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A Diachronic Study of Paleolithic and Aceramic Neolithic Settlement Patterns in the Wadi Hasa, West-Central Jordan

Introduction

The analysis of hunter-gatherer settlement subsistence systems in the Levant has benefited in recent years from the development of both general and regional models of positioning strategies. The best-known general model is probably Binford's forager-collector continuum, in which foragers use high residential mobility to 'map on' to resources in largely undifferentiated environments through encounter-type procurement strategies. Collectors are typically less mobile residentially, relying on logistically-organised food procurement and storage to solve problems of temporal and spatial incongruities in resource distribution. In basic terms, foragers tend to produce smaller and less differentiated sites than do collectors (Binford 1980, 1982).

For the Levant, the most comprehensive local land use model is probably the radiating-circulating dichotomy developed by Marks and his colleagues for data from the central Negev highlands (Marks and Freidel 1977; see also Mortensen 1972). These contrasting ideal types are argued to be related to macroclimatic changes which affected the location of environmental zones and ultimately hunter-gatherer resource abundance and distribution. A radiating pattern, which consists of a sedentary or semi-sedentary residential camp surrounded by small limited activity stations, is argued to be a response to mesic climatic conditions and is correlated with an expansion of Mediterranean phytogeographic zones. A circulating pattern, comprising scattered, small, relatively similar multi-purpose sites, is thought to be a response to the xeric climatic conditions associated with the formation of Irano–Turanian phytogeographic zones (that is, dry sub-desert and steppe environments). Marks has used paleoenvironmental and archaeological evidence to suggest that a radiating pattern was characteristic of the Negev during the relatively wet Middle Paleolithic and Natufian periods, and that a circulating pattern typified the drier Upper Paleolithic and Early Epipaleolithic (TABLE 1).

Donald Henry, working on the southern edge of the Jordan Plateau, has added the dimension of transhumance to the Marks model (Henry 1982, 1983, n.d.). He suggests that in south Jordan during the Middle, Upper and Epipaleolithic there was movement between different elevational zones on a seasonal basis which affected group size and composition, and ultimately site size and characteristics in this area. Larger residential sites tend to be located at lower elevations during the winter months and smaller sites tend to be found at higher elevations and correspond to summer encampments. Thus during the winter months, a 'radiating' settlement pattern (in Marks' terms) would have prevailed, to be replaced during the summer by a 'circulating' pattern. This model is both supported and contradicted by Bedouin ethnographic data. Both Levantine land use models have been partially tested using survey and excavation data. Are we now (1986) in a position to be able to evaluate the credibility of these models? The answer is a qualified 'yes'.

Paleoenvironments of the southern Levant

Largely as a consequence of work done in Palestine, it has recently become possible to reconstruct expected general paleoenvironmental trends from the Middle Paleolithic through the Prepottery Neolithic (Donaldson n.d.). However, there is less than complete agreement for even the southern Levant, and differences of opinion regarding the extent to which it is possible to extrapolate from north to south (Clark 1984; Donaldson n.d.).

Early Middle Paleolithic data from the Negev suggest an environment considerably wetter than today with climatic belts distributed 200–250 kms south of their present locations. Limited evidence from the Later Middle Paleolithic from both the Negev and south Jordan indicate increased aridity during this period.

The Middle-Upper Paleolithic transition and the Early Upper Paleolithic in the Negev are characterised by a dry climate with a relatively wet interval between 32 and 27,000 years BP. Evidence from south Jordan is suggestive of overall and continuing dry conditions during this time.

The Early Epipaleolithic of the Negev continues to be characterised by increasing aridity, although the climate was probably still more moist than at present. Data from south Jordan, however, indicate a wet interval between about 20,000 and 15,000 years ago.

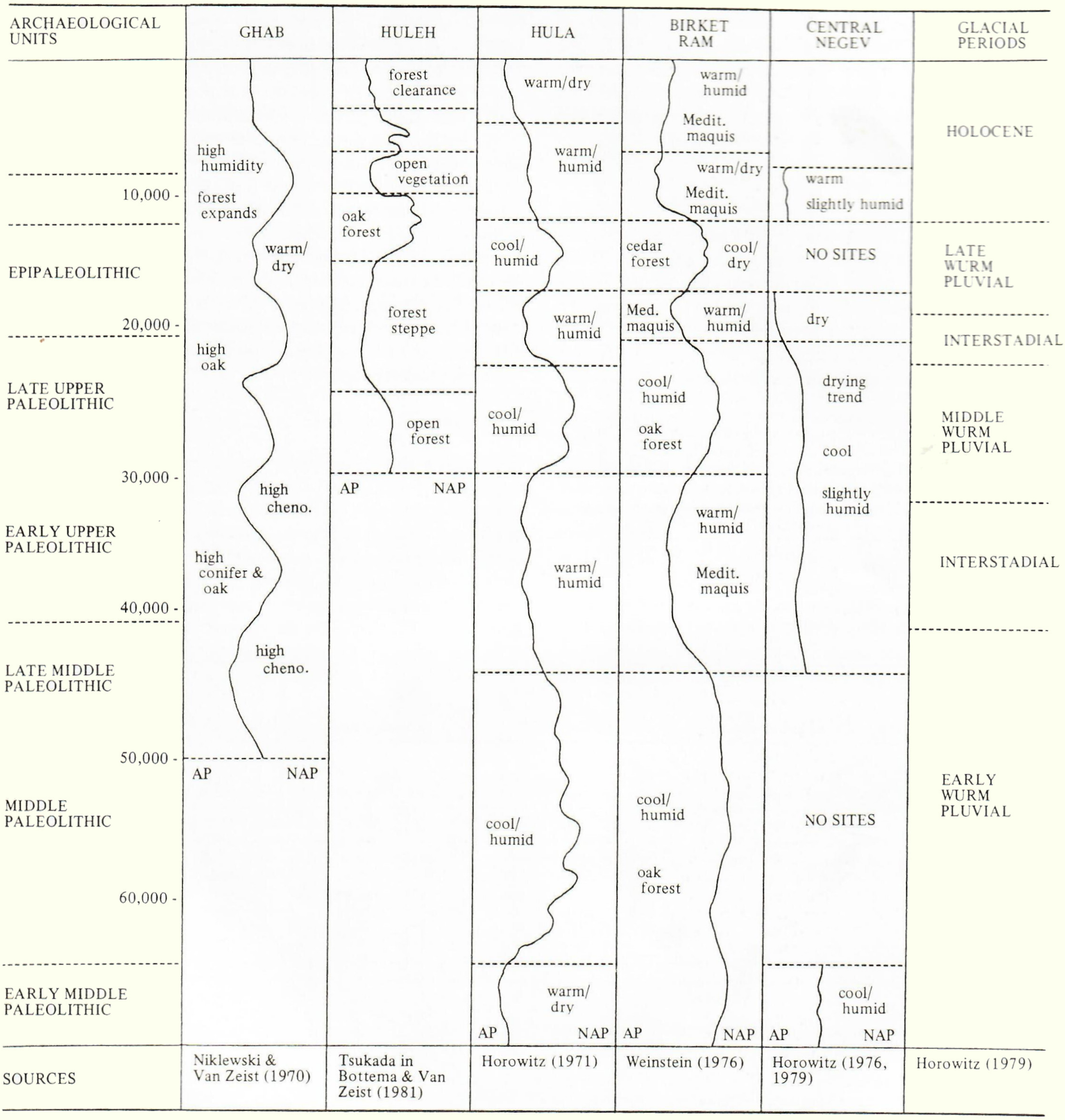
Table 1 Tentative Paleoclimatic sequence for the Late Pleistocene of the Central Negev (From Goldberg 1973, 1979, 1981; Horowitz 1976, 1979)

Archaeological units	Sedimentological & vegetational characteristics*	Avdat/Aqev Sites†	Macroclimatic Trends	Marks' (1981, 1983) Settlement pattern characteristics
EPIPALEOLITHIC-EARLY NATUFIAN [*c.* 17,000–13,000 BP]	periodic very slightly more humid oscillations 17–12,000 BP followed by contradictory evidence: drier conditions post-13,000 BP indicated by the sediments (Goldberg 1981), wetter conditions post-14,000 BP by the pollen (Horowitz 1979); by the late Natufian (*c.* 10,500 BP) a drier climate as indicated by pollen data from Rosh Zin (D-16)	D-5, Rosh Zin (D-16) D-101, Ein Aqev (D-31)	Drying Somewhat wetter	climatic evidence equivocal; possible brief return to radiating configuration during the early Natufian, followed by circulating pattern in the late Natufian
UPPER-EPIPALEOLITHIC TRANSITION [23–22,000–15,000 BP]	continuation of drying trend with arboreal fraction 7% (D-34), then 3% (D-31); NAP indicates slightly wetter conditions than present; erosion beginning *c.* 23,000 BP becomes marked after *c.* 15,000 BP; formation of colluvial silt lenses after *c.* 18,000 BP; maximum aridity *c.* 16–15,000 BP	Ein Aqev (D-31) D-34	Drying	circulating pattern continues
UPPER PALEOLITHIC [*c.* 45,000–20,000 BP]	complex sedimentary sequence with continued alluviation characterised by the accumulation of coarse, then fine terrace gravels, sands (until *c.* 27,000 BP), then silts, clayey colluvium (until *c.* 20,000 BP); decline in runoff energetics over time; climate somewhat more humid (and considerably more humid 32,000–27,000 BP) until *c.* 27,000 BP, when a trend toward greater aridity begins; 16% AP at D-22, D-27; climatic belts 150–200 km S of present locations	D-22, D-27a, b D-100 D-34	Drying Wetter Drying	circulating pattern with no significant intersite variability (i.e., more difficult to distinguish between base camps, limited activity stations); repeated reoccupation of sites (but without spatial consistency in activity area placement); more mobile settlement/subsistence system tied to increased importance in scheduling in resource procurement in a more arid environment than during the Middle Paleolithic
MIDDLE-UPPER PALEOLITHIC TRANSITION [*c.* 47,000–*c.* 45,000 BP]	new cycle of alluviation with formation of terraces up to 15 m thick; somewhat drier than previously with 17% AP at D-101; NAP much the same as early Mousterian	D-101	Dry Briefly somewhat wetter?	shift to circulating pattern with trend toward increased dessication; decline in site size, intersite variability and evidence of sedentism
LATER MOUSTERIAN [*c.* 65,000–*c.* 45,000 BP]	drying trend, erosion (wadi downcutting with destruction of many early Mousterian sites), consequently few sedimentary traps for later Mousterian industries		Drying	radiating settlement/subsistence system with base camps and associated limited activity sites; base camps characterised by high artifact density, stratified deposits and the formation of middens, spatially-consistent tool kits; a relatively sedentary pattern or, alternatively, a pattern of reoccupation at regular intervals; logistical strategy possible due to optimal climatic conditions vis a vis the Upper Paleolithic
EARLY MOUSTERIAN [c. 90,000 – *c.* 65,000 BP]	wet; formation of gravel terraces and travertines in springs; 25% AP at D-35; channel aggradation followed by colluviation; climatic belts 200–250 km S of present locations	D-35, D-15	Wet	

* should be read from bottom to top

† sites not in stratigraphic order within archaeological units

Table 2 Schematic comparison of major pollen studies in the Levant



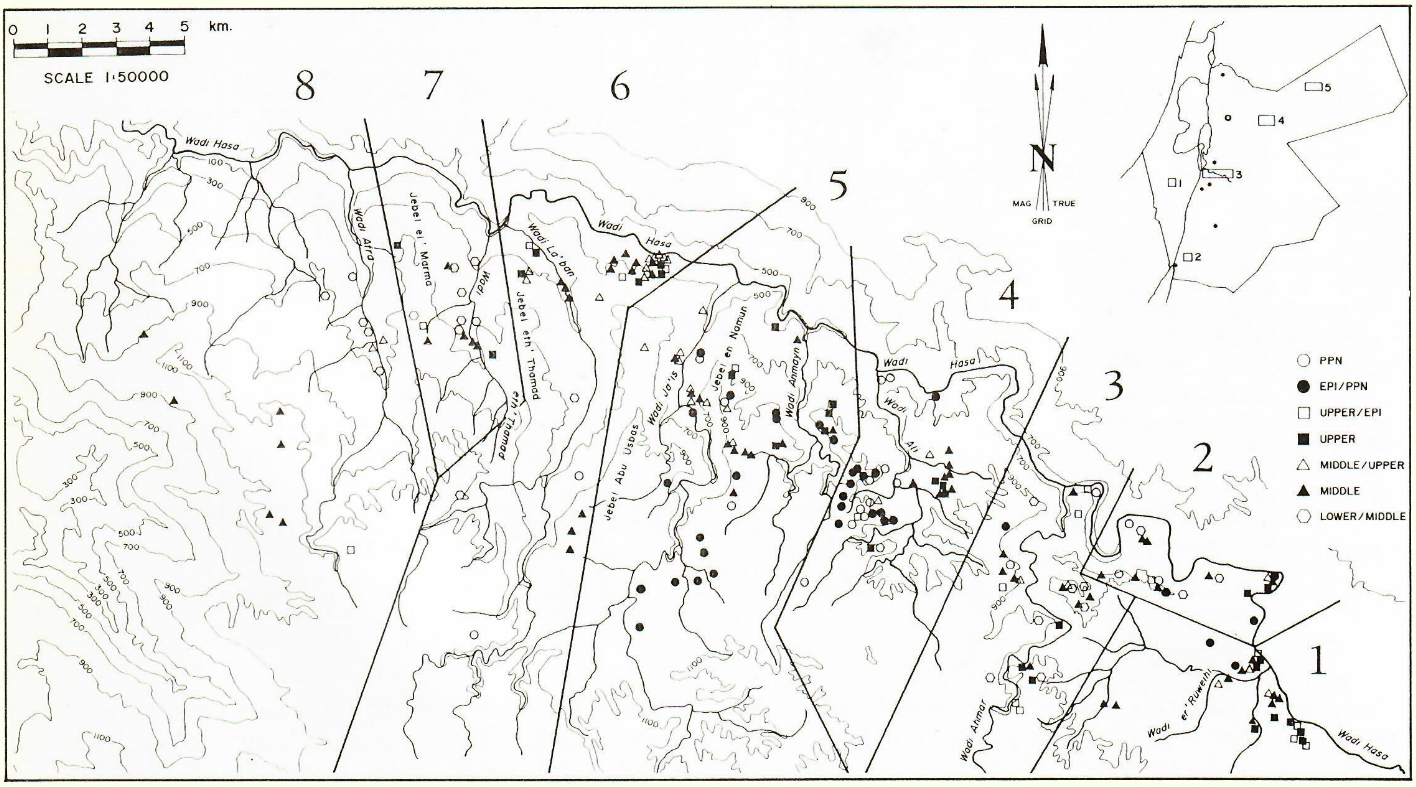
The Late Epipaleolithic in the Negev is characterised by conditions as dry as those of the present, but in the Early Natufian there is evidence for a slightly wetter interval dated to about 13000 to 11000 BP. This wetter climatic episode is also detected in Henry's south Jordan sequence. The Later Natufian, dated from about 11–10000 BP in both areas, is apparently drier than the preceding interval. Paleoclimatic data for the Prepottery Neolithic in the Negev comes from a single PPNB site and indicates a climate slightly wetter than that of the present. The climate of south Jordan at this time has been interpreted as dry. These climatic sequences and the settlement-subsistence models reviewed earlier provide a set of expectations against which to examine survey data from the Wadi el-Hasa, west-central Jordan (TABLE 2).

The Wadi el-Hasa survey

From 1979 to 1983, Burton MacDonald of St Francis Xavier University conducted a survey of the south bank of the Wadi el-Hasa drainage system, encompassing the entire 70 km length of the wadi from its source near the Qa el-Jinz to where it empties into the Dead Sea depression near As-Safi. Some 1,074 sites were identified ranging in time from the Lower Paleolithic to the Ottoman Empire. 222 of these were classified as Lower, Middle, Upper and Epipaleolithic and as Prepottery Neolithic, with various bracketing categories and subdivisions. Although the survey was fairly systematic, MacDonald's efforts were not directed primarily at the lithic periods of interest here, nor were sampling designs employed to insure data sets representative of particular temporal or cultural periods, nor of topographical subdivisions of the environment.

We looked first at the temporal and spatial distribution of sites within the wadi by eight tributary drainage systems and by the wadi system as a whole (FIG. 1). The objective of these pattern searches was to determine whether time trends existed in the data, and to see whether patterns of association among environmental and topographic variables, site sizes and densities could be detected that might have meaning in behavioural terms. Identifying settlement-subsistence systems which corresponded to the various subdivisions of the paleolithic, epipaleolithic and early neolithic allowed us to make comparisons with the models proposed by Marks and Henry.

1. Distribution of sites by time-stratigraphic unit along the S bank of the Wadi el-Hasa, west-central Jordan (base map courtesy of Burton MacDonald). The large numbers *on the map* indicate major tributary drainages of the Hasa: (1) Wadis Abu Ar-Riwaq and er-Ruweihi, (2) the Wadi Hasa lowlands, (3) Wadi Ahmar, (4) Wadi Ali, (5) Wadis Anmayn and Ja'is, (6) Wadi La'ban, (7) Wadi eth-Thamad, (8) Wadi Afra. The small numbers *on the key* indicate major paleolithic survey projects: (1) Avdat/Aqev area, C Negev highlands (Marks), (2) Wadi Hisma/S Jordan Plateau (Henry), (3) S bank of the Wadi Hasa (MacDonald), (4) Azraq Basin (Garrard), (5) Black Desert (Betts). Major Jordanian cities and towns are indicated by dots.



Site frequencies

A preliminary assessment of gross site frequencies in the tributary drainages of the Hasa indicated fairly similar distributions over time. When the distributions of sites in each of the seven time periods were taken into account, however, marked differences became apparent. Drainage 3 and Area 7 contain 60 per cent of sites occupied during the Lower and Middle Paleolithic, while during the Middle Paleolithic sites are more evenly dispersed along the wadi course. During the Middle and Upper Paleolithic, sites are concentrated in Drainages 5 and 6, whereas in the Upper and Epipaleolithic they occur primarily in Drainages 1, 4 and 6. In the Epipaleolithic and Prepottery Neolithic, 82 per cent of the sites are concentrated in adjacent Drainages 4 and 5. During PPN times, 63 per cent of the sites are located in these same drainages with another 13 per cent in Area 2, the neighbouring wadi lowlands. The pattern that emerges is one in which the areas utilised most heavily *contract* over time, with the Epipaleolithic and PPN sites most heavily concentrated in Drainages 4 and 5.

Site areas

Site areas ranged from 12 to 48,000 sq m, but 69 per cent of the sites are classified as 'small' (<2,500 m^2). The mean site area for all time periods was 3,468 m^2 with a large standard deviation of 7,380 m^2. About 9 per cent of the sites were 'very large'—over 10,000 m^2. When mean site areas by time period are considered, a striking pattern of decrease over time becomes apparent. The mean area of Lower/Middle Paleolithic sites is 7,207 m^2 contrasted with only 752 m^2 during the EPI/PPN. Moderately larger sites characterise the PPN period itself, as indicated by a mean of 2,773 m^2 (TABLE 3).

Table 3 Descriptive statistics for site area by time periods

Periods	N	Max	Min	Mean	Med	Range	St. Dev.	St. Err.	95% Confidence −S	+S
PPN	22	15,000	16	2,773	1,650	14,984	3,552	757	1,199	4,348
EPI/PPN	35	3,600	16	752	400	3,584	908	154	440	1,064
UP/EPI	18	15,000	36	2,510	1,500	14,964	3,545	836	747	4,273
UPPER	30	48,000	25	3,584	1,100	47,975	8,748	1,597	318	6,851
MID/UP	28	35,000	75	3,038	975	34,925	6,766	1,279	414	5,662
MIDDLE	66	43,750	12	4,229	800	43,738	9,082	1,118	1,996	6,462
LOW/MID	23	30,000	25	7,207	2,800	29,975	9,689	2,020	3,016	11,397
ALL	222	48,000	12	3,468	900	47,988	7,381	495	2,492	4,445

Comparisons with Marks and Freidel's data on site area from the central Negev indicate similar vectored change in site size. They found that early Mousterian sites ranged between 1,200 and 3,000 m^2 depending on the degree of *in situ* deposits. In contrast, *in situ* Upper Paleolithic sites were considerably smaller, on the order of 50–300 m^2, while disturbed deposits ranged from 400 to 1,800 m^2. Epipaleolithic sites in the Negev continued to be small, again paralleling patterns found in the Hasa data.

Site elevations

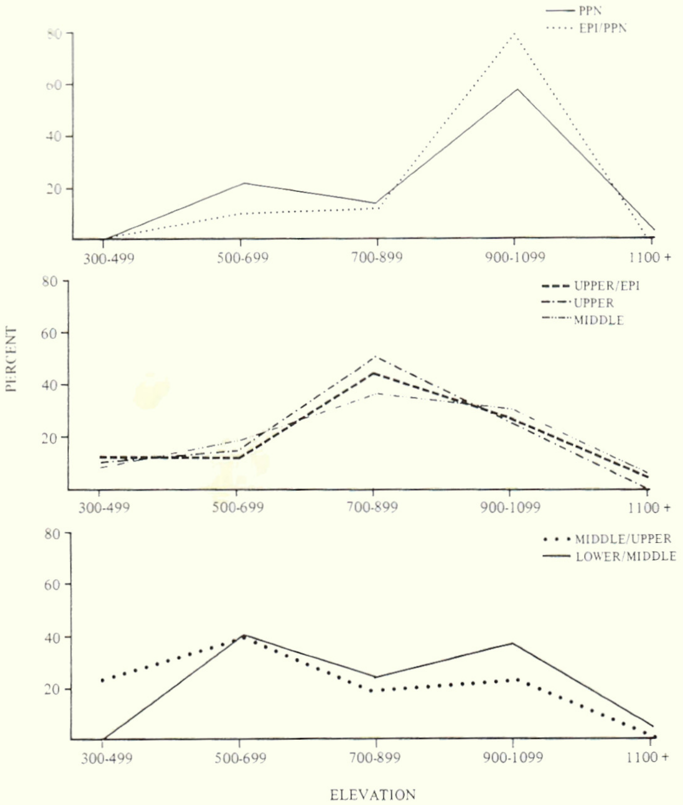
The Wadi el-Hasa Survey covered terrain ranging in elevation from about 200 to more than 1,300 m above sea level, and sites were located from 385 to 1,200 m. If we look at the distribution of sites in different elevational zones, we see that 40 per cent of the sites were located in a relatively narrow elevational band between 900 and 1,100 m. If elevational changes in site locations through time can be associated with environmental and climatic changes, the distribution of mean elevations in the various time periods indicates significant differences. While mean elevations are similar during the Lower/Middle, Middle, Upper and Upper/Epipaleolithic time frames, ranging from 773 to 816 m, the low elevation mean for the Middle/Upper Paleolithic sample is indeed a deviation from the other unit means. The high elevation mean of 905 m for the Epi/PPN combined sample also appears to be significant. By PPN times, the location of sites is again similar to that of most of the earlier periods (TABLE 4). The unanticipated outcome of the site elevation data was the demonstration that three distinct kinds of patterns existed: (1) a bimodal symmetrical distribution characteristic of the Lower/Middle and Middle/Upper Paleolithic combined samples, with site clusters at 5–700 and 9–1,100 m, (2) an essentially unimodal symmetrical distribution typical of the Middle, Upper and Upper/Epipaleolithic, with sites concentrated in the 7–900 m band, and (3) a unimodal asymmetrical configuration characteristic of the Epi/PPN and PPN periods, with the major mode at 9–1,100 m (FIG. 2).

When the survey area is partitioned into drainages, a number of significant variations in site elevation can be seen. As one moves from east to west, the elevation patterns become increasingly bimodal. FIG. 3 is a series of histograms scaled to topographic relief that illustrates the relative concentration of sites between 800 and 900 m in Drainage 3 toward a progressively bimodal distribution in Drainages 5 and 6. Elevational ranges in the western, dissected end of the wadi are of course more extreme. The dichotomous pattern of site elevations in Drainages 3–6 seems to be a significant datum, suggesting the possibility of seasonal movement and/or major temporal differences in site locations within and across the various drainages.

Table 4 Descriptive statistics for site elevations by time periods

Periods	N	Max	Min	Mean	Med	Range	St. Dev.	St. Err.	95% Confidence −S	+S
PPN	22	1,198	540	844	915	658	165	35	881	918
EPI/PPN	35	1,062	515	905	930	547	117	20	864	945
UP/EPI	18	1,175	390	797	816	785	188	44	704	891
UPPER	30	965	385	773	803	580	164	30	712	834
MID/UP	28	950	440	680	642	510	176	33	612	748
MIDDLE	66	1,200	440	816	866	760	192	24	769	863
LOW/MID	23	1,100	515	792	816	585	152	32	726	857
ALL	222	1,200	385	806	856	815	178	12	782	829

2. Global site elevation distributions by time/stratigraphic unit. The graphs show the percentages of sites represented in each of five class intervals. Graphs of similar shape are grouped together.



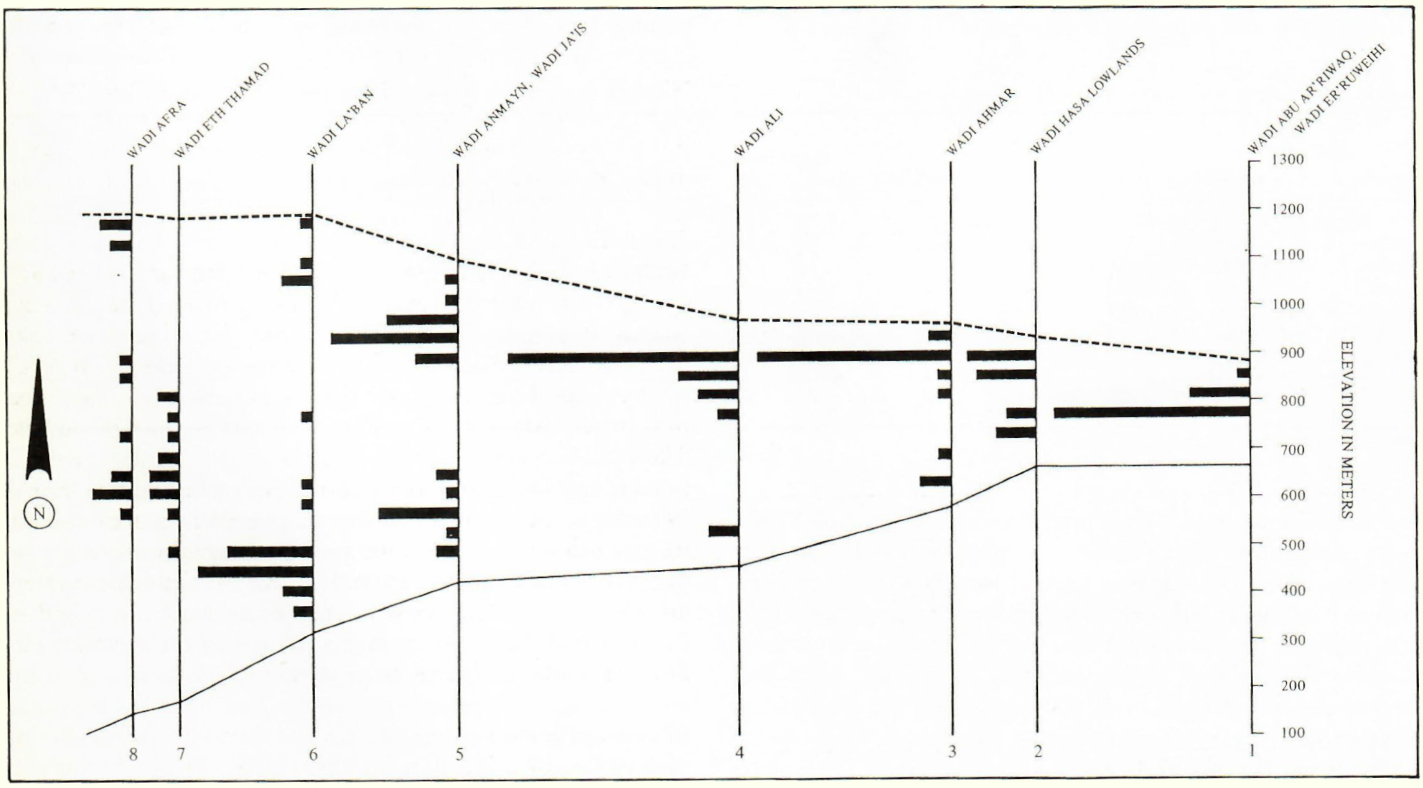
We next examined site locations for each time period in Drainages 3–6 individually, to see if similar patterns existed which corresponded to particular time periods. We found that there are distinct elevational 'bands' that were favoured within specific drainages during certain time periods, and that a bimodal pattern of site occupation was important in each drainage during at least some time periods. The variable site location patterns suggest behavioural responses to altitudinally-determined microenvironmental variability set against a backdrop of long-term climatic change during the late Pleistocene and early Holocene.

Bivariate relationships between site size and location

Most settlement pattern studies involving hunter-gatherers have been directed toward understanding a group's adaptive relationships with various aspects of the environment. It is usually assumed that a group's adaptive strategies included loci beyond a base camp and that variability in site size and function of contemporaneous sites might shed light on the organisation of a settlement system. The trick in defining discrete settlement systems, of course, is to establish simultaneously site function, contemporaneity and interpretable patterns of association.

In the absence of unambiguous site functional identifications in the Hasa survey data, site size would probably be the next

3. Histograms of site frequencies by elevation and tributary drainage with minimum and maximum elevations indicated for each drainage.



best potential indicator of site function. Because we had some indication of bimodal site distributions in elevational zones, we looked for possible correlations between site size and elevation in an effort to determine whether these two variables were directly related in meaningful and interpretable patterns. That is, elevation could be related to site function, and site size would be a preliminary step toward identifying site function associated with altitudinal variability.

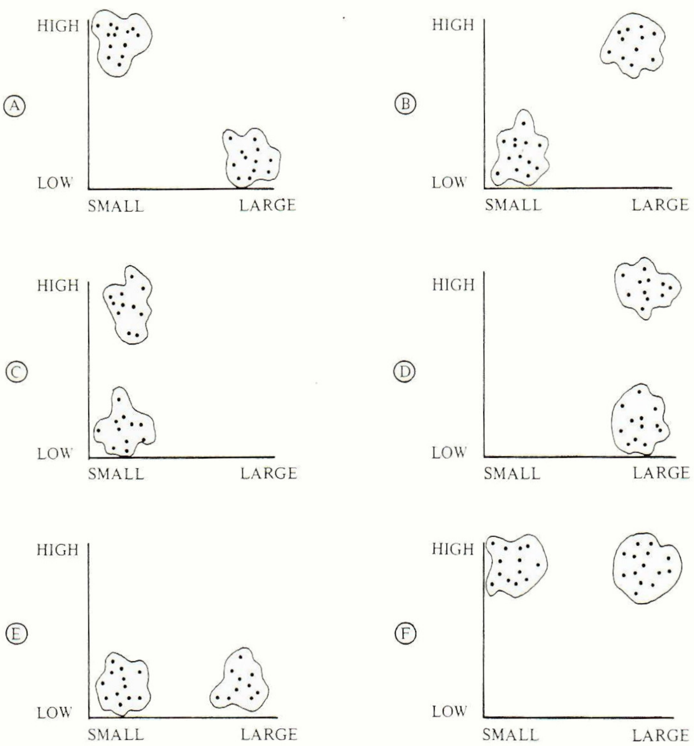
Ideal models

A variety of ideal models that express different kinds and degrees of correlation between site size and elevation are displayed in FIG. 4. Scatterplots A and B show double dichotomies in these variables. Sites are combinations of either small or large sites located at either high or low elevations. In C through E, the sites exhibit only a single dichotomy.

Archaeologists have previously suggested similar models for Levantine hunter-gatherers. For instance, if sites in Plots A and B were contemporaneous, they would reflect what Marks and Freidel (1977) call the 'radiating' settlement patterns typical of early Mousterian sites in the Negev. The larger sites would function as base camps while the smaller sites would indicate a range of procurement and processing activities. Seasonal and environmental variability might constrain choice in the elevations at which satellite sites such as hunting locations, field camps, stations or caches might be located.

If sites in Plots C and D were contemporaneous, the single dichotomy between the either site size or elevation might reflect Marks and Freidel's 'circulating' pattern. Residential mobility is high and sites are relatively undifferentiated, but the different elevations might indicate site locations in a seasonal round.

4. Six ideal models expressing dichotomous relationships between site size and elevation.



Global comparisons ignoring time

We first examined site size and elevation ignoring time, to illustrate the nature and degree of site clustering relative to the two variables. Drainage 5, 6 and to some extent 7 best resemble Model C with small sites at both high and low elevations. The sites in Drainage 7 only minimally resemble Model A, with a dichotomy in site size but little difference in site elevation.

Global comparisons by time-stratigraphic units

The relationship of site size and elevation by time/stratigraphic units is less well defined relative to the ideal models. As might be expected, a greater degree of variability is present as indicated by multiple clusters and considerable dispersion through the range for each variable. Plots for the Middle-Upper Paleolithic, Upper Paleolithic, the Epi-PPN combined sample and the Prepottery Neolithic best fit the ideal models because each indicates a fairly well-defined dichotomy in site elevation while varying in site size similarity and in the discreteness of site size clusters (FIG. 5). The Middle-Upper Paleolithic combined sample indicates a relatively wide range in site area for low sites, but a much more restricted size range for sites at higher elevations. The Upper Paleolithic sites are interesting in that they represent three clusters: relatively few small sites at low elevations, relatively many small and a few large sites at high elevations. The Epi-PPN sites are all relatively small and clustered at medium-to-high elevations. There are only three sites at low elevations. The PPN sites have extended size ranges but quite good altitudinal differentiation, making the PPN plot most similar to Model C.

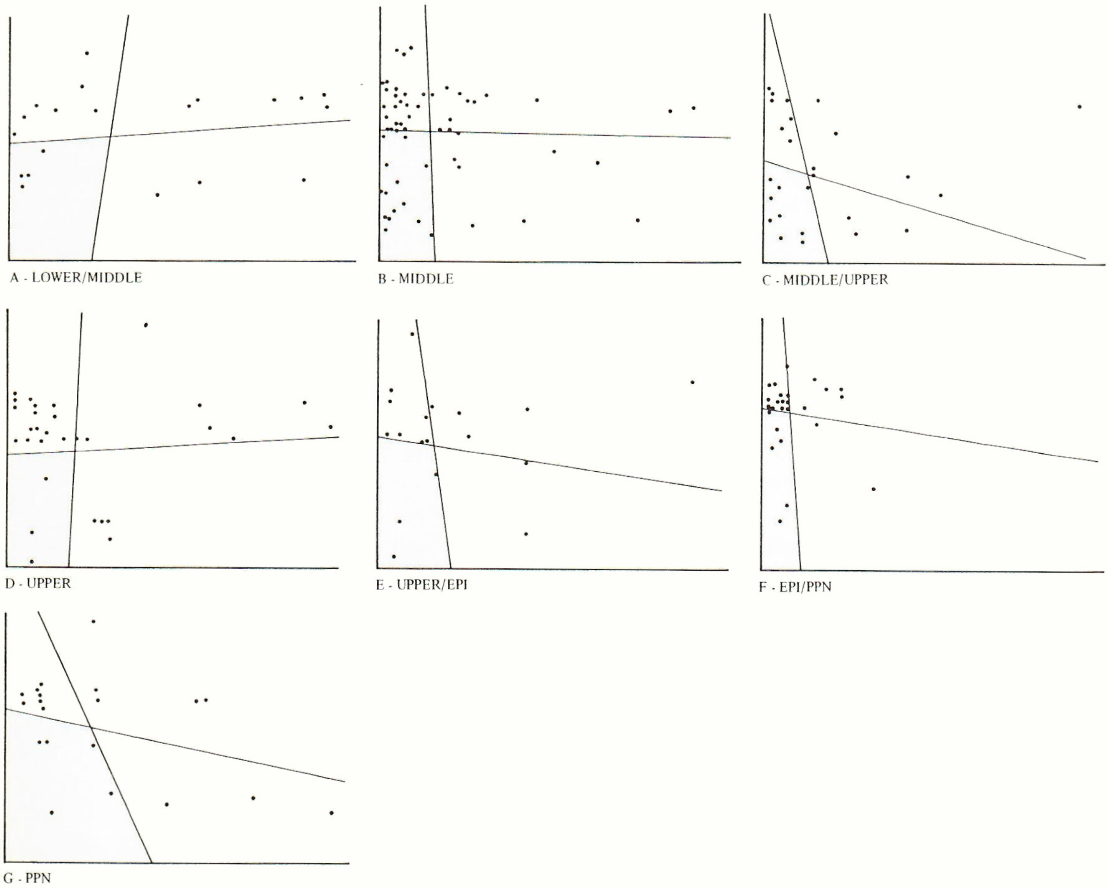
Conclusions

In sum, examination of the temporal distribution of sites indicates that settlement systems in the survey area exhibit differentiation in site size and elevation but that the correlation between these variables does not correspond closely to time-stratigraphic boundaries nor does it agree with the patterns of vectored change predicted by the Marks and Henry models. There is also some fairly obvious distortion due to variations in relief among the different subsidiary drainages of the Hasa. In order to carry the study further, we will need to look at temporal distributions by time-stratigraphic units within drainages to determine if correlations between site size and elevation are more clearly indicative of temporal factors or whether they reflect altitudinally-determined 'bands' of resources specific to particular drainages and elevational zones.

Acknowledgments

This is Contribution No. 7 of the Wadi el-Hasa Paleolithic

5. Global scatterplots of site size and elevation for (A) the Lower/Middle, (B) Middle, (C) Middle/Upper and (D) Upper Paleolithic; (E) Upper/Epipaleolithic, (F) Epipaleolithic/Prepottery Neolithic, (G) Prepottery Neolithic.



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References

Binford, L. 1980. Willow smoke and dogs' tails: hunter-gatherer settlement systems and archaeological site formation. *American Antiquity* 45(1): 4–20.

—— 1982. The archaeology of place. *Journal of Anthropological Archaeology* 1(1): 5–31.

Bottema, S. and Van Zeist, W. 1981. Palynological evidence for the climatic history of the Near East, 50,000–6,000 BP. In *Prehistoire du Levant* (Colloques Internationaux du CNRS No. 598) (J. Cauvin and P. Sanlaville, eds), pp. 111–132. Paris: CNRS.

Clark, G. 1984. The Negev model for paleoclimatic change and human adaptation in the Levant. *Annual of the Department of Antiquities of Jordan* 28: 226–248.

Donaldson, M. n.d. Paleoenvironments of the southern Levant. Manuscript on file with author, Department of Anthropology, Arizona State University.

Goldberg, P. 1973. Sedimentology, stratigraphy and paleoclimatology of et'Tabun Cave, Mt. Carmel, Israel. Unpublished Ph.D dissertation, Department of Anthropology, University of Michigan.

—— 1976. Upper Pleistocene geology of the Avdat-Aqev area. In *Prehistory & Paleoenvironments in the Central Negev*, Vol. I (A. Marks, ed.), pp. 25–53. Dallas: SMU Press.

—— 1981. Late Quaternary stratigraphy of Israel: an eclectic view. In *Prehistoire du Levant* (Colloques Internationaux du CRNS No. 598 (J. Cauvin and P. Sanlaville, eds), pp. 55–66. Paris: CNRS.

Henry, D. 1982. Paleolithic adaptive strategies in southern Jordan. In *Studies in the History & Archaeology of Jordan*, Vol. I (A. Hadidi, ed.), pp. 41–47. London: Routledge & Kegan Paul, Ltd.

—— n.d. Patterns of transhumance in southern Jordan: ethnographic and archaeological analogs. Paper presented at the Annual Meeting of the American Schools of Oriental Research (Chicago, December 1984).

Henry, D., Hassan, F., Henry, K. and Jones, M. 1983. An investigation of the prehistory of southern Jordan. *Palestine Exploration Quarterly* 115: 1–24.

Horowitz, A. 1971. Climatic and vegetational developments in northeastern Israel during Upper Pleistocene–Holocene times. *Pollen et Spores* 8(2): 255–278.

—— 1976. Late Quaternary paleoenvironments and prehistoric settlements in the Avdat/Aqev area. In *Prehistory & Paleo-*

environments in the Central Negev, Vol. I (A. Marks, ed.), pp. 57–68. Dallas: SMU Press.

—— 1979. *The Quaternary of Israel*. New York: Academic Press.

Marks, A. 1981. The Upper Paleolithic of the Negev. In *Prehistoire du Levant* (Colloques Internationaux du CNRS No. 598) (J. Cauvin and P. Sanlaville, eds.), pp. 343–352. Paris: CNRS.

—— 1983. The Middle to Upper Paleolithic transition in the Levant. *Advances in World Archaeology* 3:51–98

Marks, A. and Freidel, D. 1977. Prehistoric settlement patterns in the Avdat/Aqev area. In *Prehistory & Paleoenvironments in the Central Negev*, Vol. II (A. Marks, ed.), pp. 131–159. Dallas: SMU Press.

Mortensen, P. 1972. Seasonal camps and early villages in the Zagros. In *Man, Settlement & Urbanism* (P. Ucko, R. Tringham and G. Dimbleby, eds), pp. 293–297. London: Gerald Duckworth.

Niklewski, J. and Van Zeist, W. 1970. A late Quaternary pollen diagram from northwestern Syria. *Acta Botanica Neerlandica* 19: 737–754.

Weinstein, M. 1976. The late Quaternary vegetation of the northern Golan. *Pollen et Spores* 18(4): 553–562.