

Socioecological factors influence hunter-gatherers

Group size, lifetime interactions, and emergent properties of culture

Brian F. Coddling, Kasey Cole, and Kurt M. Wilson

Introduction

The size of hunter-gatherer societies varies across multiple scales. In one dimension, individuals may experience a very different number of co-residing others, often referred to as band size.

Consider a Martu woman living in the western Australian desert in the 1940s: she may spend most of her days in a small, tight-knit, highly mobile community of kin that includes her mother and sister co-wives, who cooperate in an all-female division of labor to feed themselves and their kids (Scelza and Bliege Bird 2008; Peterson and Long 1986); yet she also maintains a broad social network linking her to a large number of kin and non-kin who might rarely see one another (Bird et al. 2019).

Contrast this with the life of a Dogrib woman living in the western Canadian subarctic in the 1930s: she may spend the summer fishing with her extended family and many non-kin, the winter processing caribou hunted or trapped by members of her nuclear family plus a few other close kin, and the spring and fall in other task-specific aggregations of varying sizes (Helm 1965, 1968; Andrews and Zoe 1997); her core social network might be built from no fewer, and no more, than these same individuals with whom she co-resides for part of every year on a seasonal round.

These two women may experience very different lives in terms of the number and relatedness of the people with whom they live on a day-to-day basis, but they may interact with nearly the same number of others throughout their lifespan. This is another dimension across which individuals living in hunter-

gatherer societies might experience variation: the total number of interactions they experience with a unique other during their lifetime.

Consider an Ache woman living in the neotropics of Paraguay in the 1960s. She might spend her days in a band of about 20 individuals, to most of whom she is unrelated save only her brother whose family also camps with hers (Hill et al. 2011). Nearly every day she packs up her family and their belongings to transport them to a new camp, pausing along the way to forage and assist her current husband in spotting game (Hurtado et al. 1985). From time to time new families join the band, others leave, and throughout her lifetime she may end up interacting with nearly all Ache living in the region (Hill et al. 2014).

This differs from what a Ju'/hoansi woman experiences through her lifetime in the arid Kalahari savanna of Botswana in the 1930s (Lee 1968, 1972, 1979). While she too lives with a similar number of bandmates on an average day, between 15 to 30 (Hill et al. 2011; Wiessner 2014), she experiences remarkable seasonal and inter-annual variation. During the wet season, she might be living in a smaller than average group made up of her immediate family camped in the mongongo groves where she works two or three days a week harvesting and processing nuts (Lee 1968, 1972, 1979). During the dry season, she and her husband might join up with her parents and a few other families to camp near permanent water in a group of about 30 individuals. During the dry season in an extremely dry year, she may be joined by her husband's parents, along with many other families as they congregate at the largest water source in the region in a group that tops 80 people (Lee 1972). Repeated throughout her lifetime, and strengthened by the formal exchange partnerships she cultivates (Wiessner 2002, 2014), she may end up interacting with a large number of people, despite living in a smaller than average band.

These four women may share a similar mode of subsistence — hunting and gathering — but they experience a different number of co-residents day-to-day, and a disparate number of interactions with unique others aggregated over their lifetimes. Moreover, how they interact with others varies, suggesting meaningful differences in the quality, not just the quantity, of interaction spheres. This variation is often averaged over by researchers seeking to find a single number characteristic of human social organization (e.g., Dunbar 1993). Yet doing so is a missed opportunity to explore, and possibly explain, the variation.

Here we build on recent synthetic analyses (Hill et al. 2011; Hill et al. 2014), and case studies (Bird et al. 2019; Wiessner 2014) summarized in a recent review (Coddling et al. *nd.*) to further explore this variation in hunter-gatherer

group size and the degree of interaction, specifically focusing on the influence of ecological, economic, and social factors, and the sociocultural consequences of these socioecological dynamics. We begin with a summary of our theoretical approach, and specific expectations derived from it.

Theory First

Our research strategy follows a tradition established by anthropologists leveraging theory from behavioral ecology to examine variation in hunter-gatherer socioecology (Winterhalder and Smith 1981; Codding and Kramer 2016). A core part of this strategy is an emphasis on individual decision making within a local environmental context, wherein environment is broadly defined to include the natural and social worlds within which an individual resides. The assumption is that individuals will do the best they can to make a living, given the opportunities and constraints afforded by their local context. This assumption is akin to extending the principal of charity (Gauker 1986) or of humanity (Dennett 1987) from interpreting an individual's thoughts and words in the most reasonable way possible, to interpreting their decision making and behavior with the same charitability. Though in this case, we also have a general theory of behavior that provides a function to identify the objective of behavior (*cf.* Gauker 1986: 2-3).

To derive expectations *a priori* about how individuals should behave within a specific context, researchers rely on formal models. These models can examine optimal decisions relative to the distribution and abundance of resources (i.e., resource-contingent decisions; e.g., Charnov 1976), to how many others co-reside in that environment (density-dependent decisions; e.g., Fretwell and Lucas 1969), and to the strategies others employ (frequency-dependent decisions; e.g., Barnard and Sibly 1981). Model predictions are compared quantitatively or qualitatively to observed behavior (or their material correlates in the case of archaeology), with mismatches indicating problems with model specifications, not that the behavior is suboptimal or maladaptive. In other words, following the adaptationist program (Mayr 1983), behaviors are assumed to be near optimal within constraints, with research focused on the simplest explanation possible without being overly reductionist or deterministic.

Out of these decisions, broader patterning emerges, such as sustainable land use (Moritz et al. 2018), divisions of labor (e.g., Codding et al. 2011), hierarchy (e.g., Smith and Codding 2021; Wilson and Codding 2020), ethno-

linguistic diversity (Coddington and Jones 2013), and other cultural phenomena (e.g., Smith et al. 2017). As the product of individual decisions in a local context, explanation of these sociocultural phenomena requires research focused on individuals and their relations, not on the emergent properties themselves. Thus, the approach provides a way to look at the socioecological foundations of behavior that aggregate to produce patterning expressed as cultural phenomena, including its material correlates studied by archaeologists (O'Connell 1995; Bird and O'Connell 2006; Coddington and Bird 2015).

Implementing this general research strategy using cross-cultural evidence, here we propose that three factors derived from three core principals in the ecological and behavioral sciences can be used to predict how and why band size and interaction spheres may vary among hunter-gatherers (Coddington et al. nd.). We refer to these as Allee-effects, the maximum sustainable yield, and social dilemmas.

First, we suggest that band size should be structured by returns-to-scale, or Allee effects, associated with focal resources. Within an ideal distribution model framework (Fretwell and Lucas 1969), the decision of any one individual to settle in a resource patch or habitat will depend in part on the number of others who already reside there. For many resources, this relationship takes the form of negative density dependence, wherein everyone does worse with each additional joiner. However, there are also often benefits to aggregation, such that everyone does better up to some threshold as more people co-reside. These Allee-like benefits can arise when aggregations result in increased habitat quality (e.g., Bird et al. 2019), shared defense costs (e.g., Coddington et al. 2019), or returns-to-scale in resource acquisition (e.g., Smith 1985). We suggest that those resource acquisition activities with positive density dependence should encourage more individuals to cooperate, thus aggregating to produce larger mean experienced band sizes. In a very simple example, we previously showed that returns-to-scale increase from economies focused on plants, to those focused on aquatic and hunted resources (Coddington et al. nd.).

Second, we suggest that the size of an individual's interaction sphere is in part structured by the maximum sustainable yield (MSY) of focal resources. MSY is the highest number of resources that can be taken at that rate in perpetuity. Because foraging depletes resources (e.g., Alvard 1994), individuals may be better off moving camp more or less frequently depending on MSY. This can be modeled following the marginal value theorem (Charnov 1976), which shows that individuals should move and resettle elsewhere following depletion to the point of diminishing returns. Available evidence supports these

model predictions (e.g., Aswani 1998; Codding et al. 2016; Venkataraman et al. 2017), though individuals are likely to stay longer than what is sustainable when doing so maximizes their immediate returns, leading to long-term unsustainable outcomes (Alvard 1993; Hardin 1968). Of course, there are also other factors that structure mobility and interaction rates, but all else being equal, individuals should move more frequently if their focal resources have a lower MSY. If individuals reshuffle co-residents when they move, then this should influence interaction rates, though more detailed analysis is required to unpack how strong this association may be relative to other causal factors.

Finally, the strategies that others employ should structure band size and interaction rates through complex dynamics influenced by frequency-dependent decisions (Barnard and Sibly 1981). Specifically, larger band sizes may increase social dilemmas by increasing opportunities to “free ride” on the production of others (e.g., Olson 1965). Producers may find it in their best interest to tolerate an increasing number of non-producers (Blurton Jones 1984, 1987) up to some threshold at which they may decide to “vote with their feet” and leave (Lee 1972; Woodburn 1982) or remain and punish those who do not contribute, the latter being extremely rare (e.g., Gaula 2012; Marlowe 2010). The former may result in high mobility and residential reshuffling that increases interaction rates (e.g., Lewis et al. 2014). In some circumstances, these dynamics may also encourage institutions that restrict who can join groups of producers working in Allee-like (e.g., Codding et al. 2019) or economically intensive (Parker et al. 2019) subsistence activities, which may reduce interactions with outsiders. As such, band size and interaction rates likely feedback on one another depending on how individuals resolve social dilemmas.

This final point highlights how individual decisions might interact with one another to propagate broader social and cultural institutions. Specifically, socioecological factors that incentivize large cooperative groups may encourage “solutions” to collective action problems, while those that induce high lifetime interaction rates may facilitate institutions to manage large social networks. The former may encourage practices and institutions governing group membership, such as territoriality, property rights, and inter-group conflict (Codding et al. 2019; Parker et al. 2019). The latter may encourage practices that help regulate frequent encounters with distantly known others, or that foster long-distance ties with many others, such as ritual practices (e.g., Bird et al. 2019; Hill et al. 2014) or economic partnerships (e.g., Wiessner 2002). If this is supported by further analysis, understanding variation in past socioecology may also help archaeological inquiry ascertain the kinds of social

institutions formed by past societies to solve these problems, even if they are otherwise materially invisible.

In summary, building on theory and models from behavioral ecology, we suggest that individual decisions structured by density-dependent, resource-contingent, and frequency-dependent factors will aggregate to produce emergent group-level patterning observed as forager band size and lifetime interactions, which may further feed back to structure decisions that produce emergent social and cultural institutions.

This approach flips some previous perceptions on their head. For example, Barth (1978: 11) notes that "...it is taken for granted that the social institutions of the Andamans simply do not have the capacity to organize large populations" – we would argue it is the other way around: social institutions create capacity in response to population size and interactions, which are in part structured by the local environment. Individuals adapt to their local circumstances; social institutions are the epiphenomenal product of those decisions interacting with and feeding back on one another. In this way, the approach is not environmental determinism, rather, individuals have the agency to determine their actions (Bird and O'Connell 2012). The approach assumes that individuals, having near-to-perfect knowledge of local conditions and expected immediate outcomes, will generally make the best decisions possible out of the available options, which are limited by local conditions. As noted above, this is a charitable assumption. To think otherwise would implicitly assume that individuals lack either the capability or knowledge to do what is best within their local context. Of course, individuals acting in their best interest will not produce outcomes that are best for everyone (e.g., Hardin 1968; Olson 1965), and may result in profoundly negative unintended consequences in the long term (anthropogenic climate change being a prescient example).

Applied to the case at hand, we previously found some support for our predictions (see Coddling et al. nd.): mean experienced band size (Hill et al. 2011; Bird et al. 2019) and lifetime interactions with unique others (Hill et al. 2014; Wiessner 2014) seem to co-vary respectively with the primary focus of subsistence and net primary productivity (Binford 2001). Additionally, total population size (and lifespan) will influence the total number of interactions possible (Hill et al. 2014). Finally, a qualitative review of the ethnographic evidence (Coddling et al. nd.) also suggests that band size may further influence interaction rates through increased residential reshuffling in response to free-riders (Blurton Jones 1987). Leveraging these predictions, here we explore how these dynamics may structure the range of variation in hunter-

gatherer band size and lifetime interactions, and the sociocultural institutions that may emerge from these dynamics.

To explore the empirical record of hunter-gatherer social space relative to our theoretical expectations, here we seek to examine the range of variation in hunter-gatherer band size and lifetime interactions in a sample of 25 societies (see Codding et al. nd.). However, the available evidence required to assess this expectation about lifetime interactions are restricted to only three cases for which data have been quantified: Hadza, Ache (Hill et al. 2014), and San (Wiessner 2014).

Thankfully, this is not an insurmountable problem. Using other information recorded about each society, we can impute estimated lifetime interactants for all societies in this sample. Specifically, here we impute estimates of lifetime interactants for the 22 societies without empirical estimates using a non-parametric imputation method from Stekhoven and Buhlmann (2012) based on the random forest algorithm (Breiman 2001) implemented by Liaw and Wiener (2002). Specifically, we ask the model to predict the 22 missing lifetime interactants based on the three recorded lifetime interactants (lifetime conversations from Hill et al. 2014; interaction sphere from Wiessner 2014) plus documented information on mean experienced band size (Hill et al. 2011; Bird et al. 2019), net primary productivity, the primary source of food (gathered, hunted, or aquatics), and the total population size (Binford 2001).¹

One other issue stems from the fact that lifetime interaction spheres are estimated differently across studies. For San, Wiessner (2014: Table 2) calculates the number of interactants as the number of adults who co-reside with exchange (*xaro*) partners, with whom individuals will likely interact during aggregation events. She notes this is likely an underestimate of lifetime interaction spheres. For Hadza and Ache, Hill et al. (2014: Table S16) calculate the number of interactants from the results of 16 questions about specific types of dyadic interactions men have with other men, and women have with

1 As imputation error of the *missForest* function varies with the number of variables randomly sampled at each split in a tree (m_{try}) and the number of trees grown in each forest (n_{tree}) (see Stekhoven and Buhlmann 2012), we iterate models through every combination of each parameter from 1 to 100 trees (the default) and 1 to 5 (the maximum number of variables) to select the combination that minimizes the root mean square error (RMSE) of lifetime interactions, a measure of model fit in the same units as the imputed variable (for the best model, $m_{try} = 5$ and $n_{tree} = 4$). Error rates reported in text are out-of-bag error.

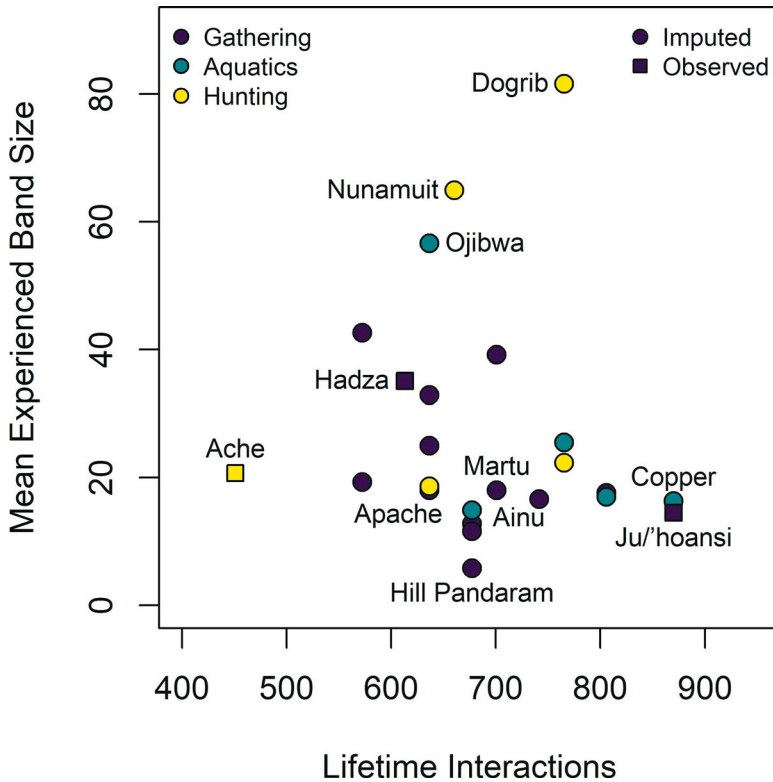
other women, from which they estimate a yearly interaction rate, and a consequent lifetime estimate based on the total population size and lifespan. We take the average number of men's interactants across all arenas and double them to account for interactions with women, which is likely an overestimate for Hadza though may be appropriate for Ache given closer gender parity in interactions (Hill et al. 2014). Together, these provide relative estimates of lifetime interactions that we can use to explore the likely interaction spheres that individuals in different societies might experience.

The model results, shown in Figure 1, predict lifetime interactants for all societies with an error rate (root mean square error [RMSE]) of about 162; meaning the model can on average predict lifetime interactions within plus or minus 162 individuals. This equates to a mean normalized error (NRMSE) of 0.25 (zero being perfect, and one being very poor), which suggests the model is performing reasonably, but not remarkably well. With this in mind, and given the full range of observed variation is between 451 individuals (for Ache) and 870 individuals (for Ju/'hoansi), we can interpret the predicted values as showing meaningful separation at the extremes, but having overlapping errors near the central tendency. In other words, the point estimates in Figure 1 should not be taken as a measure of actual precision, but can be used to explore the possible parameter space characterizing hunter-gatherer group size and interaction rates. Keeping the limitations in mind, we use this graphical result as an opportunity to scope the general bounds and possible range of variation in band size and interaction rates. Here we examine ethnographic cases at the boundaries of this parameter space.

The range of variation in band size is bounded by 5.8 for Hill Pandaram to 81.6 for Dogrib. That of lifetime interactions is bounded by the estimated empirical range from 451 for Ache to 870 for Ju/'hoansi (note, the model cannot impute estimates outside the observed range). Hadza appear near the center of this envelope, which supports Marlowe's (2010) observation about the representativeness of Hadza for warm climate foragers.

Shown in Figure 1, societies living in similar regions and with similar subsistence targets sometimes cluster near one another in this constructed social space, such as Nunamnit and Dogrib. Other societies living in disparate ecosystems and employing varying subsistence practices find themselves near one another within this social envelope, such as Martu focused on gathering, Apache on hunting, and Ainu on aquatic resources, all of whom cluster toward the central tendency of interaction rates and lower bounds of band size. To explore the socioecological factors that may structure a society's position within

Figure 1: Range of variation in mean experienced band size and interaction sphere for 25 hunter-gatherer societies. Points are color-coded by the main source of subsistence (gathered, aquatic, and hunted resources) with point shape indicating if the interactions value is observed (square) or imputed (circle). Societies mentioned in the text are labeled.



this social space, and the possible sociocultural institutions that emerge from it, we next examine a few cases at the extremes in a bit more detail.

Hill Pandaram

Beginning with the smallest mean recorded bands, an individual living in Hill Pandaram society in the Ghat Mountains of south India may on average live with their nuclear family plus two or three other couples and their children

(Morris 1982). Our analysis suggests this individual might interact with a relatively moderate number of others throughout their life, totalling near 677. Small band size and intermediate lifetime interactions seems to be structured in part by local resources.

Morris (1982) reports a very limited economy of scale, with each individual being responsible for acquiring their own food. Additionally, individuals seem to have intermediate levels of mobility driven by the depletion rate of local resources: “[t]hey remain for a week, and move on when the food supply is exhausted” (Iyer 1937: 97; quoted by Morris 1982: 453). These moves every 7–8 days also result in group fissioning down to a single family and fusion up to as many as 20 people on rare occasions. Interestingly, aggregations are not linked with seasonal variation in resource abundance, as is the case for populations with significantly higher interaction rates such as the Ju/’hoansi and Copper Inuit (more below).

These socioecological dynamics may further influence emergent cultural patterning, including their societal emphasis on individual autonomy and self sufficiency, as well as egalitarian roles between women and men, and the lack of institutions to facilitate corporate organization (Morris 1982), all of which may stem in part from such limited returns-to-scale. Further, there are no ritual aggregations, and kinship is “geared to mating and adhesion, not filiation” (Morris 1982: 454), both of which may in part result from the limited need to maintain larger than average social networks.

Dogrib (Tlicho)

At the opposite extreme of mean experienced band size, an individual living in Dogrib (Tlicho) society in the Northwest Territories of Canada may on average co-reside with 82 others (Hill et al. 2011). This average derives from individuals in Marten Lake Dogrib communities residing in about twenty households (Helm 1967; Denham 2010), who regularly aggregate and disaggregate into specific task group formations. These include two to three men who go out trapping, a trapping party of a few families, the aggregation of many families for caribou hunting, and further aggregations for fishing camps, each of which may last from a few days to several weeks (Helm 1965: 378).

Our analysis suggests that the typical person might interact with 765 others through these settlement dynamics, which is high relative to the range of variation and might encourage institutions to facilitate this scale of interactions. Indeed, in discussing kinship, Helm (1965) argues bilateral ties allow

flexibility in residence while linking individuals together in a “social chain” (Helm 1965).

While kin ties may be structured to facilitate within-group connectedness, larger – though not necessarily coordinated – seasonally-specific task groups focused on the acquisition of reliable and abundant resources may also incentivize territorial property rights to exclude outsiders (Dyson Hudson and Smith 1978; Codding et al. 2019). Helm (1965: 363) notes some possible support for this, given that the four socio-territorial groups of Arctic Drainage Dene (two Hare, one Slavery, and one Dogrib) who occupied the region at the time of her study acquired resources “in their own region” to which they tied their identity. The lack of even stronger territorial boundaries is not surprising given the spatio-temporal brevity (see Dyson Hudson and Smith 1978) of these larger aggregations, and that the activities undertaken did not require coordinated labor (Helm 1965: 378).

Northern Ache

Northern Ache living in the neo-tropical forests of eastern Paraguay experience relatively small mean experienced band size and the lowest observed lifetime interactions (Hill et al. 2011, 2014). As the hypothetical story in the introduction highlights, Ache live in small, fluid, highly mobile bands with women's tasks focused on plant resources, and moving camp, while men's are focused on hunting mid- to small-sized game (e.g., nine-banded armadillo). Men tend to search for prey independently, but keep close enough so that they may call on other hunters to aid in pursuit. Modeled Ache hunting returns increase with group size (peaking at about 2-7 or more depending on the prey), but observed pursuit group size tends to be smaller than optimal (about 1-5 depending on the prey; McMillan 2000). This may result from trade-offs between maximizing individual search efficiency by distancing further away from other hunters than is optimal to facilitate cooperation, or from frequency-dependent decisions leading some not to call for help, or others not to join, resulting in failures of coordination (McMillan 2000).

Evidence of high mobility, but low interaction rates seems contrary to our proposed hypothesis. The pattern may result from relative group stability, or the relatively small total population size which limits the possible number of interactants (Hill et al. 2014). The former seems an unlikely explanation, given that individuals are likely to interact with nearly all other Ache through their lifetime, and that they maintain formal ritual relationships which foster

connections and ties among highly mobile bands (Hill et al. 2014). As such, their low population size (about 560; compared to 950 for Hadza and 2200 for Ju/'hoansi) is likely the most limiting factor. Further unpacking this finding will require research into the determinants of total demic population size and total territory size, which may also result from the interaction of dynamic socioecological factors (e.g., Parker et al. 2019) to structure the possible number of interactants in a society, and the density of interactions.

Ju/'hoansi (San)

Ju/'hoansi (San, or !Kung) living in the semi-arid Kalahari savanna of Botswana and Namibia have the highest interactions and total population size, though live in smaller than average bands (San mean experienced band size = 14.5 compared to 28.2 for all 32 societies in Hill et al. 2011) and at relatively low population densities (0.16 people per square kilometers; Lee 1968).

The relatively small groups may result in part from the limited economy of scale of focal resources, such as mongongo nuts which are acquired by individual women and men with “one tree to a person” (Lee 1979: 192), though children may help maximize returns by processing nuts back at camp (Blurton Jones et al. 1994). While plants, and especially mongongo nuts, make up the bulk of Ju/'hoansi diet, there are some other resources that encourage cooperation. For example, hunting is more likely to be successful in larger groups (Yellen 1977), men most often pursue game in pairs, and larger cooperative groups formed for game drives (Hitchcock et al. 1996).

High lifetime interactions appear driven by high mobility and seasonal aggregations, which are in part influenced by resource depletion rates and seasonal water availability respectively. Hitchcock et al. (1996: 162) note that in the 1960s “[g]roup aggregation and dispersal patterns were related to the abundance of resources... as resources were depleted in an area, people tended to move out, in part to avoid conflict among group members over the remaining resources.” Water availability, and its influence on resource abundance, is one of the major factors that determines aggregation. Lee (1972) reports Ju/'hoansi aggregation and dispersion events in the /gam-/ai/ai areas during the 1920s and 1930s. During the rainy season, a minimum of 11 bands would disperse across the region. During a typical dry season, these bands may aggregate into five groups centered on permanent water sources. During an extreme dry year, the 11 bands would aggregate into as few as two or three locations,

resulting in as many as seven bands at a single water hole. One of these locations, “ai/ai was a trading center where people from all points of the compass came to visit, dance, and do *hxaro* trading (and sometimes fight)” (Lee 1972: 138). The need to maintain connections with others for dry season aggregations when resources are scarce are facilitated by social institutions that foster long-term, long-distance relationships of mutual aid known as *hxaro* exchange (Wiessner 2002).

Copper Inuit (Kitlinermiut)

Copper Inuit (Kitlinermiut) and Ju/’hoansi have similar mean empirical band sizes, and our analysis predicts that they might have similarly high lifetime interactions as well, despite the disparate nature of these ecosystems and adaptations. This invites a more detailed review of the factors structuring Copper Inuit band size and interactions. Specifically, we might predict that both societies have different resources which structure similar Allee-like groupings, depletion-driven mobility, and frequency-dependent fission-fusion. To evaluate this, we examine how focal resources structure band size, interactions, and social dilemmas.

Copper Inuit bands are organized around the nuclear family (Damas 1972). Sometimes nuclear family bands may camp alone, fishing on the winter ice or searching for dispersed caribou outside of the migration season (Jenness 1928; Damas 1972). These bands may aggregate when resource acquisition encourages Allee-like cooperation of one form or another, and may disaggregate when resources are depleted or when seasonal changes alter prey behavior. Three resource acquisition activities are illustrative: intercept caribou hunting, fish trapping, and breathing-hole sealing.

Jenness (1928: 156) notes that during the caribou migration, a collection of family bands would travel to locations where herds are expected, camp for a few days searching for and hunting game, then travel as a group about 10-15 miles (16-24 km) and repeat the process. During one summer, hunters “went on ahead to intercept a herd of caribou they had sighted... This hunt well illustrated the unity of an [Inuit] band. Every individual, man, woman, and child, took part in it...both men and women contributed to the discussion that decided the tactics to be employed.” Using coordinated labor and natural topography, they drove 15 caribou, after which they “feasted and idled for two days”. This hunt illustrates a relatively extreme example of coordinated labor

wherein every member of the extended co-residing band cooperates in the acquisition of a focal resource.

Similar patterns seem to influence group size associated with fish trapping, when families aggregate in the spring and build “three barriers of stones across the streams, leaving narrow openings in the two that lay nearest the sea, and completely closing the highest; whenever a shoal gathered in the upper chamber, they blocked its entrance and stabbed the struggling fish with long, three-pointed spears. Nearly a hundred salmon each weighing from three to twelve pounds lay spread out on the flat boulder around the camp.” (Jeness 1928: 237).

While these two activities clearly show how cooperation in resource acquisition may structure co-residence size, perhaps the most well known aggregation events – winter sealing camps – are not a direct product of an economy-of-scale. Smith (1984) notes that winter sealing camps of 50-200 people (reported by Damas 1969) would have 12-50 hunters, while the optimal number of cooperating hunters is around three per breathing hole. He suggests this discrepancy is not due to crowding of prime sealing sites (as individuals would be better off distributing proportionally to the suitability of sealing sites; per Frewell and Lucas 1969), to reduce variance in returns (as harvest rate variance does not decline with group size), or to smooth over acquisition variance via sharing (as storage would be sufficient to accomplish this without invoking collective action problems). Instead, these larger-than-optimal sealing camps may serve another function: information-sharing. Specifically, while larger-than-optimal settlements may accelerate the rate of depletion and exacerbate free-rider problems, these costs may be outweighed by the benefits each individual receives from sharing information on the location and abundance of seals in the area around the camp. He argues this may also explain variation in winter sealing camp size, as the greater the unpredictability, the greater the optimal size of the information-sharing network.

Resource and information sharing may also facilitate connections that strengthen interaction networks, such as enduring social bonds and formal partnerships outside of kin relations (Damas 1972). Though individuals may alter their behavior based on what others are doing, producing frequency-dependent variation that may help resolve social dilemmas. In a contemporary arctic community, Ready (2018) shows that high producing households form reciprocal ties, which indicates that producers bias shares to other producers who are more likely to reciprocate. This may be part of a general trend in which individuals are more likely to cooperate with other cooperators. For

example, in public goods games Hadza increase cooperation when they co-reside with more cooperators (Apicella et al. 2012; Smith et al. 2018). If similar dynamics occurred at winter sealing camps, positive assortment of cooperators may serve to reduce collective action problems. Moreover, formal sharing institutions such as seal sharing “flipper associates” may be particularly important to maintain connections among Copper Inuit, who have less defined kin structure than neighboring groups (Damas 1972).

Conclusion

Building on theory and models from behavioral ecology, here we suggest that individual decisions structured by density-dependent (returns-to-scale), resource-contingent (maximum sustainable yield), and frequency-dependent (social dilemmas, specifically free-riders) factors will aggregate to produce emergent patterning in experienced band size, lifetime interactions, and subsequent properties of cultural institutions.

Exploring cases that define the social envelope of mean experienced band size and unique lifetime interactions (Figure 1) reveals some support for this proposed socioecological principle. Mean experienced band size does in part appear influenced by returns-to-scale with focal resources, evidenced well by the extreme cases of Hill Pandaram and Dogrib. The number of lifetime interactions with unique others does seem to vary at least partly as a function of the depletion rate of focal resources, as well as broader patterns of resource availability that lead to seasonal aggregations, such as among Ju/'hoansi and Copper Inuit. Total population size also seems to have a strong influence on lifetime interactions, as shown by Ache. Finally, how these scales of society size interact creates variation in the form of social institutions that emerge to facilitate interactions and solve social dilemmas. In this final dimension, socioecological dynamics seem to aggregate in ways that inform the quality, as well as the quantity, of interactions across these two scales of society size.

While many details remain to be worked out, here we suggest that differences in the scale of hunter-gatherer societies may in part be due to differences in socioecology. Through this exercise, we hope that we have allowed the “scale” of hunter-gatherer societies to emerge not “as an artifact of analysis, but rather [as] an empirical property of the things we study” (Barth 1978: 11). Though our approach does have at least two limitations in this regard.

First, we recognize that generating *a priori* predictions limits initial analysis to those factors which are deemed theoretically important. Second, we

recognize that our analytical approach imputes lifetime interactions for a much greater number of societies ($n=22$) than what is empirically observed ($n=3$). These may indeed generate artifacts of analysis. However, while these are weaknesses, we also see strengths in these elements. Specifically, understanding variation in the scale of hunter-gatherer social organization requires a framework to distinguish signal from noise. Here we present a conceptual grounding framed in established theory as for why two scales may vary across societies, which allows analysis to focus on the signal. Further, while the specific imputed values are certainly imprecise, and may be wrong altogether, the exercise offers a view into how we might be able to understand patterned variation in the potential social envelope in of hunter-gatherer social organization.

Together, these help move debate away from simple dichotomies regarding whether hunter-gatherer societies are “large” or “small”. As illustrated by the hypothetical vignettes in the introduction of this chapter, there is tremendous variation in the scale at which hunter-gatherer societies operate. There is likely even greater variation beyond the reach of ethnography, which may be revealed through archaeological analyses that leverage theory to circumvent issues with direct ethnographic analogy (see O’Connell et al. 1995). We hope future work can build on this chapter, and this volume overall, to explore the full range of variation in the scale of hunting and gathering societies.

Acknowledgement

We are grateful for the opportunity to present these ideas alongside so many eminent scholars in hunter-gatherer research. We thank the organizers, especially Thomas Widlok and M. Dores Cruz for their support and guidance. We are in debt to Kenneth Blake Vernon for directing us to the principal of charity, and for general comments on an earlier version of this manuscript. We thank members of the University of Utah Archaeological Center and two anonymous reviewers for thoughtful comments on this work.

References

- Alvard, Michael S. 1993. Testing the “ecologically noble savage” hypothesis: Intraspecific prey choice by Piro hunters of Amazonian Peru. *Human Ecology*, 21(4), 355-387.

- Alvard, Michael S. 1994. Conservation by native peoples. *Human Nature*, 5(2), 127.
- Andrews, Thomas. D., and John. B. Zoe 1997. The Idaa trail: Archaeology and the Dogrib cultural landscape, Northwest Territories, Canada. *At a crossroads: Archaeology and First Peoples in Canada*. Burnaby, British Columbia: Archaeology Press, Simon Fraser University, 160-177.
- Apicella, Coren, Marlowe, Frank, Fowler, James H. and Nicholas A. Christakis. 2012. Social networks and cooperation in hunter-gatherers. *Nature* 481, 497-501. DOI: 10.1038/nature10736.
- Aswani, Shankar. 1998. Patterns of marine harvest effort in southwestern New Georgia, Solomon Islands: resource management or optimal foraging?. *Ocean & Coastal Management*, 40(2-3), 207-235.
- Barnard, C. J., and Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal behaviour*, 29(2), 543-550.
- Barth, Fredrik 1978. Introduction, in *Scale and Social Organization*, edited by Fredrik Barth. Columbia University Press, 9-12.
- Binford, Lewis R. 2001. *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets*. University of California Press, Berkeley.
- Bird, Douglas W., and James F. O'Connell 2006. Behavioral ecology and archaeology. *Journal of Archaeological Research*, 14(2), 143-188.
- Bird, Douglas W., and James F. O'Connell 2012. Human behavioral ecology. In *Archaeological Theory Today*, 2nd edition, edited by Ian Hodder, pp. 37-61. Polity Press.
- Bird, Douglas W., Bleige Bird, Rebecca, Codding, Brian F., and Zeanah, David W. 2019. Variability in the organization and size of hunter-gatherer groups: Foragers do not live in small-scale societies. *Journal of Human Evolution*, 131, 96-108.
- Bliege Bird, Rebecca and Brian F. Codding 2021. Promise and peril of ecological and evolutionary modelling using cross-cultural datasets. *Nature Ecology & Evolution*, 1-3. <https://doi.org/10.1038/s41559-021-01579-w>.
- Blurton Jones, Nicholas G. 1984. A selfish origin for human food sharing: tolerated theft. *Ethology and Sociobiology*, 5(1), 1-3.
- Blurton Jones, Nicholas G. 1987. Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Social Science Information*, 26(1), 31-54.

- Blurton Jones, Nicholas G. 2016. *Demography and evolutionary ecology of Hadza hunter-gatherers*. Cambridge, Cambridge University Press.
- Blurton Jones, Nicholas G., Kristen Hawkes and Patricia Draper. 1994. Foraging returns of! Kung adults and children: why didn't! Kung children forage? *Journal of Anthropological Research*, 50(3), 217-248.
- Breiman, Leo. 2001. Random forests. *Machine Learning*, 45(1), 5-32.
- Charnov, Eric L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, 9(2), 129-136.
- Coddig, Brian F., and Dougals W. Bird. 2015. Behavioral ecology and the future of archaeological science. *Journal of Archaeological Science*, 56, 9-20.
- Coddig, Brian F., and Karen L. Kramer (eds.). 2016. *Why forage?: hunters and gatherers in the twenty-first century*. Albuquerque, University of New Mexico Press.
- Coddig, Brian F., and Terry L. Jones. 2013. Environmental productivity predicts migration, demographic, and linguistic patterns in prehistoric California. *Proceedings of the National Academy of Sciences*, 110(36), 14569-14573.
- Coddig, Brian F., Ashley K. Parker, and Terry L. Jones. 2019. Territorial behavior among Western North American foragers: Allee effects, within group cooperation, and between group conflict. *Quaternary International*, 518, 31-40.
- Coddig, Brian F., Kasey Cole, and Kurt M. Wilson (nd.) Exploring the ecological foundations of uniquely human social organization.
- Coddig, Brian F., Rebecca Bliege Bird and Douglas W. Bird. 2011. Provisioning offspring and others: risk-energy trade-offs and gender differences in hunter-gatherer foraging strategies. *Proceedings of the Royal Society B: Biological Sciences*, 278(1717), 2502-2509.
- Coddig, Brian F., Zeanah, David W., Bliege Bird, Rebecca, Parker, Christopher H., and Bird, Douglas W. 2016. Martu ethnoarchaeology: Foraging ecology and the marginal value of site structure. *Journal of Anthropological Archaeology*, 44, 166-176.
- Damas, David. 1969. Environment, history, and Central Eskimo society, in *Ecological Essays*, edited by David Damas, pp. 40-64, Bulletin 230, Ottawa, National Museums of Canada, 40-63.
- Damas, David. 1972. Central Eskimo systems of food sharing. *Ethnology*, 11(3), 220-240.
- Denham, W. W. 2010 [1978]. Group Compositions in Band Societies (GCBS) Database Manual. https://www.kinsources.net/kidarep/dataset_attachment-/60/216/GCBSManualREADFIRST.pdf.

- Dennett, Daniel C. 1987. *The intentional stance*. MIT press.
- Dunbar, Robin I. 1993. Coevolution of neocortical size, group size and language in humans. *Behavioral and Brain Sciences*, 16(4), 681-694.
- Dyson-Hudson, Rada, and Smith, Eric Alden. 1978. Human territoriality: an ecological reassessment. *American Anthropologist*, 80(1), 21-41.
- Fretwell, Stephen D., and H. L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19(1): 16-36.
- Gauker, Christopher. 1986. The principle of charity. *Synthese* 69(1), 1-25.
- Guala, Francesco. 2012. Reciprocity: Weak or strong? What punishment experiments do (and do not) demonstrate. *Behavioral and Brain Sciences*, 35(1), 1-15. DOI: 10.1017/S0140525X11000069.
- Hardin, Garrett. 1968. The tragedy of the commons: the population problem has no technical solution; it requires a fundamental extension in morality. *Science*, 162(3859), 1243-1248.
- Helm, June. 1965. Bilaterality in the socio-territorial organization of the Arctic Drainage Dene. *Ethnology*, 4(4), 361-385.
- Helm, June. 1968. The nature of Dogrib socioterritorial groups. In *Man the hunter*, edited by R. B. Lee and I. DeVore, Chicago: Aldine, 118-125.
- Hill, Kim R., Brian M. Wood, Jacopo Baggio, Magdalena Hurtado, and Robert T. Boyd. 2014. Hunter-gatherer inter-band interaction rates: Implications for cumulative culture. *PLoS One*, 9(7), e102806.
- Hill, Kim R., Robert S. Walker, Miran Božičević, James Eder, Thomas Headland, Berry Hewlett, Magdalena Hurtado, Frank Marlowe, Polly Wiessner, and Brian Wood. 2011. Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 331(6022), 1286-1289.
- Hill, Kim, Kaplan, Hillard, Hawkes, Kristen, and Hurtado, A. Magdalena. 1985. Men's time allocation to subsistence work among the Ache of eastern Paraguay. *Human Ecology*, 13(1), 29-47.
- Hitchcock, Robert K., John E. Yellen, Diane J. Gelburd, Alan J. Osborn and Aron L. Crowell. 1996. Subsistence hunting and resource management among the Ju/'hoansi of Northwestern Botswana. *African Study Monographs*, 17(4), 153-220.
- Hurtado, A. Magdalena, Hawkes, Kristen, Hill, Kim, and Kaplan, Hillard. 1985. Female subsistence strategies among Ache hunter-gatherers of eastern Paraguay. *Human Ecology*, 13(1), 1-28.
- Jenness, D. 1928. *The people of the twilight*. New York: Macmillan.

- Lee, Richard B. 1968. What hunters do for a living, or, how to make out on scarce resources. In *Man the Hunter*, edited by R. B. Lee and I. DeVore, Chicago: Aldine, 30-48.
- Lee, Richard B. 1972. !Kung spatial organization: an ecological and historical perspective. *Human Ecology*, 1(2), 125-147.
- Lee, Richard B. 1979. *The !Kung San: men, women and work in a foraging society*. Cambridge University Press.
- Lewis, Hannah M., Lucio Vinicius, Janis Strods, Ruth Mace, and Andrea B. Migliano. 2014. High mobility explains demand sharing and enforced cooperation in egalitarian hunter-gatherers. *Nature Communications*, 5(1), 1-8.
- Liaw, Andy, and Matthew Wiener. 2002. Classification and regression by randomForest. *R news*, 2(3), 18-22.
- Marlowe, F. 2010. *The Hadza: hunter-gatherers of Tanzania*. University of California Press.
- Mayr, Ernst. 1983. How to carry out the adaptationist program? *The American Naturalist*, 121(3), 324-334.
- McMillan, Garnett P. 2001. Ache residential grouping and social foraging. Unpublished PhD. Dissertation, University of New Mexico.
- Moritz, Mark, Behnke, Roy, Beitel, Christine M., Bleige Bird, Rebecca, Chiaravalloti, Rafael M., Clark, Julia K., Crabtree, Stefani A., Downey, Sean S., Hamilton, Ian .M., Phang, Sui C. and Scholte, Paul, and Wilson, James A. 2018. Emergent sustainability in open property regimes. *Proceedings of the National Academy of Sciences*, 115(51), 12859-12867.
- Morris, B. 1982. Economy, affinity and inter-cultural pressure: notes around Hill Pandaram group structure. *Man* 17(3), 452-461.
- O'Connell, James F. 1995. Ethnoarchaeology needs a general theory of behavior. *Journal of Archaeological Research*, 3(3), 205-255.
- Olson, Mancur. 1965. *Logic of collective action: Public goods and the theory of groups*. Harvard University Press.
- Parker, Ashley K., Parker, Christopher H., and Coddington, Brian F. 2019. When to defend? Optimal territoriality across the Numic homeland. *Quaternary International*, 518, 3-10.
- Peterson, Nicholas, and J. P. M. Long. 1986. *Australian territorial organization: a band perspective*. Sydney: University of Sydney.
- Ready, Elspeth. 2018. Sharing-based social capital associated with harvest production and wealth in the Canadian Arctic. *PloS One*, 13(3), e0193759.

- Scelza, Brooke, and Rebecca Bliege Bird. 2008. Group structure and female cooperative networks in Australia's Western Desert. *Human Nature*, 19(3), 231-248.
- Smith, Daniel, Philip Schlaepfer, Katie Major, Mark Dyble, Abigail E. Page, James Thompson, Nikhil Chaudhary, Gul Salali, Ruth Mace, Lenora Astere, Marilyn Ngales, Lucio Viniscus, and Andrea Migliano. 2017. Cooperation and the evolution of hunter-gatherer storytelling. *Nature Communications* 8(1): 1-9.
- Smith, Eric Alden. 1984. Approaches to Inuit socioecology. *Etudes/Inuit/Studies* 8(1), 65-87.
- Smith, Eric Alden. 1985. Inuit foraging groups: Some simple models incorporating conflicts of interest, relatedness, and central-place sharing. *Ethology and Sociobiology*, 6(1), 27-47.
- Smith, Eric Alden and Brian F. Coddling. 2021. Ecological variation and institutionalized inequality in hunter-gatherer societies. *Proceedings of the National Academy of Sciences*, 118(13).
- Smith, Eric Alden and Bruce Winterhalder. 1981. New perspectives on hunter-gatherer socioecology, edited by B. Winterhalder and E.A. Smith, pp. 1-11, *Hunter-gatherer Foraging Strategies: Ethnographic and Archaeological Analyses*. University of Chicago Press.
- Stekhoven, Daniel J., and Peter Bühlmann. 2012). MissForest—non-parametric missing value imputation for mixed-type data. *Bioinformatics*, 28(1), 112-118.
- Venkataraman, Vivek V., Kraft, Thomas S., Dominy, Nathaniel J., and Endicott, Kirk M. 2017. Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proceedings of the National Academy of Sciences*, 114(12), 3097-3102.
- Wiessner, Pauline W. 2014. Embers of society: Firelight talk among the Ju/'hoansi Bushmen. *Proceedings of the National Academy of Sciences*, 111(39), 14027-14035.
- Wiessner, Pauline. 2002. Hunting, healing, and hxaro exchange: A long-term perspective on! Kung (Ju/'hoansi) large-game hunting. *Evolution and Human Behavior*, 23(6), 407-436.
- Wilson, Kurt M., and Coddling, Brian F. 2020. The Marginal Utility of Inequality. *Human Nature*, 31(4), 361-386.
- Winterhalder, Bruce and Eric Alden Smith. 1981. *Hunter-gatherer Foraging Strategies: Ethnographic and Archaeological Analyses*. University of Chicago Press.

Woodburn, James. 1982. Egalitarian societies. *Man* 17, 431-451.

Yellen, John E. 1977. *Archaeological approaches to the present: models for reconstructing the past*. Academic Press.

Comment by Andreas Maier

It is not only in times of social distancing that contacts between people are an essential parameter for human societies. Interpersonal contact is at the base of transmitting information and skills throughout networks and thus fundamental to innovation dynamics, material cultural evolution, and social organization. While the quality of interpersonal contacts certainly plays an important role in this regard (see Damm, this volume), the quantity of interactions with unique others throughout a person's lifetime also holds a high explanatory potential for social phenomena at different spatial and temporal scale levels. Coddling et al. offer highly insightful estimates on the quantity of lifetime interactions for different groups of hunters, fishers, and gatherers. They find that the individuals in their case studies interact with 451 to 870 ± 162 unique other individuals throughout their lifetime. While the personal network size can thus be quite different, and irrespective of whether or not these estimates are accurate by plus or minus 200 people, Coddling et al. provide a sound idea about the order of magnitude of interpersonal contacts within foraging societies. These numbers are highly valuable also for researchers interested in quantitative analyses of foraging communities of the past. Here it is interesting to note, however, that a low total population size seems to be a limiting factor for total lifetime interaction, as discussed in the example of the Northern Ache. It can also be assumed that the distance between interacting bands plays a role, since it relates to energy investments for movements. If that was the case, it would follow that the number of lifetime contacts for individuals living during the Palaeolithic should be found at the lower end of the inferred spectrum. Against this background, it would be promising to estimate unique lifetime contacts for Upper Palaeolithic hunter-gatherers based on the palaeodemographic data provided by the Cologne Protocol (see Maier et al., this volume). The approach presented by Coddling et al. has the advantage that it does not rely on direct observations or counts of interactions over an entire lifetime. To the contrary, observations from only a few well-studied key-communities are transferred to other groups using additional parameters

such as mean band size, net primary productivity of the environment, the primary source of food (gathered, hunted, or aquatics), and the total population size. All these additional parameters can be provided for the Upper Palaeolithic in Western and Central Europe. This of course would imply shifting from an emphasis on individual decision making within a local environmental context to averaging contacts per group in a regional environment. Such an upscaling approach appears permissible, given that the transfer functions used by Codding et al. also imply a certain abstraction from purely individual decisions. An attempt in this direction would certainly be worthwhile, since it promises to deliver quantifiable data highly relevant for the study of cultural evolution that is otherwise outside the reach of inferences from the archaeological record. Such estimates on lifetime interactions could then be compared with independent data on regional and large-scale movements of people as can be derived from the transport patterns of lithic raw materials and fossil mollusc shells. Together with information from palaeogenetic studies, they can help refining models about the regional and supra-regional network structure of Palaeolithic hunter-gatherers. Seen in a diachronic perspective, the expected findings may yield explanatory potential for differences in artefact diversity in communities in Western and Central Europe, or for the development of networks during the process of the repopulation of Central Europe after roughly 20,000 years ago.

