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The hierarchy of virtue: mutualism, altruism and signaling in Martu women's cooperative hunting☆

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Abstract

Cooperative hunting is often assumed to be mutualistic, maintained through returns to scale, where, by working together, foragers can gain higher per capita return rates or harvest sizes than they can by hunting alone. We test this hypothesis among Martu hunters and find that cooperation only provides increased returns to poorer hunters while disadvantaging better hunters. Even so, better hunters still cooperate as frequently as poorer hunters. We ask whether better hunters are advantaged in secondary sharing distributions or whether they bias their partner choice to kin or household members. We find that better hunters are not more likely to pair up with kin and they do not gain consumption benefits from acquiring more. They share a greater proportion of their harvest than poorer hunters: no matter how much one produces — better hunter, worse hunter, cooperator, solitary hunter — all eat the same amount in the end. Such a result suggests the hypothesis that cooperation might be a costly signal of commitment to the public interest on the part of better hunters, which generates trust among camp members and facilitates strong social networks, particularly among women, who cooperate more than men. While some foragers may benefit through cooperation from returns to scale or risk reduction, others may benefit more through signaling commitment and generating trust.

Keywords: Cooperation; Martu; Australian aboriginal; Women's hunting; Sharing; Costly signaling

1. Introduction

When hunters have the option of jointly pursuing prey, they are expected to do so primarily when there are direct, mutualistic benefits in the form of increasing returns to scale. Previous work has shown that cooperative hunting is likely to be maintained when coordinated action increases individual hunting success, prey encounter rates or harvest size obtained, or reduces the costs of search and pursuit leading to increasing per capita foraging return rates (Alvard, 2001; Alvard & Nolin, 2002; Packer & Ruttan, 1988; Smith, 1981, 1991). The benefits achieved by cooperative hunting are gained through distribution of the subsequent harvest among the members of the hunting party, such that those who cooperate gain increased individual consumption return rates (measured as kilocalories consumed per unit of time spent foraging) relative to what they could achieve through hunting alone.

Despite the synergistic benefits possible with cooperative hunting, conflicts of interest, failures of coordination, extensive free riding and heterogeneity among individual foragers in ability and access to group production can produce differential benefits to cooperation, raising questions about how collective action in group hunting and other forms of production is sustained (Hawkes, 1992; Ostrom, 1991). If group foraging involves striking a balance between the benefits of cooperating and the costs of interference competition, groups might become larger than optimal for all members if solitary foragers still do better to join them rather than hunt alone (Smith, 1981, 1985, 1991). When group members find it costly to exclude joiners, the benefits of cooperative hunting will be lower for all than if group sizes are kept close to optimal. Cooperation may also fail to

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provide higher per capita benefits if the distribution of prey following the hunt is biased or non-cooperators are allowed to gain access to the group's production. This can lead to a reduction in cooperation; Sosis, Feldstein and Hill (1998) found that the distributions of cooperative fishing groups on Ifaluk were biased toward canoe owners and large landholders, and, as expected, such individuals fished cooperatively more often than small-holders and men who did not own canoes. Cooperation is also sensitive to partner choice if hunters differ in their hunting abilities or effort, especially when solitary hunting offers returns that are just a bit lower than those from a cooperative hunt. If better hunters do not pair up with other good hunters, or exclude poor hunters from the party, they might not see any synergistic effects of cooperation relative to what they could achieve by hunting alone (Packer & Ruttan, 1988; Winterhalder, 1996). If it is too costly for hunters to assert control over the composition of hunting groups, better hunters are expected to hunt alone more often than poorer hunters. Finally, cooperative hunting can only provide synergistic benefits if the benefits of cooperation are outweighed by the costs of harvest losses to non-hunters through demand sharing. Among Lamaleran whale hunters, crews of at least eight gain higher returns from whale hunting than from solitary fishing, but the payoffs to this strategy depend upon strict rules for division that specify certain portions to those who play certain roles on the hunt, thus minimizing losses to free riders (Alvard & Nolin, 2002).

In this article, we ask whether or not returns to scale structure the benefits of cooperative hunting among Martu, Aboriginal foragers of the Western Desert in Australia. Martu are the indigenous owners of the estates that surround Lake Disappointment and the Percival Lakes in the northwest section of Australia's Western Desert (see Tonkinson, 1974, 1978, 1988, 1991, 1990, 2007; Walsh, 1990). As highly mobile hunter–gatherers in one of the most remote and arid regions of Australia, many Martu managed to maintain their lifeway relatively autonomous of colonial influence well into the second half of the 20th century. We focus particularly on Martu women, who frequently hunt small animals, and supply half of the bush meat that people consume (Bliege Bird & Bird, 2008). Historic band composition and contemporary residential patterns among Martu may have been critically shaped by the extent to which women engage in cooperative task specialization (Scelza & Bliege Bird, 2008). Sharing among Martu can also be extremely equitable for some resources, despite variance in productive effort (Bird & Bliege Bird, 2010; Bliege Bird & Bird, 2008). Some of this variability stems from gender- and age-related specialization on different productive activities: some individuals spend more time hunting, others more time collecting; some produce more small game, others produce more large game (Bliege et al., 2008; Bird, Bliege Bird & Codding, 2009). Such variability provides an ideal case study of the factors influencing cooperative production.

We first take a broad perspective on cooperative foraging among Martu, asking whether cooperation provides increasing returns to scale across foraging activities and how gender affects cooperation. We then narrow our focus to the hunting activity that provides the most meat by weight and comprises the majority of all hunting bouts, sand monitor hunting, asking whether cooperation on monitor hunts provides increasing returns to scale over solitary hunting, and whether there is individual heterogeneity in the benefits of cooperation. We ask whether better hunters compensate for losses incurred in cooperating with poorer hunters by cooperating less often, keeping more for themselves after sharing, or choosing to cooperate more often with kin.

1.1. Cooperation among Martu

Extensive descriptions and analysis concerning the nature of different types of Martu foraging activities are provided elsewhere (Bird & Bliege Bird, 2005; Bird et al., 2009; Bliege Bird & Bird, 2005; Bliege et al., 2008; Codding, Bird & Bliege Bird, 2010; Bliege Bird, Codding & Bird, 2009). Below we focus on the most frequent hunting activity (sand monitor hunting) and provide some brief comments on the cooperation and patterns of distribution associated with other foraging activities used in our analyses.

1.1.1. Sand monitor hunting

Sand monitor (*Varanus gouldii*) hunting is the most common foraging activity and mostly conducted by women. In this foraging activity, there are several different ways individuals might cooperate. In the winter season, where successful hunting involves targeting patches of old-growth spinifex grass for burning (Bird et al., 2005; Bliege Bird et al., 2008), two or more individuals often burn the same patch and share search costs for the prey revealed within. Each hunter will separate by about 100 m, calling the other over to assist in pursuit and capture if they find fresh tracks or a likely burrow. The hunters then coordinate in probing around the burrow in wide concentric circles with the point of their digging sticks to locate the den. One might dig up the entrance hole to determine the direction of the tunnel, the other probing for the terminal chamber. Depending on the depth of the den, hunters may then take turns in its excavation. In the summer season, when sand monitor are active on the surface, two or more hunters might cooperate to track and chase a single prey item, attempting to capture it before it retreats to its deep summer den. During a cooperative hunt, most partners pool their harvest: one hunter, usually the older or more skilled hunter, will transport all prey in her own bag. Typically, she will then take responsibility for cooking their pooled returns at the dinner-time camp (hereafter, DTC). As the individual monitor lizards are removed from the fire, she initially divides the harvest evenly between the partners she cooperated with while hunting (primary distribution). Each individual hunter then distributes her own portion to others in the DTC: her family, her children, her spouse, her brother or others with whom she did not hunt (secondary distribution). This is the only hunting activity that is usually characterized by producer control over distributions. While there is a strong negative relationship between the number of people in the DTC and the amount a producer keeps, some producers keep more than others, and it is in these secondary distributions where reputations for stinginess or generosity can be built and maintained. On cooperative hunts there are thus two ways that a hunter might bias the amount she keeps for herself: she might give less or more to her hunting partner (s) in primary distribution, and she might keep a portion for herself that is smaller or larger than the individual portions she gives away to others in secondary distribution.

1.1.2. Perentie and cat hunting

Men and women are equally represented on feral cat (*Felis catus*) and perentie (*Varanus giganteus* and *V. panoptes*) hunts (Bird et al., 2009). For these medium-sized mobile prey, cooperation generally entails two or more individuals searching separately and then coordinating in tracking the same animal when fresh tracks are found, pursing it to exhaustion. Unlike with sand monitors, but as with larger animals like kangaroo and bustard, the hunters typically do not cook and distribute their own harvests. If an older individual is present, she will generally take responsibility for cooking and dividing prey into between four and six standardized portions. Like the primary distribution of kangaroo, if the DTC is large, shares from medium-sized animals like these are sometimes distributed to “hearth groups” (individuals sitting at separate fires) within a DTC, rather than to individuals, and secondary distributions occur among members of the hearth group. This contrasts with the distribution of sand monitor, which is always from the acquirer to individual consumers.

1.1.3. Vehicle hunting

Long-distance search using a vehicle is most common for hunts targeting the Australian bustard (*Ardeotis australis*), although if other high-ranked prey are encountered (perentie, kangaroo, monitor lizards, skink or patches of Solanum fruit) they will usually be pursued. Vehicle hunts are nearly always cooperative to some extent: large-mixed sex groups are common, and even if there is only a single rifle in the party, others will act as spotters and trackers, tracking prey and following it while in the vehicle. Mothers and grandmaternal caretakers often leave young children with vehicle hunters while they hunt on foot, in order to avoid having to carry them long distances. At the dinner camp, distributions of cooked bustard proceed in the manner described for other medium- to large-sized prey.

1.1.4. Kangaroo hunting

While men most frequently hunt hill kangaroo (*Macropus robustus*) alone, they do sometimes cooperate. Cooperation often involves one hunter moving ahead on the hilltop, another in the acacia brush at the base of the hill to drive prey out of hiding and toward the rifle. If more than one hunter has a rifle, hunts became less coordinated, with each hunter separating on opposite sides of the rocky range so that prey missed by one might be shot at by the other. Sharing of kangaroo is highly formal, with the hunter playing no role in preparation or distribution but for exceptional circumstances. The formality allows for the cook/distributor to make the parcels in primary distribution equal for each recipient or hearth group present at the dinner camp (see Bird & Bliege Bird, 2010; Bird et al., 2009; Bliege et al., 2008 and Codding et al., 2010, for detailed description and analysis of kangaroo hunting and sharing).

1.1.5. Collecting

Collecting activities include picking Solanum fruit (*S. centrale* and *S. diversifolium*), digging roots or corms (*Vigna lanceolata* or *Cyperus bulbosis*), chopping tree-boring grubs from trunks or roots (*Endoxyla* spp.), harvesting the nectar of *Hakea* and *Grevillia* flowers, or collecting feral European bee (*Apis*) honey. For most of these non-hunting activities, cooperation is minimal, usually involving acquiring resources in the same patch or in close proximity, and pooling prior to returning to the dinner camp. An older woman with a large harvest might dump a portion of her surplus into the container of a younger person with less prior to leaving the patch, “so they could take home more to share”. This type of cooperation is most common for fruit, nectar, root or bulb digging or in acquiring grubs. Honey is the only collecting activity in which pursuits were necessarily collective: several individuals often took turns with the axe to extract honey from a single hive, some staying below the tree to tend smoky fires to keep the bees calm.

1.2. Hypotheses

The first step in our analysis is to investigate whether or not cooperative foraging in general seems to be maintained through the benefits of increasing returns-to-scale; that is:

H1: Cooperation increases per capita return rates in all foraging activities.

The pattern of variability in the frequency of cooperation across foraging activities by the gender of the forager could tell us something about the benefits that influence cooperation. If cooperation is patterned by the benefits of returns-to-scale, then it should be most frequent in activities that show strong positive effects of cooperation on returns, less frequent in activities that show weak effects on returns and most infrequent in activities that show negative effects on returns.

As an alternative, cooperation could be a means to overcome risk by increasing the chances of a successful harvest. If so, we might expect to see a correlation between the proportion of bouts in any activity that are cooperative and the expected probability of failure in that foraging activity. As we have suggested in previous publications (Bliege et al., 2008), Martu women may be more risk sensitive than men and, accordingly, we would expect this relationship to be much stronger for women than for men. Specifically we suggest that:

H2: Men and/or women both cooperate more frequently in activities that are associated with higher chances of bout failure.

We then focus our analysis on sand monitor hunting, which offers the most variability in cooperation and thus the greatest opportunity to link cooperative effort and its benefits. Sand monitor hunting parties are cooperative 40% of the time, women cooperate more often than men (65% of women's vs. 43% of men's bouts are cooperative) and these hunts account for nearly half of all foraging bouts on dinner camps (713 of 1532), giving us a large sample of both cooperative and noncooperative hunts. Furthermore, the number of hunts per individual is quite high, allowing us to examine intra-individual variability in hunting returns. The mutualism hypothesis suggests that:

H3: Cooperation within a single foraging activity (sand monitor hunting) should (a) increase the per capita return rate, (b) increase total harvest weight (in kilocalories of edible flesh), (c) reduce the time needed for foraging in sand monitor hunting or (d) increase the chances of a successful hunt.

Because our statistical methods are correlative, we also attempt to test for directional causality: does cooperation cause changes in return rates, or do external changes in return rates affect whether or not people cooperate? For example, a correlation between low returns and cooperation could mean either that cooperation causes low returns or that people are more likely to cooperate when returns are likely to be low. If so, we would expect a greater percentage of individuals to hunt cooperatively on dinner camps where solitary hunting offers lower returns than cooperative hunting. We would also expect solitary and cooperative hunting returns to be correlated across time and space: camps that see lower solitary returns should also see lower cooperative hunting returns.

Because sand monitor harvests are always shared (on average an individual keeps 55±3% of any catch), return rates for cooperative vs. solitary hunting should be based on what a hunter (and his or her dependents) actually consumes after all sharing has taken place. Cooperative hunting may not provide higher acquisition returns, but cooperative hunters may be able to collectively defend a greater percentage of their catch and thus keep more for themselves and dependents (lose less to sharing) than will solitary hunters (producer priority). Or, alternatively, cooperative hunters may be able to collectively exert stronger claims to the catches of other hunters, receiving more than solitary hunters. The end result should be that cooperative hunters have higher consumption returns (grams of meat consumed by self and dependents per hour of foraging) than solitary hunters:

H4: Cooperators have producer priority: higher consumption returns (grams of meat consumed by self and dependents per hour of foraging) than solitary hunters.

Behavioral ecologists have long recognized that if individuals consistently differ in their pre-distribution foraging return rates due to skill or effort, and do not assort according to those skill levels, better or more productive hunters will be disadvantaged by cooperative hunting. If in the sharing of the harvest, better hunters do not receive a greater proportion of the catch than poorer hunters, they will not gain from cooperation and so should cooperate less frequently than poorer hunters:

H5: If there is heterogeneity in forager skill or production, better hunters should cooperate less frequently than poorer hunters.

If we find that better hunters continue to cooperate at the same frequency as poorer hunters, we can ask what direct or indirect benefits they might be receiving. We first focus on explanations for why there are consistent differences in hunter production — why do better hunters not simply quit earlier? One plausible explanation for overproduction is that it does benefit hunters to produce more in the short-term because those who demonstrate that they are better hunters may eat more in the end, either because others might be more likely to give to them (reciprocity) or they might be able to keep more of their own production for themselves (producer priority). We then turn toward explaining why better hunters cooperate so much. One plausible explanation is that better hunters have the social capital to be able to discriminate against their partners more readily, and while they may not be choosing to assort based on hunting skill, they may be more likely to pair up with kin or co-resident household members than are poorer hunters. Thus, while good hunters take on a cost to cooperate, they mediate that cost by directing the benefits of cooperation to close kin or other with whom they interact reciprocally on a daily basis.

If better hunters choose more often to cooperate with kin or members of their own residential camps, they ensure that the subsequent pooling in primary distribution provides benefits to kin or residential camp members who might reciprocate in other ways. If so, we would expect a strong interaction between kinship and/or residency and the difference in hunt rank between partners. As the difference in rank between two cooperating partners increases, the effects of kinship and residential camp membership on the percentage of time partners affiliate should become stronger, thus:

H6: Better hunters should (a) benefit directly through having higher consumption returns or (b) benefit indirectly through biasing cooperative partner choice to kin or co-resident household members.

2. Methods

The contemporary foraging data described here were collected over 27 months between 2000 and 2009, primarily in the region surrounding the Parnngurr community, but trips were also made to more remote locations and to locations surrounding the communities of Punmu and Kunawarritji. Given that Martu now operate out of permanent communities (ranging in size from 5 to 20 residential camps), foraging parties usually use vehicles to access more remote foraging locales. The foraging party typically leaves the community together and establishes a temporary logistical camp, what Martu refer to as a "dinner-time camp", after arriving at an agreed-upon foraging locale. Sometimes a dinner camp is used only on a single day, sometimes repeatedly. Dinner camp locations are established proximate to particular resource patches; thus most camps are characterized by strong correlations among foragers in the types of resources acquired. After foraging, all participants reconvene at the dinner camp to butcher, cook, share and consume the resources acquired over the course of the day's hunting and gathering activities. The dinner camp thus has both social and spatial dimensions that change daily with the nature of foraging and contrasts with the less ephemeral (albeit still flexible) residential camp.

Between 2000 and 2009, we accompanied a total of 230 single and multi-day dinner camps, averaging 8.0±3.3 (S.E.) participants (2.3±1.1 men, 3.6±0.8 women, 2.1±1.4 children), although groups of over 20 are not uncommon. On dinner camps, we recorded 1324 individual adult foraging bouts conducted by 105 different adults. Bouts were defined as the time an individual forager spent away from a camp engaged in one of 11 mutually exclusive foraging activities (see Bird et al., 2009, for details). Because resource distributions are patchy in time or space, generally individuals engaged in only a single bout per day. On a few occasions, foragers came back to the camp for lunch and went out again in the afternoon; such episodes were scored as separate bouts. Adult foraging bouts across all activities averaged 159±88 min (not including travel time between the community and the dinner camp). A subset of these bouts were detailed focal individual follows (n=649 adult follows), where a researcher recorded all of the time a specific individual allocated to the different components of foraging (search, pursuit, capture, field processing and transport) and the yield from all items of all resource types. Each individual in the dataset was assigned membership to an age class, given that few individuals over the age of 40 know their birthdates: 0–5, 6–10, 11–20, 21–40, 41–60, 61–80 and 80+. Membership to younger age classes was assigned using actual birthdates, but the oldest age classes were assigned following Howell (1979).

A foraging bout was scored as cooperative using two criteria: (1) individuals were observed to come together at least once to search for or pursue the same prey item(s) and/or (2) individuals pooled their harvest while foraging in the same patch prior to returning to the central place. In the monitor hunting dataset, there are 226 solitary and 168 cooperative hunting bouts. Of the 168 cooperative hunts, prey from 124 hunts were evenly pooled among members that hunted together; on the remaining 44 hunts (35%), harvests were divided unevenly. The sand monitor hunting dataset includes 84 individual hunters, 29 of which we recorded more than four bouts each, distributed over 139 dinner camp days. On a subset of these monitor hunts secondary distributions were fully recorded. The secondary distribution database consists of 153 observations of potential recipients over 18 different dinner camps where all foragers focused on sand monitor hunting and we were able to record how much in total recipients acquired, kept, distributed to others and received from others. 81.2% of those recipients were hunters themselves.

Because we wished to control for individual heterogeneity in foraging returns in addition to the effects of cooperation by foraging activity, we analyzed the data for most analyses using linear mixed models, which incorporate individual differences as a random effect in the model. As the database consists of individual observations of per capita hunting returns, but those returns are correlated for all members of a cooperative hunting party, we include a weighting term for each individual corresponding to the inverse of the party size in which that individual collaborated. For the analysis of proportional data, including percentage of cooperative or successful hunts, we use a generalized linear model with a logit link function. All analysis was performed using JMP (SAS Institute, 2008).

3. Results

3.1. Are per capita return rates higher with cooperation across all foraging activities?

Hypothesis 1 predicts that cooperation should increase mean per capita return rates across all foraging activities, but as Table 1 shows, there were few consistent effects of cooperation on foraging return rates. For nearly all *collecting* activities, cooperation had no significant effect on foraging return rates. The one exception was grub collecting return rates, which were significantly lower for cooperative bouts. The only *hunting* activity to show weakly significant effects of cooperation was sand monitor hunting, but in the opposite direction predicted: cooperation is correlated with reduced, rather than increased mean per capita returns.

3.2. Does cooperation reduce the chances of a failed bout?

Hypothesis 2 predicts that women particularly should cooperate more often in activities that have a higher chance of a failed bout. Men and women cooperated at the same frequency when foraging for collected resources (honey, grubs, fruit or nectar), but women cooperated significantly more often than men when hunting (Table 2). Across all foraging activities, the proportion of bouts that failed significantly predicted women's proportional cooperation in that activity, but not men's (Fig. 1).

Table 1
The effect of cooperation across foraging activities

Foraging activity (model)	No. of parties (% Coop)	Model parameter	Model estimate	Effect test *F*	*p* value	Return rate(±S.E.) by group size and gender				
						Solitary female	Cooperative female	Solitary male	Cooperative male	Mixed sex
Solanum fruit	61 (19%)	Intercept	1859		.0004	1664±455	1969±537	2196±756		
		Year [ran]		1.50	.2200					
		Forager [ran]		.74	.7951					
		Cooperation	231	.53	.4690					
Apis honey	7 (86%)	Intercept	7419		.0536	6867±2956			3976±1240	6355±897
		Year (ran]		.22	.6519					
		Forager [ran]		.42	.8895					
		Cooperation	−1890	.36	.5738					
Hakea nectar	13 (23%)	Intercept	10,239		.0001	10,746±3069	8779±3001	10,954±3657		10,371±3380
		Year [ran]		11.06	.0127					
		Forager [ran]		2.60	.1185					
		Cooperation	−1172	1.86	.2140					
Grub	53 (11%)	Intercept	262		.0008	454±48	236±104	413±141		502±189
		Year [ran]		4.92	.0023					
		Forager [ran]		1.05	.4433					
		Cooperation	−138	5.31	.0288					
Sand monitor	447 (41%)	Intercept	639		.0001	727±68	570±63	656±88	558±216	686±77
		Year [ran]		4.01	.0003					
		Forager [ran]		1.90	.0001					
		Cooperation	−46	3.80	.0517					
Feral cat	15 (61%)	Intercept	1140		.2616	1174±65	717±107	2371±1278		
		Forager [ran]		.23	.9924					
		Cooperation	−894	.04	.8386					
Perentie	49 (53%)	Intercept	389		.1913	21±352	699±310	605±367	561±478	901±337
		Year [ran]		.42	.7892					
		Forager [ran]		.41	.9927					
		Cooperation	204	1.61	.2096					
Bustard	159 (47%)	Intercept	17,018		.1374		10,673±22,614	20,563±9043	4171±7704	9730±9751
		Year [ran]		3.62	.0010					
		Forager [ran]		2.03	.0002					
		Cooperation	−3692	.64	.4320					
Kangaroo	81 (31%)	Intercept	1316		.2322			2280±705	425±806	1147±1329
		Year [ran]		.25	.9691					
		Forager [ran]		.77	.7724					
		Cooperation	−641	1.09	.2978					

To test whether cooperation increases per capita foraging returns over solitary hunting, we analyzed separate linear mixed models within each foraging activity predicting per capita foraging returns with one fixed effect (cooperative or solitary group) and two random effects: the identity of each forager, and year of observation. As the unit of analysis is the bout, and some bouts involve multiple individuals cooperating, we weight each bout by the inverse of the number of individuals in the party. For each model, we report the *F* statistic for the effect tests on each covariate and its associated *p* value, as a measure of its significance in predicting variation in foraging return rates for that activity. Whole model statistics: fruit collect (*df*=75, *F* ratio=1.107, *p*=.3755), honey (*df*=18, *F* ratio=.801, *p*=.6578), nectar (*df*=15, *F* ratio=3.211, *p*=.0710), grub (*df*=58, *F* ratio=1.806, *p*=.0598), sand monitor (*df*=680, *F* ratio=2.305, *p*=.0001), cat (*df*=25, *F* ratio=.403, *p*=.9453), perentie (*df*=80, *F* ratio=.501, *p*=.9810), bustard (*df*=297, *F* ratio=2.930, *p*=.0001), kangaroo (*df*=124, *F* ratio=.812, *p*=.7524).To the right, we also report the mean foraging returns for each activity by type of foraging party. These are the estimated marginal means derived from analyzing the same models separately by type of foraging party (solitary female, solitary male, cooperative female, cooperative male and cooperative mixed sex).

3.3. Does cooperation in sand monitor hunting increase per capita returns, harvest sizes, success probabilities or reduce foraging time?

We now turn toward examining the effects of cooperation within the most common hunting activity, sand monitor hunting. Hypothesis 3, Prediction (a) of the mutualism hypothesis states that cooperation should increase the per capita return rate. Our previous analysis showed that cooperative sand monitor hunting has only a weakly significant effect on foraging returns, but in the opposite direction predicted: cooperative hunting predicts lower return rates. When we analyze men's and women's cooperative monitor hunting separately (Table 3), we find that cooperation does significantly decrease women's foraging returns, but has no effect on men's. Cooperation reduces women's mean marginal foraging returns by 114 kcal/h, from 704±77 to 590±74 (here, and below, we report the estimated marginal mean±S.E., which controls for the effects of the other covariates on harvest size).

A correlation between low returns and cooperation could mean either that cooperation causes low returns or

Table 2
Logistic regression models within each foraging activity predicting cooperation (as a dichotomous outcome vs. solitary hunting) with gender

Activity	Main prey/ patch	Frequency of failed bouts	No. of female bouts cooperative (%)	No. of male bouts cooperative (%)	Likelihood ratio χ^2: sex	Odds ratio cooperative F/M	p value
Collecting	Roots/corms	0.083	0 (0%)	0 (0%)			
	Solanum fruit	0.084	26 (38.2%)	3 (30%)	0.25	1.44	.6101
	Apis honey	0.105	6 (85.7%)	12 (100%)	2.09	0	.1479
	Hakea nectar	0	4 (36.6%)	2 (40%)	0.02	0.86	.8895
	Grub	0.016	10 (18.2%)	2 (50%)	1.90	0.22	.1684
Hunting	Sand monitor	0.108	358 (65.2%)	57 (43.2%)	21.21	2.47	.0001
	Feral cat	0.077	18 (94.7%)	2 (28.5%)	8.25	44.99	.0006
	Perentie	0.372	43 (78.2%)	14 (56.0%)	3.98	2.81	.0460
	Bustard	0.536	50 (98.0%)	163 (65.9%)	29.76	25.73	.0001
	Kangaroo	0.848	6 (100%)	63 (52.9%)	7.37	23,981	.0066

Odds ratio gives the log odds of a female forager cooperating in that activity relative to a male forager. The odds ratio for kangaroo hunting is anomalously high because women were always observed to cooperate.

that people are more likely to cooperate when returns are likely to be low, and that cooperation is simply making the best of a bad situation. If the latter, we would expect a greater percentage of individuals to hunt cooperatively on dinner camps where solitary hunting offers lower returns. We would also expect solitary and cooperative hunting returns to be correlated across time and space: camps that see lower solitary returns should also see lower cooperative hunting returns. Out of a total of 149 days with monitor lizard hunts, there were 73 days that had both cooperative and solitary hunting bouts, with an average of 3.76 individuals hunting alone and 2.24 individuals cooperating per day. Mean return rates for solitary hunters did not predict the proportion of individuals who cooperated (GLM model: log likelihood=.003; Estimate$_{\text{solitary}}$=.00003, likelihood ratio χ^2=.0069, p=.9334). Solitary and cooperative returns were not correlated across camp days either (least squares model: r=.160, p=.1749). Return rates on days when there were both cooperative and solitary hunts were significantly lower for individuals who cooperated compared to those who did not (paired t test: mean difference=−201, t_{72}=−2.84, p=.0058).

Hypothesis 3, Prediction (b) states that cooperation in sand monitor hunting might allow foragers to acquire larger harvests than they could by hunting alone, but we find that cooperation among women reduces per capita harvest size by 280 kcal when controlling for other sources of variability (foraging time, season, year and individual; see Table 3). Prediction (c) suggests that cooperating might also allow foragers to find prey more quickly, reducing total foraging time, but we find that cooperation among women increases foraging time by an average of 20 min. For male foragers, however, cooperation has no significant effect on mean harvest size or foraging time.

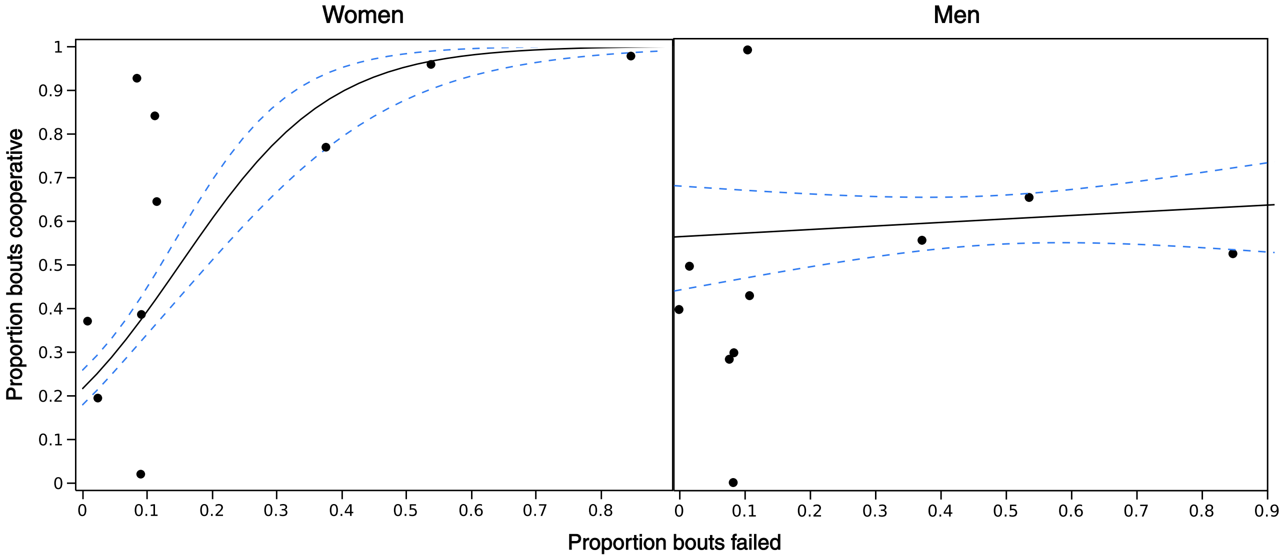

Fig. 1. Generalized linear models predicting the proportion of cooperative bouts in that foraging activity by the proportion of bouts that fail. Women: log estimate of success on % cooperation=8.59, χ^2=89.79, p<.0001; men: log estimate of success on % cooperation=.327, χ^2= .5303, p=.4665.

Table 3
Least squares mixed models predicting per capita bout return rates (kcal/h), total harvest size (kcal) and foraging time (min) with cooperation

	DF	Estimate	Effect test *F* ratio	*p* value
Model 1: Women's return rate (kcal/h)				
Intercept		647		.0001
Season	2		0.01	.9908
Forager [random]	40		1.94	.0007
Year [random]	7		4.04	.0003
Cooperation=yes	1	−57	5.82	.0162
Model 2: Women's harvest size (kcal)				
Intercept		190.7		.4358
Foraging time	1		100.01	.0001
Season	2		2.61	.0747
Forager [random]	40		2.82	.0001
Year [random]	7		4.04	.0003
Cooperation=yes	1	−140.0	4.51	.0341
Model 3: Women's foraging time (min)				
Intercept		159.3		.0001
Season	2		14.24	.0001
Forager [random]	40		1.80	.0024
Year [random]	7		3.72	.0006
Cooperation=yes	1	9.9	9.00	.0028
Model 4: Men's return rate (kcal/h)				
Intercept		938.8		.0001
Season	2		6.55	.0021
Forager [random]	18		1.51	.1003
Year [random]	7		1.95	.0912
Cooperation=yes	1	19.2	0.05	.8138
Model 5: Men's harvest size (kcal)				
Intercept		1617		.0169
Foraging time	1		4.94	.0283
Season	2		10.81	.0001
Forager [random]	18		1.64	.0634
Year [random]	5		1.01	.4154
Cooperation=yes	1	74.9	0.09	.7591
Model 6: Men's foraging time (min)				
Intercept		134.8		.0001
Season	2		2.15	.1206
Forager [random]	18		1.58	.0786
Year [random]	5		1.01	.4100
Cooperation=yes	1	−8.9	0.79	.3758

Each model includes the covariates' year of observation (which stands as a proxy for climatic effects due to rainfall), season of observation and forager ID as a random effect to account for multiple observations of hunting by the same individuals, with per capita values weighted by the inverse of the number of foragers in the foraging party. Harvest size model includes minutes foraging time as a covariate to control for the strong effect of foraging time on total harvest size for both cooperative and solitary hunts. Statistics for the sand monitor whole models: women (df=548): return rates F ratio=2.495, p=.0001; harvest size F ratio=6.424, p=.0001; total foraging time F ratio=3.02, p<.0001. Men (df=131): return rates F ratio=1.788, p=.0210; harvest size F ratio=2.827, p=.0001; foraging time F ratio=2.37, p=.0011.

Hypothesis 3, Prediction (d) states that even if cooperation (for women) reduces per capita returns and increases foraging time, it may still provide risk minimization benefits if individuals are more likely to successfully acquire any prey at all when cooperating. In total, there were 38 out of 268 solitary bouts and 33 out of 423 cooperative bouts that failed. A simple analysis of failure frequency by foraging group type (solitary male, solitary female, cooperative female and mixed sex, excluding cooperative male, as there were only three cooperative male hunting parties) shows that cooperation has little effect on failure for women: solitary female parties failed 9.1% of the time, and cooperative parties 7.8%. Cooperation did have big effects for men, dropping the chances of failure from 21.2% when foraging alone to 5.6% when foraging with a female partner. To test for the significance of these differences, we use a logistic regression model that controls for the effects of foraging time on the log odds of success. When women cooperated with other women, there was no significant effect of cooperation on the log odds of success ($\text{Estimate}_{\text{solitary}}$=.039, χ^2=.040, p=.8495). However, solitary men had significantly lower odds of success compared to men cooperating with women ($\text{Estimate}_{\text{men}}$=−0.822, χ^2=6.35, p=.0117).

3.4. Do cooperators keep more or receive more meat from others?

Hypothesis 4 states that the benefits of cooperation are gained not through acquisition, but through distribution: cooperators have higher consumption returns (grams of meat consumed by self and dependents per day) than solitary hunters because they keep more or receive more from others.

In focusing on this prediction and others involving consumption returns, we used the secondary distribution dataset of 153 individual-based observations on all members of 18 sand monitor hunting camps, where monitors were the only resource acquired and shared. Because the consumption returns any individual gained is necessarily a function of a variety of variables including cooperation, in order to compare across different camp days we used a multivariate linear mixed model predicting net grams of meat consumed per day by whether or not that individual cooperated while hunting, controlling for potential confounds including the time recipient spent hunting, the total harvest of all camp members, total camp population and the amount the recipient acquired through his or her own hunting effort. We found that cooperators were actually at a disadvantage relative to solitary hunters in consumption returns (Table 4). With all other covariates held at their median values, cooperation reduces mean consumption returns by 79 g/day. There were also strong effects of total camp production on the amount consumed: the more everyone produced, the more individuals ate, but individual production was only a weakly significant predictor of individual consumption because those who failed to acquire did not eat significantly less than those who acquired something. Holding all covariates at their median values, consumption returns go from 616 g/day when individuals did not acquire anything themselves, to 880 g/day at an individual harvest of 3 kg. Increasing the total harvest of all camp members provides more than a threefold increase in consumption, from 538 g/day at a total camp

Table 4
Modeled effects of cooperation on post-consumption net returns as grams of meat consumed per day

Parameter	Estimate	Likelihood ratio χ^2	Significance	Predicted value over range of parameter (range)
Model 1: Cooperation				
Intercept	6.478	200.02	0.0001	650
Cooperation=yes	−0.067	5.70	0.0170	561–642 (yes, no)
Total camp harvest (gram whole weight)	0.0001	73.48	0.0001	538–1535 (3096–14,860)
Amount forager acquired (gram whole weight)	0.0001	9.20	0.0024	616–880 (80–2950)
Total camp population	−0.078	40.89	0.0001	947–344 (5–18)
Time forager spent hunting (min)	0.0009	3.21	0.0733	553–834 (0–452)
Model 2: Cooperation by hunt rank				
Intercept	6.578	150.92	0.0001	719
Cooperation=yes	−0.07	5.50	0.0190	571–651 (yes, no)
Hunting rank	−0.004	1.13	0.2766	657–643 (1–31)
Cooperation=yes by rank	−0.003	0.91	0.3406	610–509 (1–31)
Total camp harvest (gram whole weight)	0.0001	62.16	0.0001	523–1598 (3096–14,860)
Amount forager acquired (gram whole weight)	0.0001	5.92	0.0150	618–850 (80–2950)
Total camp population	−0.080	35.89	0.0001	963–399 (5–18)
Time forager spent hunting (min)	0.0009	2.52	0.1123	602–839 (0–452)

Generalized linear model using a normal distribution and log link function. Model 1: −2LL=66.66, *df*=5, χ^2=133.3, *p*=.0001. Model 2: −2LL=58.48, *df*=7, χ^2=116.93, *p*=.0001. Predicted values are the model estimate of the grams of meat consumed per day across the range of that covariate, holding all other covariates at their median values.

harvest of 3 kg, to more than 1500 g of meat per person at a camp production of 15 kg. Increasing camp size reduces individual consumption, from 947 at a small camp of 5, to 344 in a large camp of 18. These data show that sand monitor harvests are subject to a strong form of pooling that resembles tolerated scrounging, where consumption tends to be equalized across all hunting camp members. As a result, the individual consumptive benefits of high production are much lower than the benefits to the group as a whole.

3.5. Do better hunters cooperate less frequently than poorer hunters?

Hypothesis 5 predicts that if there is heterogeneity in forager skill or production, better hunters should cooperate less frequently than poorer hunters. In our previous analysis of the effects of cooperation on return rates, harvest size and foraging time, we found forager identity to have a strongly significant effect on all three outcome variables (Table 3), suggesting that there was a great deal of heterogeneity among foragers. Some hunters seem to have higher returns, larger harvests and spend more (or less) time hunting than others. This may be why we do not see any benefits to cooperation when we average across all individuals. Because of this substantial variability among hunters in production or skill levels, if better hunters do not positively assort with one another, they will often end up cooperating with poorer hunters, and while poorer hunters will show an increased per capita return with cooperation, better hunters will do worse because they are supporting poorer hunters. If this is the case, better hunters maximizing personal returns should simply choose to cooperate less often.

To test this hypothesis, we used a paired means comparison of 22 women and 11 men foraging alone and cooperatively. Hunters were included in the analysis if there were more than 10 hunts in both treatments (cooperative and solitary) for which return rates could be calculated (the average was 29 hunts per individual, ranging from 10 to 153). We ranked each hunter according to the highest average acquisition return rate when hunting alone. Hunters are ranked from 1 to 33, where 1 was the best hunter and 33 the poorest. We used rank as a continuous variable in a least squares regression to predict the relative difference in return rates between cooperative and solitary hunting. We then asked whether hunter rank predicted the frequency of cooperative hunting.

We found that heterogeneity among foragers did affect the relationship between cooperation and per capita foraging acquisition returns. Only the consistently less productive female hunters had higher acquisition return rates when cooperating: each unit drop in rank (e.g., from 1 to 2) resulted in an average 20.7 kcal/h increase in relative acquisition return rate when cooperating (Fig. 2, Panel A). Hunters ranked 20 and lower had consistently positive relative returns, meaning they did better when cooperating, and hunters ranked above 20 (better hunters) had consistently negative relative returns. The model predicts a hunter at Rank 1 to lose out by −457 kcal/h, and a hunter at Rank 35 to gain by 247 kcal/h with cooperation, a 185% difference in returns. There was no corresponding effect of hunter rank for male hunters (Estimate=55.37, t_{30}=1.71, *p*=.1209). Because higher ranked female hunters had lower returns when cooperating, we expected them to cooperate less often, but the relationship was surprisingly weak (Fig. 2, Panel B). The model predicts only a 10% difference in cooperation between high-ranked and low-ranked hunters.

3.6. Do better hunters compensate for the cost of cooperation by keeping more or biasing partnerships toward kin?

Our analysis of cooperative hunting reveals that cooperation tends to disadvantage better female hunters by as much

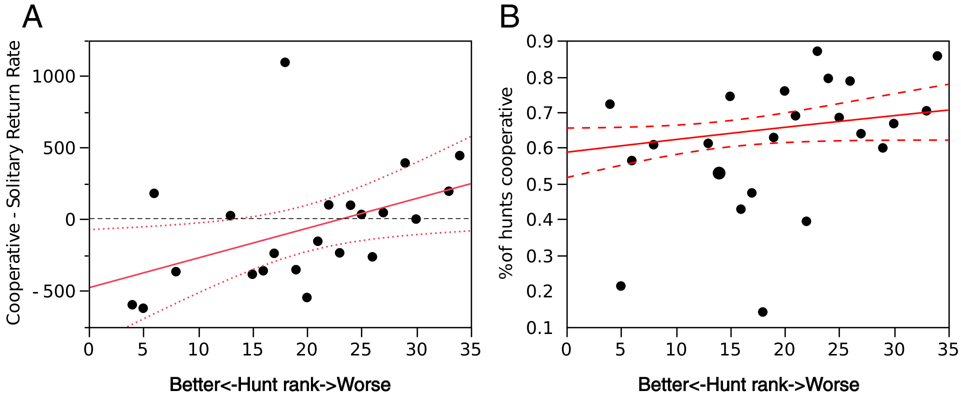

Fig. 2. (Panel A) Linear regression model (with 95% confidence intervals) of women's hunt rank as a predictor of the difference in foraging returns when cooperating compared to hunting alone. The mean difference across women was −61.7 kcal/h. A positive difference score indicates that individuals do better with cooperative hunting; a negative score that individuals do better with solitary hunting. The model predicts a hunter at Rank 1 to lose out by −457 kcal/h, and a hunter at Rank 35 to gain by 247 kcal/h with cooperation, a 185% difference in returns (Estimate=20.7, F=5.27, p=.0326). (Panel B) Generalized linear model (with 95% confidence intervals) of women's hunt rank as a predictor of the proportion of monitor hunts cooperative. The mean proportion of cooperative hunts across women was 61.7%. There was a weakly positive relationship between hunt rank and proportion of hunts observed to be cooperative (−2LL=1.54, log estimate=.015, χ^2=3.07, p=.0793). The model predicts only 11% difference in cooperation between the highest and lowest ranked hunters: 59% at Rank 1 and 70% at Rank 35.

as 185%, yet they are only 10% less likely to cooperate. Because we find that better hunters still cooperate at a fairly high rate compared to the poorest hunters, Hypothesis 6 expects them to compensate for this cost by keeping more of their production for themselves or by biasing cooperative partner choice to kin or co-resident household members.

If better hunters were rewarded for their cooperation with more food from others and/or were better able to keep their production for themselves, we would expect there to be a positive interaction between hunting rank and cooperation on consumption returns, that is, high-ranked hunters should end up with larger consumption portions when they cooperate compared to lower ranked hunters when they acquire a harvest of a given size. Because consumption returns are a function of many other factors, we must also control for the effects of total camp production, total camp population and the time the forager spent hunting. But as Table 4 shows (Model 2: Cooperation by hunt rank), there is no interaction between rank and cooperation on consumption returns: solitary hunters gained significantly higher consumption returns at any given harvest size and over all ranks than did cooperating hunters. Thus, we are able to reject the hypothesis that high-ranked hunters are more likely to benefit through cooperation: they do not eat more at a given harvest size than low-ranked hunters. This suggests that high-ranked hunters must be sharing a greater proportion of the meat they produce relative to other camp members on that day, and, indeed, overall, the highest ranked hunters (Ranks 1–10) gave away an average of 34±4% of all their meat income (acquired by themselves and others), medium-ranked hunters (11-21) gave away 27±4% and low-ranked hunters (21-35) 16±6%.

In the second test, we ask whether better hunters cooperate so much because they gain nepotistic benefits through the initial pooling with close kin or residential camp members. If so, we would expect to see an interaction between the differences in rank between potential cooperative partners and both relatedness and residential camp membership as predictors of the probability that any two individuals at the dinner camp will cooperate with each other on a sand monitor hunt (the affiliation score). In other words, when rank differences are larger between potential partners, we would expect the probability of affiliation to be higher for closer kin or members of the same residential camp.

Our analysis looks at the probability of affiliation for female–female dyads in three separate generalized linear models: the first explores the relationship between the affiliation score and the covariates relatedness, rank differences between partners and the interaction between the two; the second model includes only the effect of household membership, differences in rank and the interaction between the two on affiliation, and the third model includes both relatedness and household membership, along with differences in rank and its interactions. The first model (Table 5) showed no significant effect of rank differences and no significant interaction between rank differences and relatedness. The second model predicts affiliation with rank differences and residential camp co-residency and again shows no effect of rank differences and no interaction between rank and co-residency. In the third model, we control for the fact that residential camp membership and relatedness will obviously covary and find that only kinship remains a significant predictor of affiliation, indicating that any effects of residency are driven by the interaction between camp residency and relatedness. Because there was no significant interaction between rank differences and kinship or residential camp membership, we can reject the hypothesis that cooperative hunting

Table 5
Results from three generalized linear models predicting affiliation with differences in rank, household co-residency and relatedness between potential cooperative partners

Term	Estimate	S.E.	χ^2	*p* value
Model 1: The effects of rank differences (DIFFRANK) and kinship (RELATE) on the probability of affiliation				
Intercept	−1.998	0.443	26.657	.0001
DIFFRANK	0.017	0.041	0.180	.6716
RELATE	5.738	1.334	19.061	.0001
(RELATE−0.047)∗(DIFFRANK+9.222)	−0.038	0.235	0.027	.8698
Model 2: The effects of rank differences (DIFFRANK) and household co-residency (HH) on the probability of affiliation				
Intercept	−0.916	0.504	3.205	.0734
DIFFRANK	0.028	0.048	0.337	.5615
HH [cores]	0.745	0.283	6.119	.0134
HH [cores]∗(DIFFRANK+9.222)	0.012	0.048	0.059	.8088
Model 3: The effects of rank differences (DIFFRANK), household co-residency (HH) and kinship (RELATE) on the probability of affiliation (binomial logit GLM)				
Intercept	−1.60	0.744	5.274	.0216
DIFFRANK	0.049	0.069	0.529	.4671
HH [cores]	0.094	0.549	0.028	.8670
HH [cores]∗(DIFFRANK+9.222)	0.040	0.068	0.353	.5523
RELATE	5.632	1.819	11.992	.0005
(RELATE−0.047)∗HH [cores]	−0.726	1.793	0.157	.6913
(RELATE−0.047)∗(DIFFRANK+9.222)	−0.154	0.291	0.283	.5949

For all three models, we constructed a matrix database of all possible dyadic partnerships in a subsample of sand monitor hunting dinner camps (*n*=24) for which the cooperation status of all camp members was recorded. This resulted in 381 possible dyadic partnerships for which we recorded the type of dyad (MM, MF or FF), the affiliation score (AFFIL) calculated as the number of days cooperation was observed divided by the number of days the dyad was "at risk" to cooperate, the genealogical relatedness of the pair (RELATE), and whether or not the pair resided in the same residential camp while in the community (HH). Each dyad member was given a hunting rank based on their overall mean foraging return rate when hunting solitarily. The difference in ranks (DIFFRANK) was constructed by subtracting the lower ranked member of the dyad from the rank of the higher ranked member, with higher numbers indicating poorer hunters. Thus more negative numbers are associated with pairs far apart in rank (high-low dyad types), while numbers closer to zero are associated with dyads composed of members of similar ranks. Because our dependent variable, AFFIL, is a proportion representing the percentage of time a partner was available to cooperate that they actually did so, we used a generalized linear model with a binomial distribution and a logit link function.

partners far apart in rank are more likely to be close kin or members of the same residential camp.

4. Discussion

Cooperative hunting among Martu does not predictably increase per capita foraging returns for any hunting or collecting activity. Sand monitor cooperative hunting in particular is associated with a significant decrease in per capita foraging returns on average. This seems to be due primarily to forager heterogeneity in skill or effort, and to the lack of positive assortment among hunters of disparate skill levels. Men (who mostly cooperate with women) and poorer hunters who cooperate with better hunters tend to see their per capita returns increase, while better female hunters tend to do worse. Cooperation reduces per capita returns through both decreasing per capita harvest size and increasing the time each forager spends hunting. Although women's frequencies of cooperation across foraging activities correlate well with the expected chances of hunt success, cooperation among women does not increase the chances of a monitor hunt being successful and only increases men's chances of success because their solitary hunting is much more unsuccessful than women's. Given the 185% difference in returns gained by the poorest hunters compared to the best hunters when they cooperate, it was surprising that the poorest hunters were only 10% more likely to cooperate.

These results spurred us to ask what benefits compensated better sand monitor hunters for their relatively poor returns in cooperation: did better hunters get more meat from others, keep more for themselves or favor kin or co-residents more often as cooperation partners? We found that better hunters did not gain more in secondary distributions and actually gave away a greater proportion of their own harvest than poorer hunters, leading to consumption payoffs that did not reward productive effort. Better hunters were not likely to choose kin or co-residents as cooperation partners than poorer hunters: no one favored cooperating with other members of their residential camp, and all hunters, regardless of rank, cooperated more often with kin. Because Martu do not choose hunt partners on the basis of skill, better hunters often pair up with poorer hunters and end up subsidizing their partners, working harder to produce more. But better hunters do not keep the surplus they gained in primary distribution, but give away relatively more of their harvest than poorer hunters in secondary distributions, leading to an equalization of consumption across all people present at the DTC regardless of their productivity (see similar results in Bird et al., 2009).

4.1. Signaling, generosity and the hierarchy of virtue

While a poor hunter may be motivated to cooperate by the increase in his or her per capita foraging returns, better hunters are not receiving direct benefits, either through mutualism, reciprocity or nepotism. However, the cultural contexts surrounding hunting and sharing do give us some clues about other pathways through which benefits might flow. Better hunters may be trading off an immediate loss in foraging return rates against future increased benefits achieved through building or maintaining a reputation for generosity, which in turn builds one's social capital (Gurven et al., 2000; Smith & Bliege Bird, 2005). To do so requires communicating honest information about one's hidden qualities: here, one's motivation to work for the benefit of others in provisioning public goods. Costly signaling theory predicts that the most honest signals of hidden qualities will be those that involve quality-linked costs, where the guarantee for honesty is the cost the signaler pays in sending the signal. The costs linked to public interest motivations are often those of pecuniary disinterest (Gambetta, 2009), that is, individuals fail to claim an individual benefit they have every right to take, instead directing that benefit toward the promotion of other individuals. In so doing, however, they do gain social capital (prestige, influence, social network position) that can be translated into material benefit.

As signaling is an act of communication, understanding the nature of the information being signaled requires first an attention to the cultural meanings surrounding hunting and sharing. Among Martu, the road to influence, renown and power is through generosity, rather than through accumulation (Myers, 1986; Sackett, 1979). Social distinctions are generated not through material possession, but through dispossession, what has often been described as a disengagement with property (Bird & Bliege Bird, 2010; Tonkinson, 1988). When Martu talk about hunting, they often describe their underlying motivation as "hunting to share" (Bliege et al., 2008). One who produces more and shares more of that production with others is *mirtilya*:

> "When a mirtilya goes out hunting she has a good feeling that she's going to get so much and be able to feed others. Good hunters always think that when they go out and it helps them to hunt better...When a really good hunter goes out, she gives so much away and takes home only a small piece for herself. But she will always walk away feeling pukurrpa."

Mirtilya refers to a skillful hunter who consistently acquires and shares production, particularly in the context of providing food not only for his or her own family, but for those with whom she has little obligation to share. A *mirtilya* is a person who not only frequently gives, but a person who frequently has things to give — a person who works harder than others so that surplus production can be distributed to all (see Bliege et al., 2008, for additional details). Implicit within the definition of *mirtilya* is that it is "other-regarding": one does not share for gain, but because one genuinely cares about feeding others — *yunkupayi*, sharing without the expectation of return. But Martu do believe that *mirtilya* gain benefits from their effort. *Pukurrpa* is what many Martu see as the reward for *mirtilya*: *pukurrpa* means generally "warmth and happiness", but a happiness that is the product of *yunkupayi* that binds people together (see also Myers, 1986). Without *yunkupayi*, "you feel you're not in a family. You're just for yourself, not for everybody. You don't share things". This does not mean that all sharing is expected to be *yunkupayi*, but that *yunkupayi* is idealized as the process that creates cooperative and familial social relationships.

This would seem to suggest that better hunters should avoid cooperating, as they could gain even more *pukurrpa* through sharing the larger harvests they acquire while hunting alone. The solution to this puzzle may lie in the concept of *kanyininpa*, which means holding and nurturing and can refer to nurturing the autonomy of others (see Myers, 1986, for an extensive discussion). As Mauss (1924) noted in *The Gift*, and Martu recognize, one who is constantly giving and never receiving gains social power through the creation of hierarchy. Consistent one-way flows might appear to maximize one's generosity, but in fact they do the opposite: they create tension and inequality. To be considered truly generous in the Martu way, one must be "honestly" generous and to share in such a way that fosters egalitarian relationships and social autonomy: one must share not only one's economic production, but one's social capital gained through that production. Through unrestricted cooperating, a hunter gives others the opportunity to gain social capital and thus signals that she is willing to contribute to the holding of others.

Cooperating without regard for your partner's skill or level of effort and pooling equally is one way to share the social rewards gained through hunting: as one woman put it, "I like to hunt with someone who is going to share. If we hunt together, I will give you half of what I get. Then you have something to share even if you didn't get lucky yourself. You're looking out (*kanyinin*) for someone else [by cooperating]" (Nola Taylor, personal communication, 2004). There may also be social costs to restricting cooperation: if a good hunter were to eschew cooperation in favor of solitary hunting, she would be accused of being greedy, of not wanting to split her harvest with a partner. Excluding others from hunting with you, especially if you are a good hunter, may mean you prevent them from acquiring and thus exclude them from gaining the benefits of being able to demonstrate their own generosity. Martu do not simply gain social capital through giving, but through costly giving: the benefit better hunters gain is ascendance in the hierarchy of virtue (cf. Bourdieu, 1991). Cooperation becomes the better hunter's handicap, ensuring the honesty of the signal of one's commitment to *kanyininpa*. Such commitments are inextricably intertwined with *Yulpiriti*, the Law, which identifies the ideal conduct expected for a Martu person. As such, hunting, cooperation and sharing might be more appropriately compared to costly forms of religious ritual that promote cooperation and serve to mark and identify members of a religious group (Alcorta & Sosis, 2005; Sosis & Alcorta, 2003; Tonkinson, 2005).

There may be material benefits that flow to those who signal in this way. As Martu describe it, the benefits of being *mirtilya* (*pukurrpa*) come more indirectly from being at the center of a wide, cohesive social network created through looking after others. This conceptualization of the benefits of sharing echoes the argument Wiessner (2002) makes on behalf of the Ju/'hoansi, and one that Clutton-Brock (2002) makes for social animals in general: in sharing widely and generously, one might support an extensive family from which one might draw a variety of indirect benefits, including help in childrearing, deterrence from intergroup aggression and improved health and well-being. Similar benefits have been proposed to motivate individuals to engage in costly religious ritual and adhere to obligatory codes of conduct: for example, Orthodox Jewish men who pray frequently are more trusted to cooperate in experimental economic games (Ruffle & Sosis, 2007; Sosis & Ruffle, 2003), and religious communes with more strict obligations and ritual requirements tend to last longer than those with fewer, lower cost expectations (Sosis & Bressler, 2003).

Our ethnographic observations suggest a complex interpretation of signaling: we have hypothesized that overproduction might serve as a signal of skill (Bliege et al., 2008) and here argue that sharing such overproduction might be a signal of one's commitment to the public good — one's disinterest in gaining economically from one's skill. We also suggest here that cooperating indiscriminately with others is a signal of one's disinterest in the status gains from consistently giving. Signaling one's disinterest in pecuniary gain (and, conversely, one's interest in providing public goods) is a powerful way to earn respect from others (Gambetta, 2009). By cooperating with poorer hunters, better hunters make it possible for others to have the opportunity to give, which is an honest signal of their disinterest in gaining from the inequality that they have generated through overproduction. They have demonstrated that they are willing to assist others in gaining social capital. Such actions thus signal a commitment to material equality that, ironically, ends up perpetuating more social inequality. A better hunter who cooperates with others is still giving away more than anyone else, whether she is giving meat directly or giving others the opportunity to give. But what she accomplishes through the latter is a sharing network that is more egalitarian and which may foster trust and cooperative interactions in other arenas.

4.2. Women's cooperative hunting

The second issue we would like to explore here is why women cooperate more frequently than men. We had initially suspected that gender differences in cooperation, especially in the pursuit of mobile prey, might be due to women's greater risk aversion. We have already shown that much of Martu women's foraging time allocation decisions can be predicted by the degree of economic risk or variance in returns and harvest sizes (Bliege et al., 2008). If foragers are risk averse, they are likely to value a smaller reward with a higher probability of acquisition as much as a larger reward with a lower probability (Caraco, 1981) and so might trade off reductions in per capita returns with an increased chance of harvest success. Our results were somewhat equivocal: we did see an overall trend toward more cooperation in activities with higher risks of harvest failure, but cooperation did not increase the chances of success for sand monitor hunting.

We think that women may cooperate more than men in this context because they spend more time acquiring sand monitor, men in acquiring kangaroo and other larger prey. These decisions interact with differences in social strategies, particularly the way women organize child care and other productive labor. Women average more than 70% of their foraging time on hunting sand monitor, men only 30%. If cooperation is in part spurred by the need to give others the opportunity to share, sand monitor hunting creates more opportunities for inequalities in giving among women over the long-term than kangaroo hunting does among men. Kangaroo hunting is a stochastically varying activity, one where variability due to individual skill and effort is swamped by external sources of variability that are difficult, if not impossible, to predict. As such, it may be very difficult to tell whether one hunter is more productive than another (see Hill and Kintigh, 2009). Sand monitor hunting is very different. It is much more reliable than kangaroo hunting and associated with a positive correlation between foraging time and harvest size (Codding et al., 2010). This, together with low stochastic variation relative to forager skill/effort, leads to some hunters consistently being able to out-produce others.

Women may cooperate in order to reduce these inequalities because they have more to gain by doing so. Cooperative female social relationships may be more likely where cooperation is essential to female reproductive success, as it is among many communally breeding species (Clutton-Brock, 2002; Silk, 2007). There are many potential direct and indirect benefits females can gain by maintaining a network of cooperative relationships, but their ability to do so may vary with the extent to which they can remain in close proximity to other female kin (Yanca & Low, 2004). Elsewhere we have shown the importance of matrifocality in Martu historic residential patterns (Scelza & Bliege Bird, 2008) and the predominance of intergenerational cooperative partnerships, primarily for childcare (Scelza, 2009), and here we show that kinship ties are the most important predictor of cooperative hunting affiliation. Martu women's reproductive strategies may be critically linked to the formation of social ties with female kin. Martu women may thus cooperate more often than Martu men because they benefit more from maintaining closeness (spatial and social) to female kin, and better hunters reap more of the benefits from cooperative caretaking by virtue of the cohesive social networks they create around them (Scelza, 2009; Scelza & Bliege Bird, 2008).

5. Some conclusions and broader implications for understanding cooperative hunting

Despite the importance of understanding what sustains and maintains cooperation in the face of temptations to free-ride, especially under circumstances where labor and its products are shared, there has been comparatively little attention paid to the factors that influence variability in human cooperative foraging. While mutualism may often drive the benefits of hunting cooperatively, conflicts of interest, failures of coordination and heterogeneity among individual foragers in ability, foraging goals and access to jointly produced resources can interfere with attaining these benefits. Optimal group sizes for hunting may also fail to be achieved because of the social costs of exclusion and the social benefits of appearing generous. In societies characterized by egalitarian social structures and extensive demand sharing, cooperation might be particularly costly, especially for more successful hunters (see Hill, 2002). In such societies, some individuals consistently produce more than others, and in so doing support free riders to varying degrees. Our results show that any analysis of the benefits maintaining cooperation must consider how forager heterogeneity affects how those benefits are realized. Some foragers may benefit in immediate ways through increases in per capita returns, reductions in the chances of harvest failure or increases in harvest size, but others may use cooperation to gain other, more indirect benefits. Hunters may engage in cooperation as a social signal, using it to gain political capital or build a reputation for public goods provisioning (e.g., Smith & Bliege Bird, 2005), or cooperation may simply be a way to gain indirect benefits from being in a group, such as protection from predation or alloparental care (e.g., Clutton-Brock, 2002). As such, the individual benefits to cooperation may not always lie in direct material rewards, but also may facilitate the accumulation of social capital that can be used as currency to gain material rewards in other realms.

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References

Alcorta, C., & Sosis, R. (2005). Ritual, emotion, and sacred symbols: the evolution of religion as an adaptive complex. *Human Nature*, *16*, 323–359.

Alvard, M. S. (2001). Mutualistic hunting. In C. Stanford, & H. Bunn (Eds.), *Meat-eating and human evolution* (pp. 261-278). NY: Oxford U. Press.

Alvard, M. S., & Nolin, D. (2002). Rousseau's whale hunt? Coordination among big-game hunters. *Current Anthropology*, *43*(4), 533–559.

Bird, D. W., & Bliege Bird, R. (2010). Competing to be leaderless: food sharing and magnanimity among Martu Aborigines. In J. Kanter, & K Vahn, & J. Earkins (Eds.), *The Evolution of Leadership: Transitions in Decision Making From Small-Scale to Middle-Range Societies* (pp. 21-49). Santa Fe: SAR Press.

Bird, D. W., & Bliege Bird, R. (2005). Mardu children's hunting strategies in the Western Desert, Australia: foraging and the evolution of human life histories. In B. S. Hewlett, & M. E. Lamb (Eds.), *Hunter Gatherer Childhoods* (pp. 129-146). New York: Aldine de Gruyter.

Bird, D. W., Bliege Bird, R., & Codding, B. F. (2009). In pursuit of mobile prey: Martu hunting strategies and archaeofaunal interpretation. *American Antiquity*, *74*, 3–29.

Bird, D. W., Bliege Bird, R., & Parker, C. H. (2005). Aboriginal burning regimes and hunting strategies in Australia's Western Desert. *Human Ecology*, *33*, 443–464.

Bliege Bird, R., & Bird, D. W. (2005). Human hunting seasonality. In D. Brockman, & C. van Schaik (Eds.), *Primate Seasonality* (pp. 243-266). Cambridge: Cambridge University Press.

Bliege Bird, R., & Bird, D. W. (2008). Why women hunt: risk and contemporary foraging in a Western Desert aboriginal community. *Current Anthropology*, *49*(4), 655–693.

Bliege Bird, R., Bird, D. W., Codding, B. F., Parker, C., & Holland Jones, J. (2008). The fire-stick farming hypothesis: anthropogenic fire mosaics, biodiversity and Australian Aboriginal foraging strategies. *Proceedings of the National Academy of Sciences*, *105*(39), 14796–14801.

Bliege Bird, R., Codding, B. F., & Bird, D. W. (2009). Determinants of gendered foraging and production inequalities among Martu. *Human Nature*, *20*, 105–129.

Bourdieu, P. (1991). [1972] *Outline of a Theory of Practice*. New York: Cambridge University Press.

Caraco, T. (1981). Risk sensitivity and foraging groups. *Ecology*, *62*, 527–531.

Clutton-Brock, T. (2002). Breeding together: kin selection and mutualism in cooperative vertebrates. *Science*, *296*(5565), 69–72.

Codding, B. F., Bird, D. W., & Bliege Bird, R. (2010). Interpreting abundance indices: some zooarchaeological implications of Martu foraging. *Journal of Archaeological Science*, *37*, 3200–3210.

Gambetta, D. (2009). *Codes of the Underworld: How Criminals Communicate*. Princeton: Princeton University Press.

Gurven, M., Allen-Arave, W., Hill, K., & Hurtado, M. (2000). It's a wonderful life: signaling generosity among the Ache of Paraguay. *Evolution and Human Behavior*, *21*(4), 263–282.

Hawkes, K. (1992). Sharing and collective action. In E. A. Smith, & B. Winterhalder (Eds.), *Evolutionary Ecology and Human Behavior* (pp. 269-300). New Brunswick: Aldine Transaction Press.

Hill, K. (2002). Altruistic cooperation during foraging by the Ache, and the evolved human predisposition to cooperate. *Human Nature*, *13*, 105–128.

Hill, K., & Kintigh, K. (2009). Can anthropologists distinguish good and poor hunters? Implications for hunting hypotheses, sharing conventions, and cultural transmission. *Current Anthropology*, *50*, 369–378.

Howell, N. (1979). *Demography of the Dobe !Kung*. New York: Academic Press.

JMP, Version 8. SAS Institute Inc., Cary, NC, 1989-2008.

Mauss, M. (1924). *The Gift*. New York: Norton.

Myers, F. R. (1986). *Pintupi Country, Pintupi Self: Sentiment, Place and Politics Among Western Desert Aborigines*. Berkeley: Univ. California Press.

Ostrom, E. (1991). *Governing the Commons: The Evolution of Institutions for Collective Action*. Cambridge: Cambridge University Press.

Packer, C., & Ruttan, L. (1988). The evolution of cooperative hunting. *American Naturalist*, *132*(2), 159–198.

Ruffle, B., & Sosis, R. (2007). Does it pay to pray? Costly ritual and cooperation. *The BE Journal of Economic Analysis and Policy*, *7*, 1–35.

Sackett, L. (1979). The pursuit of prominence: hunting in an Australian Aboriginal community. *Anthropologica (NS)*, *21*, 223–246.

Scelza, B. (2009). The grandmaternal niche: critical caretaking among Martu Aborigines. *American Journal of Human Biology*, *21*, 448–454.

Scelza, B., & Bliege Bird, R. (2008). Group structure and female cooperative networks in Australia's Western Desert. *Human Nature*, *19*, 231–248.

Silk, J. (2007). Social components of fitness in primate groups. *Science*, *317* (5843), 1347–1351.

Smith, E. A. (1981). The application of optimal foraging theory to the analysis of hunter-gatherer group size. In B. Winterhalder, & E. A. Smith (Eds.), *Hunter-Gatherer Foraging Strategies* (pp. 36-65). Chicago: University of Chicago Press.

Smith, E. A. (1985). Inuit foraging groups: some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethology and Sociobiology*, *6*, 27–47.

Smith, E. A. (1991). *Inujjuamiut Foraging Strategies: Evolutionary Ecology of an Arctic Hunting Economy*. Hawthorne, NY: Aldine de Gruyter.

Smith, E. A., & Bliege Bird, R. (2005). Costly signaling and cooperative behavior. In H. Gintis, & S. Bowles, & R. Boyd, & E. Fehr (Eds.), *Moral Sentiments and Material Interests: The Foundations of Cooperation in Economic Life* (pp. 115-148). Cambridge: MIT Press.

Sosis, R., & Alcorta, C. (2003). Signaling, solidarity, and the sacred: the evolution of religious behavior. *Evolutionary Anthropology*, *12*, 264–274.

Sosis, R., & Bressler, E. (2003). Cooperation and commune longevity: a test of the costly signaling theory of religion. *Cross-Cultural Research*, *37*, 211–239.

Sosis, R., Feldstein, S., & Hill, K. (1998). Bargaining theory and cooperative fishing participation on Ifaluk Atoll. *Human Nature*, *9*, 163–203.

Sosis, R., & Ruffle, B. (2003). Religious ritual and cooperation: testing for a relationship on Israeli religious and secular kibbutzim. *Current Anthropology*, *44*, 713–722.

Tonkinson, R. (1974). *The Jigalong Mob: Aboriginal Victors of the Desert Crusade*. Menlo Park: Cummings Press.

Tonkinson, R. (1978). Aboriginal community autonomy: myth and reality. In M. C. Howard, Ed. *Australian Aboriginal Concepts* (pp. 81-90). Atlantic Highlands: Humanities Press.

Tonkinson, R. (1988). Egalitarianism and inequality in a Western Desert culture. *Anthropological Forum*, *5*, 545–558.

Tonkinson, R. (1990). The changing status of Aboriginal women: "Free agent" at Jigalong. In R. Tonkinson, & M. Howard (Eds.), *Going it Alone? Prospects for Aboriginal Autonomy* (pp. 125-144). Canberra: Aboriginal Studies Press.

Tonkinson R. (1991). *The Mardu Aborigines: living the dream in Australia's desert*. Fort Worth: Holt, Rinehart and Winston.

Tonkinson, R. (2005). Individual creativity and property-power disjunction in Australian Desert society. In T. Widlok, & W. G. Tadesse (Eds.), *Property and Equality: Ritualisation, sharing, egalitarianism* (pp. 32-46). New York: Berghahn Books.

Tonkinson, R. (2007). Aboriginal "difference" and "autonomy" then and now: four decades of change in a Western Desert society. *Anthropological Forum*, *17*, 41–60.

Walsh, F. (1990). An ecological study of traditional Aboriginal use of country: Martu in the Great and Little Sandy Deserts, Western Australia. *Proceedings of the Ecological Society of Australia*, *16*, 23–37.

Wiessner, P. (2002). Hunting, healing, and *hxaro* exchange: a long term perspective on !Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior*, *23*, 407–436.

Winterhalder, B. (1996). Social foraging and the behavioral ecology of intra-group resource transfers. *Evolutionary Anthropology*, *5*, 46–57.

Yanca, C., & Low, B. S. (2004). Female allies and female power: a cross-cultural analysis. *Evolution and Human Behavior*, *25*, 9–23.