities are highest in the areas Martu most intensively hunt (Bliege Bird et al. 2012). Similar relationships may have caused local extinctions of indigenous small marsupials when the mid-twentieth century interruption of Martu burning led to the loss of fine-grained mosaics of successional vegetation (Bliege Bird et al. 2012). Long-term Martu burning for sand monitors also has beneficial effects on hill kangaroo (*Macropus robustus*) populations, which tend to peak at intermediate levels of human disturbance (Cudding et al. 2014).

Despite the immediate pay-off of burning to hunt sand monitors, Martu follow strict customary rules controlling rights to burn any given tract, and sometimes undergo punishment or consternation for lighting fires that threaten totemic sites in estates owned by someone else or for burning areas larger than feasible to harvest. Because of such cultural prohibitions and years of experience setting broadcast fires, many Martu are expert at controlling their fires and skilfully use prevailing winds and natural firebreaks to control the spread and size of ignitions (Bird et al. 2016b). Nevertheless, with unpredictable conditions, anthropogenic fires sometimes get out of control, and estate owners will hold the burner responsible. Such traditions hint that longer-term benefits of burning were more important causes of pre-colonial Martu burning practices than they appear to be in the contemporary setting.

The MVT, Martu monitor hunting, and small seed utilisation

Despite the historical importance of small seeds as dietary staples (Veth and Walsh 1988) and the desire of Martu to maintain their traditional foraging lifestyle, contemporary Martu rarely harvest wild grass seeds (Bliege Bird and Bird 2008). Other Aboriginal foragers across arid Australia also ceased harvesting seeds in the 20th century, while still foraging for other foods, even though they retained the necessary expertise and technology (Brokensha 1975; Cane 1987; Devitt 1988; O’Connell et al. 1983; Palmer and Brady 1991). The availability of commercial flour and the work required to make traditional damper seem obvious reasons for dropping seeds from traditional diets (Altman 1987; Balme 1983). Elsewhere (Zeanah et al. 2015), we have demonstrated that among contemporary Martu, milled white flour provides a much higher caloric return per unit of wage
labour than do traditional seed resources per unit of foraging labour. Yet, simple substitution of higher cost foraged foods with similar, but lower cost, commercial options does not adequately explain why Martu no longer harvest seeds, because they do not make similar substitutions elsewhere in their diet. For example, Martu enthusiastically hunt relatively low ranked game, despite the availability of affordable meat products in community stores.

Based on principles of the prey choice model, O’Connell and Hawkes (1981, 1984), argued that availability of commercial foods eased depression of highly ranked foraged foods. Consequently, Alyawara foragers achieved sufficiently high overall returns to exclude lower-ranked seeds from their optimal diet. But this does not explain the Martu case. We analysed Martu foraging bouts targeting sand monitor lizard in recently burned tracts of manguu and kunarka, that occurred during the prime window for harvesting grass seed between April and June (Zeanah et al. 2015). The mean overall foraging return for successful hunts was 663 kcal/h, with a standard deviation of 557 kcal/h. Including seed season monitor bouts that produced no energetic return (at 10% of the total) produces a much more skewed distribution: Mean = 547 kcal/h; Stdev= 565 kcal/h; Median = 4434 kcal/h; Median Absolute Deviation = 439 kcal/h. Available accounts of Australian foragers processing seeds suggest that 300–1000 kcal/h is a good estimate of the range of post-encounter caloric return rates feasible for seeds that must be wet milled. Since overall returns for monitor hunting commonly fall below the post-encounter return range expected for seeds, the prey choice model predicts that seeds should frequently enter the optimal diet breadth of hunters seeking monitor lizards burrowed in the sand. Contemporary Martu foraging behaviour falsifies this prediction.

We argued (Zeanah et al. 2015) that the Martu choice to ignore seeds is best understood as resulting from their use of 4-WD vehicle transport to access new hunting patches (including community stores) and avoid the extensive post-harvest handling costs required to process seeds. The availability of 4-WD vehicles and diesel fuel have altered the cost-benefit ratio of foraging, making seed harvesting uneconomical by imposing an opportunity cost between time spent processing seeds and traveling to new patches. The classic formulation of the Marginal Value Theorem (MVT) models trade-offs between foraging within a patch and traveling to a new patch (Charnov 1976), and is a useful framework for investigating hunter-gatherer subsistence and mobility decisions (Coddington et al. 2016b; Venkataraman et al. 2017). However, it does not distinguish in-patch handling and search time, which we have shown is a major difference between the costs of most of the resources that Martu still forage and seeds (Zeanah et al. 2015). This conflict can be modelled using Bettinger and Grote’s (2016) equation for the MVT incorporating handling time as a variable for calculating diminishing patch returns. Prey of uniform energy content are randomly encountered and taken individually, adding the time necessary to handle each prey item as separate cost to those necessary to find each prey item as patch returns diminish.

Following this approach, Figure 1 shows marginal gains for Martu sand monitor foraging bouts and hypothetical seed harvesting bouts. Detailed explanation of the derivation of the curves is provided elsewhere (Zeanah et al. 2015). Foragers should always prefer the sand monitor lizard patch (a) to the seed patch (b) because it initially offers a higher rate of return. If travel costs to alternative patches are relatively low (<i), foragers should abandon one monitor patch for another without switching to harvesting nearby grass seeds. With longer travel times between monitor patches (>i), foragers are more apt to find switching to seeds an economic alternative to traveling to a new monitor patch.

Contemporary Martu utilise 4-WD vehicle transport to access hunting patches from the outstations. Assuming an average driving speed of 20 km/h, a forager could access alternative monitor patches nearly 20 km distant before finding harvest of the highest ranked seeds (1000 kcal/h) and 120 km distant before the lowest ranked (300 kcal/h) became economical. The driving distance between the outstation communities of Parnngurr and Punmu, geographically discrete centres of Martu hunting fires (Kauhanen 2011), is a little over 100 km. Thus, a vehicle equipped Martu foraging party can journey to a completely different anthropogenic mosaic before finding the lowest ranked seeds worthwhile to harvest. Given these thresholds, it is unsurprising that contemporary Martu rarely harvest seeds.

Yet travel thresholds are dramatically different for pedestrian hunters. Assuming walking speeds of 4 km/h on sand plains (Bird and Bliege Bird 2005) a forager on-foot could only access alternative monitor lizard patches in less than a 4 km radius before they would find it profitable to switch to the highest ranked seeds but a 24 km radius before they would find taking the lowest ranked seeds profitable. The highest ranked seeds in patches of nyukura should enter the diets of foragers seeking monitor lizard burrows in a freshly burned tract of manguu/kunarka, whenever the returns for foraging fall within one standard deviation below the mean of sand monitor lizard bouts and the distance to the next patch of manguu/kunarka exceeds the average daily foraging range from a dinnertime camp
(3 km). Lowest ranked seeds will enter diets when travel time to the next patch exceeds a full-days march (6 h at 4 km/h). This suggests that small cereal grains offer pedestrian foragers a critical alternative for variability in varanid hunting returns, but only if seed patches fall within easy walking distance of monitor lizard hunting patches.

Pre-contact Aboriginal foragers would have thus faced similar opportunity conflicts between travel time to new patches and seed processing time, at a pedestrian scale, as do contemporary vehicle-equipped Martu. Foragers on-foot who harvested seeds were obliged to spend the rest of the day processing them for consumption, forgoing the opportunity to travel up to 24 km to a new locale where they may have encountered fresh foraging opportunities. Thus, the costs of travelling to a new hunting patch must have been an important consideration whenever pre-contact foragers chose to process seeds. Considering the ecological consequences hunting fires have for seed patch distributions, the opportunity conflict between pedestrian travel and seed processing has direct implications for the antiquity of firestick farming and seed usage.

**Martu fire regime and seed distributions**

Figure 2 monitors the probability of encountering important plant resources in the five emic successional stages. These transects were anchored on Martu dinnertime camps occupied during cool-season monitor lizard hunting forays. The diverse plants present in nyukura include fast reproducing, seed-bearing annuals that cannot compete with spinifex, but were traditionally important food plants (Figure 3). The effects of fire treatment on seed availability are fully apparent and document a direct link between Martu burning and the creation of patches that yield edible grass seeds 1–3 years after the burn.

Although contemporary Martu are fully aware that burning enhances seed productivity, their intent cannot be to create seed stands because they rarely harvest seeds (Zeanah et al. 2015). Nonetheless, we predict that sand monitor lizard hunting fires should significantly alter the distribution of seed-bearing patches of nyukura at the scale of Martu foraging activities in a manner that would have proven crucial for traditional foragers who used seeds. Sustained burning of the same region should induce the emergence of anthropogenic vegetation mosaics in which mid-succession patches of nyukura occur within pedestrian access of late-succession patches of manguu/kunarka more often than they do in non-anthropogenic fire regimes. Such mosaics would ensure that small grained grass and forb seeds would be available whenever monitor hunting returns fell short.

**Methods**

To examine the effects of the current Martu burning regime on the distribution of grass and forb seed patches at the scale of Martu foraging, we compared
the distribution of *nyukura* in a series of circular areas selected from anthropogenic fire regimes with circles selected from landscapes burned only by naturally occurring lightning ignitions. Kauhanen (2011) analysed circular buffers set at 1 km increments up to 15 km in radius around a sample of control points selected from areas Martu frequently burn (most anchored at Martu dinnertime camps) and a sample of points randomly drawn from lightning fire regimes. He demonstrated that significant differences in fire-age diversity were greatest between 2 and 5 km around the control points, closely matching the 3 km foraging radius typical of contemporary Martu dinnertime camps (Bliege Bird

**Figure 2.** Kernel density plot of the predicted probability of presence of resources by successional age (derived from a logistic regression model) per 100 metres along ten separate 10 km transects surveyed in 2003. Successional Stage 1 = Nyumma, Stage 2 = Waru-waru, Stage 3 = Nyukura, Stage 4 = Manguu, Stage 5 = Kunarka. Green = seeds, Blue = acacia shrubs, Orange = Solanum fruit, Red = Hakea/Grevillia nectar.

**Figure 3.** Stand of wollybutt grass (*Eragrostis eriopoda*) in *nyukura*. D. Zeanah photographer.
and Bird 2008). Significant differences in diversity between anthropogenic and lightning fire regimes steadily diminished with buffers greater than 10 km from centre points. For these reasons, we chose to compare the distributions of seed bearing nyukura patches in buffers of 3 km and 10 km catchments.

To characterise variability in fire regimes at these scales, we generated a raster data set using a time series of 21 30 × 30 m resolution Landsat (7TM + for 1999–2002, 5TM for 2003–2010) taken in about six-month intervals from November 1999 to April 2010 (see Bliege Bird et al. 2012). Fire scars were digitised by hand using a ratio of bands 7 and 4 in ENVI version 4.8 (Exelis Visual Information Solutions, Boulder, Colorado) by comparing the current image with the previous time-step (Kauhanen 2011). Ground-truthing in May 2011 revealed a 10% error rate (Bliege Bird et al. 2012).

We defined regions as being under an Anthropogenic or Lightning fire regime following Bliege Bird et al. ( 2012). Spatial distributions of seed-bearing habitats were estimated using remotely sensed fire scars in roughly six month intervals from 1999 to 2010. Stages of vegetative succession were assigned to each burned patch corresponding to the age of each burned area from 2010. Because seed-bearing patches can only occur within defined stages of post-fire regrowth, these data estimate the total areas possibly containing seed patches. Detailed methods on the generation of fire histories from remote-sensing data have been outlined previously (Bliege Bird et al. 2012).

Using Hawths Tools (Beyer 2004), a grid of regular (offset) points was laid out with each point separated by 10 km (the max distance buffered) in equal intervals. Buffers of 3 km and 10 km were placed around each of 49 points within the anthropogenic regime and 158 points within the lightning regime point and used to summarise raster values. Fire scars were merged to correspond to Martu ethnocological successional stages of mid-succession (nyukura), defined as 1–3 years following fire, and late-succession (manguu and kunarka) being older than 5 years (Bliege Bird et al. 2008; Codding 2012; Codding et al. 2014). In this case, the dependent variable is calculated as amount of each successional stage that would have been observed within in each catchment in 2010. Data are summarised by pixel (30 × 30 m).

Analyses were run in R (R Development Core Team 2013).

Results

Table 1 compares the number of catchments with and without nyukura, as well as with and without manguu/kunarka at both 3 km and 10 km scales. Figure 4 illustrates a sample of these catchments. Both lightning and anthropogenic catchments always contain refuge patches of manguu/kunarka in both 3 km and 10 km buffers. Thus, both fire regimes readily offer patches of climax vegetation suitable for burning to hunt burrowed monitors. On the other hand, the representation of nyukura patches in 3 km anthropogenic and lightning buffers are significantly different (Chi-square = 5.63, df = 1, p-value = .0177) with only 4% of anthropogenic buffers lacking nyukura but 20% of the lightning regimes

**Table 1.** Presence/absence of Nyukura and Manguu/Kunarka in anthropogenic and lightning regime catchments.

<table>
<thead>
<tr>
<th>Buffer radius</th>
<th>Fire regime</th>
<th>3 km</th>
<th>10 km</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of catchments</td>
<td>Anthropogenic</td>
<td>49</td>
<td>49</td>
</tr>
<tr>
<td>Number with Nyukura</td>
<td>Anthropogenic</td>
<td>47</td>
<td>49</td>
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<tr>
<td>Number without Nyukura</td>
<td>Anthropogenic</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Number with Manguu/Kunarka</td>
<td>Anthropogenic</td>
<td>49</td>
<td>49</td>
</tr>
<tr>
<td>Number without Manguu/Kunarka</td>
<td>Anthropogenic</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
lacking nyukura. No significant differences in nyukura occur at the 10 km buffer (Chi-square = 0.083, df = 1, p-value = .7737). The results indicate that sustained anthropogenic burning maintains seed-bearing patches of nyukura within easy pedestrian access of Martu dinnertime camps.

Contrary to our prediction, mean percent coverage by manguu/kunarka is greater in anthropogenic circles, whereas coverage by nyukura is virtually identical in both buffers despite differences in presence/absence of nyukura (Table 2). These averages are skewed, however, by the non-normal distribution of fire sizes, particularly of lightning-set wildfires, which are significantly more biased toward larger fires than Martu-set fires (Bliege Bird, et al. 2012). Catchments within anthropogenic fire mosaics always contain higher median coverage of both nyukura and manguu/kunarka than do lightning fire regimes. More importantly, variances of percent coverage are significantly smaller in both 3 km and 10 km anthropogenic catchments than their lightning regime counterparts for both nyukura (Levene’s Test for Homogeneity of Variance: 3 km Radii- Df = 1,205, F value = 4.44, Pr (>F) = 0.0364; 10 km Radii- Df = 1,205, F value = 12.24, Pr (>F) = 0.0006), and manguu/kunarka (Levene’s Test for Homogeneity of Variance: 3 km Radii- Df = 1,205, F value = 13.295, Pr (>F) = 0.0003; 10 km Radii- Df = 1,205, F value = 16.455, Pr (>F) = 0.00007). Thus, the primary effect of Martu hunting fires on seed patches is to minimise the likelihood of having no patches of seed bearing grasses available within pedestrian distance of a late successional hunting patch and its associated dinnertime camp. Sustained burning thus creates mosaics of successional vegetation communities that are fine-grained at the scale of Martu foraging activities, ensuring that patches of manguu/kunarka and nyukura almost always occur near one another. This minimises the risk that an individual hunting sand monitor lizards in late-succession manguu/kunarka will be more than 3 to 10 km of a seed-bearing patch of mid-successional nyukura (Bliege Bird et al. 2012, 2013).

Note the implications of the distributions of manguu/kunarka and nyukura in anthropogenic and lightning fire regimes for pre-contact foraging. In anthropogenic mosaics, small seed patches and monitor hunting patches are likely to occur within easy pedestrian distance of one another, making seeds a reliable alternative whenever monitor hunting returns were poor. In the coarser grained landscapes structured by lightning fires, the nearest seeds may be beyond the range where they can economically serve as a backup to monitor hunting. Yet, vast expanses of manguu/kunarka would probably have been easily accessible to pedestrian foragers, encouraging journeys to new hunting patches.

### Discussion

Relationships between hunting fires, grass seed distribution, and mobility have profound implications for understanding the Aboriginal past. Based on the higher average returns contemporary Martu obtain from monitor hunting than seed gathering, we expect that pre-contact foragers seeking to provision offspring reliably preferred hunting small reptiles and marsupials to harvesting seeds (Bliege Bird, et al. 2013; Codding 2012; Codding et al. 2011). Nonetheless, achieving best returns for hunting burrowing prey required setting fires to improve encounter rates (Bird et al. 2005; Bliege Bird et al. 2013), which in turn had significant, yet unintentional, effects on the productivity and distribution of seed bearing grasses and forbs. Since improved hunting returns immediately rewarded burning, there was initially no need for social sanctions on free riders to justify burning to achieve longer-term goals. Nonetheless, long-term benefits were real and tangible because burning fostered the development of future seed crops that could buffer future variability in small game hunting returns. A freshly burned tract of manguu/kunarka hunted for sand monitor,
became a future patch of *nyukura* offering seeds when monitor returns were poor.

Yet, pre-contact hunters of burrowing prey would have achieved higher returns by moving on to fresh hunting patches than by harvesting small-grained seeds if travel distances between hunting patches were relatively short (Figure 1). Moreover, harvesting of successional seed grasses and forbs was not a feasible alternative for small game hunting if no patches of *nyukura* occurred within 3 km of the hunting patch, a situation that we have shown is more likely in lightning than in anthropogenic fire regimes. A reliable juxtaposition of the two successional stages occurred only if the same area had several small fires in close proximity in space and time, leading to the emergence of a fine-grained, anthropogenic fire mosaic. This suggests that traditional foragers were unlikely to capitalise fully on long-term benefits of hunting fires for seed patch creation until constrained mobility led them to revisit the same region over several consecutive decades.

Australian archaeologists (Hiscock 2008; Smith 2013) have posed climate change and population fluctuations as driving adaptive change and intensification of the arid zone (Figure 5). Adverse cold and drought conditions of the Last Glacial Maximum (LGM), and climatic variability associated with middle to late Holocene ENSO activity both appear to have caused population contractions, but the Holocene also witnessed a general trend of population growth, culminating in a rapid population increase during the late Holocene (Williams 2013; Williams et al. 2013, 2015a, 2015b, 2015c). A trajectory of population growth, punctuated by episodes of adverse climatic change should have had predictable effects on hunter-gatherer mobility and patch choice.

Bettinger and Grote (2016) discuss the effects of population growth and climatic change for the MVT, which we utilise here for the specific case of hunting fires and seed use in the Australian arid zone. In Figure 6, we use the marginal value curve for monitor lizard hunting during the seed season to predict how climate change and population growth affected traditional foraging patch choice. To simulate the effects of environmental deterioration, we halve prey count in the monitor lizard patch in Figure 6(a), but keep travel time constant, as when patch productivity declines without reducing the number of patches (thereby keeping inter-patch travel costs constant). The MVT predicts that foragers should slightly reduce patch residence time during periods of low patch productivity (because of the reduced handling time necessary for processing fewer small game), but use the same proportion of patch resources as they do when patch productivity is high. Sand monitor lizard hunters faced with this sort of environmental variability should emphasise mobility as the best way to deal with depressed hunting returns, with little or no need to fall back on seeds. High mobility would further depress female fertility, leading to low population growth rates.

Figure 6(b) keeps in-patch prey count constant, but doubles travel time to the next patch.
Bettinger and Grote (2016) argue that this better captures circumstances where population growth fills nearby patches thereby increasing travel distance to the next available patch, without lowering pristine patch quality. Here, in line with predictions of classic formulations of the MVT (Charnov 1976), increased travel time should encourage foragers to prolong the time they spend in patches as well as increase the proportion of patch resources they use. Under these circumstances foragers should intensify their use of seeds in response to reduced mobility and a greater need to supplement variability in small game hunting returns.

At least two factors pertaining to arid Australia complicate the simple distinction that Bettinger and Grote draw between climate change and population growth. First, climate change may differentially affect some patches more than others, thereby increasing travel costs between fewer high quality patches (Elston et al. 2014). This is particularly likely in arid Australia, where population density was directly tied to the distribution of potable water (Bird et al. 2016c; Birdsell 1953) and water sources served as hubs of residential mobility (Gould 1969). Arid climatic intervals that desiccated some water sources would increase inter-patch travel costs between the

![Figure 6. Marginal gains and travel costs for Martu foragers illustrating returns for sand monitor hunting following Bettinger and Grote 2016. Under situations where prey quantity in patch is halved but travel time kept constant (a) patch residence time is reduced ($r1 > r2$) while the proportion of patch remaining is constant ($p1 = p2$). Bettinger and Grote expect this scenario to be representative of circumstances where climate change deteriorates patch quality but does not affect patch abundance. Under circumstances where prey quantity is kept constant, but travel time doubled (b), patch residence time ($r2 > r1$) increases, whereas the proportion of patch remaining ($p1 > p2$) decreases. We expect scenario b to be representative either of climate change that reduces patch abundance or population growth.](image)
few that remained. Reduced mobility would have inadvertently created fine-scale anthropogenic fire mosaics bearing stands of seed grasses (Bliege Bird et al. 2008). Although this would have reduced travel distances between hunting patches within the mosaic, drought would have increased the distances a forager would have to travel to access a mosaic associated with a different water source. Pedestrian mosaics faced with local shortages of game would have turned to seed damper as the most reliable means of provisioning offspring in a manner like that Bettinger and Grote (2016) predict for demographic pressure.

Second, the emergence of fine-grained anthropogenic mosaics around water sources with sustained burning should improve the productivity of associated foraging patches over the long term by increasing the abundance of large and small game and enhancing the diversity of gathered resources (Bliege Bird et al. 2012, 2013; Coddington et al. 2014). Furthermore, Aboriginal burning activities are sensitive to climatic fluctuations and should buffer adverse climatic effects in anthropogenic fire regimes by dampening the adverse effects of lightning fires during droughts (Bliege Bird et al. 2016a). Because of such emergent properties, patches associated with fine-grained anthropogenic mosaics should rise in rank relative to patches in lighting fire regimes over time. A landscape of fewer, widely distributed, higher quality anthropogenic mosaics would persist even after the return of more mesic climate increased the number of intervening water sources. Intensification of patch use in this case, could be the catalyst for, rather than consequence of, population growth.

Bearing these caveats in mind, we evaluate several scenarios that have been posed concerning the effects of climate change and population growth on seed use intensification in arid Australia, pointing out testable implications based on the MVT for each. We argue that current understandings of traditional Aboriginal economies in arid Australia, particularly regarding the late Holocene fluorescence of formal wet-milling technology, suggest that intensive seed use closely followed the emergence of fine-grained, fire mosaics of vegetation communities (Bliege Bird et al. 2008), in response to intensified ENSO activity between 4.5 and 2 kya, followed by a surge in population growth.

We expect that Pleistocene foragers should have regularly set hunting fires and used seeds whenever hunting returns were low and seeds were available. Low population densities, however, allowed Pleistocene foragers to emphasise mobility over intensification, inhibiting developments of fine-grained anthropogenic mosaics and formalised milling technology (Coddington 2012). Extreme and prolonged droughts of the LGM probably reduced the number of water sources thereby increasing travel times between patches in the absence of demographic pressure. If so, the LGM plausibly could have caused seed usage to intensify (Edwards and O’Connell 1995; Veth 2005), but evidence for LGM seed use is contradictorily rare (Smith 2013).

Climatic conditions of the LGM led Pleistocene foragers to abandon the most arid portions of Australia for relatively well-watered refugia (Veth 1993; Williams et al. 2013), and radiocarbon curves suggest that population densities were quite low (Figure 5) even within refugia (Williams 2013; Williams et al. 2013). Most archaeological evidence suggests that LGM foragers were more mobile than their late Holocene successors (Veth et al. 2017; Veth 2005). Smith (2013:123) argues that a ‘point to point’ land use strategy involving frequent residential moves between reliable water sources within refuges best accounts for the LGM pattern.

Figure 7 shows the distributions of permanent water sources (Bird et al. 2016c) in biogeographic provinces intersecting or adjoining Martu Native Title boundaries.1 Radiocarbon dates falling within the LGM suggest that the Pilbara and Gascoyne bioregions were refuges, whereas the Great Sandy, Little Sandy and Gibson deserts lack LGM radiocarbon dates and were probably abandoned (Morse et al. 2014; Williams et al. 2013, 2015b). Observed mean distances between the 2822 Pilbara and Gascoyne water points are significantly shorter than the 252 sandy desert sources (Table 3), suggesting that it was feasible for LGM foragers to pursue the ‘point to point’ land use pattern in refuges. If so, we expect that LGM foragers resisted including seeds into their diets.

This may explain why evidence for Pleistocene seed-grinding appeared episodically in arid Australia and usually involved casually manufactured and multifunctional milling equipment (Denham et al. 2009; Fullagar et al. 2015; Smith 2015a, 2015b; Smith et al. 2015). Then again, some archaeologists have argued that the archaeological record is biased against the recovery of representative samples of Pleistocene milling technology and the intensity of seed usage in the Pleistocene may have been comparable to the late Holocene (Fullagar and Field 1997; Gorecki et al. 1997; Hayes 2015). The complex ecological relationships between firestick farming,

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1Two of the authors (RBB & DWB) have compiled a comprehensive record of Indigenously known water sources in Martu territory. It reveals that the continental scale of the database compiled by M. Bird and colleagues (2016c) from modern 1:250,000 maps, drastically underestimates the number of usable water sources known to contemporary Martu foragers. Nonetheless, we assume for analytical purposes here that the continental database provides a reasonably accurate regional measure of the relative abundance of water sources that would have persevered though periods of pre-contact aridity and served as suitable hubs of long-term residential activity.
seed-bearing grasses and forbs, and seed-consuming fauna evident among contemporary Martu suggest deep-time, coupling. It is possible that co-evolutionary relationships between anthropogenic burning, hunting, and small prey and seed ecology emerged in yet-to-be identified Pleistocene contexts. We predict that archaeological evidence for Pleistocene mosaic burning and intensive seed-grinding, if it occurs at all, should be found in landscapes imposing long travel times between hunting patches, such as the sandy deserts.

Archaeological evidence for the earliest sustained occupation of the sandy desert bioregions appears associated with more mesic climatic conditions and growing populations at the Early Holocene Climatic Optimum (9-6ka) (Williams et al. 2015b). Logic based on the MVT suggests that foragers would have incorporated the more far-flung water sources of sandy deserts only after rising population densities (Smith and Ross 2008; Williams 2013) filled the most productive habitats in better-watered refugia, leading to longer patch residence times and imposing high travel costs on foragers seeking to transit from one hunting patch to another, consistent with Bettinger and Grote’s (2016) population growth scenario.

As populations grew, travel costs to new mosaics and the likelihood of depressed small game hunting returns would have increased accordingly. Reduced mobility and temporary aggregation of larger groups in better watered areas should have caused foragers to intensify seed production, rather than small game patches, as soon as seed patches provided a higher rate of return (Figure 1). If pre-contact arid Australian foragers ever used firestick farming to intentionally create and manage seed stands for their long-term benefit, it would have been under such circumstances. Williams and colleagues (Williams et al. 2015b) speculate that population growth stimulated ‘low-level food production’ in the early Holocene, consistent with these inferences based on the MVT. If this scenario is correct, we expect evidence for intensive seed use and mosaic burning to appear first in the Pilbara and Gascoyne bioregions, where more densely-packed water sources would have fostered higher population densities than in the

Table 3. Nearest neighbour statistics for refuge (Pilbara and Gascoyne) and sandy desert (Great Sandy, Little Sandy, and Gibson deserts) bioregions.

<table>
<thead>
<tr>
<th></th>
<th>Refuges</th>
<th>Sandy deserts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>2822</td>
<td>252</td>
</tr>
<tr>
<td>Observed mean distance (km)</td>
<td>2.61</td>
<td>14.23</td>
</tr>
<tr>
<td>Expected mean distance (km)</td>
<td>7.25</td>
<td>33.18</td>
</tr>
<tr>
<td>Nearest neighbour index</td>
<td>0.355</td>
<td>0.424</td>
</tr>
<tr>
<td>Observed median distance (km)</td>
<td>1.10</td>
<td>5.08</td>
</tr>
<tr>
<td>Standard deviation distance (km)</td>
<td>4.17</td>
<td>20.39</td>
</tr>
<tr>
<td>Z-Score</td>
<td>-65.555</td>
<td>-17.478</td>
</tr>
</tbody>
</table>

Figure 7. Map of Western Australia showing location of Martu Native Title, permanent water sources (from Bird et al 2016c) and boundaries of the Gascoyne, Pilbara, Great Sandy, Little Sandy, and Gibson Desert biogeographic regions.
sandy deserts. Demographic pressure would have stimulated the early development of territoriality and storage requiring the emergence of institutional property regulations. This should be accompanied by functionally specialised and curated seed-milling technology, as seeds assumed a primary economic role for provisioning social gatherings at aggregation sites (Fullagar and Wallis 2012).

However, it seems more likely that it was not population growth, but the onset of intensified ENSO activity, in the context of fluctuating, yet generally low population densities, that triggered mosaic burning and intensive seed usage in arid Australia. Summed calibrated radiocarbon probabilities suggest that although Australian populations grew during the early Holocene climatic optimum, density and growth rates did not peak until the late Holocene (Williams et al. 2015b). Williams and colleagues (Williams et al. 2015b, 2015c) suggest that intensified ENSO activity between 4.5 and 2 kya fragmented earlier foraging territories, and initiated cycles of population collapse and rebound that stimulated technological innovations. These included the development of formalised seed milling tools, the technological basis of the seed-based foraging economies.

The abundance of permanent water sources in the Pilbara and Gascoyne refuges may have allowed sub-maximal, middle to late Holocene populations to retain a point-to-point mobility strategy through adverse ENSO conditions (Bird et al. 2016a, 2016b, 2016c). In contrast, generally warmer and drier climates would have had greater impact in sandy deserts by desiccating ephemeral and seasonal clay pans and pools. This would have reduced the number of water sources available, thereby increasing inter-patch travel costs. Prolonged patch residence times at remaining sources should have encouraged the emergence of fine-grained anthropogenic mosaics and formalised wet-milling seed-grinding technology. If so, we anticipate earliest archaeological evidence for these activities to be associated with more isolated water sources in the sandy deserts.

Further, the emergent properties of improved hunting returns and climate buffering associated with these mosaics should have discouraged intentional seed cultivation. Foragers could have capitalised on the emergent properties of landscapes maintained vis-à-vis the payoffs of burning for small game hunting, with only some reduction in residential mobility and in the absence of institutional property regulations. But the return of more benign climatic conditions coupled with emergent benefits of mosaic burning should have fuelled the spread of anthropogenic landscapes and further population growth. Under this scenario, we expect little evidence for intentional seed cultivation or social institutions of the sort implied by contemporary Martu rules governing burning rights until population levels neared their zenith in the late Holocene. The earliest specialised seed milling tools should thus date to the period of intensified ENSO activity, significantly pre-dating evidence for regional population pressure or changes in social institutions that managed ownership of material property.

We expect that this latter scenario best captures the course of population growth and technological development in the arid Australian past as it is currently understood. If we are correct, the late Holocene fluorescence of formal wet-milling technology is closely associated with the development of firestick farming; both were stimulated by ENSO-related climatic variability and served as catalysts for late Holocene population growth. Earlier archaeological evidence for Pleistocene and early Holocene milling technology and anthropogenic burning probably accommodated seed distributions created in fire regimes other than the mosaic burning conducted by Martu today. We predict that residue and phytolith evidence for spinifex seed milling should be particularly strongly associated with such contexts.

Of course, the true test of our predictions lies in further archaeological investigations. But productive archaeological research must be guided by firm expectations of what questions to ask and where to look. Regardless of whether our expectations are borne out by further archaeological research, we point out that formal consideration of the contemporaneous relationships between Martu hunting fires and seed ecology, considering the MVT, bear testable predictions about when and where mosaic burning and intensive seed usage should have occurred in arid Australia. These, in turn, provide a framework for interpreting archaeological evidence for seed milling and paleoenvironmental proxies of anthropogenic burning that bear implications for the emergence of seed cultivation and changes in social institutions.

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