

17 A DNA signature for the expansion of irrigation in Bali?

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Introduction

Archaeologists infer changes in social structure indirectly from the distribution of artifacts in space. But the chain of assumptions required for such inferences can sometimes become tenuous. Genetic markers offer a more direct approach to tracing not only the movement of populations on the landscape, but also patterns of genetic relatedness within communities. Here we utilize non-coding regions of DNA with rapid mutation rates to analyze changes in social structure associated with the historical development of wet-rice farming on the Indonesian island of Bali. We begin by reviewing current debates about irrigation in Bali. Subsequently, we present a model to explain the origins and spread of irrigation systems on Balinese volcanoes. We then test some of the model's predictions by means of a comparative analysis of genetic relatedness in 21 villages and nine regions of Bali.

The puzzle of Balinese irrigation

Anthropologists and historians have long debated the respective roles of princes and villagers in the creation and management of irrigation systems in Bali (Hauser-Schaublin 2003). Elsewhere in Southeast Asia, the spread of irrigated rice agriculture was usually linked with the expansion of pre-colonial kingdoms. Typically, the earliest irrigation systems were constructed by particular villages, and then later consolidated and expanded by their rulers (Kulke 1986). But because of Bali's steep volcanic topography, 'the spatial distribution of Balinese irrigation canals, which by their nature cross community boundaries, made it impossible for irrigation to be handled at a purely community level' (Christie 1992). Thus even the earliest Balinese irrigation systems required a system of management that could extend beyond the boundaries of villages. The problem was solved by a new institution called *subak*, which begins to appear in 11th-century royal inscriptions. *Subak* were associations of farmers who shared water from a common source, such as a spring or irrigation canal. Typical ancient irrigation systems included multiple *subaks*, strung like melons on a vine to take advantage of water flowing through irrigation tunnels, aqueducts, and canals. For example, an inscription

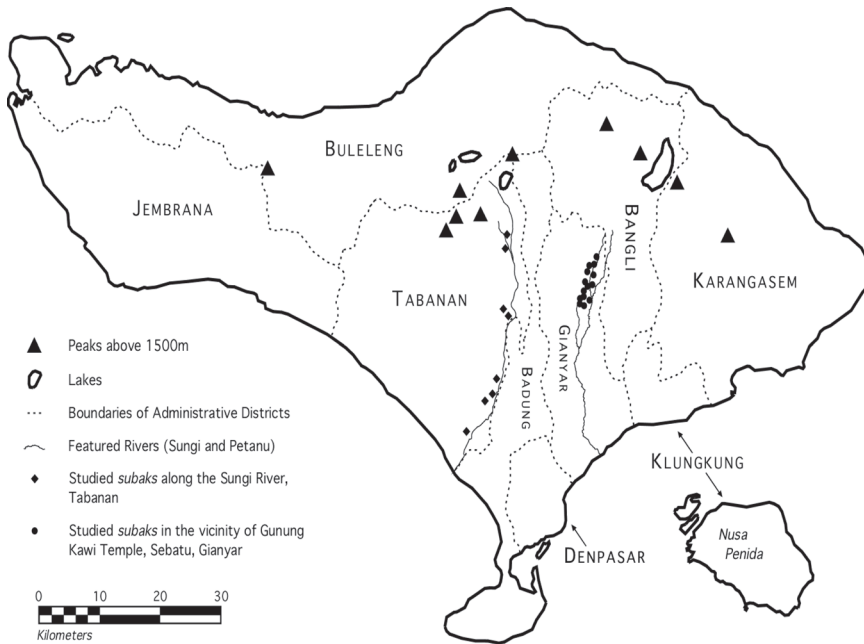
dated AD 1072 refers to a single *subak* comprising fields located in 27 named hamlets (Atmodjo 1986).

But while Balinese volcanoes gradually became honeycombed with irrigation tunnels, canals, and aqueducts, the spread of irrigation in Bali was largely unrecorded because Balinese kingdoms never entered an imperial phase, and stopped issuing inscriptions altogether by the middle of the 14th century. Half a millennium later, in 1811, Sir Stamford Raffles visited Bali and recorded his surprise that the rajahs of Bali were merely one group of landowners among many others; ‘The sovereign [that is, the Raja of Buleleng] is not here considered the universal landlord; on the contrary, the soil is almost invariably considered as the private property of the subject, in whatever manner it is cultivated or divided’ (Raffles 1817). The marginal role of Balinese kings in irrigation, also noted by later colonial observers (Geertz 1980), prompted a question that has been debated for nearly a century: does Bali provide an exception to the thesis that irrigation encourages the centralization of power? Some scholars envision a slow process of irrigation expansion driven by the needs of villagers, while others argue that the key role was played by the rajahs, with the *subaks* serving as merely a reservoir of manpower (Hauser-Schaublin 2003; Lansing 2005). In the absence of definitive written records, the evidence needed to resolve this dispute must come from archaeology and, as we shall show, population genetics.

Archaeology of irrigation in Bali

The earliest Balinese irrigation systems were probably simple canals channeling water from natural springs into adjacent valleys. A few systems of this type are still functioning today, and in 1997 we undertook an archaeological study of one of them: the Gunung Kawi irrigation system, which is located near the upper reaches of one of Bali’s major rivers, the Petanu (Map 17.1).

The temple of Gunung Kawi encloses two natural springs located in a deep natural depression, just south of the village of Sebatu. Closest to the springheads are fountains where water can be collected for ritual purifications. Below them the water is led into pools for bathing, and then into a fishpond. The spring water then enters a short tunnel and emerges a few hundred meters downstream, where it irrigates 0.89 hectares of rice terraces. From there the unused water enters a canal that continues for 4 km before emerging atop a terraced hill where it is used to irrigate 31 hectares of paddies near the village of Dlod Blungbang (Figure 17.1). This system of irrigation canals includes five tunnels, the longest of which is 1.5 km long. We speculated that, long before the start of irrigation in Bali, farmers would have been drawn to this site as an ideal place to grow typical Austronesian crops such as coconuts, taro, bananas, and possibly rice. Later, with the appearance of irrigation technology, the site would have become even more desirable. Water from the spring could easily be channeled into the depression downstream. Digging the short surface canal needed for this purpose would have been much easier than carving irrigation tunnels through the volcanic rock, so this site would likely have been one of the first to be exploited by early farmers.



Map 17.1 Map of Bali showing locations of Gunung Kawi (Gianyar) and Tabanan *subaks*, site of archaeological study (Sebato), and boundaries of the nine regions from which DNA samples were taken.

We mapped the temple, the irrigation canals that flow out of it, and the fields that depend on this flow (Figure 17.2). We also sank 18 soil cores to a depth of up to 5 meters and carried out analyses of sediment, pollen, and phytoliths on the samples thus extracted. We found that, as predicted, before the advent of irrigated rice cultivation, the valley bottom was a swampy forest dominated by palms and bananas. Taro was probably also grown but because it does not produce pollen, this could not be directly confirmed. Later, irrigated rice was grown in the small concave depression immediately downstream from the water temple. Sedimentology indicated a very rapid buildup of sediments after the appearance of irrigation systems. For example, a radiocarbon date from a core extracted from a currently unutilized terrace surface north of the temple showed that nearly 3 meters of soil had been deposited at this location in the past 500 years. Local farmers showed us how the predictable buildup of sediments could be managed to contour the landscape, enlarging the area suitable for terracing and facilitating the flow of water in small canals. The little basin located south of the temple widened as a result of sediment buildup, but even today it is much too small to use more than a small fraction of the water that flows from the springs. So at some point, the farmers began to construct a series of small tunnels, aqueducts, and canals, which now transport most of the flow 4 km downstream to the *subak* of Dlod Blungbang. Three of our 16 cores struck defunct irrigation tunnels, evidence for the frequency

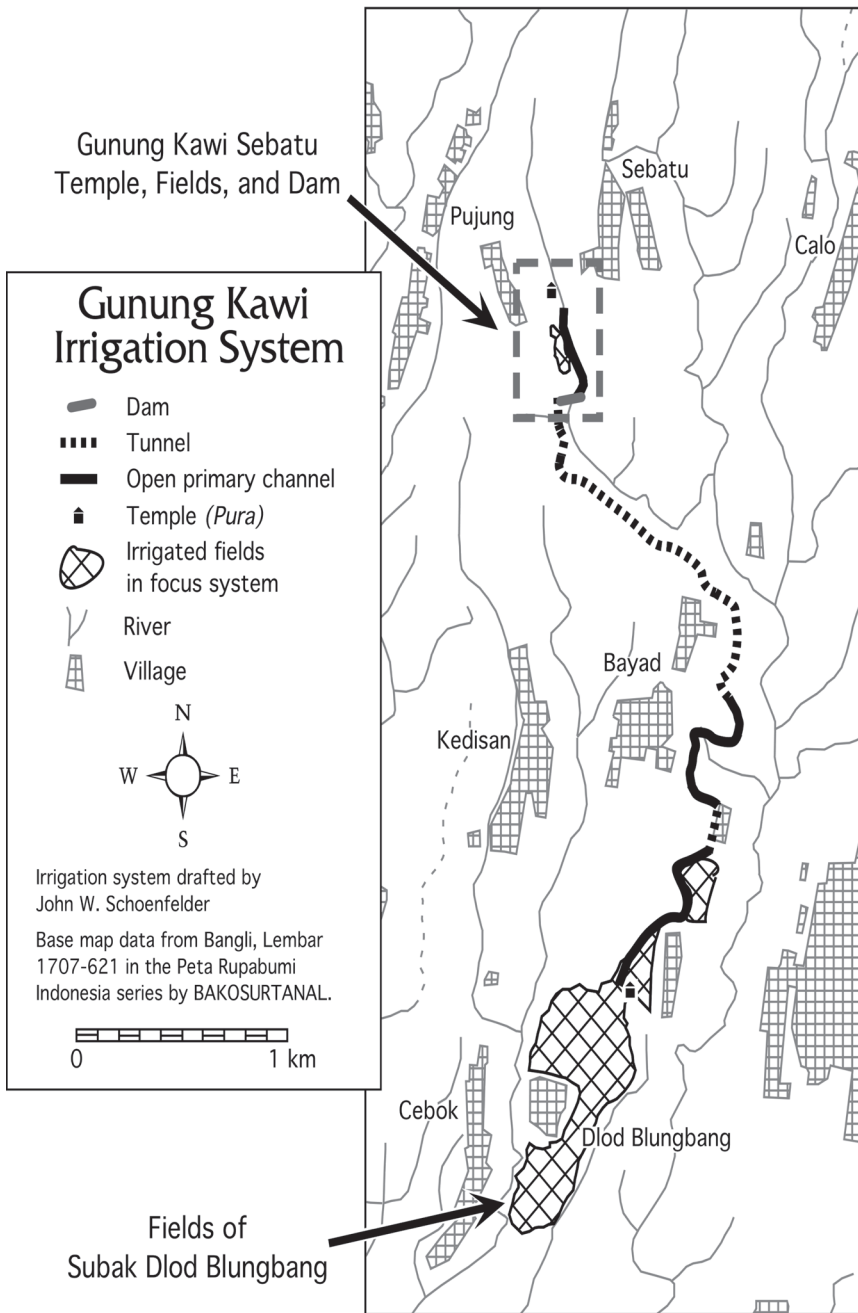


Figure 17.1 Irrigation systems originating from springs at Gunung Kawi Sebato, the site of our archaeological investigation.

with which landscape changes, including the accumulation of sediment, compelled the farmers to modify their irrigation systems. We spoke with older farmers who recalled participating in the demolition of a weir and construction of new tunnels and canals leading out of the topmost fields about 40 years before. Altogether, these results suggested that, over a period of centuries, small teams of farmers were continuously engaged in skilled micro-engineering to maintain control of the flows of water and sediment. There was no evidence for the mobilization of large teams of laborers, or the use of more sophisticated technology than that available to the villagers (Scarborough *et al.* 1999, 2000).

The problem of cooperation

The results of the Gunung Kawi study are consistent with a slow, accretive expansion of irrigation systems organized and executed by local farmers. There is no obvious technical need for a higher authority to carry out the construction of these irrigation works. But irrigation water is often in short supply during the dry season. Consequently there is a need for some mechanism or authority to safeguard the water rights of downstream communities such as Dlod Blungbang. A solution to this problem must have been found centuries ago; otherwise the kilometers-long irrigation systems linking multiple *subaks* would be pointless, and the total area of terraced fields on the island could never have reached its historic extent.

To find out how the problem of water sharing is solved by farmers today, we undertook ethnographic studies of the *subaks* located in the vicinity of our archaeological investigations at Gunung Kawi. In general, every *subak* collectively manages its irrigation system and flows as a form of common property. Monthly meetings provide a venue for *subak* members to make plans, organize work teams, and assess fines or other penalties on members who do not fulfill their obligations. In addition, all of the *subaks* located near the site of our excavations belong to the congregation of a nearby water temple, Pamos Apuh. Each *subak* elects a leader to represent them at monthly meetings of the 'Greater Subak of the Pamos Apuh Temple', a group of fourteen *subaks* that has the right to adjudicate inter-*subak* issues pertaining to irrigation. To find out how well this system works, or in other words whether *subaks* located downstream receive their fair share of irrigation water, we measured the flows to eleven *subaks* during the month of July in 1997 and 1998, at the height of the dry season (Table 17.1).

Sebatu, Jasan, Timbul, and Calo, the *subaks* located furthest upstream, have a slight advantage over their downstream neighbors. However, this is probably a consequence of the way that flows are measured, not a deliberate attempt to cheat. Water rights are based on proportional division (*tektek*) at the points where the flow is divided. This method does not take into account downstream losses from percolation and evaporation. Consequently it is to be expected that downstream *subaks* will receive slightly less water. It is also apparent that the *subaks* furthest downstream (Kebon, Kedisian Kelod, and Pakudui) are only slightly disadvantaged. A survey of 150 farmers from ten *subaks* supports this conclusion. In answer to

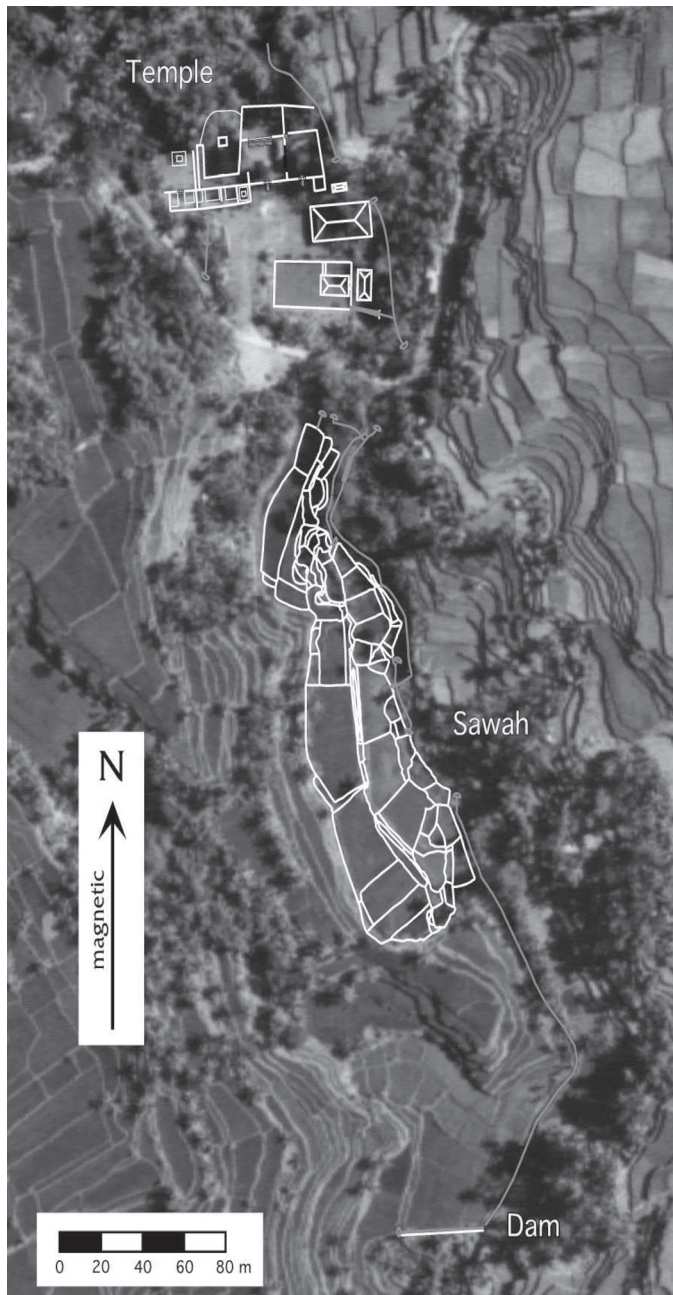


Figure 17.2 Aerial photograph with outline of the Gunung Kawi water temple and adjacent rice paddies superimposed. The small area of irrigated rice paddies (sawah) shown in outline lies at a slightly lower elevation than the temple with its springs.

Table 17.1 Comparison of average measured irrigation flows (in liters per second) and water rights for 11 subaks in the vicinity of Gunung Kawi (Gianyar) during the dry season, July 1997 and July 1998

<i>Subaks</i>	<i>Average flow (liters/sec)</i>	<i>% of flow</i>	<i>Water rights in tektek</i>	<i>% of tekteks</i>
Jasan, Sebatu	368	19.42	16.0	17.02
Timbul, Calo	460	24.27	21.0	22.34
Pujung kaja	207	10.92	11.5	12.23
Kedisan kaja, Kedisan kelod	214	11.29	16.0	17.02
Bayad	198	10.45	7.0	7.45
Pujung kelod	111	5.86	5.5	5.85
Kebon, Kedisan kelod, Pakudui	337	17.78	17.0	18.09
Total	1895	100.00	94.0	100.00

Water rights are measured in proportional shares of the total flow (tektek).

the question, 'Is the division of water by the Pamos Water Temple equitable?', all said yes.

Mechanisms to promote cooperation

Both our flow measurements and the survey results support the conclusion that farmers in downstream *subaks* can rely on a steady supply of irrigation water reaching their fields after it passes through, beneath, or alongside the terraced fields of their upstream neighbors. Although it would be easy for the upstream farmers to take more than their agreed-upon share of water, in our surveys most farmers reported only mild anxiety with regard to the danger of water theft. There was a single exception: in one *subak*, weak leadership triggered a need for the farmers to organize teams to police the irrigation works several times a day during the dry season of 1997 (Lansing 2006). But this was the exception that proved the rule: ordinarily there appears to a very high level of cooperation within and between *subaks*. How is such cooperation sustained? We identified two relevant mechanisms. One has its roots in the ecology of the rice paddies, and the other in marital alliances. We begin with the ecological mechanism.

Rice is vulnerable to a variety of pests, including rodents, insects, and bacterial and viral diseases spread by insects. But Balinese farmers are able to reduce pest populations by synchronizing fallow periods in large contiguous blocks of rice terraces. After harvest, the fields are flooded, depriving pests of their habitat and thus causing their numbers to dwindle. The need to minimize losses from pests provides a strong motivation for farmers to cooperate with their neighbors in synchronous planting schedules. This gives downstream farmers a bargaining lever in negotiations over water with their upstream neighbors: if the downstream

farmers don't receive enough water to synchronize their planting schedule with upstream farmers, then there will be no widespread fallow interval, and rice pests may migrate upstream. Pest control is an important consideration for the farmers: after a few seasons of unsynchronized cropping schedules, losses from pest outbreaks can approach 100 per cent.

To test whether this logic reflects the thinking of the farmers, in the summer of 1998 we carried out a survey of farmers in ten *subaks* that belong to the congregation of the Pamos water temple. In each of the ten *subaks*, we chose a random sample of fifteen farmers. Of these fifteen, five were selected whose fields are located in the upstream part of their *subak*; five more from the middle of the *subak*, and the last five from the downstream section of the *subak*. We asked 'Which problem is worse, damage from pests or irrigation water shortages?' The results, shown in Figure 17.3, show that upstream farmers worry more about pests, while downstream farmers are more concerned with water shortages.

The same dynamics can occur at the next level up (Figure 17.4). Not only individual farmers, but whole *subaks* must decide whether or not to cooperate. In our sample, six of the ten *subaks* were situated in upstream/downstream pairs, where the downstream *subak* obtains most of its water from its upstream neighbor. Thus it was also possible to compare the aggregate response of all the farmers in each downstream *subak* to the response of their upstream neighbors.

Here also, upstream farmers are more concerned with potential damage from pests than from water shortages, and so have a reason to cooperate with downstream neighbors. By adjusting their own irrigation flows the upstream *subaks* have the power to promote a solution that is beneficial for everyone. In a recent publication, we presented a formal model showing that cooperation is the predicted outcome for farmers faced with this tradeoff between water sharing and pest control, for a wide range of field conditions (Lansing and Miller 2005).

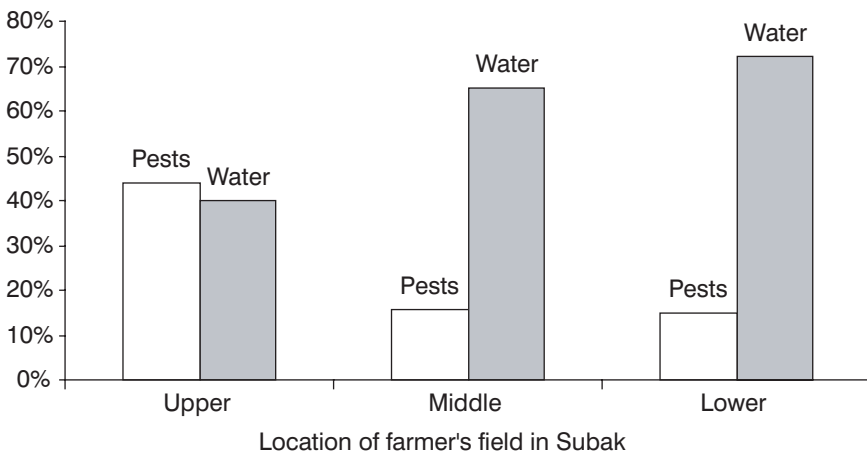


Figure 17.3 Relationship of the location of a farmer's fields to his views on the relative importance of losses from pests or water shortages, based on a sample survey of 150 farmers in ten subaks in the Gunung Kawi Sabtu region.

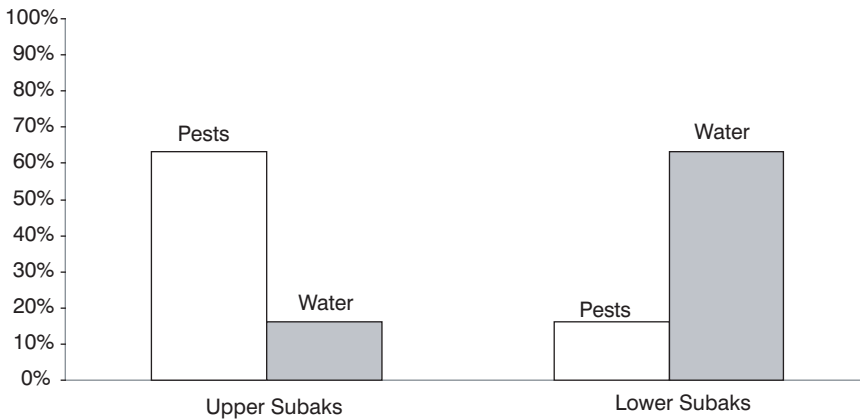


Figure 17.4 Aggregate responses of 90 farmers in 3 upstream subaks and 3 downstream subaks.

The observed pattern of marriages by the farmers suggests a second mechanism sustaining cooperation. If cooperation is vital to the success of the *subak* as an egalitarian institution managing a vital common resource (water), then marital alliances provide a way to create bonds between farm families. We asked about twenty married men in each of thirteen *subaks*, a total of 252 individuals, whom they had married: 84 per cent had chosen a wife from among the daughters of men belonging to their own *subak*. Interestingly, a survey of marriage preferences in two highland villages (where *subaks* do not exist) showed that these men are much less likely to marry within their communities; the rate of endogamous marriages falls to 34 per cent. A fuller analysis of these mechanisms is presented by Lansing (2006).

Insights from genetics on the history of the subaks

Results from our archaeological studies are consistent with a model of expansion of wet-rice irrigation carried out by villagers rather than the state: demographic pressure provided an incentive for villages to gradually bud off daughter settlements downstream as the island's population grew. This is similar to Peter Bellwood and James Fox's Austronesian expansion model, in which some younger siblings become pioneers who create new communities. Bellwood suggests that 'junior founders ... could establish senior lines, aggrandize their resources, and attempt to ensure methods of genealogical inheritance which would retain privileges for their descendants' (Bellwood 1996: 19). Kinship bonds would provide a motive for cooperation with daughter settlements in the first phase of this process. Later on, cooperation could be sustained by the joint need to control rice pests. Consequently, there would be little need for an external coercive authority (e.g. the state) to enforce water rights for downstream *subaks* in large multi-*subak* irrigation systems.

In the absence of historical documents for the relevant period (14th–19th centuries), how could this model be tested? Conventional archaeological methods (such as those we used at Gunung Kawi) provide insights into the historical development of irrigation technology but permit only indirect inferences about the social management of irrigation. However, in the last decade, geneticists have developed tools to assess variation in non-coding regions of the human genome that are subject to very rapid rates of mutation. Using these markers it is possible to trace micro-migrations and changing patterns of relatedness within small communities in the recent past. The amount of genetic variation observed in populations is deeply influenced by demography and thus can shed light on settlement patterns (Hurles *et al.* 2005).

We can construct two alternative scenarios for the expansion of irrigation and rice cultivation, which would produce contrasting signals in the genetic structure of farming villages. If the expansion of irrigation was accomplished by the farmers rather than their rulers, then population movement of males (patrilineages) would occur only as a result of demographic pressure leading to the formation of new daughter settlements close to the parent villages. This budding model would predict the formation of small communities located along irrigation systems, with the oldest settlements located at the irrigation outtakes located closest to the most ancient weirs or springs. Small population size and reproductive isolation would produce high rates of genetic drift; the older the community, the more evidence of drift. On the other hand, the younger *subaks* would undergo a substantial founder effect, in particular for the male part of the population. Patrilineages should exhibit less evidence of movement on the landscape than matrilineages, because only males inherit rights to farmland. But matrilineages should also be very localized because of the preference for marriage within one's own *subak*. Thus a budding model of irrigation expansion by the *subaks* would predict a clear pattern of population structure for both patrilineal and matrilineal inheritance in the rice-growing regions of Bali.

In the alternative scenario in which the expansion of irrigation was managed by the state, none of these constraints would be in evidence. Instead, the population would serve as a reservoir of labor, which could be relocated by the rulers to build and service new irrigation systems. Overall, this scenario would predict a more fluid population structure with less nucleation of settlements and less genetic drift within settlements, compared with the budding model. In 2001, we began to gather the genetic data needed to test these hypotheses.

A genetic test of the budding model

DNA samples

We analyzed a total of 507 Balinese males. One group consisted of 287 farmers from 13 *subaks* belonging to the Pamos Apuh water temple, in the vicinity of Gunung Kawi as described above. These 13 *subaks* are located in the region where most of the earliest Balinese kingdoms appeared. Irrigated rice cultivation

is frequently mentioned in royal inscriptions addressed to villages in this region in the 10th through the 13th centuries (Ardika 1986, 1994; Goris 1954; van Stein Callenfels 1926). Although they obtain irrigation water from numerous sources, including three weirs and the springs described above, these *subaks* are all located in a relatively small cluster (with average geographic distances among *subaks* only 3.2 km), and are of similar size, averaging 63 hectares.

The second group consists of 120 farmers belonging to eight *subaks* located along the Sungai river in the regency of Tabanan (Map 17.I). These *subaks* were included in the study to provide a contrast with the Gunung Kawi *subaks*. The absence of archaeological evidence for early kingdoms in Tabanan suggests that rice cultivation began later there than in the Gunung Kawi region; consequently the Tabanan *subaks* should be younger. The Tabanan *subaks* were also chosen to shed light on the relative permanence of farming villages. The eight *subaks* in the sample were selected from sites spanning the full length of the Sungai River, from the uppermost reaches to the sea (average geographic distance is 13.9 km). While the upper *subaks* are about the same size as the 13 Gunung Kawi *subaks*, several of the lower *subaks* are much larger. Thus, our sample of *subaks* encompasses a range of contrasts, including ages, sizes, and regions. The third group comprises 100 random samples from each of the nine administrative districts on the island (Map 17.I), to provide context for the *subak* samples. All sampling protocols were approved by the Human Subjects Committee of the University of Arizona and the Eijkman Institute for Molecular Biology.

Genetic markers and data analyses

The Y chromosome polymorphic sites in our survey included 71 single nucleotide polymorphisms (SNPs) and 12 short tandem repeats (STRs) published by Karafet *et al.* (2005). Sequence data for the hypervariable segment 1 (HVS1 – 519 bp) of mtDNA were analyzed with the SEQUENCHER software program. Parameters of within-population diversity, including Nei's (1987) haplotype diversity (h), which is based on the frequency and number of haplogroups, and the mean number of pairwise differences among haplogroups, population genetic structure indices, and relationships between genetic and geographic structure by the Mantel test were estimated by using the ARLEQUIN 2.000 software (Schneider *et al.* 2000). The standardized measure G'_{ST} (Hedrick 2005) was calculated to compare the levels of differentiation between Y-chromosome and mtDNA data. Median-joining (MJ) networks (Bandelt *et al.* 1999) were constructed by using the NETWORK 2.0c program. For network calculations STRs were weighted according to their repeat number variances. The reduced median output was used as input for the median-joining network.

Genetic structure of Balinese subaks

Genetic diversity based on mtDNA and Y-chromosome data for all populations are given in Table 17.2. The trend for all three genetic systems demonstrated lower

diversity in the Gunung Kawi region, compared with Tabanan and Bali as a whole. For Y-chromosome SNP markers in the Gunung Kawi *subaks*, the average h and p values were 0.52 and 1.99, respectively. These very low diversity values may be explained by the fact that 7 out of 13 Gunung Kawi *subaks* possess only one to three predominant haplogroups belonging to lineage O. The Tabanan *subaks* had substantially higher Y-SNP diversity (0.67 and 2.86, respectively for Nei's h and p). Nine different geographic regions of Bali showed an intermediate h (0.65) and the highest p (2.99) values. Diversity values for 12 Y-chromosome STRs also showed a general decline in h and p values for *subaks* in the Gunung Kawi region compared with those for Tabanan *subaks* and nine geographic regions in Bali. The finding of *both* Y-SNP and Y-STR diversity reductions is important because the tandem repeat markers do not suffer from a potential SNP's ascertainment bias (Hammer *et al.* 2001; Jobling and Tyler-Smith 2003). The first hypervariable segment of the mtDNA (519 bp) once again revealed significantly reduced variation in Gunung Kawi. Given the archaeological data indicating an older age of Gunung Kawi *subaks* compared with Tabanan, these results are consistent with a smaller effective population size for the Gunung Kawi region. This supports the hypothesis that Gunung Kawi *subaks* were established as small communities over a long period of time, perhaps experiencing sequential founder effects as predicted by the budding deme model (Fix 2002). Moreover, since migrants comprised a biological kin group, migration may actually increase local genetic differentiation (Fix 2004).

To further investigate the putative effects of serial founder effects on the Gunung Kawi *subak* system, we compared diversity parameters of the older (Bayad, Pujung, Sebatu, and Timbul) and younger *subaks* (Jati, Jasan, Bonjaka, and Tegal) of Gunung Kawi. As predicted by the budding deme model, the mean diversity in the younger Gunung Kawi *subaks* was lower than that in the older *subaks* in all parameters except pairwise differences (p) among mtDNA HVS sequences (Y-SNPs: 0.644 versus 0.411 for h , 2.49 versus 1.55 for p ; Y-STRs: 0.933 versus 0.929 for h , 6.36 versus 5.16 for p ; mtDNA: 0.926 versus 0.898 for h , 7.24 versus 7.39 for p). We also constructed a median-joining network for the most frequent haplogroup O-M95 in Bali (Plates 17.Ia and 17.Ib). The network of the O-M95 haplotypes in older *subaks* showed a notable microsatellite differentiation with several reticulations and without single shared haplotype (Plate 17.Ia). The majority O-M95 chromosomes in the younger *subaks* were connected in a simple way with one haplotype shared by all four *subaks*, and with seven haplotypes found in more than one population (Plate 17.Ib).

A budding deme model also predicts an increase in genetic differentiation among subpopulations as the process continues over time (Fix 2002). The F_{ST} values for the Gunung Kawi *subaks* were notably higher for all three genetic systems than those for Tabanan *subaks* and the nine randomly collected samples in Bali, indicating a significant degree of genetic differentiation within Gunung Kawi region (Table 17.3). For Y-SNPs Gunung Kawi exhibited a high F_{ST} value (0.141), nearly twice as high as for the regional Bali sample (0.075). Interestingly, Tabanan *subaks* were not significantly differentiated from one another. The same

Table 17.2 Genetic diversity parameters based on Y-SNP haplogroups, Y-STR haplotypes and mtDNA HVSI sequences for individual populations

Subsaks	Y-SNP					Y-STR					mtDNA							
	Na	nb	h	SE	p	Na	nb	h	SE	p	Na	nb	h	SE	p	SE		
<i>Gunung Kawi subsaks</i>																		
Bayad	20	5	0.62	0.11	2.31	1.32	20	13	0.93	0.04	6.31	3.12	20	12	0.93	0.04	7.51	3.66
Bonjaka	21	6	0.65	0.10	3.03	1.64	21	14	0.95	0.03	6.21	3.07	21	10	0.87	0.05	7.72	3.75
Calo	23	4	0.64	0.09	2.04	1.19	23	16	0.96	0.02	6.09	3.01	22	11	0.91	0.04	7.42	3.60
Jasan	23	1	0.00	0.00	0.00	0.00	23	15	0.94	0.03	3.58	1.89	23	13	0.94	0.03	7.01	3.42
Jati	20	3	0.49	0.12	1.69	1.03	20	12	0.93	0.03	5.62	2.81	20	12	0.90	0.05	7.52	3.66
Kaja	20	3	0.51	0.04	1.90	1.13	20	13	0.93	0.04	6.09	3.03	20	9	0.89	0.04	7.07	3.46
Kebon	20	1	0.00	0.00	0.00	0.00	20	9	0.88	0.05	3.23	1.74	20	6	0.62	0.11	4.44	2.28
Kelod	20	3	0.58	0.05	2.75	1.52	20	15	0.96	0.03	6.45	3.19	18	10	0.90	0.05	6.57	3.26
Pakudui	19	6	0.74	0.09	3.02	1.65	19	12	0.94	0.04	6.67	3.29	18	6	0.81	0.07	10.10	4.84
Pujung	20	6	0.78	0.06	3.79	1.99	20	12	0.95	0.03	6.79	3.34	20	10	0.91	0.04	5.74	2.87
Sebatu	38	4	0.67	0.04	2.32	1.30	38	19	0.90	0.04	5.64	2.67	38	16	0.91	0.03	8.02	3.81
Tegal	23	3	0.50	0.08	1.48	0.93	22	10	0.89	0.04	5.25	2.64	23	10	0.89	0.05	7.30	3.55
Timbul	20	3	0.51	0.09	1.56	0.97	20	13	0.95	0.03	6.72	3.31	18	12	0.95	0.03	7.69	3.76
Mean			0.52		1.99				0.93		5.74				0.88		7.24	
Total	287	14	0.60	0.03	2.82	1.49	286	125	0.99	0.00	6.36	3.03	281	72	0.96	0.01	7.85	3.67
<i>Tabanan subsaks</i>																		
Apit Yeh	7	3	0.67	0.16	2.38	1.47	7	6	0.95	0.10	5.95	3.23	7	7	1.00	0.08	9.33	4.89
Bena	20	5	0.75	0.07	3.54	1.88	20	15	0.97	0.03	7.60	3.70	18	12	0.95	0.03	7.95	3.88
Gadon	20	7	0.64	0.12	2.82	1.55	17	14	0.99	0.02	6.76	3.34	19	16	0.98	0.03	7.92	3.85

continued...

Table 17.2 continued

Subaks	Y-SNP						Y-STR						mtDNA						
	Na	nb	h	SE	p	SE	Na	nb	h	SE	p	SE	Na	nb	h	SE	p	SE	
Jaka	10	2	0.47	0.13	1.87	1.16	10	7	0.96	0.06	5.78	3.02	10	7	0.91	0.08	6.29	3.26	
P.Akitan	10	4	0.78	0.09	3.51	1.95	10	6	0.91	0.08	6.28	3.25	10	7	0.91	0.08	7.56	3.85	
Sungi	20	6	0.73	0.07	2.60	1.45	20	15	0.98	0.02	6.84	3.36	20	11	0.92	0.04	7.73	3.76	
Tungkub	20	6	0.73	0.07	3.59	1.90	20	18	0.99	0.02	6.99	3.43	18	14	0.97	0.03	8.07	3.93	
Uma Poh	13	3	0.62	0.08	2.62	1.49	13	12	0.99	0.04	6.55	3.31	12	7	0.83	0.10	8.79	4.36	
Mean			0.67		2.86				0.97		6.59				0.93		7.95		
Total	120	15	0.69	0.04	3.03	1.59	118	90	0.99	0.00	6.91	3.27	114	58	0.98	0.00	8.32	3.88	
<i>Geographic regions in Bali</i>																			
Badung	11	4	0.49	0.18	2.40	1.41	11	10	0.98	0.05	5.85	3.03	11	9	0.96	0.05	9.24	4.60	
Bangli	9	3	0.67	0.10	2.89	1.67	9	5	0.81	0.12	6.50	3.40	9	9	1.00	0.05	7.50	3.87	
Buleleng	9	2	0.22	0.17	0.89	0.68	9	9	1.00	0.05	4.78	2.58	9	8	0.97	0.06	7.83	4.03	
Denpasar	8	4	0.64	0.18	3.25	1.87	8	8	1.00	0.06	6.57	3.47	7	7	1.00	0.08	10.00	5.21	
Gianyar	25	5	0.71	0.05	3.83	1.99	25	23	0.99	0.01	7.26	3.52	23	17	0.97	0.02	7.84	3.79	
Jembrana	4	4	1.00	0.18	4.00	2.52	4	4	1.00	0.18	7.67	4.53	4	4	1.00	0.18	7.17	4.26	
Karangasem	12	5	0.80	0.09	4.23	2.26	12	12	1.00	0.03	7.74	3.88	9	8	0.97	0.06	9.06	4.61	
Klungkung	12	4	0.74	0.08	3.82	2.07	12	10	0.95	0.06	7.38	3.71	12	9	0.95	0.05	8.56	4.26	
Tabanan	10	2	0.53	0.09	1.60	1.03	10	7	0.87	0.11	5.80	3.03	10	10	1.00	0.04	8.07	4.09	
Mean			0.65		2.99				0.96		6.62				0.98		8.36		
Total	100	11	0.69	0.04	3.27	1.70	100	77	0.99	0.00	7.06	3.34	94	81	1.00	0.00	8.66	4.04	

N: number of individuals; n: number of haplotypes; h: gene diversity; SE: standard error; p: p-value.

Table 17.3 Fst parameters for Y-SNP haplogroups, Y-STR haplotypes and mtDNA HVSI sequences

	Y-SNP		Y-STR		mtDNA	
	Fst	p a	Fst	p	Fst	p
Gunung Kawi (N = 13) b	0.141	0.000	0.061	0.000	0.086	0.000
Tabanan (N =8)	0.009	0.274	0.024	0.000	0.052	0.000
Bali (N = 9)	0.075	0.011	0.034	0.000	0.008	0.097

p: p-value; N: number of individuals.

trend was observed for Y-STRs; however, genetic differentiation for Tabanan *subaks* was statistically significant (Table 17.3).

The Bali regions exhibited significant population structure for both Y-SNPs and Y-STRs (Table 17.3), but not for mtDNA ($F_{ST} = 0.008$, $P = 0.097$). Many studies of local populations have shown the similar pattern, which has been attributed to sex-biased migration associated with the common practice of patrilocality (Seielstad *et al.* 1998; Jorde *et al.* 2000). (But for alternate findings and explanations see Destro-Bisol *et al.* 2004; Wilder *et al.* 2004; Wood *et al.* 2005.) Interestingly, we found a higher F_{ST} value for mtDNA variation than for Y-STR variation in Gunung Kawi and Tabanan *subaks*. Because the interpretation of genetic differentiation based on measures of F_{ST} is complicated by its dependence on levels of genetic diversity associated with different loci (e.g. see Table 17.3), we computed a standardized measure of genetic variation described by Hedrick (2005). This measure (G'_{ST}), which is related to the widely used G_{ST} parameter, allows more appropriate comparisons between loci with different mutation rates. G'_{ST} estimates showed similar levels of differentiation for mtDNA and Y-STR data in the Bali region (mtDNA $G'_{ST}/Y-STR G'_{ST} = 1.054$), while Gunung Kawi and Tabanan *subaks* demonstrated higher population structuring for Y chromosome (0.828 and 0.890, respectively). Moreover, within Gunung Kawi region Y-chromosome differentiation was higher for Y-SNPs and Y-STRs in older *subaks* (0.167 and 0.069, respectively) than in younger *subaks* (0.103 and 0.055, respectively), while mtDNA was less differentiated in older *subaks* (0.060) than younger *subaks* (0.072). These results are consistent with the predictions of the budding deme model: the level of endogamy is higher for males because of the strong tendency for patrilocality in rice-growing villages, while females migrate more often, albeit at only a low rate.

Genetic and geographic variation over short areas

To test for associations between genetic and geographic variation in Bali we performed Mantel tests (Table 17.4). Genetic distances were calculated based on haplogroup or haplotype frequencies, without taking into account their allelic content and the molecular distances between the haplogroups and haplotypes. Geographic and genetic distances were not correlated for Y chromosome and mtDNA data in Tabanan or Bali as a whole. In contrast, Y-STR variation was

Table 17.4 Mantel test: correlation between geography and genetics, and between mtDNA and Y-chromosome genetic distances

	Correlation coefficient <i>r</i>	<i>p</i>
<i>Gunung Kawi (N = 13)</i>		
mtDNA – geography	0.361	n.s.a
Y-SNP's – geography	-0.001	n.s.
Y-STR's – geography	0.541	0.000
Y-STR-mtDNA	0.629	0.000
Y-SNP-mtDNA	-0.067	n.s.
<i>Tabanan (N = 8)</i>		
mtDNA – geography	-0.046	n.s.
Y-SNP's – geography	0.060	n.s.
Y-STR's – geography	-0.189	n.s.
Y-STR-mtDNA	-0.159	n.s.
Y-SNP-mtDNA	-0.046	n.s.
<i>Bali (N = 9)</i>		
mtDNA – geography	-0.227	n.s.
Y-SNP's – geography	-0.050	n.s.
Y-STR's – geography	-0.164	n.s.
Y-STR-mtDNA	-0.223	n.s.
Y-SNP-mtDNA	0.133	0.278

n.s. not significant

highly correlated with geographic distances in Gunung Kawi ($r = 0.541$), as was mtDNA variation ($r = 0.361$). While the Y-chromosome association was highly statistically significant, the mtDNA correlation was not (Table 17.4). These results are especially noteworthy because the geographic distances among the Gunung Kawi *subaks* are very small (averaging 3.2 km). Not surprisingly, genetic distances based on slowly evolving Y-SNPs did not demonstrate any association with geography ($r = -0.001$).

To investigate the correspondence between paternal and maternal genetic variation, we also estimated correlation coefficients among different loci. The results indicate a strong correlation between Y-STR and mtDNA structure in Gunung Kawi ($r = 0.629$), possibly reflecting the same events in population history. In contrast, there was no positive correlation among Y-chromosome and mtDNA genetic distances in Tabanan or the geographic regions of Bali ($r = -0.159$ and $r = -0.223$, respectively).

Summary

The genetic analyses presented here provide several clear insights into the origins and expansion of the *subaks*, all of which are consistent with a kin-structured budding model of gradual expansion carried out by rice farmers. In this model, demographic pressure drives increases in population size, and downstream budding of the *subak* system. *Subaks* located at the furthest positions upstream on their respective irrigation systems demonstrate greater levels of genetic differentiation and diversity, suggesting that they must have been built before their downstream neighbors. The evidence from the Y chromosome is consistent with key features of the budding deme model: patrilocality with very little movement on the landscape except for occasional micro-movements to nearby daughter settlements. The older the *subak*, the more evidence for this pattern. Evidence from mtDNA is consistent with the contemporary observed pattern of patrilocality and preferential village or *subak* endogamy, but occasional marriages outside the *subak*. Again, this pattern is most strongly evidenced in the oldest villages, and scales with time. The all-Bali sample shows none of these patterns.

We conclude with the observation that the budding model imposes a very restrictive set of constraints on the genetic structure of farming communities in Bali. These include strong founder effects accompanied by genetic drift and directional micro-movements; more structure in patrilineages than matrilineages; and a strong contrast between *subaks* versus background relatedness of the whole population. These are not the patterns expected under the alternative scenario of state-controlled expansion of irrigation – that is, the *rajahs* transporting whole villages to newly constructed irrigation areas, or alternatively bringing settlers from nearby villages.

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