

Modes of Religiosity and the Evolution of Social Complexity at Çatalhöyük

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One of the greatest unsolved puzzles in the study of cultural evolution is the first emergence of large-scale, complex civilizations. Social scientists and historians have long puzzled over the dynamics of large hierarchical societies and the mechanisms responsible for their survival and spread. But less is known about the origins of complex societies, which first emerged in only a few places around the world, leaving behind no written records of the process by which this quantum leap in human social organization occurred. The excavations at Çatalhöyük may help solve the puzzle. We argue that a major factor driving the emergence of complex society was *religious routinization*. The frequency of rituals appears to have increased over the course of settlement at Çatalhöyük and this may have had major consequences for the scale and structure of Neolithic society.

This argument permits a conciliatory stance on the relationship between religion's "vitality," as conceptualized in much of this volume, and its "functionality" in bolstering a social order. In fact these two aspects of religion are intimately interconnected – stripped of its vitality religion's social functions could hardly be fulfilled. The evidence from Çatalhöyük suggests that the earliest functions of religion were not to legitimate political and economic inequalities. Initially religion's function was to bind together small tribal groups, but gradually, as agriculture intensified, this ancient function faded and religion became a means of reproducing much larger (if more diffuse) group identities. This entailed a change also in religion's vitality – a shift from esoteric mystery cult to something more ideologically uniform, in some ways less awe-inspiring and more controlling. The exploitation of this new kind of religion by elites occurred much later, however, entailing the evolution of new forms of religious vitality.

Modes of Religiosity at Catalhöyük

The connection between ritual frequency and social morphology has been the subject of considerable research in recent years. A central hypothesis is that low-frequency, “dysphoric” (frightening and/or painful) rituals with others promote prosocial behavior in cooperative endeavors rather more than the sharing of either euphoric or neutral ritual experiences, and that the amount of reflection and rumination triggered by the experience and/or the fusion between the individual participant and the group will mediate this effect (Whitehouse 1996; Richert, Whitehouse and Stewart 2005). Dysphoric rituals are thought to bind small face-to-face groups based on networks of relational ties (Swann et al. 2012). Such rituals may be especially adaptive where survival depends on high levels of cooperation despite strong incentives to defect, such as chronic tribal warfare or systems in which meat is procured by hunting large and dangerous animals with simple weapons. This clustering of features (especially low-frequency dysphoric ritual and intense social cohesion in small groups) has become known as the “imagistic mode of religiosity” (Whitehouse 2004).

By contrast, participation in high-frequency (e.g., daily or weekly) religious rituals is thought to foster identification of group members within large “imagined” communities, efficient spread of authoritative dogma that is standardized by means of speech and text, and multiple levels of jurisdictional hierarchy (Whitehouse 1995). High-frequency religious rituals, like many other culturally shared behavioral conventions, are recalled as procedural scripts and semantic schemas (Baddeley 1997). Scripts and schemas specify what typically happens in a given ritual and what is generally thought to be its significance. In a group whose identity markers are composed mainly of scripts and schemas, what it means to be a member of the community may be generalized to everyone who performs similar acts and holds similar beliefs. This route to the construction of communal identity, based on routinization, may be especially conducive to the establishment of large populations sharing a common tradition and capable of behaving as a coalition in interactions with nonmembers, *despite* the fact that no individual in the community could possibly know all the others, or even hope to meet all of them in the course of a lifetime (Whitehouse 2000). Routinization also may also allow very complex networks of dogma and narrative to be learned

and stored in collective memory, making it relatively easy to spot unauthorized innovations. High-frequency rituals would seem to be adaptive for large populations requiring standardized identity markers to facilitate trust among strangers, for example, when competing for partners in trading networks, or to facilitate participation in large-scale cooperation. This nexus of features (high-frequency ritual and large-scale, hierarchical social morphology) has come to be known as the “doctrinal mode of religiosity” (Whitehouse 2004).

Evidence for the theory of modes of religiosity was originally based on a large body of detailed historical and ethnographic case studies (e.g., Ketola 2002; Martin and Pachis 2009; Martin and Whitehouse 2005; McCauley 2001; McCauley and Lawson 2002; McCauley and Whitehouse 2005; Naumescu 2008; Whitehouse and Laidlaw 2004; Whitehouse and Martin 2004; Whitehouse and McCauley 2005; Xygalatas 2007). Qualitative evidence of this kind was useful in refining the theory but is inevitably vulnerable to the criticism of “cherry picking” examples that confirm the predictions and ignoring those that do not. To address the problem, more systematic data on this topic are now being assembled. For instance, in a recent survey of 644 rituals selected from a sample of 74 cultures Atkinson and Whitehouse (2010) found an inverse correlation between ritual frequency and levels of dysphoric arousal, with most rituals clustering around the high-frequency/low-arousal (doctrinal) and low-frequency/high-arousal (imagistic) poles of the continuum. One of the predictions of the modes theory supported by this cross-cultural evidence was that high-frequency rituals correlate with larger-scale farming societies while more dysphoric rituals prevail in smaller communities exhibiting lower reliance on agriculture. Extrapolating these findings to the transition from foraging to farming in the prehistory of the Middle East and Mediterranean Atkinson and Whitehouse observed:

The first appearance of the doctrinal mode in human prehistory would seem to presage the first appearance of large-scale, hierarchical political systems in Mesopotamia and Egypt. Was this seismic shift in social evolution driven by a change from imagistic to doctrinal practices? Although the question of causality cannot be determined here, the link between agriculture and relatively low arousal, high frequency rituals in our survey of contemporary societies offers support for this hypothesis. Whereas the exploitation of wild resources requires only sporadic group co-operation (e.g. in hunting larger game), the domestication of animals and plants fosters increasingly

routinized forms of collaborative labour (e.g. clearing, planting, harvesting, and fencing). In traditional societies such activities are typically punctuated by rituals.... If the emergence of agriculture drives an overall increase in the frequency of communal rituals, it also indirectly opens up opportunities for other features of the doctrinal mode to appear ... including the homogenization of regional traditions and in time the emergence of professional priesthoods.

This chapter builds on an earlier study suggesting that changes in ritual life at Çatalhöyük were linked with and may have facilitated the shift to large-scale agricultural societies (Whitehouse and Hodder 2010). Of course, Çatalhöyük was always agricultural and the site was always large. But we argued that a shift could be observed from imagistic to doctrinal modes of religiosity. Following Mithen (2004) we suggested that the clearest evidence from Çatalhöyük concerned low-frequency rituals that would have had high-arousal components. Such evidence seemed to predominate in the earlier occupation of the site. The socialized and ritualized interactions with large and dangerous animals, and concomitant feasting, would have occurred relatively infrequently and would have been high-arousal events. Other aspects of the Çatalhöyük data could be interpreted as conforming to the expectations of the imagistic mode. For example, as the hard pointed parts of the animals killed in hunting or teasing and baiting were taken into individual houses there was much variation in the specific interpretations that were made – so there were multivocality and multivalence, as indicated by the great diversity of specific interactions with the bucrania and other animal body parts in individual houses. For example, usually the benches with bull horns occur on the east side of main rooms in houses, but in Building 52 a bench with bull horns occurs on the west side. In the upper levels of the site, Whitehouse and Hodder (2010) argued that the emergence of the doctrinal mode could be discerned not only in the evidence for recurring themes in the construction of acts and artifacts at the site but, more tellingly, in the evidence for an increasingly discursive deployment of those themes in standardized ways and the emergence of authoritative versions.

While Whitehouse and Hodder (2010) noted a concomitant shift from less to more social differentiation in the sequence at Çatalhöyük, little attention was given to possible links among the changing modes of religiosity, community size, and agricultural intensity. Atkinson and Whitehouse's (2010) cross-cultural analysis of contemporary cultures

from around the globe found that modes of religiosity are indeed associated with synchronic variation in community size and agricultural intensity. The analysis showed that high-arousal, low-frequency rituals are associated with both hunting/gathering and smaller community size. Conversely, low-arousal, high-frequency rituals are associated with increased agricultural intensity and larger community size. One explanation for this pattern is that ritual is partly a cultural adaptation supporting different scales of cooperation suited to varying challenges of resource extraction and intergroup competition. The aim in this chapter is to move beyond these synchronic data to look in detail at evidence from a single site to see whether the shift to a doctrinal mode of religiosity is linked to increasing agricultural intensity and greater community size and density of population.

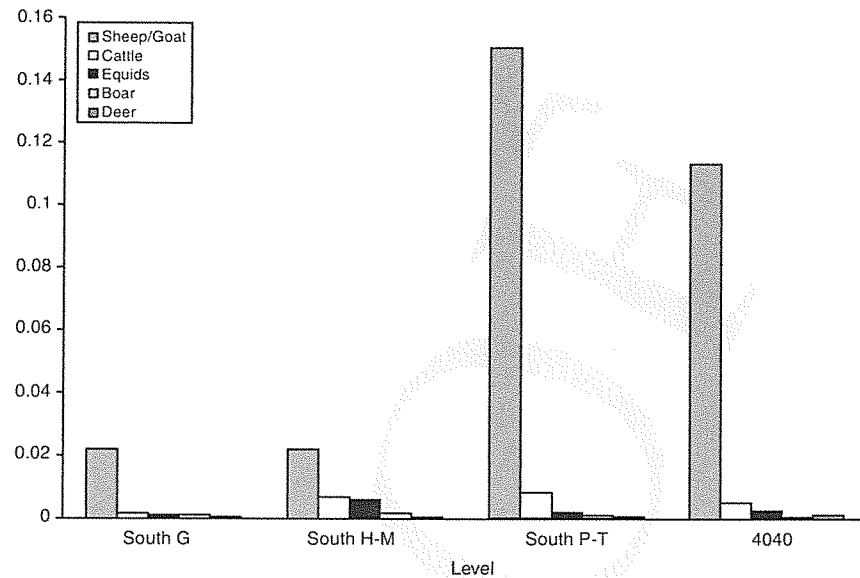
In the earlier levels of Çatalhöyük, the best evidence of the imagistic mode is the installations of parts of wild animals within houses. In particular, the horns of bulls and the tusks of wild boar were placed within walls or pedestals; these animals and animal parts seem also to be associated with feasting. After Level South O/P the frequency of such installations declines. In their place are found paintings of people teasing and baiting wild animals. In the material culture inventory there is an increased occurrence of stamp seals and pottery with decoration including representations of bulls. This more discursive and perhaps doctrinal mode occurs from South P to TP. The new recently collected evidence from the site allows evaluation of changes in population size and agricultural intensity through the entire sequence of occupation.

Overall Population Size and Density

Regional survey by Baird (2002, 2005) shows increasing population densities through the Ceramic Neolithic and early Chalcolithic (eighth to sixth millennia BC) on the Çarşamba alluvial fan on the Konya Plain, but also concentration through time into the one large site of Çatalhöyük, followed by dispersal into multiple tells in the Chalcolithic. As far as densities on site are concerned, while we cannot yet map the whole East Mound and each level, there is some evidence to suggest that population gradually rose until Levels South M, N, and O. We know very little of the extent of the earliest occupation of the site, but excavations in the twenty meter by twenty meter area in the South Area found no buildings

in the lowest levels, and the midden deposits discovered may have been toward the edge of the site. By Level South J this South Area was more densely populated, and the density of houses increased into Level South N. The number of burials per building is greatest in these middle levels (Cessford 2005), and the densely packed clusters of households (Düring 2006; Düring and Marciniak 2006) suggest that the site's population reached its peak in South M–O and 4040 G. There is also significant change in indicators of human fertility, diet, activity, and disease. Larsen et al. (2013) identify clear evidence for higher levels of fertility in the middle period of occupation (South M and North G). The prevalence of osteoperiostitis among adult individuals is also at its peak in the middle levels (27.9 percent) and declines dramatically in the upper levels (8.6 percent). This evidence suggests heightened conditions of nonspecific stress, especially during the peak population. Evidence of accidental skeletal trauma also suggests a rather more accident-prone population in the middle levels, perhaps linked to the increased workload. The middle period appears to be characterized by higher overall amounts of labor, perhaps stemming from intensified resource exploitation and food production, while in the upper levels there appears to be a decrease in overall workload and an increase in mobility as a wider range of resources was exploited. From South P onward we see more open space between buildings, and habitation seems increasingly dispersed, with contracted settlement in the South Area of the site, sparse settlement in the northern zone, and scattered occupation to the east of the East Mound (Hodder 1996) and in the IST Area. A femoral midshaft index was used (Larsen et al. 2013) to assess the mobility of individuals, and a general trend from less to more mobility through time was noted for both males and females (although only statistically significant for males). Study of long bone cross sections suggested that females show some indication of an increase in mobility through the occupation of the site. All this evidence for increased mobility in the upper levels fits very well with the evidence for increasingly wide use of the landscape for herding sheep and managing domestic cattle (see later discussion).

In summary, population numbers and densities increase into South M–O and then decline or population dispersal occurs. This South M–O period is also the time of greatest fertility and most skeletal evidence of stress on health. In the upper levels this high level of stress is replaced by greater skeletal evidence of mobility.



6.1. Midden deposits: density of animal taxa through time.

Agricultural Intensity

The relative proportion of taxa (sheep/goat, cattle, boar, equid, deer) through time shows a rise in sheep/goat in levels South P–T (Russell et al. 2013). But more telling is that the analysis of the densities of faunal remains in midden units by level shows a sharp rise in sheep/goat (Figure 6.1) and a constant level of cattle consumption. The increase in sheep/goat on site from South P onward appears to indicate the intensification of caprine herding in the late levels. It is not clear exactly when this change occurred, as in the South levels the recent excavations have not explored N and O; and in the North we are unsure of the exact chronological relationships with the South levels, but we can say the change occurred somewhere in the South N to P bracket, that is, around 6500 BC.

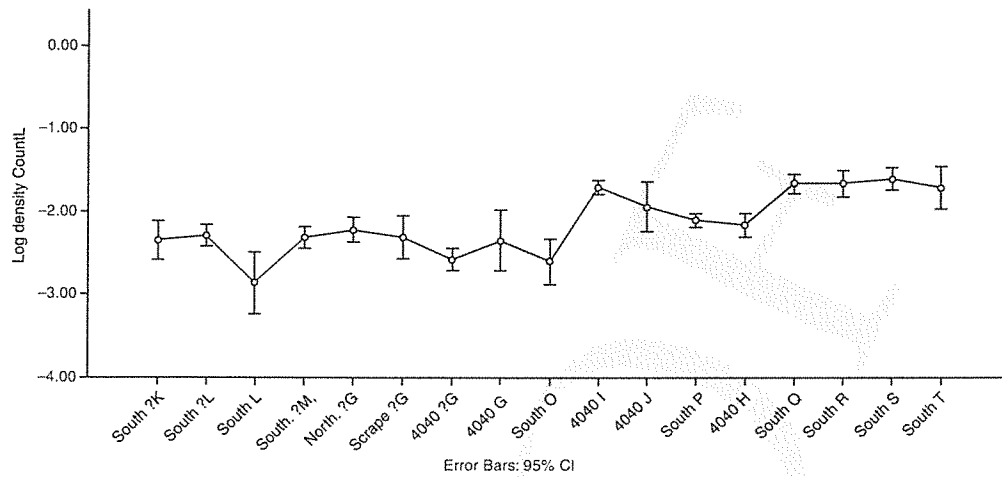
This increased focus on sheep suggests a major input of labor. There is also evidence for the introduction of domesticated cattle at this time (Russell et al. 2013). Together these shifts suggest a significant increase in the intensification of agricultural production that continues on into the West Mound Chalcolithic. There is some slight indication that this increase in intensification was associated with a shift from collective management of sheep herds to separate house-based control. This argument

is based on an interpretation of age and sex profiles in the upper levels (Russell et al. 2013) and on variability in sheep isotopes (Pearson 2013). There is also slight indication (see later discussion) that the shift to herding cattle may have allowed a degree of wealth accumulation, although this always seems to have competed with strong leveling mechanisms at Çatalhöyük.

The botanical remains do not show marked change through the main sequence at Çatalhöyük. Rather they show continuity but with hulled barley introduced as a new, more intensive crop in the uppermost levels and on the West Mound (as seen in both phytolith and macrobotanical remains – Ryan 2013; Bogaard et al. 2013). The clearest evidence of change in the phytolith assemblage is an increase in *Australis* phragmites in the upper levels, after South P. In general terms phragmites is an indicator of disturbance to the local environment through increased human intervention. Possible causes of the increase are the digging of deeper quarry pits around the mound (in order to provide sandy clays for bricks and pottery), over-wintering of sheep and perhaps local managing of cattle near the site, and the provision of reeds for roofs and mats. The expansion of phragmites would have led to lowered water tables and a decrease in biodiversity. Management of and response to the proliferation of phragmites would have required greater inputs of labor.

Increased Activity in the House and Settlement

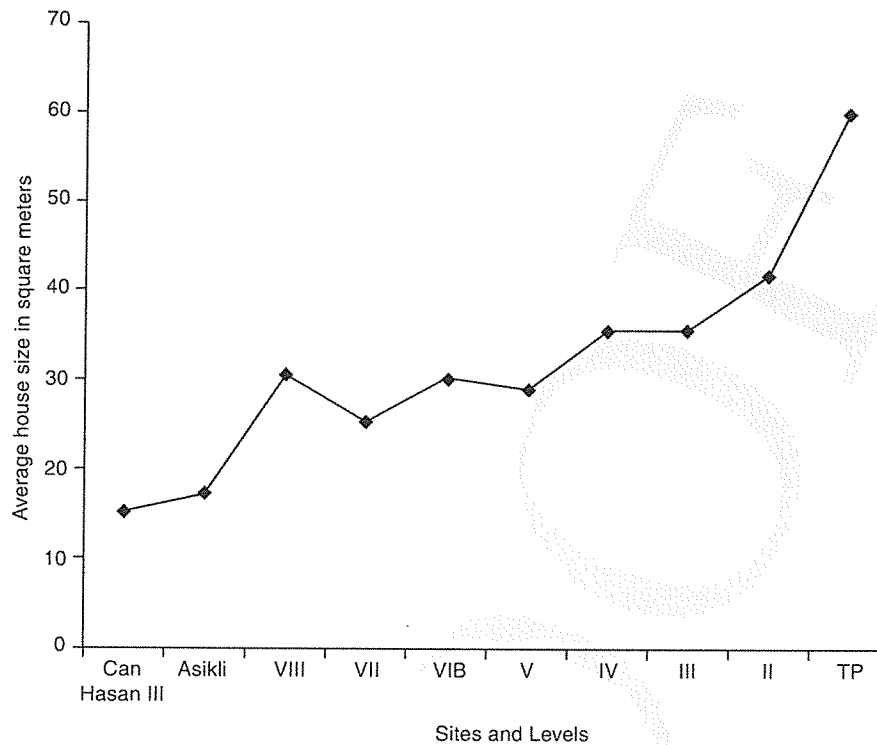
The increased evidence for agricultural activity in the post-P South levels can be related to increased intensity of activity in the house. Many aspects of the economy seem to have been organized through a domestic mode. There is much evidence for the intensive processing of sheep bones and meat in the house, using pottery to extract grease and fat as well as to cook meat. We also have much evidence that cereals were stored in the house with spikelets attached. As needed the grains were removed from storage bins, dehusked, and then ground. Given this degree of house processing of sheep and cereal resources it might be expected that as the intensity of animal and plant exploitation in the landscape increased so there should be increased evidence for processing in and around the house. The introduction of pottery and its gradual increase in densities through time (Figure 6.2; a Kruskal Wallis test reported a statistically significant difference between levels) is one indicator of this increased



6.2. Density of pottery through time.

processing since the cooking pots were largely used to process sheep meat and fat (Pitter, Yalman, and Evershed 2013); there is also phytolith evidence that pots were used in processing cereals. Ground stone was used to grind and process foods, and there is greater specialization of production of ground stone tools in the upper levels (Wright 2013). There is also incipient small-scale specialization of bone tool manufacture in the upper levels (Russell et al. 2013), and the same can be said of obsidian (Carter and Mili 2013). Mini clay balls, tokens, and stamp seals all increase in the upper levels, and it is possible that all these were used in early forms of accounting (Atalay 2013; Bennison-Chapman 2013). Although not involved in agricultural production, beads demonstrate a greater diversity of raw materials in the upper levels of the site, and greater technical skill was involved in their production (Baines 2013). They thus contributed to the overall increased levels of productive activity.

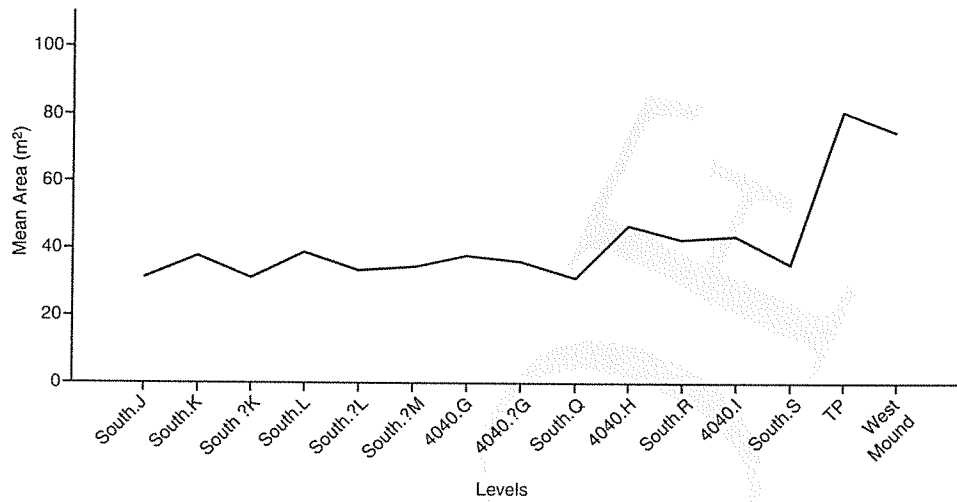
Since most of these productive activities (final processing of sheep and cereal resources, manufacture of ground stone, bone and obsidian tools, and the production of beads) all took place in the house it might be expected that houses would become larger in the upper levels. Such a trend is clear if we consider the average increase in house size in Çatalhöyük and adjacent sites, incorporating both recent data and the larger sample collected by Mellaart (Figure 6.3). When only the recent excavations are considered, in this smaller set of data the relationship is not found, except for an increase in TP and on the West Mound



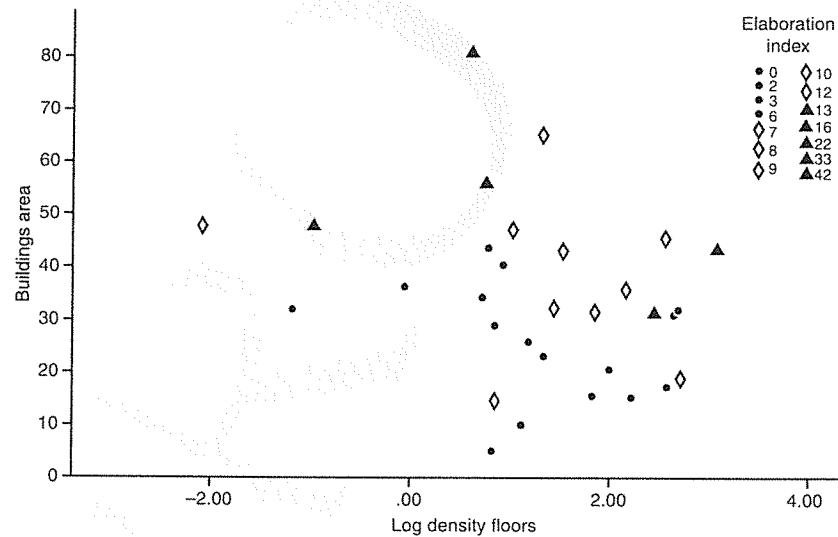
6.3. Average internal area of houses (not including walls) in levels at Çatalhöyük and at two earlier sites in central Anatolia. The Çatalhöyük data include buildings excavated by Mellaart.

(Figure 6.4; a Kruskal Wallis test did not find a statistically significant difference between levels). In the larger data set, the later bigger houses have more storage and side rooms, and there is a very large “farmlike” house that has been excavated on the West Mound (Building 25). While some buildings get larger, there is little evidence of change in the ratio of main rooms to side and storage rooms. The evidence does not suggest substantive social differentiation, but rather a general increase in variation between smaller and larger buildings. The same conclusion is reached by considering the scatterplot in Figure 6.5 that shows floor density in relation to building size and elaboration. While this plot confirms earlier evidence (Hodder and Pels 2010) that more elaborate buildings tend to be larger, there is no evidence of greater or lesser densities of activity on floors of larger or more elaborate buildings.

We have noticed that buildings in the upper levels of the site seem to have cleaner floors. This is perhaps shown in the very slight and gradual

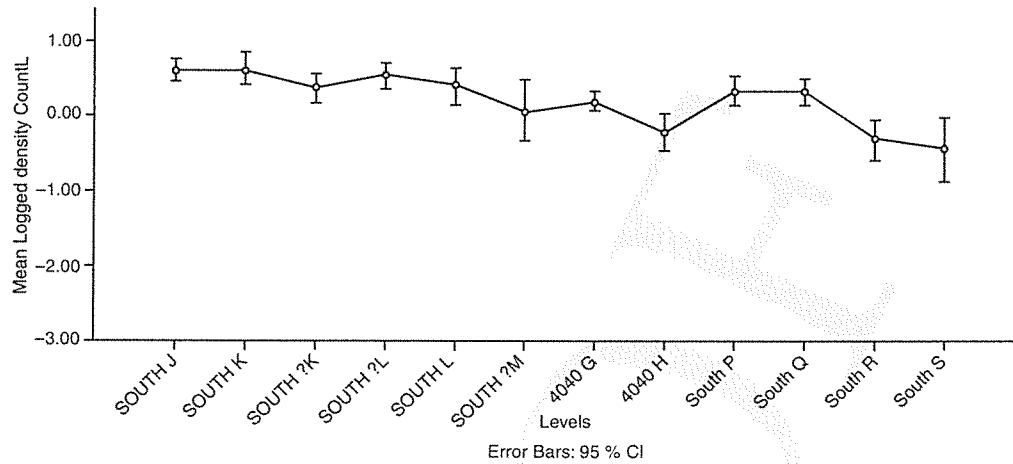


6.4. The area of buildings excavated by the current project in different levels at Çatalhöyük (area calculated from GIS incorporating building walls).

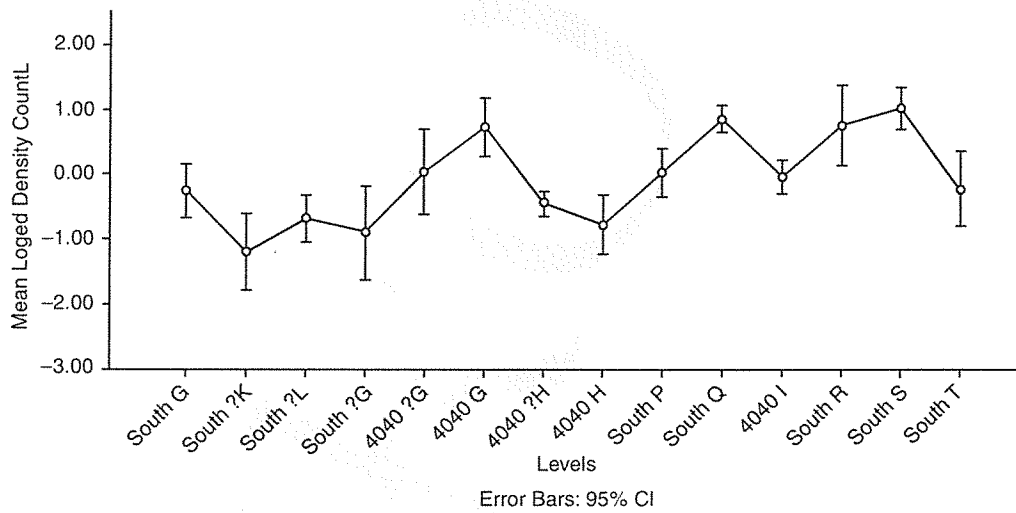


6.5. Scatterplot of logged density on floors (faunal remains, chipped stone, pottery, and ground stone) versus building size, by elaboration index.

change in densities on floors in Figure 6.6 (e.g., a Kruskal Wallis test found a statistically significant difference in pottery densities on floors between levels). On the other hand, there is slight evidence of greater densities of residues in middens in the upper levels (Figure 6.7 and again a Kruskal Wallis test found a statistically significant difference in pottery

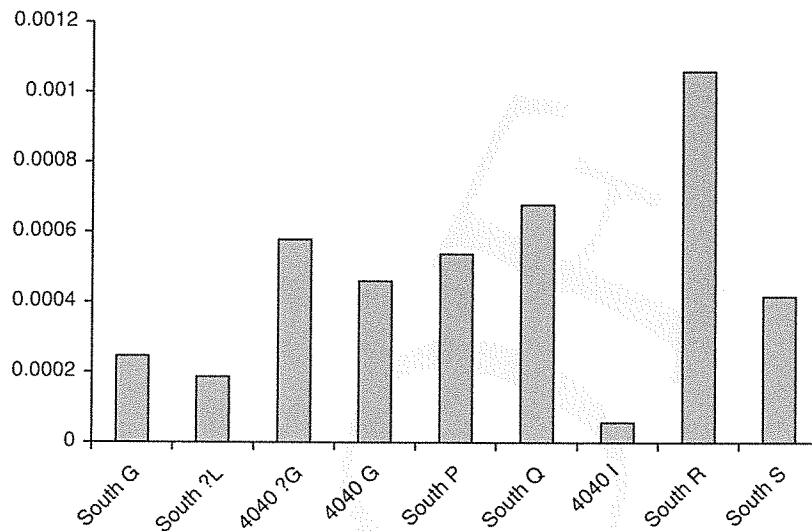


6.6. Density of pottery, chipped stone, faunal remains, and ground stone in floors through levels, 4040 and South for data collected 1995–2008. (Botanical remains have been excluded because of missing samples for the early levels.)



6.7. Density of pottery, chipped stone, faunal remains, and ground stone in middens through levels, 4040 and South for data collected 1995–2008. (Botanical remains have been excluded because of missing samples for the early levels.)

densities in middens between levels). In the upper levels, then, houses are cleaned out more thoroughly, but also activities that used to take place inside houses now occur more frequently outside – and this is supported by the slight increase in fire spot density in middens in the upper levels (see Figure 6.8) (though with perhaps a final decrease in

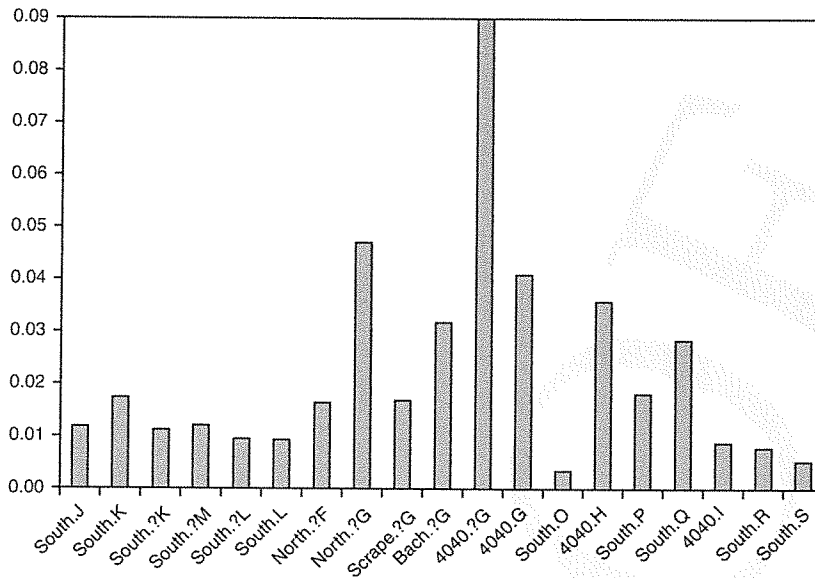


6.8. Densities of fire spots in middens and other external areas by level.

4040 I and South S). As buildings grew bigger and multiroomed they also increasingly made use of adjacent open areas. There seems to be a pattern of increased encroachment onto adjacent midden areas in the 4040 Area of the site, especially onto Sp.60 midden. Similarly ovens and hearths increasingly appear in yards and middens in the South Area from P onward and some buildings (e.g., in the 65-56-44-10 sequence) have openings into adjacent yard or midden areas. The archaeological evidence for increased use of open space between buildings for a range of domestic and productive activities is described elsewhere (Hodder 2013). All the evidence suggests the gradual expansion of the house into a multifunctional productive unit.

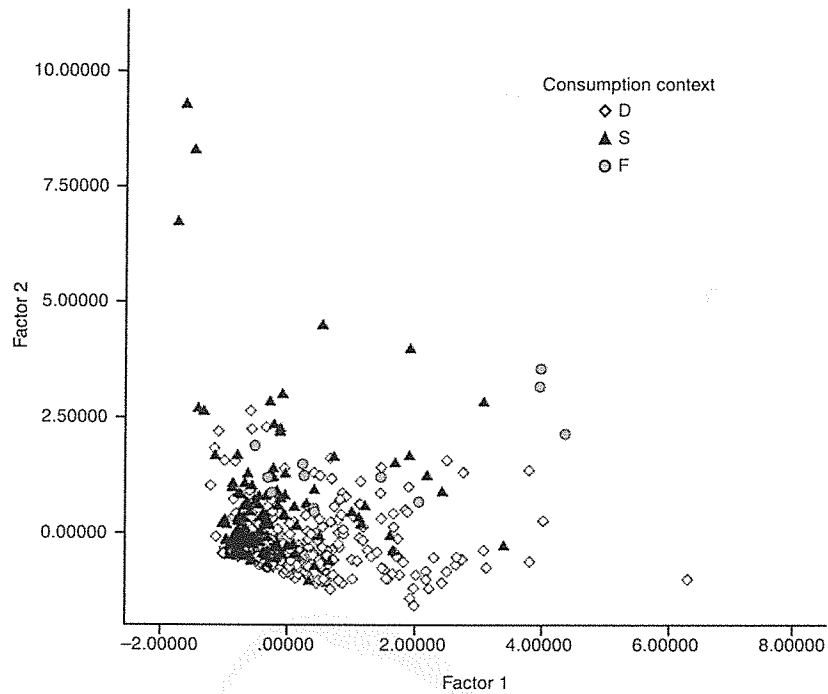
Ritual Changes

Overall, therefore, there is evidence for increased productive intensity in the upper levels of Çatalhöyük associated with greater activities in houses and surrounding yards and middens. Settlement both on the site and regionally started to disperse. At the same time there is evidence for greater mobility and the exploitation of a wider range of locales in the landscape for sheep and cattle herding. There is a parallel change in ritual practices in the upper, post-South P levels.

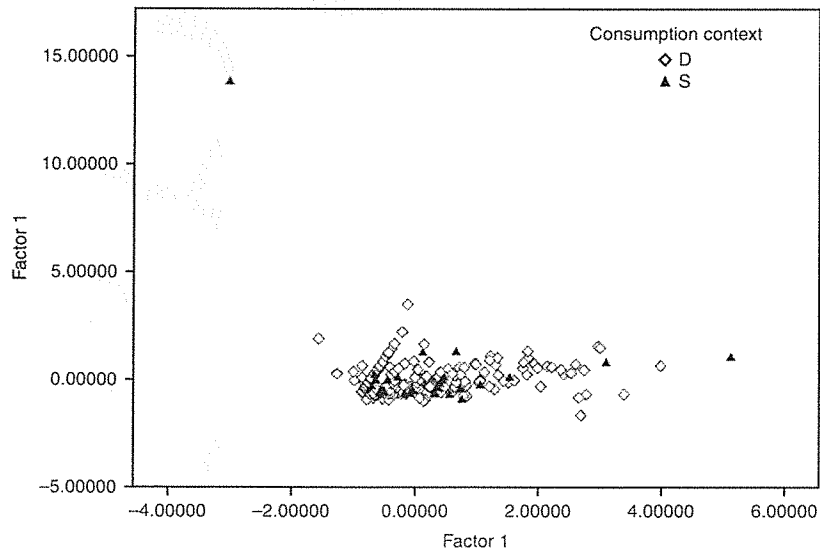


6.9. Chronological distribution of densities of special deposits among all excavated units.

The analysis of faunal deposition has identified special deposits as those with high concentrations of relatively unprocessed large bones. Such special deposits occur, for example, in house abandonment and foundation deposits. In the lower levels of the site such special deposits, as well as feasting deposits, are associated especially with wild bulls (Russell and Martin 2005). The density of these deposits reaches a high point in Level 4040 G, equivalent to South N–O (Figure 6.9). In the upper levels the densities of special deposits decrease again, while sheep/goat proportions increase in special consumption contexts as the overall amounts of sheep/goat increase. Reciprocally, cattle appear to be consumed more often in quotidian settings in the upper levels. A principal component analysis of faunal densities together with pottery, chipped stone, and figurine densities has confirmed these trends. In levels before South P, the special and feasting deposits have less sheep and more cattle, as well as well as less chipped stone. After South P, on the other hand, there is less clear distinction among special, feasting, and daily contexts (Figures 6.10 and 6.11). And indeed cattle now associate with domestic pottery on component 1. So, while feasting and special deposits decline in frequency in the upper levels they are less commonly associated with



6.10. First two factors resulting from principal components analysis of densities of animal remains, chipped stone, figurines, and pottery in pre-South P level equivalents in the southern and northern parts of the site. Special deposits (S) and feasting deposits (F) cluster on the plot differently from daily consumption deposits (D).



6.11. First two factors resulting from principal components analysis of densities of animal remains, chipped stone, figurines, and pottery in post-South P level equivalents in the southern and northern parts of the site. Special deposits (S) are less distinctive in relation to daily consumption deposits (D) in the upper levels of the site.

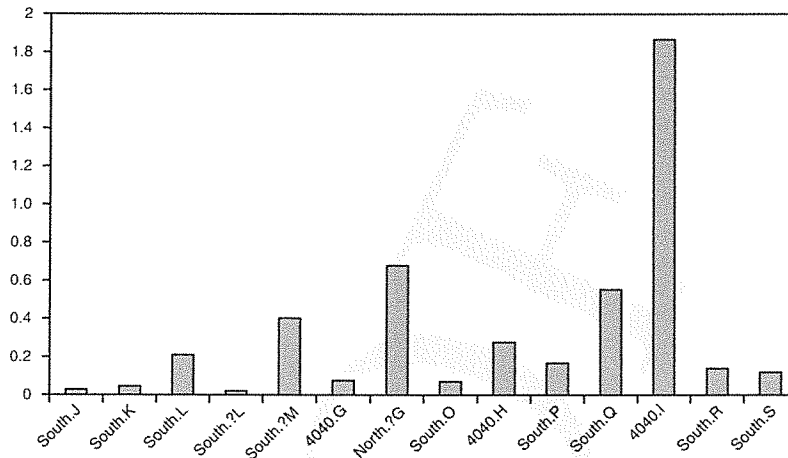
wild cattle and other wild animals. As noted previously, the upper levels also see a decline in the use of wild animal parts in installations in houses. There is thus less focus on special events associated with high-arousal experiences and less focus on the direct presencing of dangerous wild animals within the routine practices of everyday life within the house. This confirms the general pattern of a decrease in special events associated with wild cattle and other wild animals and a decrease in installations that memorialize these events.

Burial

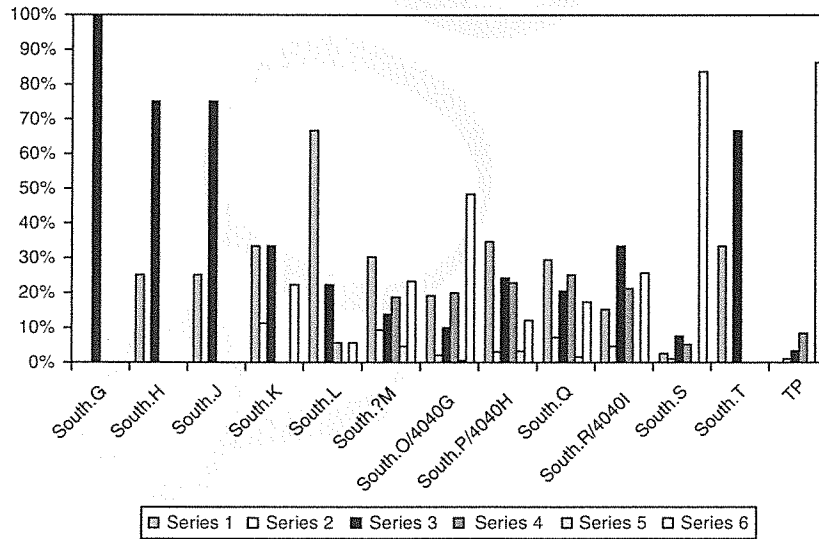
The greatest richness and diversity of burial goods occur in South M–O (Nakamura and Meskell 2013), coinciding with the concentration of animal part installations in buildings during the same period. The significance of burial events was perhaps heightened by the incorporation of burial goods in graves. The density of burials, however, changes little through time. In Figure 6.12 the density appears to increase, but the high point of 4040 I is a small sample of baby burials mainly in one building.

There is more focus on foundation burials in the upper levels at the same time as there is less continuity from building to building through time. It is as if continuity of the house building was no longer taken for granted and had to be established through foundation burials of people. There is also increased disturbance of the burials in houses as is seen in an increase in the percentage of primary disturbed loose bones in burials in South S and TP and their absence in the lowest levels (Figure 6.13). In the very uppermost levels of the East Mound there is evidence of major change in burial rites, with “tombs” discovered in the TP Area in which multiple burial and burial of humans with animals now occurred. By the time of the Chalcolithic West Mound there is little evidence of adult burial in houses, and it is possible that separate cemeteries will be discovered.

In general terms, then, as with evidence of installations and special deposits, the role of burial in creating house-based continuities changes after South P, although only gradually. Through the later occupation of the site, burial is increasingly separated from the routines of daily life in the house, where it had earlier aroused notions of continuity. In the



6.12. The density of individuals buried beneath floors in the different levels.



6.13. Percentage of burial types through levels (series1: primary, series2: secondary, series3: tertiary, series4: primary disturbed, series5: unknown, series6: primary disturbed loose).

earlier levels the burial process reaches its apogee in terms of numbers of objects placed in graves in South M–O, but in the upper levels the dead were increasingly disturbed and then distanced and separated from daily life even if they retained an importance, at least on the East Mound, in founding new buildings.

Conclusion

In sum it seems that two trends can be identified that relate to the proposal that a shift to a doctrinal mode of religiosity in the upper levels at Çatalhöyük was linked to increasing agricultural intensity and greater community size and population density.

The first trend identified is increased intensity of agricultural and other forms of production in the upper levels. This shift is associated with a decreased focus on the continuity of the house, fewer installations in the house, and a decrease in special ritual and feasting events focused on the killing of wild animals. It thus appears that these low-frequency rituals, which are likely to elicit high arousal, decreased through time as intensity of production increased. As discussed by Whitehouse and Hodder (2010), there is an increase in the upper levels in discursive mobile symbols as seen on stamp seals and pottery. Feasting or special deposits become more “everyday.” The main factor linked to a shift away from high-arousal, low-frequency rituals seems to be productive intensity not community size because we see a decrease in the overall size of the population in the upper levels as houses dispersed and became more separate and independent. Houses do themselves get larger, or some of them do, but the overall density and size of the settlement decrease.

There is a second trend that does relate to the increased density of occupation. Increased population size, density, and fertility occur in South M–O. What we see in South M–O, that is toward the end of what may be a more imagistic mode of religious life in the lower levels, is a heightening of the classic early Çatalhöyük pattern of elaborate symbolism in houses, installations of wild animals, special animal feasting and deposits, and elaborate burial. So, again, the data suggest that settlement size and density are not predicting these changes in ritual form. At Çatalhöyük the highest population size and density are associated with the greatest elaboration of imagistic-type features. There is evidence of stress in the population at this point (South M–O), and it is not until these stresses are relieved with a more intensive and more mobile economy in the upper levels that there is more evidence for aspects of the doctrinal mode. The evidence overall suggests that at Çatalhöyük a shift away from more imagistic, low-frequency high-arousal rituals is linked to increasing intensity of agricultural production rather than population size and density, although this shift may

also have entailed a transition of tribal fragmentation toward settlementwide or even regional cultural homogenization and more encompassing forms of group identity. This pattern is broadly consistent with parallel findings from the analysis of ritual variation in contemporary cultures. Doctrinal religious practices are associated with both larger population size and increased agricultural intensity, but in a multiple regression analysis only agricultural intensity remains a significant predictor (Atkinson and Whitehouse 2010).

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