Conservation or Co-evolution? Intermediate Levels of Aboriginal Burning and Hunting Have Positive Effects on Kangaroo Populations in Western Australia

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Abstract. Studies of conservation in small scale societies typically portray indigenous peoples as either sustainably managing resources, or forsaking long-term sustainability for short-term gains. To explain this variability, we propose an alternative framework derived from a co-evolutionary perspective. In environments with long histories of consistent interaction, we suggest that local species will frequently be well adapted to human disturbance; but where novel interactions are introduced, human disturbance may have negative environmental consequences. To test this co-evolutionary hypothesis, we examine the effect of Aboriginal burning and hunting on hill kangaroo (*Macropus robustus*) abundance. We find that hill kangaroo populations peak at intermediate levels of human disturbance, showing that in ecosystems characterized by long-term human-environmental interactions, humans can act as trophic mediators, resulting in patterns consistent with epiphenomenal conservation. Framing the question within this co-evolutionary perspective provides an explanation for the underlying mechanisms that drive environmental outcomes of subsistence practices.

Introduction

Studies of conservation among small scale societies produce varied characterizations. Some see sustainable practices as evidence of purposeful management grounded in traditional ecological knowledge (e.g., Lepofsky and Caldwell, 2013; Lightfoot et al., 2013; Welch et al., 2013). Others point to the negative effects of human subsistence practices on biotic communities as evidence that individuals optimize short-term gains at the expense of long-term conservation (e.g, Alvard, 1993, 1994; Kay, 1994).

Debates that cast indigenous peoples as either intentional conservationists or environmental devastators oversimplify human-environment interactions and ignore existing theoretical frameworks in ecology that account for greater diversity in species interactions. These include direct interactions between species with positive effects

to one (i.e., commensalism) or both species (i.e., mutualism) and indirect interactions which can benefit species several trophic levels removed (e.g., habitat facilitation), all of which result from interspecific co-evolution. Such positive effects, whether direct or indirect, are increasingly recognized as a significant force in community assembly, and may be critical in sustaining population stability in complex food webs (Bruno et al., 2003; Kikvidze and Callaway, 2009). Indirect stabilizing effects are often associated with "keystone species" which have a disproportionate effect on other species (Paine, 1969; Power et al., 1996) and are crucial to ecosystem function (Cottee-Jones and Whittaker, 2012). Keystone species include those with strong directional ties (such as top predators, Ripple et al. 2014), many weak ties (such as generalist omnivores, Neutel et al. 2002) or those that modify their environments, sometimes referred to as ecosystems engineers (Jones et al., 1994; Smith and Wishnie, 2000; Smith, 2013) or niche constructors (Odling-Smee et al., 1996, 2003, 2013). The latter may be particularly important where species interactions cause intermediate levels of environmental disturbance (Connell, 1978; Huston, 1979; Sousa, 1979), thereby producing direct or indirect benefits to species at intermediate levels of interaction.

Though rarely included as a keystone species, humans can frequently meet these criteria in having strong top-down links, many weak ties and subsistence practices that significantly alter the environment. Species that have co-existed with stable human activities for long spans of time should become adapted to intermediate levels of anthropogenic disturbance. In ecological communities that have co-evolved alongside human subsistence strategies, traditional practices may introduce positive and stabilizing effects on complex community networks (e.g., Bliege Bird et al., 2013). Within such environments, we should expect human interaction to produce outcomes consistent with what some have called "epiphenomenal conservation" (e.g, Alvard, 1993, 1998; Borgerhoff Mulder and

Coppolillo, 2005; Smith and Wishnie, 2000) or "emergent sustainability" (Moritz et al., 2013). These outcomes are neither intentional conservation, which requires short-term loss for long-term gain, nor are they sustainable management, which requires planned intent. Rather, they are an emergent outcome resulting from co-evolved interactions between humans and other organisms in a biotic community. However, these co-evolutionary outcomes are expected only in communities associated with a long history of stable human-environment interactions. When the scale and scope of human interaction changes rapidly, as with initial colonization, the introduction of new technologies, new forms of ownership or mobility, or sudden shifts in subsistence strategy, it may result in extensive ecosystem disruption and a wave of species extinctions in the short term (e.g., Estes et al., 2011). The co-evolutionary approach therefore provides predictions about where and when we should expect to find practices consistent with sustainable resource management in small-scale societies, and when the results of subsistence practices may be detrimental. Such a framework provides the means to explain variability across diverse societies and environments; specifically, to understand why some indigenous practices seem to produce effects consistent with conservation, while others do not. We suggest that the underlying patterning can be explained as a process of co-evolution between human subsistence practices and those of other organisms in the local environment.

Here we test predictions from this co-evolutionary hypothesis by examining the spatially variable effects of Aboriginal burning and hunting practices on hill kangaroo (*Macropus robustus*, also known as the common wallaroo or euro) in Western Australia. In Australia's remote western deserts, Martu, Aboriginal owners of their ancestral estates, maintain a number of traditional foraging practices, including fire-stick farming (Jones, 1969)—a practice that may date back several thousand years (Codding, 2012; Smith, 2013) or more (Miller et al., 2005).

Martu light fires for many reasons, but most frequently in the context of winter-time sand monitor lizard (*Varanus gouldii*) hunts (Bliege Bird et al., 2008; Bird et al., 2005). Sand monitor lizards are burrowed in the winter and hunters burn off patches of mono-specific climax vegetation composed of spinifex grass (*Triodia* spp. or *Plectrachne* spp.) in order to more easily spot the fresh mounds of sand at their entrances. This practice increases in-patch foraging returns on winter hunts, and increases foraging efficiency in the summer months when foragers can more easily track animals across the newly burned sandplain (Bird et al., 2005; Bliege Bird et al., 2008, 2013).

Because these hunting fires are smaller and more numerous than lightning caused fires, repeated burning and hunting results in the build-up of a more fine-grained and locally diverse mosaic of vegetation communities that vary in the time since fire (seral stages) (Burrows et al., 2006; Bliege Bird et al., 2008, 2012). Many of the species endemic to the desert region seem to be adapted to a tightly woven mosaic of alternating post-fire successional stages; especially well-documented are the smaller marsupials, such as the brushtail possum (*Trichosurus vulpecula*) and the spinifex hare-wallaby (*Lagorchestes hirsutus*), both of which have been argued to be dependent upon an aboriginal fire regime (e.g., Lundie-Jenkins et al., 1993). Beyond reducing the likelihood of devastatingly large fires that could destroy habitat or actually cause mortality (Bliege Bird et al., 2012; Bradstock et al., 2005), the greatest benefits may center on the reduced costs of access to alternating patches of varying seral stages, allowing for predator refugia in older seral stages adjacent to high quality foods occurring in patches of younger ages (e.g., Firth et al., 2010).

We recently showed that the unintentional benefits sand monitor lizards receive from anthropogenic fires outweigh the associated negative impacts of human hunting pressure (Bliege Bird et al., 2013). Along with sand monitors and other small marsupials, larger species

such as the hill kangaroo may also benefit from living within an anthropogenic fire mosaic. Previous research has shown that fire can have a positive affect on in-patch kangaroo densities. In the eucalyptus forests of Arnhem Land, kangaroos seem to prefer newly emerging shoots in the first stages of post-fire succession (Murphy and Bowman, 2007). In the hummok sedgelands of Tasmania, fire incidence has a positive effect on kangaroo densities by removing dominant climax vegetation with limited forage value, and replacing it with a diverse set of colonizing plants that provide a higher density of high quality forage (Styger et al., 2011). However, studies examining the impact of fire on mammal populations typically look only at the in-patch effects, and as such, there is still very little research on how landscape-level patterning in fire affects kangaroo populations. Because hill kangaroo range over unusually small areas for their body size, especially in more arid regions (Clancy and Croft, 1990; Croft, 1991; Fisher and Owens, 2000), hill kangaroo may benefit from living within more fine-grained vegetation mosaics as they might more easily transition between shelter in old growth patches to resource-rich patches of younger seral age. The greater diversity of seral patches available within the average hill kangaroo day range may also buffer individuals from seasonal and inter-annual variability in resource distributions. However, hill kangaroo are commonly hunted by Aboriginal foragers, who favor regions with higher kangaroo population densities. The balance between the negative effects of predation and the positive effects of anthropogenic fire should vary such that intermediate levels of disturbance will positively effect hill kangaroo populations. If however, there are no co-evolutionary relationships between humans and kangaroos, we would expect only negative effects of predation: spatial variation in kangaroo populations should peak in regions more distant from anthropogenic influence.

To better understand the dynamics between Aboriginal subsistence practices and desert

fauna, we collected data on hill kangaroo scat densities in the Little Sandy Desert Bioregion across different Martu Aboriginal hunting regions. These data were coupled with remotely-sensed and on-the-ground measures of seral diversity and habitat heterogeneity. We test three predictions to determine the combined effects of Aboriginal burning and hunting on hill kangaroo populations. First, we examine hill kangaroo distributions across patches of different seral stages to determine if they do indeed prefer particular stages of vegetation regrowth. If so, then more fine-grained mosaics of these different stages of vegetation regrowth should provide hill kangaroo with greater access to preferred resources within their daily foraging range. Second, if hill kangaroo benefit from living within a fine-grained mosaic of alternating seral stages, then their densities should be higher in regions with greater seral-stage diversity and heterogeneity. Finally, because hunting pressure may co-vary spatially with burning, hill kangaroo populations may be greatest at intermediate levels of human activity, where the net benefits of Aboriginal burning are high enough to offset any negative impact of Aboriginal hunting.

Materials and methods

Study area and context

In the Little Sandy Desert Bioregion of Western Australia, Martu have Native Title to a vast expanse of their traditional estates (Fig. 1). Of the three Martu communities within the Native Title Determination Area (Punmu, Parnngurr and Kunawarritji), this work is centered on Parnngurr community. Residents of all three communities are highly mobile, frequently traveling between different communities, to nearby towns (e.g., Newman, Port Hedland) and along hunting tracks to establish temporary 'dinner-time camps' from which they will forage for, prepare and consume wild foods.

Martu classify post-fire succession in five ethnoecological stages that correspond to the dominant vegetation (Table 1). Following an initial period during which the ground is bare, (*Nyurnma*), early regrowth (*Waru-Waru*) begins typically six months to one year following the first post-fire precipitation. The mid-seral stage (*Nyukura*) begins one to five years following fire with herbaceous and fruiting plants (e.g., *Solanum* spp.), which are an important dry season resource for Martu and, according to Martu informants, for *M. robustus* as well. Spinifex reestablishes dominance between five and fifteen years since fire. Martu differentiate this late seral stage into two types: *Manguu*, when spinfiex is mature enough that a fire can carry and *Kunarka*, when old spnifex dominates with a decaying center. Because a fire generally cannot spread well until spinifex again dominates the vegetation, fire-return intervals are limited based on the structure of *Triodia* growth.

This *Triodia* spp. and *Plectrachne* spp. (spinifex) sandplain dominated environment is interspersed with *Acacia* spp. (mulga) woodlands, eucalypt dominated water-course margins and rocky ranges of mixed cover. Hill kangaroo spend most of their days in the shade of shrubs, trees and caves atop these rocky ranges, traveling down to the sandplains in the mornings and evenings to forage. Since most Aboriginal patch mosaic burning occurs in the sandplains, reshuffling the mosaics of post-fire vegetation may alter the distribution of plants available within a hill kangaroo foraging radius. Our analysis tests for this in-patch effect of increasing forage quality, as well as for a landscape level effect on kangaroo populations.

Data collection

The context of hunting and burning was recorded over a long-term ethnographic project starting in 2000 (Bird et al., 2005; Bliege Bird et al., 2008, 2012, 2013). Hunting bouts—defined as the total time spent searching for and pursuing a particular resource-type—were monitored through a combination of focal-individual follows and continuous camp-scans (Altmann, 1974). Intensive focal-follows of kangaroo hunters occurred be-
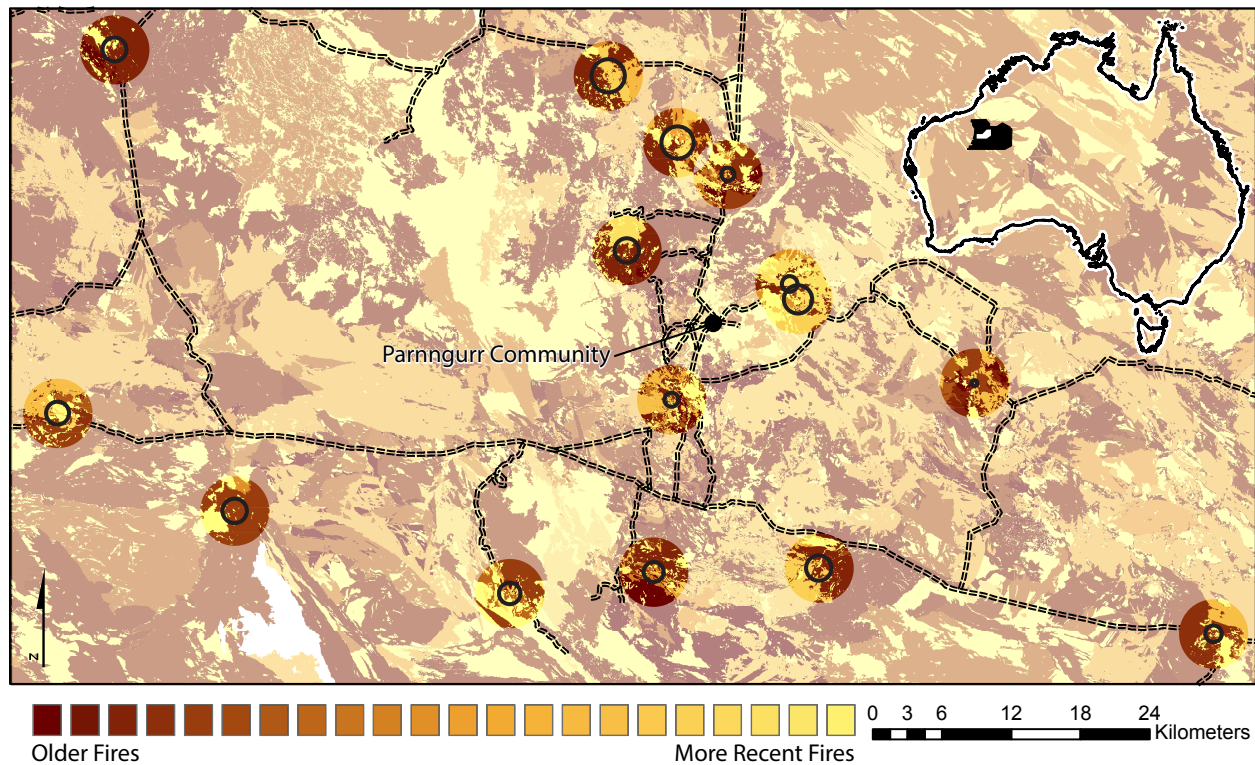
Figure 1: Map showing locations of scat transects relative to a 10 year history of fires classified by remote sensing. Highlighted circles mark the 3-km radii around each hill kangaroo habitat. Black circles are scaled proportionally to kangaroo scat counts. Dashed lines are 4WD tracks around Parnngurr community. The insert shows the location of the Martu Native Title Determination Area in black with Karlamilyi National Park in white.

tween 2007–2010 (Codding, 2012). These provide fine-grained detail on Aboriginal hunting practices and quantitative data on hunting time and returns which can be used to generate estimates of hunting pressure.

In order to investigate potential anthropogenic influences on populations, hill kangaroo distributions were quantified through a series of two stratified-random 1-km-x-4-m pedestrian transects in each Martu hunt region (Codding, 2012). Transects were restricted to rocky ranges and adjacent sand plains, occasionally crossing watercourse margins. The relative densities of kangaroo were measured using fresh scat-event counts as a proxy (Hill, 1981; Murphy and Bowman, 2007; Styger et al., 2011). Fresh scat-events were tallied within each discrete succes-

sional patch. While intra-genus identification is unreliable (Telfer et al., 2006), hill kangaroo are the most abundant, if not the only, macropod in these hunt regions. In-patch fire-history was recorded following the ethnoecological stages identified by Martu (Table 1). To control for variability due to substrate/habitat, each (rocky, sand plain or watercourse margin) was also recorded. Transects were walked from 2007–2009. The results include scat densities recorded across 30 transects in 15 different hunt regions.

Seral-stage diversity was calculated by developing fire histories for the area using a time series of 22 30-m resolution Landsat 7 TM+ (1999-2002) and Landsat 5 TM (2003-2010) images taken at roughly six month intervals (barring cloud-free days) from November 1999 to April

Table 1: Ethnoecological stages of vegetative succession following fire.

Seral Stage	Aboriginal Stage Name	Min Age (years)	Max Age (years)	Description
Burned-ground	*Nyurnma*	0	≈ 0.5	Burned ground
Early	*Waru-Waru*	≈ 0.5	≈ 1	Green shoots emerge
Mid	*Nyukura*	≈ 1	≈ 5	Herbaceous and fruiting plants
Late	*Manguu*	≈ 5	<15	Spinifex begins to dominate
Late (climax)	*Kunarka*	>10	>15	Old spinifex dominates

2010 (see Fig. 1). Each fire scar was hand-digitized in ENVI using a ratio of bands 7 and 4. A sample of 50 randomly distributed points was ground-truthed in May 2011. Remote sensing data was used to calculate the number of different seral patches ("Seral Richness"), a measure of seral-stage diversity. Seral diversity was measured as the number of different Martu classification stages within a 3-km buffer encompassing both transect locations in each region constructed using ArcMap (ESRI, 2011). Each 3-km radii polygon was then used to summarize values from a raster (30-m^2 pixels) dataset classified by burn age calibrated appropriately according to the year the transect was walked (see Fig. 1). Diversity values were calculated from the raster data by treating each seral stage as a 'species'; values were extracted from the raster dataset using Hawth's Analysis Tools for ArcGIS (Beyer, 2004) and then imported into R where richness values were calculated using the Vegan library (R Development Core Team, 2012; Oksanen and Simpson, 2011). On-the-ground measures included the area of each seral stage along each transect, the area of each substrate (habitat) and the number of seral transitions, or edges ("Seral Edge"), used as a measure of seral-stage heterogeneity.

Statistical analyses

To determine the effect of each measure of anthropogenic burning and hunting on counts of kangaroo scat events, analyses relied on generalized linear models of the poisson family (or distribution) with the canonical log-link (Faraway, 2006). These were implemented in R (R Development Core Team, 2012). Model results report the null deviance (D_0), which includes only the intercept, and the deviance explained by the model (D_M) reported in negative two log-likelihood.

Models constructed to determine the in-patch effect of each seral stage (Table 1) on scat counts controlled for substrate and area, and interactions between seral stages and habitats. Additionally, Wald's test was used to determine if the parameters significantly improve model predictions (R Development Core Team, 2012). For display purposes, these values are shown (Fig. 2) following a continuity corrected log or $log(x + 0.5)$ (Zeileis et al., 2008). Because models assume a log link, interpretation relies on the exponent of model coefficients.

Models examining the effects of seral-stage diversity (richness) and heterogeneity (edge) on scat counts across hunt regions controlled differences in the area surveyed (due to unnavigable terrain) by weighting each observation by the max possible area less the area surveyed. A second-order polynomial was introduced if it improved the model fit as determined through an increase in the amount of deviance (D_M) explained. Because spatial variability in the distribution of hill kangaroo scat may be biased by underlying nonrandom neighboring relationships (Valcu and Kempenaers, 2010), we tested for spatial autocorrelation using the *spdep* package in R (Bivand, 2013).

To examine the effects of hunting on hill kangaroo abundance, a measure of hunting pressure was derived by summing the amount of time spent hunting in each region between July 2007 and August 2010 (Codding, 2012). Because observations did not occur in precisely the same locations as transects, hunting pressure across the region was described by a polynomial surface that represents the spatial trend in hunting time observed from 2007-2010. This was generated using the *spatial* package (Ripley, 2011) in R (R Development Core Team, 2012). The degree polynomial was selected from alternatives based on the greatest amount increase in r^2 and decrease in AIC. The surface was converted to a raster and values corresponding to the location of each scat transect were extracted using the *raster* package (Hijmans and van Etten, 2012). A secondary measure of human influence was calculated as the average travel time from the community to each hunt region. Because Martu are central place foragers, the amount of time required to travel from the community should provide a broad measure of human influence on the landscape. As above, the predictive effect hunting pressure and travel time on scat counts were determined through generalized linear models of the poisson family with a log link controlling for area surveyed and including a second-order polynomial where it improved model fit.

Results
Succesional patch preference

Hill kangaroo differentially distribute themselves across patches of post-fire succession ($D_0 = 3006.1$, $D_M = 1508.3$, $p < 0.0001$, Table 2, Fig. 2). Scat densities are higher in early seral patches characterized by newly emerging green shoots and in mid-seral patches where they are able to target fruiting and herbaceous browse. The aggregate effect of these preferences should result in *M. robustus* being more abundant in areas characterized by greater seral-stage diversity and heterogeneity, where these patches have a higher probability of falling within their daily foraging range.
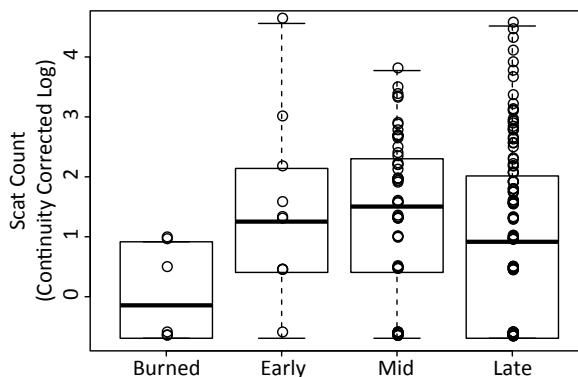

Figure 2: In-patch scat counts (continuity corrected log) across seral stages. Circles represent the raw data. Box plots show the distribution of the data outlining the first and third quartile.

Effects of Fine-Grained Vegetation Mosaics

The distribution of hill kangaroo scat counts across each hunt region is not biased by spatial autocorrelation (I=-0.04, p=0.419), but is predicted significantly by seral-stage diversity and heterogeneity. Scat counts increase significantly as a function of remotely sensed estimates of successional richness (D_0=511.89 , D_M=89.64, p<0.0001, Fig. 3) and as a function of on-the-ground observations of successional edge density (D_0=1312543, D_M=372597, p<0.0001, Fig. 3). However, scat counts decline at the highest levels of edge density. This may signify that too many small fires may have a detrimental effect on hill kangaroo populations, but it is more likely a function of covariance between Aboriginal burning and hunting pressure. Areas characterized by greater successional diversity as a result of burning while sand monitor hunting may also be areas where kangaroo are hunted more intensively. To further investigate these factors, we examine the interactive effects of Aboriginal burning and hunting on hill kangaroo abundance.

Table 2: Summary of generalized linear model results examining in-patch variation in hill kangaroo density as a function of successional stage and habitat.

Parameter †	Estimate	Std. Error	z	p	
Intercept	-1.06	0.74	-1.43	0.15204	
Early Succession	1.51	0.72	2.10	0.03603	*
Mid Succession	2.45	0.81	3.03	0.00242	*
Late Succession	1.14	0.71	1.60	0.11032	
Rocky Range	0.11	0.93	0.12	0.90651	
Sand Plain	0.24	0.20	1.21	0.22678	
Watercourse Margin	-0.26	0.45	-0.59	0.55647	
Area (m^2)	0.00	0.00	30.51	<0.0001	*

* Denotes statistical significance at $p < 0.05$. † Wald's Test suggest that the inclusion of these parameters significantly improves model prediction (F=140.17, <0.0001). There were not enough observations of scat in freshly burned area to be included in the model.

Interactive effects of burning & hunting

While hill kangaroo appear to benefit from living within fine-grained vegetation mosaics caused by Aboriginal burning, they may also be negatively affected by over-hunting. To test this, we first examine scat counts as a function of the mean amount of time kangaroo hunters spend in each region. A second-order polynomial surface significantly explains spatial variability in the distribution of hunting pressure across the landscape (r^2=0.3727, F=6.06, AIC=461.93, p<0.0001). Interpolated estimates of hunting pressure significantly predicts scat counts across each hunt region (D_0=1312543, D_M=827375, p<0.0001, Fig. 4). Hill kangaroo scat counts initially increase with the amount of time spent hunting in each region, but begin to decline at intermediate levels (Fig. 4). This could be caused by covariance between hunting and burning. Indeed, the amount of time spent hunting kangaroo in each region significantly predicts the amount of successional edge encountered along each transect (D_0=62053, D_M=38812, p<0.0001). As Martu burn in the context sand monitor hunting, but not kangaroo hunting, this reveals significant co-variance between the time spent hunting both taxa in each region.

As a proxy measure for the costs of access for central place foragers, travel time should provide a rough measure of the positive and negative effects that humans may have on hill kangaroo densities. Travel time significantly predicts variability in the distribution of hill kangaroo (D_0=511.89, D_M=160.98, p<0.0001, Fig. 5). Fig. 5 shows that densities are low closest to the Aboriginal community and increase until the limits of anthropogenic fire mosaics (approximately sixty minutes away from the community, see Bliege Bird et al., 2008, 2012). After this threshold, their relative abundance declines. This shows that hill kangaroo benefit most from intermediate levels of human influence, where the benefits of burning outweigh the effects of hunting.

Discussion

Hill kangaroo are significantly more abundant in regions dominated by fine-grained seral-stage mosaics developed by Aboriginal burning. Because Aboriginal fires shuffle the spatial distribution of seral patches so that they occur in more fine-grained mosaics (Bliege Bird et al., 2008), areas characterized by greater levels of habitat heterogeneity and seral diversity are more likely to provide hill kangaroo with access to a greater
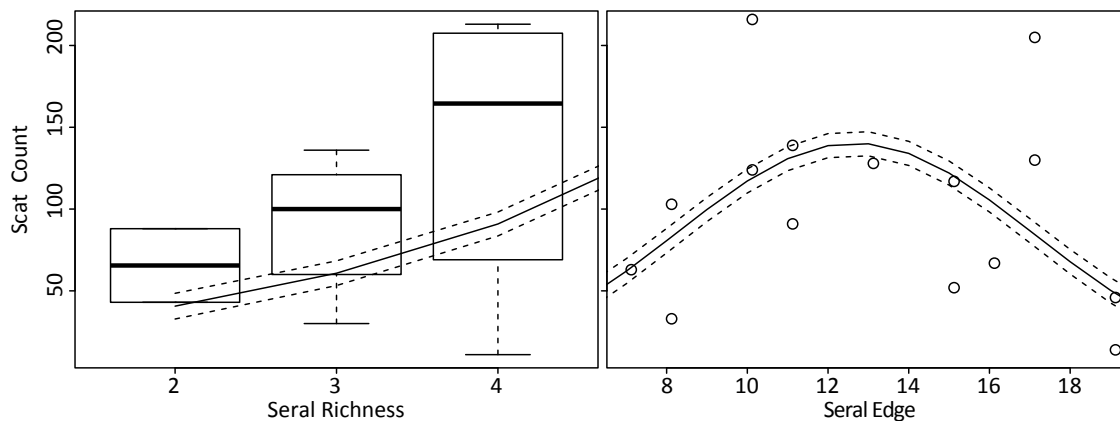
Figure 3: Scat count per hunt region as a function of (left) remotely sensed observations of seral-stage diversity (richness) and (right) on-the-ground observations of seral-stage heterogeneity (edge) shown with predicted model fits (solid line) and standard errors of the model fit (dashed).

diversity of vegetation and a greater number of preferred patches within their foraging range. This effect is likely so pronounced because Martu fire regimes differ most from lightning regimes at scalar extents ranging from 3 to 5 km (Kauhanen, 2011), which brackets the estimated home ranges of hill kangaroo (Clancy and Croft, 1990; Croft, 1991; Fisher and Owens, 2000). Gathering data at a scalar extent appropriate to the hill kangaroo home range was also likely crucial to revealing this pattern, as others have highlighted (Kelly et al., 2012). Our results are robust across measures derived from remote sensing and on-the-ground observations. However, the overall positive effect is complicated by hunting pressure, which is negatively correlated with increasing travel distance from the community.

Hunting pressure appears to have a negative effect on hill kangaroo populations so that their populations are highest at intermediate levels of human interaction. Aboriginal burning occurs most frequently in the context of sand monitor hunting (Bird et al., 2005; Bliege Bird et al., 2008). Because sand monitor and hill kangaroo hunters (frequently women and men respectively, Bliege Bird and Bird 2008; Bliege Bird et al. 2009; Codding et al. 2010, 2011) often travel to the same regions and divide their labor between these two hunt-types, the positive and negative effects of burning and hunting tend to covary with one another. The fact that hill kangaroo are most abundant at intermediate levels of human predation likely reflects the dynamic interactions between hunters' decisions, fire regimes and prey abundance. Hunt regions currently characterized by low prey abundance and low predation pressure likely represent locations that have already been over-hunted. It is unknown whether the effects of predation pressure causes populations decline due to increased mortality or as a function of prey behavior which leads kangaroo to vacate areas frequented by hunters (*sensu* Charnov et al., 1976), though these effects are likely a combination of the two. The intermediate areas probably represent sweet spots where hunters are targeting dense kangaroo populations enhanced by the cumulative and indirect effects of anthropogenic burning. Here, hill kangaroo have increased access to anthropogenic landscapes characterized by higher densities of seral patches with early and middle stages of regrowth. In such areas hunting pressure has yet to, and may never, cause kangaroo populations to decline.

These results show that at intermediate levels of human disturbance, Aboriginal fire regimes
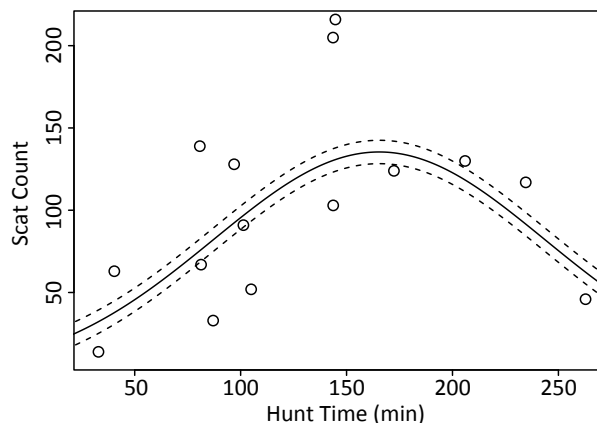
Figure 4: Scat count as a function of the amount of time spent hunting in each region shown with the predicted model fit (solid line) and standard errors around the model fit (dashed).
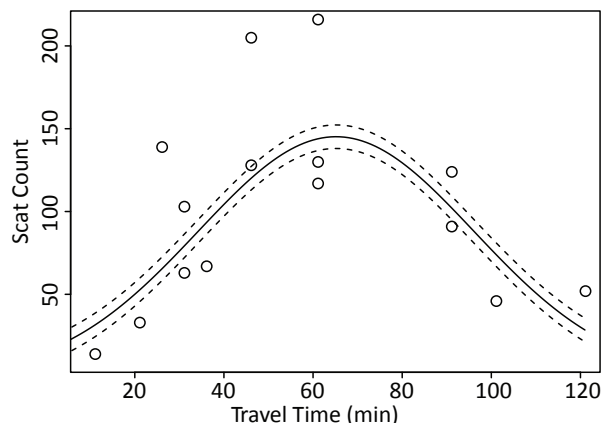

Figure 5: Scat count as a function of travel time from the community shown with the predicted model fit (solid line) and standard errors around the model fit (dashed).

have the greatest net effect on hill kangaroo populations, with populations declining outside the range of anthropogenic fire mosaics. Prior to European contact, this positive effect may have been more widespread as highly mobile hunter-gatherers traveling on foot would have a ranged across greater areas of the desert than today, where the impact of anthropogenic fires is restricted to the foraging radius around permanent communities and the vehicle tracks that provide access to the desert (Bliege Bird et al., 2012). Moreover, the negative impact of hunting would have been more dispersed, with greater periods of time between hunts in the same region, allowing prey populations to recover. However, hill kangaroo populations still persist near the community at densities similar to those regions far removed from human influence. This persistence is a direct outcome of the adaptive foraging decisions of kangaroo hunters. Post-encounter pursuit of hill kangaroo frequently results in acquisition failure due to their escape velocity (Bird et al., 2009); in regions of low kangaroo density, a failed pursuit typically results in failed overall hunting bout as a second encounter is unlikely (Codding, 2012). After several failed bouts, hunters are unlikely to return to

that hunt region for some time. As with many predator-prey interactions at equilibrium, prey seem to persist largely due to the adaptive pre-switching decisions by predators—either to take other prey, or as in this case, to take the same prey from other locations (e.g., Abrams, 1993; Winterhalder and Lu, 1997).

Our results show that hill kangaroo benefit from living within regions dominated by anthropogenic fire regimes, which suggests that hill kangaroo may have co-evolved alongside an extensive history of Aboriginal burning and hunting practices. The onset of anthropogenic fire regimes may have allowed hill kangaroo (and likely other endemic fauna) to extend their range into more marginal landscapes and to occur at higher densities within their extant range. Because these processes represent behavioral responses that would increase kangaroo somatic and reproductive success, the patterns observed here would likely emerge quickly after initial introduction of anthropogenic fire and would likewise disappear with the removal of anthropogenic fire mosaics. However, these outcomes should not be confused with conservation management.

Sustainable Subsistence

While the subsistence practices of indigenous populations are often considered to be directed at either long-term management or short-term gains, here we show that the outcomes of human-environmental dynamics may have more to do with the co-evolutionary histories of human subsistence practices. While hill kangaroo benefit from living within fine-grained vegetation mosaics established through anthropogenic fire, these positive effects should not be confused with management. Because Martu fires are lit most frequently in the context of sand monitor lizard hunting, any effect on other species, like hill kangaroo, is necessarily indirect. While Martu are well aware of these indirect effects, they clearly state that they are not managing these populations. Instead, they suggest that these interactions are part of broader patterns of ecological and spiritual relationships known as the Jukurrpa or law passed down by the Dreamtime ancestors (Bliege Bird et al., 2013; Tonkinson, 1993). This belief places people within, not apart from, ecological interactions. The empirical patterns shown here, supported by traditional Aboriginal knowledge, suggest a long history of interactions between humans and the environment in which the distribution of plants and animals is partially structured by anthropogenic fire regimes. While shaped over millennia, patterns observed today reveal a positive ecological effect of intermediate human interaction.

Such positive effects of indigenous resource use may also occur in other regions where human-fire dynamics have existed *in situ* for long periods of time, as in North and South America (e.g., Keeley, 2002; McAdoo et al., 2013; Welch et al., 2013). These indirect positive effects need not be limited to fire (e.g., Fowler and Lepofsky, 2011). For example, Moritz et al. (2013) suggest that what seems to be effective management of grazing commons among Fulbe pastoralists actually emerges from patterns of mobility that are in each individual's best interest. In such cases, indigenous practices may indeed promote species health, but again, this does not mean that sub-

sistence practices are designed to have these conservation effects. However, better understanding these co-evolutionary dynamics can inform conservation strategies.

Applying Co-evolutionary Dynamics to Conservation

Today, Australia is experiencing some of the highest rates of mammalian species decline in the world (Cardillo and Bromham, 2001; Short and Smith, 1994), which is hypothesized to result not only from novel human intervention (including invasive species introduction), but also by the removal of traditional Aboriginal fire regimes. In Australia's arid center, species loss began coincident with the departure and removal of Aboriginal foragers (Burbidge and McKenzie, 1989; Letnic and Dickman, 2005). Because most of the extinct and endangered small mammal species are hypothesized to be sensitive to the scalar extent and grain of seral-stage habitat heterogeneity (Bolton and Latz, 1978; Burbidge et al., 1988; Southgate et al., 2007), the removal of Aboriginal fire regimes is potentially to blame for the observed increase in fire extent and intensity and the reductions in small mammal abundance and diversity (Burbidge and McKenzie, 1989; Letnic and Dickman, 2005; Woinarski et al., 2010).

Our results suggest that Aboriginal burning may provide a benefit to species whose distributions overlapped with these fine-grained mosaics for prolonged periods of time, including now vulnerable or extinct species. Other research suggests that fine-grained seral mosaics may be crucial in supporting threatened mammal populations within Australia's desert ecosystems (Burbidge and McKenzie, 1989). For example, the vulnerable rufous hare wallaby (*Lagorchestes hirsutus*) likely benefits from Aboriginal fire regimes through reduced dietary variability (Lundie-Jenkins et al., 1993); further, Aboriginal fire regimes may also reduce mortality by introducing fire-breaks that significantly reduce the probability of large fires which would otherwise cause heavy mortality in individual small- to medium-sized mammals (Bur-

bidge and McKenzie, 1989; Bliege Bird et al., 2012). Given this, the recovery of these populations may depend on reestablishing these mosaics (Richards, 2005; Richards et al., 2008). As Aboriginal hunters do not target these threatened species today, reestablishing Aboriginal fire regimes would likely have a very positive effect on their populations without the negative feedbacks from anthropogenic hunting. This suggests that managing Australia's desert ecosystems requires understanding the long-term impacts of traditional land-use strategies employed by Aboriginal Australians. We suggest that in order to be successful, management schemes will need to facilitate traditional hunting and burning regimes in remote communities and incorporate this traditional ecological practice into future management protocols.

Conclusion

Characterizations of human-environment interactions among small-scale societies that emphasize only the negative effects of predation, or the conscious attempts to minimize it, miss an opportunity to explore the diverse ecological dynamics that structure human interactions with the ecological communities of which they are a part. Human subsistence practices that have a long history in a particular region likely have keystone effects in the broader ecological community due to long-term co-evolutionary dynamics between human decisions and endemic species. Because endemic fauna likely adapted to living in environments where these practices were central to people for long durations, the outcomes of such practices may serve to mediate trophic interactions and facilitate the persistence of diverse species assemblages and ecosystem stability. Understanding the processes that sustain these ecological communities, regardless of whether they are intentional or not, will allow for more effective design of management protocols that can simultaneously satisfy conservation goals while facilitating the survival, well-being, and autonomy of traditional subsistence practices.

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