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LONG ARTICLE

Permanent Group Membership

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Abstract This article is divided into two main sections. The first discusses "Female Inheritance and the Male Retention Hypothesis." Permanent groups (groups with no inherent limit on group longevity) exist in several species because over generations members share important interests. Considering the association between cooperation and degree of relatedness, it seems to follow that a collective interest is more likely to be achieved when members show a higher degree of relatedness. I argue that if membership is inherited by only one sex, and this is the female sex, this results in a higher degree of relatedness between group members than when membership is inherited by both sexes, or by males only. Indeed, this is found in the overwhelming majority of species of insects, fish, birds, and mammals living in permanent groups. The (few) exceptions to the rule are briefly discussed. Humans are of special interest because human preindustrial societies tend to show either male or female inheritance. The second section asks, "Do Moralizing Gods Raise Paternity Confidence?" Since males inherit valuable membership in patrilocal/lineal societies, they are expected to be more concerned about the probability of paternity than males in matrilocal/lineal societies. Moral rules, and specifically belief in moralizing gods, are expected to reflect this difference. An analysis of cross-cultural data of preindustrial societies does not refute the hypothesis that moralizing gods are more often found in patrilocal/lineal societies, nor is this hypothesis unambiguously supported.

Keywords Common interests · Cooperation · Degree of relatedness · Gods supportive of human morality · Membership inheritance · Paternity confidence · Patrilocal/lineal versus matrilocal/lineal societies

Female Inheritance and the Male Retention Hypothesis

The most stable aggregations of animals are "permanent groups," though this term is used sparingly (e.g., Pusey 1987, p. 295) in the literature—the problem being the apparently unambiguous word "permanent," signifying eternal. No groups exist forever. On the other hand, with turnover and inheritance of members there is, in theory, no inherent limit on group longevity. Examples are a pride of lions, a clan of spotted hyenas, a colony of honeybees, and a swarm of army ants. In each case groups may continue to exist even though over time all members are replaced by other individuals.

Permanent groups persist because of the valuable effects of cooperation between members. Examples are the collective occupation and defense of a territory, an early warning system against predators, babysitting for the young, or coordinated hunting. Assuming that cooperation is a function of the degree of relatedness between members (Hamilton 1964), this poses the question of how high relatedness is best achieved. Breeding exclusively within the group promotes relatedness but implies inbreeding. Sexual reproduction increases genetic variability in offspring, and may have evolved in response to arms races with parasites (Williams 1975; Hamilton 1980; Trivers 1985). Inbreeding in a sense abandons sexual reproduction (though not the act itself), since it decreases genetic variability, and should therefore be associated with considerable costs in many circumstances, especially in group-

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living creatures where parasites can easily transmit from one host to another (see also Ewald 1993). So exclusive inbreeding is in most cases not a viable option. The persistence of permanent groups suggests that there is a system, favored by natural selection, that optimizes the balance between in- and outbreeding of members.

Preventing Inbreeding While Maximizing Relatedness

If members of both sexes in a permanent group produce new group members and outbreed (i.e., mate with non-group members), then inbreeding is avoided but the average degree of relatedness in the group will be low. But if members exclusively descend from group members of *only one sex*, and individuals of this sex outbreed, then inbreeding is avoided but the average degree of relatedness in the group is augmented. To put it differently, membership inheritance through outbreeding individuals of only one sex avoids inbreeding yet increases relatedness. One reason why the average degree of relatedness in a group will rise with inheritance through only one sex is that after a couple of generations all individuals of the sex inheriting membership will be kin.

Assuming these considerations are correct, then which of the two sexes is expected to inherit membership? It has been pointed out (e.g., Alexander 1979, p. 160) that because of paternity uncertainty, a daughter's children are closer relatives on average than a son's children. This implies that if you possess something valuable you can pass on to your offspring, and you want your grandchildren to profit from it, then you should prefer, other things being equal, to pass it on to your daughters instead of your sons, since your daughter's offspring will certainly carry copies of your genes (no matter whom she mates with), while some or even all offspring of the sexual partners of your sons may not. Therefore, assuming as we did that membership of a permanent group is a valuable thing, female inheritance of membership is expected.

A Hypothesis Awaiting Further Empirical Scrutiny

Do females inherit membership in permanent groups; in other words, is the hypothesis about female inheritance viable? In many species of eusocial hymenoptera (wasps, ants, bees), fertile females ("queens") are readopted by their natal colonies after their nuptial flight, implying that these colonies are permanent groups. The hypothesis about female inheritance holds comfortably in these species, since females outbreed, and males are never readopted. Sometimes, as in army ants, queens are wingless and mated by incoming, winged males. Somewhat surprisingly, termite colonies do not qualify as permanent groups because colonies are mortal (Wilson 1975, p. 435). Following the nuptial flight, fertile offspring–of either sex–are not adopted by their natal colonies (See also Roes 2010).

In fish, permanent groups are rare. The cooperatively breeding cichlid *Neolamprologus pulcher* lives in what Balshine et al. (2001) describe as "permanent social groups." Family groups defend small territories along the rocky shores of Lake Tanganyika (Desjardins et al. 2008). Balshine et al. (2001) have shown that bigger groups live in larger territories with more shelter. Stiver et al. (2006, p. 453) conclude: "Our results suggest a sex difference in the strategy used to become a breeder; it appears that typically, males join, and females inherit to breed."

In birds, permanent groups are also rare. Social groups of females of the waterfowl common eider (*Somateria mollissima*) occur during the brood-rearing period, apparently to decrease predation risk and increase access to resources for adults (Öst et al. 2003, 2005). McKinnon et al. (2006) found that common eider females form kin-based social groups throughout several other stages of their life cycle, including migration. Jeugd et al. (2002) report about barnacle geese (*Branta leucopsis)* returning to breed in their natal colony. Females nested close to their parents and sisters, but settling of males conformed to a random pattern. Sisters also nested close to each other when settling on a different island than the one where their parents bred, pointing at a genuine preference for breeding close to kin.

Brown jays (*Cyanocorax morio*) are cooperative breeders that live in large territorial groups. Small groups may not be able to acquire or defend territories that contain suitable nesting sites (Williams and Hale 2006, p. 848). Hale et al. (2003, p. 446) write about inheritance in the brown jay: "Females usually inherit breeding positions on their natal territories.… Immigrant females are not likely to breed successfully."

As to mammals living in permanent groups, female inheritance appears to be the usual pattern, including African elephants, *Loxodonta Africana* (Archie et al. 2006); lions, *Panthera leo* (Grinnell and McComb 1996); root voles, *Microtus oeconomus* (Le Galliard et al. 2006), and other rodents; the greater horseshoe bat, *Rhinolophus ferrumequinum* (Rossiter et al. 2002), and other bats; meerkats, *Suricata suricatta* (Clutton-Brock et al. 2002); red howler monkeys, *Alouatta seniculus* (Pope 2000), and other primates. Pope (2000, p. 266) writes about red howler monkeys: "Genetic data indicate that ultimately, only one female is successful at leaving the territory to her descendants, and both behavioral data and rate of matriline development indicate that this is an outcome of competition between matrilines within the coalition."

Allosuckling, the provision of milk to non-offspring, as in the fallow deer, *Dama dama* (Ekvall 1998), indicates in most cases close relatedness between females in a group,

and thus female inheritance. Significantly, it is performed in but not between groups. There is also some evidence for allosuckling in the spermwhale, *Physeter macrocephalus* (Whitehead 1996), and it has been observed in at least 68 species, including some human societies (Roulin 2002, p. 201; see also Packer et al. 1992).

A hypothesis linked to the one presented above about female inheritance is that male offspring are expected to disperse or, if remaining in the group, not to significantly contribute to the gene pool of their group. Engh et al. (2002, p. 193) write about the spotted hyena, *Crocuta crocuta*: "Natal males comprise over 20 % of the adult male population, yet they sire only 3 % of cubs, whereas immigrants sire 97 %. This reproductive advantage to immigrants accrues despite the fact that immigrants are socially subordinate to all adult natal males."

The Male Retention Hypothesis

If the hypothesis about female inheritance in permanent groups holds, what about the exceptions? To my knowledge, the pattern is reversed (i.e., males inherit membership) in only five species, namely Ethiopian wolves, *Canis simensis* (Randall et al. 2007, p. 579–580); hamadryas baboons, *Papio hamadryas hamadryas* (Hapke et al. 2001); chimpanzees, *Pan troglodytes* (Williams et al. 2002); red colobus, *Colobus badius* (Pusey and Packer 1987, p. 251); and humans, at least in most preindustrial societies (Van den Berghe 1979, pp. 109–111).

Ember and Ember (1971) and Daly and Wilson (1983) proposed an idea about patrilocality or male inheritance in humans. In the words of Daly and Wilson (p. 105): "A selective history of inter-group conflict should have placed a premium upon the retention of active male kin-group ties." In other words, with intense between-group competition, groups are better able to stand their ground if males remain in their natal group. Humans are of particular interest to test this idea, because preindustrial groups or societies tend to show either male or female inheritance. Ember and Ember (1971) report statistical evidence that patrilocality is indeed associated with internal warfare, supporting the male inheritance hypothesis.

An inference from this hypothesis is that if females are larger than, and dominant over males, the latter will *not be retained* in species with intense inter-group competition. Spotted hyenas and ring-tailed lemurs (*Lemur catta)* neatly comply.

So is the "male retention hypothesis" a valid explanation for exceptions to the rule that females inherit membership in permanent groups? And should this rule itself be considered accepted knowledge, as well as the idea that membership is inherited through only one sex?

Thousands of publications about species living in permanent groups exist, but few address the notion of permanent groups. It is to be hoped that future contributions redress this trend. Since it seems reasonable to assume that humans lived in permanent groups through most of their history, this notion may also shed light on aspects of human sociality.

Do Moralizing Gods Raise Paternity Confidence?

Human Membership Inheritance and Paternity Confidence

Preindustrial societies tend to be either patrilocal/lineal or matrilocal/lineal, which accords with the expectation mentioned in the previous section with regard to inheritance by outbreeding individuals of only one sex. Van den Berghe (1979, pp. 109–111) reports that in the Murdock 1967 sample of human preindustrial societies, 13 % of 858 societies are matrilocal, and 68.6 % are patrilocal. An analysis (Hartung 1985) of cross-cultural data shows a strong association between matrilineal inheritance and moderate to low probability of paternity, and an even stronger relationship between patrilineal inheritance and high probability of paternity. This makes sense in light of the arguments presented above.

Males are expected to be concerned about paternity in species with internal but also in many species with external fertilization, especially when investing parentally, because of the risk of being cuckolded (investing in offspring that are not their own). Once again referring to arguments made above, in permanent groups with male inheritance additional reasons for males to be concerned about paternity should exist, since male offspring inherit valuable group membership. Furthermore, a male should also be concerned about *other males in the group* (to some degree his male relatives) being cuckolded. This should be so because not just his own, but also *their* male offspring, if sired by alien males, will profit from the advantages associated with group membership, at the expense of the inclusive fitness of his male relatives. Yet another reason is that cuckoldry lowers the degree of relatedness between males, thus potentially eroding cooperation within the group.

Cross-cultural research indeed suggests that human females are more closely monitored, less powerful, and more strictly sanctioned in patrilocal/patrilineal societies. For instance, Frayser's (1985, pp. 345–350) findings indicate that patrilineal/patrilocal systems are more sexually restrictive to women than matrilineal/nonpatrilocal systems. Patrilocal residence is also negatively associated with women's consent to marriage. In Baunach (2001, p. 75), two composite measures of childhood gender inequality are associated with patrilocality. Barry (2007) reports that matrilineal

kinship is positively associated with premarital sexual freedom, and Whyte (1978, p. 133) found that matrilineal/matrilocal societies are associated with more property control by women. Van den Berghe (1979, p. 104) writes:

> Patrilineal societies … are notorious for taking active steps to control the sexual behavior of wives, thus raising the probability of paternity …. Adultery is more severely punished …. Women may be physically isolated from men, other than their husband and their husband's kin …. In the extreme cases of some African societies, girls are subject to such painful attempts at controlling their sexuality as clitoridectomy and infibulation …. Nearly all patrilineal societies … have virilocal residence, a system wherein married women live under the constant surveillance of their in-laws, often, in the first instance, their mothers-in-law, but also their husbands' agnates."

In matrilineal societies by contrast, "divorce is easy and frequent" (1979, p. 107), and "Patrilineal societies are least likely to practice wife-sharing, while matrilineal are most likely.… As for rape, matrilineal societies are most tolerant of it—patrilineal societies least tolerant."

Morality and Paternity Confidence

In every society individuals use, interpret, change, and shape moral rules while seeking their own interests and those of their kin (Alexander 1987). When members of one sex have a power advantage over members of the other (Emerson 1962), moral rules reflect this difference. Van den Berghe (1979, p. 103) writes: "In all known matrilineal societies, it is men who are in ultimate jural authority, much the same as in patrilineal societies." But obviously, males have a greater power advantage over females in patrilocal/lineal than in matrilocal/lineal societies and, as argued above, are more concerned about sexual norms and restrictions. So more emphasis on moral norms about sexual conduct is expected in patrilocal/lineal than in matrilocal/lineal societies. As formulated by Roes and Raymond (2003, p. 135), important moral rules "should be imposed with authority. How better than by a moralizing god?" Therefore, the perhaps somewhat startling hypothesis put forward here, labeled the *paternity confidence hypothesis of moralizing gods*, is that since males in patrilocal/lineal societies are more concerned about paternity than males in matrilocal/lineal societies, moralizing gods are more often found in the former.

Other Explanations of Moralizing Gods

In addition to the paternity confidence hypothesis, two other general hypotheses about moralizing gods have been proposed. The first is the Marxist explanation: "Religion is the opium of the people." In societies with large power differences, moral rules are presented as divine creations in order to render them nonnegotiable, protecting the privileges of the powerful and wealthy (Cronk 1994, p. 90). Put somewhat differently: in order to consolidate and increase their wealth, moralizing gods are used—if not created—by the rich to manipulate the poor. The Marxist hypothesis thus expects a belief in moralizing gods more often in stratified societies.

A second hypothesis, the intergroup competition hypothesis, is based on the work of Alexander (1987). In a nutshell it says that human social groups became large as a result of between-group competition over preferred habitats and resources. Although larger social groups are more successful in competition, they also experience more pressures to fission. Morality and moralizing gods unite a society by limiting infringements upon the rights of other society members, and so a greater need for moral rules and moralizing gods is expected in larger societies. Roes and Raymond (2003) report empirical support for both the Marxist and the intergroup competition hypotheses.

Material

Ahead of his time, anthropologist George P. Murdock initiated in 1962 systematic databases of the best earliest descriptions of hundreds of human societies for the purpose of testing cross-cultural hypotheses. One is the *Ethnographic Atlas* (EA) with over one-hundred variables covering 1,267 societies. The Standard Cross-Cultural Sample (SCCS) is composed of 186 societies, chosen to represent the known cultural types of the world from among the societies in the EA. The latest edition has over 1,800 variables, so the SCCS contains much more information about fewer societies than the EA.

The variables (V) and their recoding used to evaluate the "paternity confidence hypothesis" are listed in the online appendix (see Online Resource 1) and briefly discussed here. The dependent variable is V34 in the EA, "High gods" (V238 in SCCS), recoded in such a way that gods are either moralizing (telling people what they should and should not do) or not. The independent variable in the EA is V11, "Transfer of residence at marriage: after first years" (V216 in SCCS), here called "Transfer." Two other SCCS variables served as indicators of membership inheritance by sex, namely V69, "Marital residence," and V70, "Descent–Membership in corporate kinship groups," here called "Descent." As possible confounding variables, "Region" (V91 in EA, V200 in SCCS) and "Religion" (V713 in SCCS) were chosen, and with the Marxist and intergroup competition hypotheses in mind also "Class stratification" (V66 in EA, V270 in SCCS), "Caste

stratification (endogamy)" (V68 in EA, V272 in SCCS), and "Jurisdictional hierarchy beyond local community" (V33 in EA, V237 in SCCS), here called "Society size."

Results

Ethnographic Atlas

In the EA the bivariate correlation is significant ($P < .05$) and the correlation between the two focal variables remains significant when controlling for each of the putative confounding variables.

	(Kendall's tau-b, *P* value, *n*)		
Transfer by high gods	.185	.000	638
Controlling for society size	.108	.007	615
Controlling for class stratification	.139	.001	590
Controlling for caste stratification	.113	.007	568
Controlling for region	.141	.000	635

Standard Cross Cultural Sample

In the SCCS two of the three bivariate relations are marginally significant, but when controlling for confounding variables, none is.

Marital residence by high god	.162	.044	150
Controlling for society size	.128	.121	146
Controlling for class stratification	.122	.139	147
Controlling for caste stratification	.113	.176	142
Controlling for region	.124	.132	147
Controlling for religion	.182	.117	74
Descent by high gods	.211	.042	94
Controlling for society size	.156	.137	90
Controlling for class stratification	.174	.094	91
Controlling for caste stratification	.157	.143	86
Controlling for region	.162	.122	91
Controlling for religion	.158	.293	44
Transfer by high gods	.124	.141	142
Controlling for society size	.050	.561	138
Controlling for class stratification	.060	.481	139
Controlling for caste stratification	.075	.388	134
Controlling for region	.060	.478	139
Controlling for religion	.134	.274	67

All 23 correlations are in the expected direction, and all five EA correlations are significant. However, only two of the three bivariate SCCS correlations are significant, and when controlling for third variables none is close to significance. The best conclusion, therefore, is that the idea of moralizing gods raising the probability of paternity is neither refuted nor unambiguously supported.[1]

To compare the three hypotheses about moralizing gods amongst themselves, here are, as an indication, some EA correlations:

Intergroup competition hypothesis	.371	.000	724
Marxist hypothesis (class stratification)	.293	.000	697
Marxist hypothesis (caste stratification)	.338	.000	673
Paternity confidence hypothesis (transfer by high gods)	.185	.000	638

Discussion

Even in large patrilocal/lineal societies where the average degree of relatedness between males is low, males should still be concerned about membership inheritance *within their own lineage*. Hence, following the arguments presented earlier, comes a common interest in the society as a whole, in the promotion and acceptance of moralizing gods.

Hypotheses about causes and effects of systems of matri- and patrilocality/lineality may nowadays seem somewhat irrelevant, since these systems appear absent in most contemporary human populations. Humans living in industrial societies are neolocal:

> Both bride and groom leave their respective families and establish a household of their own. This is considered the ideal in most industrial societies, but is otherwise a rare arrangement.… Neolocality limits the local family group to parents and unmarried children; this is called the *nuclear* family. This is convenient in industrial societies where the location of the family is in good part determined by the breadwinner's job and where monetary employment is nearly always outside the home. It is bad enough having to move from Kansas City to Buffalo when the company promotes you, or to follow the harvest of industrial crops as an agricultural laborer; it would be unthinkable to take a whole tribe of relatives with you. (Van den Berghe 1979, pp. 109–110)

But in a modern society there is no need to take this whole tribe of relatives with you. The state provides the collective goods (Olson 1965) that used to be the concern of the

[1] Pierre van den Berghe (personal communication, 11 January 2012): "There is, of course, an enormous amount of noise in the HRAF data, so, while positive findings are persuasive, non-significant ones don't necessarily mean much. However, since most of your correlations were weak and non-significant, but all in the predicted direction, I consider your hypothesis fairly well supported."

extended family, like national defense, justice and retribution (Chagnon 1988; Daly and Wilson 1988), protection of property, care for the young, sick and elderly, and so on. So is the extended family a phenomenon of the past?

While discussing the sometimes enormous aggregations of bats, Popa-Lisseanu et al. (2008, p. 471) suggest that "cryptic social groups" may exist within such colonies. Perhaps the same holds for aggregations of modern Western humans. Although interactions between extended family members may be limited to an annual Christmas card or less, and remain that way throughout lifetimes, in times of crisis half-forgotten family ties may rise in importance. And in environments plagued by chronic violence, street gangs and the like, the "honor of the (extended) family" may still be a vital aspect of social life.

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