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Blood is not always thicker than water: The limited effect of kin selection on human kinship in the traditional Chinese family

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Abstract To examine the importance of kin selection in shaping human societies, this study analyzed the kinship system practiced in traditional China for two millennia and teased apart its underlying genetic and other, presumably cultural, components. The results demonstrate that, in the traditional patrilineal Chinese family, both genetic relatedness and the cultural factor of generation were important in determining kinship status for male agnates (genetically related relatives). For female agnates, however, only genetic relatedness was important. Another surprising finding was that the influence of gender was not as important as genetic relatedness. The most interesting finding in this study, however, was that kin selection and culture (i.e., seniority in generation and age) played vastly different roles in different lineages in the Chinese family: for collateral (indirect) agnates, genetic relatedness was the most important factor in determining their kinship status, but for lineal (direct) agnates, its importance was overridden by seniority in generation and age, a cultural factor. Several other bio-cultural factors also explained a considerable amount of variance in kinship status. Since kinship profoundly affected, and was often the foundation of, the legal and social systems in dynastic China, kin selection, while its strength may differ remarkably between lineal and collateral relatives, could act as a selective force in Chinese families [Current Zoology 56 (2): 182–189, 2010].

Key words Kinship, Kin selection, Genetic relatedness, Chinese family, Culture

Kin selection may be the most important conceptual development in our evolutionary thinking since Darwin's idea of natural selection. It is considered a founding principle of sociobiology (Wilson, 1975), which has inspired the emergence of behavioral ecology, evolutionary anthropology, and evolutionary psychology. For three decades, kin selection has been viewed as central to the study of social behavior and social evolution (e.g., Frank, 1998). The idea of kin selection broadens traditional Darwinian fitness by adding indirect fitness (the additive reproductive success of an organism's relatives weighted by their genetic relatedness to the organism) to direct fitness (the organism's own reproductive success) in evolutionary analysis. The two components are lumped together and collectively called inclusive fitness. Selection, accordingly, favors individuals that can maximize their inclusive fitness (Hamilton, 1964). For this reason, kin selection is frequently invoked as an ultimate cause for observed altruistic behavior. It explains why animals exhibit altruism, even to the degree that they would sacrifice their own lives for their close relatives.

Recent findings in animal cooperation, however, have cast doubts on the assumed ubiquity and overall importance of kin selection (e.g., Grinnell et al., 1995; Goldberg and Wrangham, 1997; Mitani et al., 2000; Moller and Beheregaray, 2001; Clutton-Brock, 2002; Griffin and West, 2002; Wilson, 2005; Wilson and Hölldobler, 2005). Compelling evidence has surfaced to indicate that the strength of kin selection varies among species (Griffin and West, 2003), confirming the theoretical insight that the evolutionary process can be highly complex when other factors are involved in kin selection (e.g., Tylor and Frank, 1996; Frank, 1998). These new discoveries conjure up the unsettled issues that have been hotly debated for decades: can kin selection be applied to human society and, if yes, how effective does it work under the overwhelming influence of human culture? Clearly, close empirical examinations on the efficacy of kin selection in human social evolution are both urgent and necessary to resolve these important issues. Yet, few empirical studies are currently available to quantitatively assess the strength of kin selection in humans.

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Although the evidence of differential treatment favoring kin versus non-kin or close kin versus distant kin has been profusely documented in a large variety of animals (e.g., Fletcher and Michener, 1987; Hepper, 1991), it nevertheless cannot be used to support the argument that animals, including humans, are selected to maximize inclusive fitness. This is because Hamilton's model assumes that the genetic effect is additive and fitness is a linear function of genetic relatedness (Hamilton, 1964), as expressed by the formula $f_{inc} = \sum f_i r_i$, where f_{inc} is the inclusive fitness of the focal individual and f_i is the fitness of kin i who is related to the focal individual by the genetic coefficient r_i . Therefore, maximization of inclusive fitness via Hamiltonian kin selection has yet to meet two more stringent conditions. First, recognized kinship should have a strong, positive, linear correlation with genetic relatedness, as shown in the formula. Second, the distribution of altruism is scaled proportionally (or nearly so) to genetic relatedness, which is reliably mapped by kinship, for recipients of equal conditions under an ideal situation. Deviations from either of these two conditions would necessarily weaken the strength of kin selection and, at the same time, signify the involvement of other factors. Unfortunately, to my best knowledge, no such empirical data are currently available and little effort has been made to separate the importance of kin selection from those of other compounding factors.

For humans, kinship is a social interpretation of assumed genetic relatedness. Researchers have for long been aware of the overlap and difference between kinship used in practice and genetic relatedness in theory in a broad context (e.g., Gellner, 1960; Schneider, 1984; Holy, 1996; Stone, 2001). Yet, whether or not kin selection can be applied to human societies and how much influence culture exerts on human kinship are yet to be answered. Thus, quantitative analyses on the relationship between kinship and genetic relatedness become pivotal in providing key insights into these critical issues.

Fortunately, Chinese civilization, meticulously recorded for over two millennia, offers a distinctive opportunity for assessing how kinship was determined and how it was related to kin selection in human society. The fundamental and predominant social organization unit in dynastic China was the kin-based patrilineal, patrilocal family (Goody, 1990). This pattern of family organization appeared to be an adaptation to intense collective competition under little regulated social, economic, and political conditions (Sun, 2010). As a

result of this family-based competition, large families were economically richer and politically more powerful than small families. This pattern of competition also compelled patrilineal relatives to stay together. Consequently, families or clans of tens, hundreds, or even thousands of members frequently resided together, often with undivided common assets (Yang, 2000). Since polygyny was legal throughout this long period, wealth (often related to power and social prestige) became the major factor for men to have numerous women as wives and concubines and, in at least some dynasties, the relationship between the number of concubines a man could have was approximately related to his wealth (Wang, 2001). Hence, personal wealth, to a certain degree, predicted a person's direct fitness, in addition to its complex, but probably unknowable, effect on his indirect fitness. Since personal wealth was mostly acquired through kin-based inheritance or asset allocation and was critical for reproductive success, especially for men (Goody, 1990), kinship status certainly had a profound effect on a person's inclusive fitness in traditional China.

I here present an indirect way to assess the magnitude of kin selection using historical data from dynastic China. To do so, I started with the null hypothesis that the Chinese kinship system was based on kin selection alone. This hypothesis predicts that kinship correlated perfectly (or nearly so) with genetic relatedness. This is based on the logic that if kinship and genetic relatedness has no relationship, kin selection will cease to work (see the first prerequisite for kin selection three paragraphs back). By testing the prediction, I attempted to answer two questions: How was kinship related to genetic relatedness and how was the powerful selection force of Chinese criminal law related to the kinship system. The focus of my approach is to tease apart the roles of genetic and cultural factors in constructing the Chinese kinship system.

1 Materials and Methods

I define kinship as a social system or institution by which genetic relatedness is somehow recognized based on a set of common rules or conventions used by people in a society. Such societal kin recognition may differ from individual kin recognition, which is exercised by each and every member in society. Therefore, a societal kinship system, as a social norm, convention, or institution, is normally more stable than individual kin recognition, which may vary greatly among individuals under a variety of contexts (Feng, 1948). (To avoid any possi-

ble confusion, the words “kinship,” “kinship system,” “kinship status,” and “kinship rank” in this article refer to culturally normative kinship.) Under this operational definition of kinship, the Chinese had a broadly practiced kinship system that was legally supported for two millennia from the Han (206 B.C. – A.D. 220) to the Qing dynasties (1644 – 1911). This system classified agnatic (by birth) and affinal (by marriage) relatives into six kin ranks [from high to low: *zhuanshuai* (斩衰), *qishuai* (齐衰), *qinian* (期年), *dagong* (大功), *xiaogong* (小功), and *sima* (缌麻)], each having a specific set of benefits, rights, and duties, such as inheritance, wealth and asset division, and filial and mourning obligations (Ebrey and Watson, 1986).

The Chinese define family in a way markedly different from the West. “Family” in China can refer to nuclear family, extended family, or clan. A clan is also called a “grand family” or *zongzu* (宗族) in Chinese, often with the genealogical relationships among clan members clearly or even completely recorded in great detail for many generations. Such broadly defined families have been common in many Asian and African countries, and some part of Europe such as southern Italy. To comply with this Chinese conception and for the ease of discussion, I here use the word “family” as a broadly defined concept unless specified. Also, traditional Chinese families were virtually always kinship-based, but depart markedly from Hamiltonian kinship. Metaphorical kin were excluded in a strict sense. So a family, even a large clan, was composed of either agnates (consanguineal relatives) or affines. Such clear dichotomy of family membership greatly facilitated analysis (see below). Additionally, in plural families where concubines were involved, all relatives of the concubines, including their parents and their children were excluded, by law, from the families they were “married” into (they were actually bought) because their low social status, for which their genetic lineages did not “deserve” to be included in their husbands’ families (Wang, 2001). Therefore, polygyny did not complicate the analysis of the kinship system.

I constructed the Chinese kinship system from the Han to the Qing dynasties based on historical documents (Xu, 1933; Shi, 1999). To investigate the strength of kin selection, I focused my analysis on agnates of the ego (self: the person served as the reference in the center of the kinship system) in the same family (Fig. 1) because they were genetically related and male agnates mostly spent their entire lives in the family. For female agnates, I used their kin ranks before they married out to

avoid the complication and redundancy caused by the change in kinship status after marriage [A woman’s kinship status was lowered by precisely one rank after marrying out and redefined in her new marital families (Shi, 1999)]. Since the Han dynasty, marriages between relatives had been generally avoided and marriages between people with the same surnames are stiffly tabooed (Dull, 1978), I thus simplified the analysis by assuming that all women married out and no marriage happened within the lineage shown in Fig. 1. Uxorilocal marriages, where men married into women’s households, were rare in especially Northern China and, when they did occur, they were seen primarily in poor and small families (Goody, 1990).

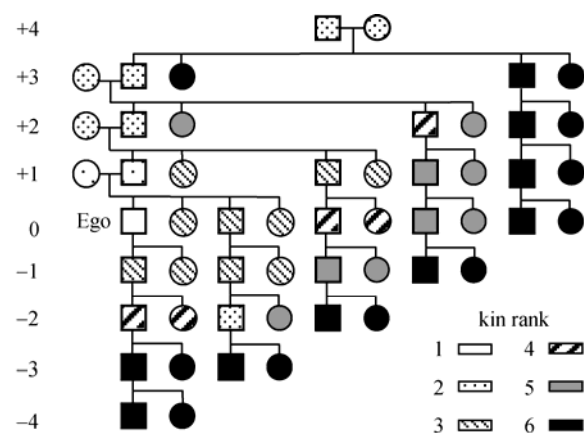


Fig. 1 The kinship system in dynastic China, showing only agnatic relatives of the male ego (white square)

All male (square) and female (circle) members with the same kinship status in reference to the ego in the lineage are represented by a single symbol. Male and female agnates were symmetrical so as to be unbiased for analysis. The numbers at the left are the number of generations up and down from the ego, depending on the ego’s age.

I calculated the coefficient of relatedness (r) as the genetic relatedness (Hamilton, 1964) between the ego and every other member of the family (Fig. 1) using path analysis (Crow and Kimura, 1970). Then, I used Spearman’s rank correlation coefficient (r_s) to investigate how kinship (kin rank, as shown in Fig. 1) was related to genetic relatedness and seniority in generation. The results were corroborated by using Kendall’s partial correlation analysis (Gibbons, 1993) through simultaneously considering the influences of genetic relatedness and generation on kinship rank. Note that r_s here is a measure of similarity between what it was in reality and what it would be expected based on the hypothesis if kin selection alone was at work. So, in a sense, it is not a usual statistical application of correlational analysis.

The importance of the genetic and cultural factors in determining a person's kinship rank was estimated using Spearman's rank correlation coefficient, which, when squared, produces the proportion of the variance explained by each factor, provided there is no significant interaction between genetic relatedness and generation. (This assumption turned out to be true, indeed, after analysis). This method of estimation, being a non-parametric alternative to ANOVA, is approximate nevertheless, as it is based on ordinal, rather than ratio, data.

Finally, I related the Chinese kinship system to kin selection by a case study to illustrate how the kin-based dynastic Chinese criminal law took inclusive fitness into consideration. Specifically, I chose the penalty for the common crime, hitting people (battery in legal terms), to probe the role of kinship in the criminal justice system based mainly on the Tang dynasty (A.D. 618–917) (Shi, 1999). In traditional China, the legal definition of battery included a large variety of physical violence, ranging from battery to aggravated assault in today's EuroAmerican legal systems. Although there were variations in severity and form, criminals were punished in a remarkably similar way according to the same kinship system in other dynasties. The trial and sentencing were proceeded by the government (*Yamen* 衙门), mostly at the county level. So usually, no kinsmen were involved for either the criminals or the victims. Spearman's rank correlation was used to examine the correlation between kinship and severity of punishment. The level of significance for all tests was set at 0.05 a priori.

2 Results

For male agnates, kinship was positively correlated with genetic relatedness ($r_s = 1$, $n = 3$, $P < 0.001$ for generation +2; $r_s = 0.949$, $n = 4$, $P = 0.051$ for generations +1 and 0; $r_s = 0.894$, $n = 4$, $P = 0.106$; $r_s = 1$, $n = 3$, $P < 0.001$ for generation -2, see Fig. 1). The influence of generation, traditionally viewed as the most important cultural factor in Chinese social life (Watson, 1986), was indeed substantial with elder relatives defined as closer kin than younger relatives for the same level of genetic relatedness ($r_s = -0.0949$, $n = 4$, $P = 0.051$ for $r = 1/4$; $r_s = -0.975$, $n = 5$, $P = 0.005$, for $r = 1/8$; $r_s = -0.655$, $n = 6$, $P = 0.158$, for $r = 1/16$). For female agnates, kinship was also positively correlated with genetic relatedness ($r_s = 1.000$, $n = 3$, $P < 0.001$ for generation +2; $r_s = 0.949$, $n = 4$, $P = 0.051$ for generations +1 and 0; $r_s = 0.894$, $n = 4$, $P = 0.051$ for generation -1; $r_s = 1$, $n = 3$, $P < 0.001$ for generation -2). The influence

of generation, however, was insignificant ($r_s = -0.866$, $n = 3$, $P = 0.333$ for $r = 1/2$; $r_s = -0.949$, $n = 4$, $P = 0.051$ for $r = 1/4$; $r_s = -0.821$, $n = 5$, $P = 0.089$ for $r = 1/8$; $r_s = -0.655$, $n = 6$, $P = 0.158$ for $r = 1/16$).

When genetic relatedness and generation were considered simultaneously using Kendall's partial correlation analysis, kinship was positively correlated with genetic relatedness ($\tau = 0.307$, $P < 0.050$) but not with generation ($\tau = -0.168$, $P > 0.200$) for all male agnates. For lineal male agnates, relatedness still had some influence ($\tau = 0.377$, $P > 0.270$), but generation also played a considerable role ($\tau = -0.252$, $P > 0.500$), though neither was significant, perhaps due to the constraint of the small sample size. Kinship for collateral (indirect) male agnates was positively correlated with genetic relatedness ($\tau = 0.570$, $P < 0.005$), but generation had virtually no influence ($\tau = 0.000$, $P = 1.000$). For all agnates or collateral female agnates, kinship was positively correlated with genetic relatedness ($\tau = 0.547$, $P < 0.010$ for all agnates; $\tau = 0.570$, $P < 0.010$ for collateral agnates), but not with generation ($\tau = -0.161$, $P > 0.200$ for all agnates; $\tau = 0.000$, $P = 1.000$ for collateral agnates). For female lineal agnates, neither factor was significant ($\tau = 0.377$, $P > 0.178$ for genetic relatedness; $\tau = -0.252$, $P > 0.400$ for generation).

Since generation and genetic relatedness were not correlated conceptually or statistically ($\tau = 0.000$ – 0.290 , $P = 0.400$ – 1.000), Spearman's rank correlation coefficient could be used to separately estimate the importance of genetic relatedness and generation in determining kinship status, in terms of how much variance in kinship rank is explained. While genetic relatedness was important in kinship in general, especially for collateral relatives, the culturally imposed generation factor had a higher influence in determining the closeness among lineal relatives (Table 1).

Dynastic Chinese criminal laws were strongly influenced by two factors: seniority in generation and age, and kinship between the criminal and the victim. Hitting people could incur harsh penalty, which was weighed according to kinship rank and seniority in generation and age. For battery between two agnates, the closer the kinship between the offender and the victim, the more severe the punishment if the offender was the younger one ($r_s = -0.937$, $n = 6$, $P = 0.002$) and the lighter the punishment if the offender was the elder one ($r_s = 0.972$, $P < 0.001$). The discrepancy in penalty scale between elder and younger offenders was reduced as their kinship rank became increasingly lower ($r_s = -0.937$, $P = 0.002$, Fig. 2).

Table 1 Influences of genetic relatedness, generation, and other bio-cultural factors on the Chinese kinship system

Gender	Kin	Correlation coefficient (r_s) ^a		Kinship variance accounted for ($r_s^2 \times 100\%$) ^b		
		Relatedness	Generation	Relatedness	Generation	Other
Male	Lineal ($n = 8$)	0.377	-0.822*	14.21	67.57	18.22
	Collateral ($n = 16$)	0.874**	-0.031	76.39	0.10	23.51
	Combined ($n = 24$)	0.781**	-0.398	61.00	15.84	23.16
Female	Lineal ($n = 8$)	0.377	-0.822*	14.21	67.57	18.22
	Collateral ($n = 16$)	0.874**	0.000	76.39	0.00	23.61
	Combined ($n = 24$)	0.782**	-0.380	61.15	14.44	24.41
Combined	Lineal ($n = 16$)	0.377	-0.822**	14.21	67.57	18.22
	Collateral ($n = 32$)	0.874**	-0.016	76.39	0.02	23.59
	Combined ($n = 48$)	0.781**	-0.389**	61.00	15.13	23.87

^a * $P < 0.05$; ** $P < 0.01$; r_s is Spearman's rank correlation coefficient, calculated similarly as the Pearson product-moment correlation coefficient using ranks in MINITAB.

^b Because no significant correlation was found between genetic relatedness and generation in any of the analyses, their respective contributions to kinship were separable.

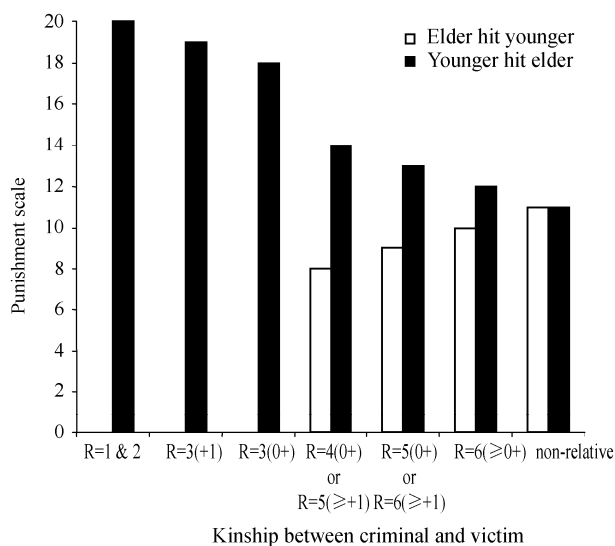


Fig. 2 Punishment for the crime of battery based on seniority in generation and age, and kinship between the offender and the victim

The vertical axis shows the 20 major penalty scales with increasing severity (0, not guilty; 1–5, whipping; 6–10, clubbing; 11–15, jailing; 16–18, exiling; 19, hanging; and 20, decapitation). The precise penalty scales are shown above the bars. The horizontal axis represents kinship rank (simplified as “R”) from the highest (1) to the lowest (6). Kinship ranks (without parentheses) and generation numbers (inside parentheses) are the same as those in Fig. 1. “0+” indicates an elder member of the same generation, and “≥+1” indicates a member senior by at least one generation. Black bars show the penalty for the younger or junior hitting the elder or senior, whereas white bars indicate the penalty for the elder or senior hitting the younger or junior.

3 Discussion

The Chinese kinship system was legally instituted in all dynasties from the Han to the Qing as a response to the long-existing genetic relatedness among family ag-

nates and the cultural norm of revering family elders. Thus, the influences of genetic relatedness and generation on kinship status were causal, despite the use of correlation analysis methods invoked in this study. The results rejected the null hypothesis, which predicted that the Chinese kinship system was constructed based solely on genetic relatedness. Therefore, other factors such as generation, a cultural factor, might also play important roles. Clearly, the results were far more intriguing than I had expected.

While both genetic relatedness and the generation factors had strong influences on the Chinese kinship system among male agnates, only genetic relatedness played a significant role in determining kinship status among female agnates. This was due to the social practice of females marrying out, mostly before 20 years old (Jiang, 1998), in patrilineal, patrilocal Chinese families. A short tenure in the family made it difficult for elder females to strongly influence younger female agnates. Among males, however, elder members had more time and opportunities to ascend to higher statuses to be dominant over younger members in the hierarchically structured family. Fig. 1 also shows that, for agnates with the same degrees of genetic relatedness, their kinship statuses were not entirely symmetrical with senior members sometimes ranked higher than junior members in the kinship system. This explains why generation and kinship were positively related. Clearly, by inflating the kinship status of senior members, the Chinese kinship system, while reflecting the traditional value of filial piety, manipulated the social cognitive system in favor of elders so as to facilitate the dominance of elders in the family (Sun, 2010). This was in conflict with the direction pre-

dicted by kin selection. For instance, the “grandmother effect,” as seen in other human societies, would favor the younger and junior members, whose reproductive values are higher, rather than the older members in the family (e.g., Lahdenpera et al., 2004; Sear and Mace, 2007). Therefore, the filial piety practice in dynastic China provided an even stronger argument for cultural involvement in the evolution of the Chinese family. From this point of view, hypotheses with the dual influence of genetics and culture (e.g., Richerson and Boyd, 2005; Henrich and Henrich, 2007) appear to have a better explanatory power than kin selection alone in the evolution of human social organization.

A surprising finding in this study is that the kinship ranks (and thus, presumably social statuses in the family) of female agnates were almost symmetrical with their corresponding male members (Fig. 1 and Table 1), despite the general perception that Chinese women were severely oppressed in traditional China. Obviously, the kinship factor seemed to be more important than the gender factor in determining social status in the family. That is to say, gender played a less important role than genetic relatedness and generation in social dominance in traditional Chinese families.

The most important finding in this study, however, is that genetic relatedness was more important in determining kinship rank among collateral agnates, whereas, for lineal agnates, the cultural factor of generation played the major role (Table 1). The separation of the relative importance of genetic relatedness versus generation in determining kinship rank allows quantitative assessment on the importance of genetic and cultural factors beyond traditional verbal arguments, especially between natural and social scientists. The difference in the importance of the genetic and cultural factors between lineal and collateral kin demonstrates that neither factor worked as a constant, uniform, or global force on human social evolution in traditional Chinese society. Their strengths varied with bio-cultural contingencies within the family.

The kinship system had a tremendous influence on dynastic Chinese criminal laws, which were characterized by filial piety and kinship (Goody, 1990). The current study shows that the penalties were affected by both kinship rank and seniority in generation and age if the criminals and the victims were relatives. The cruelty of penalties and its relevancy to kinship status necessarily rendered dynastic Chinese criminal laws a strong kin selection force on inclusive fitness. This was most explicitly asserted in statutes against family violence, notably

ably battery, as we analyzed here. Although many other crimes, such as robbery and murder, were prosecuted similarly according to the same principle (Zhang, 1999), the data were less complete, for which they were excluded from analysis.

Clearly, seniority provided an overpowering jurisprudential guidance for who should be punished more severely. Kinship rank, though less important, determined penalty on a finer scale. Among close relatives, the discrepancy in punishment remained large. By superimposing the importance of seniority on that of kinship, dynastic Chinese laws preferentially protected the elder members of the core family (mostly composed of lineal kin). Excluding the core family, kinship rank (and thus the underlying genetic relatedness) was the most important factor in criminal justice. This result shows that kin selection was indeed an important selective force among collateral agnates. Nevertheless, since correlation between kinship and penalty was not perfect, kin selection alone was unlikely to be responsible for the social evolution of the Chinese family.

Besides genetic relatedness and generation, other unspecified bio-cultural factors accounted for a considerable amount of the variance (Table 1), although I was unable to pinpoint them for the lack of further information. In all cases, kinship rank was significantly influenced by, yet not exactly congruent with, genetic relatedness. Hence, kin selection was unlikely to be the only force that had shaped the Chinese family. Indeed, several other factors, including reciprocal altruism (Trivers, 1971; Axelrod and Hamilton, 1981; Axelrod, 1984; Nowak et al., 1995), indirect reciprocity (Alexander, 1987; Nowak and Sigmund, 1998a,b; Lotem et al., 1999; Wedekind and Milinski, 2000; Leimar and Hammerstein, 2001), costly signaling (Zahavi, 1977; Zahavi, 1995; Gintis et al., 2001), altruistic punishment (Fehr and Gächter, 2002), competition among relatives (West et al., 2001; Mock, 2004), and gender segregation in the family (Zhang, 1999) can reduce or even cancel the efficacy of kin selection. Reciprocal altruism, in particular, appears to be a major reason why close relatives in humans are often perceived and treated disproportionately more altruistically than their genetic worth, in comparison with distant relatives (e.g., Hames, 1988; Burnstein et al., 1994; Barrett et al., 2002). These factors are expected to compromise the strength of kin selection.

The results of this study were based on the Chinese kinship system as a socio-cultural institution *per se* but not on what people actually practiced, which varied

across geographical regions and historical times. Any discrepancy between the kinship system and social practice would certainly affect the results presented here regarding the strength of kin selection. Although existing historical records, evidence, and signs indicate that this kinship system was closely and broadly followed in Chinese history, the exact degree of match between the social institution and social practice is probably unknowable, typical of studies using historical data. This situation may cast some uncertainty for the exact role played by kin selection in reality, but it is unlikely to significantly reduce, much less to eliminate, the importance of kin selection in the traditional patrilineal Chinese family. Of course, the limited role of kin selection was also reflected in the obvious historical fact that the genetic relatedness in the maternal lineage, which was also subject to kin selection, was rarely considered. Same could be said for polygynous marriages, where genetic lineages through concubines were also excluded. These cultural practices, although their impact was unknown, would necessarily weaken the strength of kin selection in Chinese society.

In conclusion, this study has unveiled an unexpectedly complex picture about the role of kin selection in human social evolution as exemplified in traditional China. On the one hand, the positive relationship between kinship and genetic relatedness argues for the efficacy of kin selection via especially the criminal justice system in dynastic China. This provides a solid piece of evidence against arguments discrediting the importance of kin selection in humans (e.g., Sahlins, 1976). On the other hand, it was also true that genetic relatedness could not alone determine the Chinese kinship system, which was affected by seniority and other bio-cultural factors as well. Furthermore, this study demonstrates that the strength of kin selection could vary between lineal and collateral relatives and culturally imposed institutions (such as seniority) could significantly weaken the strength of kin selection in humans.

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References

- Alexander RD, 1987. *The Biology of Moral Systems*. New York: Aldine de Gruyter
- Axelrod R, 1984. *The Evolution of Cooperation*. New York: Basic Books.
- Axelrod R, Hamilton WD, 1981. The evolution of cooperation. *Science* 211: 1390–1396.
- Barrett L, Dunbar R, Lycett J, 2002. *Human Evolutionary Psychology*. Princeton, NJ: Princeton University Press.
- Burnstein E, Crandall C, Kitayama S, 1994. Some neo-Darwinian decision rules for altruism: Weighing cues for inclusive fitness as a function of biological importance of the decision. *Journal of Personality and Social Psychology* 67: 773–789.
- Clutton-Brock TH, 2002. Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science* 296: 69–72.
- Crow JF, Kimura M, 1970. *An introduction to population genetics theory*. New York: Harper & Row.
- Dull J, 1978. Marriage and divorce in Han China: A glimpse at pre-Confucian society. In: Buxbaum D ed. *Chinese Family Law in Historical Perspective*. Seattle, WA: University of Washington Press.
- Ebrey PB, Watson JL, 1986. *Kinship Organization in Late Imperial China 1000–1940*. Berkeley, CA: University of California Press.
- Fehr E, Gächter S, 2002. Altruistic punishment in humans. *Nature*: 415: 137–140.
- Feng E, 1948. *The Chinese Kinship System*. Cambridge, MA: Harvard-Yenching Institute Publications.
- Fletcher DJ, Michener CD, 1987. *Kin Recognition in Animals*. New York: John Wiley & Sons.
- Frank SA, 1998. *Foundations of Social Evolution*. Princeton, NJ: Princeton University Press.
- Gellner E, 1960. The concept of kinship. *Philosophy of Science* 27: 187–204.
- Gibbons JD, 1993. *Nonparametric Measures of Association*. Newbury Park, CA: SAGE Publications.
- Gintis H., Smith E, Bowles S, 2001. Costly signalling and cooperation. *Journal of Theoretical Biology* 213: 103–119.
- Goldberg T, Wrangham R, 1997. Genetic correlates of social behaviour in wild chimpanzees: Evidence from mitochondrial DNA. *Animal Behaviour* 54: 559–570.
- Goody J, 1990. *The Oriental, the Ancient and the Primitive: Systems of Marriage and the Family in Pre-industrial Societies of Eurasia*. Cambridge: Cambridge University Press.
- Griffin AS, West SA, 2002. Kin selection: Fact and fiction. *Trends in Ecology and Evolution*, 17: 15–21.
- Griffin AS, West SA, 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* 302: 634–636.
- Grinnell J, Packer C, Pusey A, 1995. Cooperation in male lions: Kinship, reciprocity or mutualism. *Animal Behaviour* 49: 95–105.
- Hames R, 1988. The allocation of parental care among the Ye'kwana. In: Betzig L, Borgerhoff-Mulder M, Turke P ed. *Human Reproductive Behaviour: A Darwinian Perspective*. Cambridge: Cambridge University Press, 237–252.
- Hamilton WD, 1964. The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7: 1–52.
- Henrich NS, Henrich J, 2007. *Why Humans Cooperate: A Cultural and Evolutionary Explanation*. Oxford: Oxford University Press.
- Hepper PG, 1991. *Kin Recognition*. Cambridge: Cambridge Univer-

- sity Press.
- Holy L, 1996. *Anthropological Perspectives on Kinship*. London: Pluto Press.
- Jiang T, 1998. *Human Population and History*. Shanghai: The People's Press.
- Lahdenpera M, Lummaa V, Helle S, Tremblay M, Russell AF, 2004. Fitness benefits of prolonged post-reproductive lifespan in women. *Nature* 428: 178–181.
- Leimar O, Hammerstein P, 2001. Evolution of cooperation through indirect reciprocity. *Proceedings of Royal Society of London (Series B)* 268: 745–753.
- Lotem A, Fisher MA, Stone L, 1999. Evolution of cooperation between individuals. *Nature* 400: 226–227.
- Mitani J, Merriwether A, Zhang C, 2000. Affiliation, cooperation and kinship in wild chimpanzees. *Animal Behaviour* 59: 885–893.
- Mock DW, 2004. *More than Kin and less than Kind: The Evolution of Family Conflict*. Cambridge, MA: Belknap Press.
- Moller L, Beheregaray L, 2001. Alliance membership and kinship in wild male bottle nose dolphins of southeastern Australia. *Proceedings of Royal Society London (Series B)* 268: 1941–1947.
- Nowak MA, May RM, Sigmund K, 1995. The arithmetics of mutual help. *Scientific American* 272: 76–81.
- Nowak MA, Sigmund K, 1998a. The dynamics of indirect reciprocity. *Journal of Theoretical Biology* 194: 561–574.
- Nowak MA, Sigmund K, 1998b. Evolution of indirect reciprocity by image scoring. *Nature* 393: 573–577.
- Richerson P, Boyd R, 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
- Sahlins M, 1976. *The Use and Abuse of Biology: An Anthropological Critique of Sociobiology*. Ann Arbor, MI: University of Michigan Press.
- Schneider DM, 1984. *A critique of the Study of Kinship*. Ann Arbor, MI: University of Michigan Press.
- Sear R, Mace R, 2007. Who keeps children alive? A review of the effects of kin on child survival. *Evolution and Human Behavior* 29: 1–18.
- Shi F, 1999. *Families and Identities in Ancient China*. Beijing: Social Sciences Literature Press.
- Stone L, 2001. *New Directions in Anthropological Kinship*. Lanham, MD: Rowman & Littlefield Publishers.
- Sun L, 2010. *The Biological Roots of Chinese Culture*. Beijing: The Commercial Press, China (in press).
- Talor PD, Frank SA, 1996. How to make a kin selection model. *Journal of Theoretical Biology* 180: 27–37.
- Trivers R, 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35–57.
- Wang F, 2001. *History of Chinese Marriages*. Shanghai: Shanghai People's Publications.
- Watson JL, 1986. Anthropological overview: The development of Chinese descent groups. In: Ebrey PB, Watson JL ed. *Kinship Organization in Late Imperial China 1000–1940*. Berkeley, CA: University of California Press, 274–292.
- Wedekind C, Milinski M, 2000. Cooperation through image scoring in Humans. *Science* 288: 850–852.
- West SA, Murray MG, Machado CA, Griffin AS, Herre EA, 2001. Testing Hamilton's rule with competition between relatives. *Nature* 409: 510–513.
- Wilson EO, 1975. *Sociobiology: The New Synthesis*. Cambridge, MA: Harvard University Press.
- Wilson EO, 2005. Kin selection as the key to altruism: Its rise and fall. *Social Research* 72: 159–168.
- Wilson EO, Hölldobler B, 2005. Eusociality: origin and consequences. *Proceedings of National Academy of Science USA* 102: 13367–13371.
- Xu Z, 1933. *The Origin of Chinese Laws about Relatives*. Shanghai: The Commercial Press.
- Yang Z, 2000. *Familism and Chinese Culture*. Kunming, Yunnan: Yunnan University Press.
- Zahavi A, 1977. The cost of honesty (further remarks on the handicap principle). *Journal of Theoretical Biology* 67: 603–605.
- Zahavi A, 1995. Altruism as a handicap: The limitations of kin selection and reciprocity. *Journal of Avian Biology* 26: 1–3.
- Zhang J, 1999. *The Evolution of Chinese Legal Institutions*. Beijing: Chinese Politics and Law University.