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The Insectan Apes

Bernard Crespi

Abstract I present evidence that humans have evolved convergently to social insects with regard to a large suite of social, ecological, and reproductive phenotypes. Convergences between humans and social insects include: (1) groups with genetically and environmentally defined structures; (2) extensive divisions of labor; (3) specialization of a relatively restricted set of females for reproduction, with enhanced fertility; (4) extensive extramaternal care; (5) within-group food sharing; (6) generalized diets composed of high-nutrient-density food; (7) solicitous juveniles, but high rates of infanticide; (8) ecological dominance; (9) enhanced colonizing abilities; and (10) collective, cooperative decision-making. Most of these convergent phenotypic adaptations stem from reorganization of key life-history trade-offs due to behavioral, physiological, and life-historical specializations. Despite their extensive socioreproductive overlap with social insects, humans differ with regard to the central aspect of eusociality: reproductive division of labor. This difference may be underpinned by the high energetic costs of producing offspring with large brains.

Keywords Eusociality · Cooperative breeding · Social insects · Convergence

Since Williams (1957) posited that menopause may represent an adaptation founded in maternal care, and Hamilton (1966) suggested kin-selected benefits to grandmothering, the hypothesis that humans exhibit a breeding system that includes evolved sterility and extensive alloparental care has motivated consideration of humans as cooperative breeders (Hrdy 2009) or eusocial (Foster and Ratnieks 2005). Analyses of cooperative breeding models for helping to explain human social and reproductive evolution have centered primarily on benefits and costs of menopause, grandmothering, and other manifestations of paternal and alloparental care within and among human groups, as well as comparisons of humans with cooperatively breeding primates (especially callitrichids) and with other social mammals and birds (Hrdy 2009; Strassmann and Kurapati 2010). These applications of the comparative method, and reproductive behavioral ecology, have generated substantial insights into the selective pressures that underlie human reproductive life histories and

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behavior. Despite such progress, this field remains fraught with an extraordinary diversity of divergent results with regard to who helps and why, and the links of ecology and relatedness with human cooperative breeding behavior remain unclear (Sear and Mace 2008; Strassmann and Garrard 2011). How can such results be reconciled and extended, and such links be elucidated, to further our understanding of human social and reproductive biology?

I contend that humans have evolved convergently to eusocial insects with regard to key selective pressures and genetic substrates favoring care by individuals in addition to the mother (henceforth referred to as *extramaternal care*). As a result of this convergent evolution, humans are actually more similar to eusocial and cooperatively breeding insects than to most social vertebrates for a suite of interacting social and reproductive traits. This argument is built on five tiers of exposition and evidence.

First, I provide a brief overview of social systems and alloparental care among eusocial and cooperatively breeding insects, social nonhuman vertebrates and insects, and humans. This section assembles the framework for recognizing convergences across disparate taxa. Second, I describe a large suite of phenotypic similarities of humans with eusocial insects, each of which indicates convergent evolution from nonhuman or nonsocial related taxa as well as overlap in the selective pressures that have potentiated and driven the evolution of extramaternal care. These similarities are mediated by life-history-wide reorganization of trade-offs that leverage reproduction. Third, I describe extensive evidence, from evolutionary theory, human genetics, and anthropology, for an important role of the X chromosome in the evolution of human female reproductive physiology and behavior. Taken together, this evidence constitutes a “haplodiploidy hypothesis” for human social-reproductive evolution, whereby the male-haploid pattern of inheritance and gene expression, as in Hymenoptera and Thysanoptera, has notably influenced the evolution of extramaternal care. Fourth, I explicate a fundamental difference between humans and social insects: the presence in humans of fully retained reproductive ability, expressed in the absence of lifelong reproductive division of labor. Human females thus all follow essentially the same, single life-history trajectory, in contrast to eusocial-insect females that diverge into queens and helpers. Finally, I emphasize that human among-population diversity in ecology and social structures compels the independent treatment of populations for comparative analyses of the causes of reproductive systems. Such extreme, facultative variability stems, however, from a single trajectory of social-evolutionary changes more or less concomitant to the origin of modern humans, which has generated the insectan apes.

Sociodiversity

I compare humans with social insects in the context of the extensive literature on human “cooperative breeding.” The point of doing so is not to show that humans overlap with social insects for all or most of the phenotypes and parties involved in extramaternal care—just for a considerable suite of the most important ones. Testing for such broad-scale convergences requires clarity in the use of social terms and categories.

I use the term *eusocial*, following its original conceptualization and application, to refer to species with reproductive division of labor based on permanent life-historical differences referred to as castes (Crespi and Yanega 1995; Boomsma 2009). Reproductive division of labor necessarily involves alloparental care by workers or soldiers who normally reproduce less than the queen or reproductive pair. Formally, alloparental care refers here to tending, feeding, or defending of juveniles who are not direct descendants. More generally, *extramaternal care* can be defined as tending, feeding, or defending of juveniles by individuals other than the mother.

The term *cooperative breeding* has been used rather variably by students of different social taxa (Strassmann and Clarke 1998; Hrdy 2009). For birds and nonprimate mammals it normally refers to systems with facultative help provided to a breeding pair, usually by young descendant kin (Stacey and Koenig 1990; Solomon and French 1997). For primates, it usually refers to systems with alloparental care, most prominently as found in humans and callitrichids, but it may also be generalized to extramaternal care (Hrdy 2009).

Crespi and Yanega (1995) extended the category "cooperative breeding" to invertebrates with alloparental care (but not castes), and groups of helpers separate from reproductives, as a precondition to conducting comparative studies that include both vertebrates and invertebrates. Cooperatively breeding insects include most small-colony forms (for example, most Polistine paper wasps, halictine and allodapine bees) that lack morphological differences between reproductives and helpers, and in which helpers can become reproductives (Boomsma 2009). It is important to note that focus on "cooperative" breeding may tend to bias analyses against consideration of reproductive competition within human and social-insect groups, which is expected to constrain and structure forms of cooperation (Strassmann and Garrard 2011).

I focus on the presence and nature of convergence in phenotypic and genetic correlates of extramaternal care between humans and, taken together, eusocial and cooperatively breeding (here, "social") insects. Given the high diversity of ecological and social environments within which humans are currently found, specific human groups, populations, or cultures, rather than the human species as a whole, should be considered as units for comparison, analysis, and discussion (Strassmann and Clarke 1998). Similarly, I draw on phenotypes from a wide range of social insects that uniquely characterize some (or all) of them, and that represent differences with respect to related nonsocial forms.

The Insectan Apes

Humans have previously been compared to social insects with broad strokes depicting similarities as regards cooperation and ecological success (e.g., Kesebir 2012; Wilson 2012). Do the commonalities go deeper, to shared suites of selective pressures and to convergent responses that manifest in ways that are superficially divergent but fundamentally the same?

Hunter-gatherers and other small-scale human groups can be viewed with fresh conceptual eyes as overgrown insects. From this perspective, specific phenotypes that humans share with social insects can first be considered piecemeal and then causally connected into sets of adaptations and trade-offs. I focus first on similarities. Humans obviously also differ from social insects in diverse and important ways, but none of them take away from the core convergent overlaps.

The Colony, Nest, Hive, and Group

Groups—colonies—are composed of individuals connected by varying degrees and categories of genetic relatedness, such that within-group average relatedness is usually relatively high (at least for subsets of individuals) and relatedness to other (even nearby) colonies is relatively low (Chagnon 1988; Boomsma and Ratnieks 1996; Harpending 2002; Bowles 2006, 2009). Human groups exhibit nested hierarchical structure (from nuclear families to extended families, lineages, bands, and tribes; e.g., Service 1975), with the residential local band representing the apparent closest behavioral analog to social insect colonies. Groups of both humans and social insects have discrete boundaries and cues of unique identity (culture and language, or chemicals) that allow individuals to readily distinguish between members and nonmembers (e.g., Boyd and Richerson 1987; Nettle and Dunbar 1997; van Zweden and d'Ettorre 2010). Conflicts are well-documented, within groups, between sets of individuals harboring divergent fitness interests (e.g., parents and offspring, or factions of kin), but they are usually more or less resolved and tend to impose low costs on total group reproductive output. Within groups, prosocial behavior generally predominates (Whiten and Erdal 2012), along with repression of self-serving nepotism that would otherwise impose groupwide costs (Frank 2003; Gardner and West 2004; Úbeda and Duéñez-Guzmá 2011), commonly in the form of policing and punishment (Henrich et al. 2001; Ratnieks and Wenseleers 2005; Mathew and Boyd 2011). An individual's inclusive fitness depends to a considerable degree upon group survivorship, growth, and reproduction (e.g., Oster and Wilson 1978; Bowles 2009; Jones 2011).

A fundamental ecological basis for sociality is the "basic necessary resource," which consists of a long-lasting, highly valuable, socially improvable and defensible nest, hive, burrow, territory, or even a large, interactive group itself (Alexander et al. 1991; Crespi 1994, 2009; Kokko et al. 2001). Such resources, and accrued information in individuals and groups, represent economic capital that can mediate the evolution of extended longevity (of queens, colonies, human adults, and human groups) (Kaplan and Robson 2002). Within such highly valuable group structures, material or reproductive-opportunity inheritances following the death of a relative can greatly enhance inclusive fitness and may be strongly contested (Ragsdale 1999; Gibson and Gurmu 2011; Leadbeater et al. 2011; Hill and Hurtado 2012). Thus, relative peace is punctuated by episodes of intense conflict, usually divisive along lines of kinship or inheritance (e.g., Chagnon 1988; Heinze 2004; Heinze and Weber 2011).

Divisions of Labor

Within groups, individuals differ in behavior, with life-history, behavioral, and ecological specializations according to age, sex, condition, and skills (e.g., Wilson 1971; Ratnieks and Anderson 1999; Henrich and Boyd 2008; Gurven and Hill 2009; van Schaik and Burkart 2009). The primary group tasks include construction of material objects, foraging, hunting, harvesting, defense, reproduction, and care for offspring (feeding and otherwise tending). These tasks trade off with one another to varying degrees, but individual specializations reduce the magnitudes of the trade-offs. Success in some tasks, such as defense and foraging, are functions of group size (Bourke 1999; Kokko et al. 2001; Gautrais et al. 2002; Rodriguez-Serrano et al. 2012). Groupwide distributions of behavioral allocation are organized, across time, via summations of individual-level interactions, using salient information on environmental and social conditions.

Queens of the Apes

A small subset of individuals—insect queens, or human females aged about 20 to 35—have evolved to become relatively specialized in reproduction (Wilson 1971; Strassmann and Warner 1998; Crespi 2009; Kachel and Premo 2012). These individuals have enhanced fertility (compared with that of related nonsocial or nonhuman taxa) underlain by physiological specializations for relatively rapid production of individual offspring (Wilson 1971; Kramer and Ellison 2010). Reproductives differ from other females with regard to patterns of fat deposition and use, gluteofemoral and mammary in human and thoracic and abdominal in insects (Marlowe 1998; Lassek and Gaulin 2007; Leonetti and Chabot-Hanowell 2011). Females have also evolved to exhibit phenotypic signals of high fertility (Monnin 2006; Singh et al. 2010), which appear to solicit increased, selective investment from others (Hagen and Barrett 2009; Hill and Hurtado 2009, 2012). Colonies, or reproductive females, engage in a "bang-bang" life history pattern, with an extended period of growth and somatic investment (compared with sister taxa) followed by a relatively short period of offspring production (Oster and Wilson 1978; Crespi 2009; Kramer and Ellison 2010).

Helpers at the Colony

Reproductives are accorded help in offspring production and rearing from other individuals in the group, especially from kin who are not currently reproductive, and less commonly from other actively reproductive females. Helpers may gain inclusive fitness benefits in part from the ability to increase production of close relatives before they reach adulthood (thereby gaining fitness benefits even in the event of their death as a juvenile) (Queller 1989, 1994; Gadagkar 1991; Kramer 2011) or after they are reproductively senescent (Uematsu et al. 2010). If a reproductive dies, her offspring may still be reared to adulthood by other members of the group (e.g., Gadagkar 1991; Lahdenperä et al. 2011). Maximum lifespans are notably extended for some or all categories of females, owing in part to ecologically and socially based reductions in extrinsic mortality rates and also to benefits from the helper-reproductive system (Keller and Genoud 1997; Clutton-Brock 2009; Parker 2010; Kim et al. 2012).

The Social Stomach

Groups engage in central-place foraging, with highly generalized and diverse but relatively high-quality diets. Food is extensively shared within groups (Wilson 1971; Hunt and Nalepa 1994; Gurven 2004; Gurven and Hill 2009), resulting in a more-or-less pooled energy budget (Kaplan and Gurven 2005; Reiches et al. 2009; Haig 2010; Hou et al. 2010; Kramer and Ellison 2010), but with preferential feeding of reproductives and individuals who otherwise differentially benefit and are less able to forage on their own (e.g., juveniles) (Hunt and Nalepa 1994; Hagen and Barrett 2009; Hill and Hurtado 2009). Juveniles are fed specialized, masticated, high-quality foodstuffs (Sellen 2007; Hunt and Nalepa 1994). As a result of their large foraging labor forces, groups reduce temporal variance in food acquisition rate, which enhances the growth, survival and reproduction of social groups (Wenzel and Pickering 1991).

Larder, Barn, Harvest, Slaughter

Selective pressures for utilization of diverse foods to maintain large, dense groups have resulted in novel, socially mediated nutritional and food-gathering adaptations. Some groups have adopted forms of agriculture, which result in highly specialized diets, larger group sizes, and more-elaborated divisions of labor (Mueller et al. 1998). Animal husbandry has also been taken up by some groups or species, whereby renewable secretions are adaptively utilized as food (Schultz and Brady 2008). Nomadic lifestyles, based on local resource depletion followed by whole-group movement, have evolved in some groups and species (Kelly 1983; Gotwald 1995).

Offspring, Sex, and the Colony

Young offspring attract attention from potential caregivers with positively reinforcing and need-indicating stimuli (Hrdy 2009; Kaptein et al. 2005; Mas and Kölliker 2008; Wells 2003). However, juveniles are frequently killed by related group members at early (especially egg and newborn) life stages, particularly under poor social or ecological conditions (Crespi 1992; Hausfater and Hrdy 1984; Hrdy 1999). Among survivors, sex-biased parental and alloparental investment is common, being mediated by genetic relatedness, local socioecological conditions, and who controls different aspects of investment (Crozier and Pamilo 1996; Cronk 2007).

Hostile Forces of Nature

Groups are ecologically dominant with regard to most predators and interspecific competitors owing to their force of numbers and abilities to hunt, defend, and forage more efficiently than related species. Microparasites and intraspecific competition represent relatively important selective pressures impacting individual and group survival and reproduction (Barrett et al. 1998; Bowles 2009, 2012; Dennen 2005; Schmid-Hempel 1998). During intraspecific conflicts, some individuals specialize in self-sacrifice to increase the success of their own group in combat (“warfare”) with individuals from other groups (e.g., Keeley 1996; Hölldobler 2010). Extensive adaptations for hygiene have evolved (in the context of very high local densities of related individuals within groups) (Curtis 2007; Fefferman et al. 2007), and some aspects of mating patterns, such as choices and numbers of mates, may be driven by strong selection from parasites. Many groups have high survivorship and may persist for numerous generations, with turnover of reproductives. Individuals are highly dependent on the social group and could not survive for long without the diverse benefits it provides.

Colonizing Colonies

Groups send out dispersers of one or both sexes just before their usual age for initiation of reproduction (e.g., Wilson 1971; Strassmann and Clarke 1998). Ability to colonize rapidly, across large geographic regions, appears to be enhanced by demographic fertility benefits of social cooperation as well as by ecological generalism and flexibility, and relative ecological dominance (Wells and Stock 2007; Moreau et al. 2011). Groups may reproduce and colonize new areas by “swarming,” whereby groups of individuals disperse together, thereby avoiding a highly vulnerable stage of founding by few individuals (Loope and Jeanne 2008; Cronin et al. 2013). Demographic expansions and colonization are mediated by aspects of social structure (e.g., Wilson 1971; Jones 2011) and often have severe ecological impacts on other species (Diamond 2005; Powell 2011).

The Social Insect Brain

Group decision-making is commonly collective, being based on a summation of many independent sources of information (Wilson et al. 2004; Seeley 2010). Information salient to group survival and reproduction is stored in a distributed, dynamically maintained manner and communicated through pairwise, one-to-many and many-to-one interactions that often involve parallel processing (Hirsh and Gordon 2001). Some information transfer deploys symbolic communication systems (Seeley 2010), the only such systems well-known among animals.

The Shared Socioecological Niche

Based on these ten considerations, humans appear to resemble social insects in myriad ways, despite their profound evolutionary legacies of differences. Humans also differ from social insects in many fundamental ways, as witnessed for example by human social learning, high individual intelligence, extensive paternal care, complex hierarchical group structures, and lack of reproductive castes (as discussed below in more detail), but these differences are not relevant to the existence of convergent similarities. Most generally, the socioecological "niche" inhabited by social insects and humans centers on cooperative and collective behavior, generalist high-quality diets, food-sharing, especially valuable and long-lasting "basic necessary resources," and divisions of labor. Figure 1 depicts these similarities, and their primary causal associations with one another. The convergences between social insects and humans are fundamentally interrelated owing largely to their evolution involving changes to life history trade-offs.

Social Life Histories Alleviate Trade-offs

Trade-offs structure central aspects of ecology, behavior, physiology, and development and thus constrain inclusive fitness and demographic success of individuals, groups, and populations. Social behavior assuages trade-offs among both humans and social insects.

The energetically based size-number trade-off has shifted among humans and social insects as a result of extramaternal care, which increases the amounts and rates of resources that can be allocated to reproduction (Hrdy 2005; Kramer 2010). Among great apes, interbirth intervals have been notably reduced along the human lineage, and among human populations, shorter interbirth intervals have been associated with higher levels of extramaternal care (Hrdy 2009; Quinlan and Quinlan 2008). In social insects, queens produce eggs, and offspring biomass, at higher rates than among nonsocial insects owing to morphological and physiological specializations as well as help (Wilson 1971). Within both humans and social insects, fecundity and longevity demonstrate little or no trade-off under natural-fertility conditions (Le Bourg 2007;

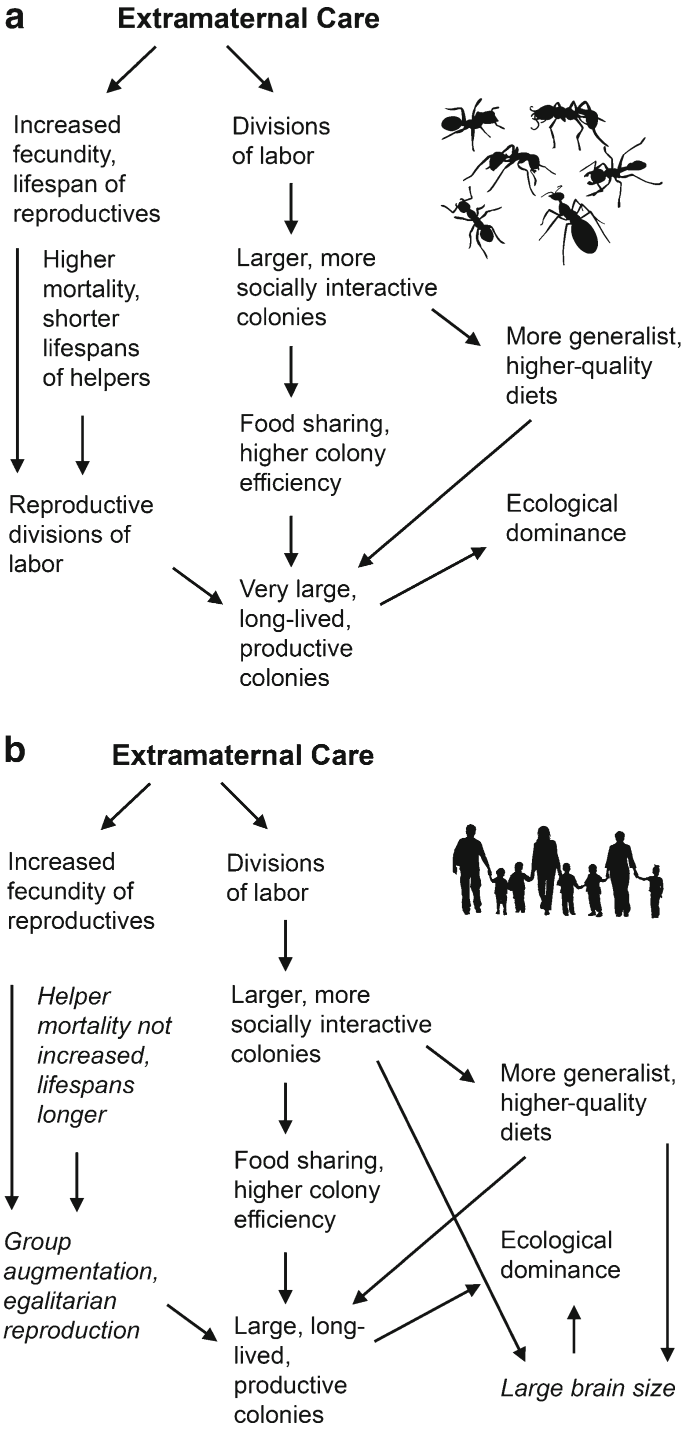

Fig. 1 Convergent relationships of extramaternal care with a set of causally associated individual-level and group-level traits, among (**a**) social insects and (**b**) humans. Differences between social insects and humans are shown in *italics*, on (**b**)

Mitteldorf 2010; Schrempf et al. 2011), presumably owing, at least in part, to direct and follow-on effects from extramaternal care.

Trade-offs are commonly alleviated via specialization. Among social insects and humans, individuals specialize for particular tasks, especially along lines of age and sex

(Ratnieks and Anderson 1999; Kramer 2010; Leonetti and Chabot-Hanowell 2011) as well as across females of similar ages. Relatively safe tasks, and tasks within the social group, are pursued more commonly by younger individuals. Among social insects, however, helping leads to increased mortality rates, which can select for increased queen-helper divergence in behavior and life history (Crespi 2009). By contrast, among humans, help in offspring production (mainly by juveniles, mates, and postreproductives) shows little evidence of strong mortality-related costs, perhaps in part because most of the tasks involved are much less dangerous, and individuals (and groups) are more ecologically dominant as regards effects from predation.

More generally, as a result of task specializations, trade-offs of reproduction with all other energy and time-demanding activities are reduced, and efficiency in specific tasks is enhanced and may additionally increase with age (e.g., Walker et al. 2002; Quinlan and Quinlan 2008). Trade-offs may also be reduced through temporal, life-historical separation of extramaternal care from reproduction, with relatively low opportunity-cost help being provided by female and male juveniles (e.g., termites, wasps, and humans) and by postreproductive females (Alexander et al. 1991; Kramer 2005; Hagen and Barrett 2009; Uematsu et al. 2010).

Relatively large human groups represent an apex of task-specific specializations given their diversity of material and informational culture, long lifespans, and broad ranges of foods utilized in different ways. Among insects, morphological caste diversity and shifts in worker task with age appear to be most pronounced among eusocial ants and bees with larger colony sizes (Grüter et al. 2012; Rodriguez-Serrano et al. 2012), where lifetime specialization need not impose strong constraints on colony-level behavioral flexibility. High levels of specialization within large social insect colonies presumably increase individual efficiencies and colony ranges of skills, as well as colony-level survivorship and reproduction as emergent social phenotypes subject to selection (Oster and Wilson 1978; Grüter et al. 2012). By contrast, within human groups of hunter-gatherers, individual and group-level costs and benefits of specialization remain largely unexplored, except in the contexts of hunting compared with gathering among males and females, and cooperative breeding as an age-structured adaptation.

Taken together, these reductions and alterations in trade-offs appear to underpin many of the convergences of humans with social insects, especially those that hinge upon reproduction. But the evolution of social-reproductive systems depends on interactions, or synergisms, of genetic with ecological, behavioral, and life-historical factors. Have the roles of genetics and relatedness in maximization of inclusive fitness shifted as well, for humans and social insects?

Homo haplodiploidus

The “haplodiploidy hypothesis” for roles of high among-sister genetic relatedness and relatedness asymmetries in the many origins of eusociality among Hymenoptera has attracted considerable attention for almost 50 years. The resulting bodies of work include evidence that haplodiploidy matters in the origins and evolution of social cooperation, conflict, and eusociality, though in ways that are complex and challenging to discern (Gardner et al. 2012).

Humans and most other mammals are also, of course, haplodiploid, though only for their X chromosome. As in haplodiploids, X ploidy mediates sexual dimorphism (Crespi 2008), though for humans this occurs in conjunction with its degenerate homologue, the Y. Among haplodiploid insects, this genetic system has been posited to influence social evolution through several interrelated effects, including 3/4 relatedness between full sisters (higher than their 1/2 relatedness to their own offspring, and 1/4 relatedness to their brothers), consequent relatedness asymmetries (deviations from all-1/2, among group members), and population-genetic effects on allele-frequency change for genes that underlie social evolution owing to higher exposure of haploid alleles to selection in males.

The hypothesis that haplodiploid X chromosomal effects modulate the evolution of human social behavior and cooperative social systems has yet to be systematically investigated. This dearth of study has probably persisted so long because the X constitutes only about 4% of the human genome and should thus represent a small, special-interest faction (Haig 2006), relative to the massive autosomal majority, in the parliament of intragenomic cooperation and conflict (Strassmann and Queller 2010)—with the X and autosomes expected to be often in conflict with one another with regard to social and sexual phenotypes (Frank and Crespi 2011). But from theory, what are the interests of X-linked genes, should they be met, and from available evidence, do they shape organism-level behavior and reproduction?

Population Genetics Theory

From population-genetic theory, the haploid nature of the X in males and the inactivation of one X chromosome in female cells (for about 80–85% of X-linked genes; Berletch et al. 2011) means that genetic and epigenetic variation on this chromosome may exert phenotypic effects and thus be visible to selection more strongly than for autosomes (Jablonka 2004). Moreover, to the extent that most adaptive variants are lost early in their allelic lives because drift is stronger than selection, the X may be more likely than autosomes to fix beneficial genes as evolutionary change proceeds (Reeve and Shellman-Reeve 1997; Graves et al. 2006; Vicoso and Charlesworth 2009; see also Hvilsom et al. 2012).

The X is also expected to harbor a preponderance of genes related to sex and reproduction, given that its different ploidy in the two sexes serves as a substrate for sex-specific phenotypic effects (Skuse 2006a,b; Crespi 2008). By these predictions, the X is uniquely "powerful" as regards generation of variation and strength of selection, the two main drivers of evolutionary change, with an emphasis on sexual and reproductive phenotypes.

Social Evolution Theory

From social-evolutionary theory, gene expression on the X is expected to favor maternal and matrilineal (inherited along female lines) interests owing to this chromosome's increased selective time spent in female bodies compared with males', and its inheritance from females twice as often as from males (Haig 2006; Frank and Crespi 2011). As such, the X may be expected to accumulate genes specialized to benefit females and mothers, and genes with sexually antagonistic effects that benefit females and mothers but also impose costs (that do not overmatch such benefits, from an inclusive fitness standpoint) on males, fathers, and offspring (Rice et al. 2010). By this body of theory, X expression should evolve to favor female and matrilineal interests (though these may sometimes differ) as regards reproduction and its socially mediated determinants.

Haplodiploidy, and by extension X linkage, is also predicted to favor the evolution of eusociality under some models via synergistic interactions with monogamy (Fromhage and Kokko 2011). This effect may be salient to humans given that increased paternal investment and a relatively monogamous mating system have evolved along the human lineage, but robust tests of such theory are challenging. More generally, socially or genetically monogamous mating systems appear to be associated with the evolution of extramaternal care among both humans and social insects (Boomsma 2009; Gardner et al. 2012; Henrich et al. 2012; Lukas and Clutton-Brock 2012), although in eusocial insects, male extramaternal care is largely restricted to the haplodiploid gall thrips (Crespi et al. 2004) and diploid termites (Bignell et al. 2011).

X Expression and Effects

How well are these predictions from theory met? From studies of tissue expression patterns and gene functions, the X chromosome clearly harbors a disproportionate preponderance of genes involved in reproduction and cognition (including so-called intellectual-disability risk genes) and genes expressed in ovary, placenta, and brain, with especially high expression of X-linked genes in the brain (Zechner et al. 2001; Vallender and Lahn 2004; Vallender et al. 2005; Graves et al. 2006; Nguyen and Disteche 2006). Offspring-expressed genes that reduce demands on mothers also appear to be concentrated on the X (Haig 2006), as do genes for prosocial behavior and verbal skills (Loat et al. 2004). The human evolutionary trajectory towards shorter interbirth intervals may also reflect maternal and female interests relative to interests of offspring (Haig and Wharton 2003; Crespi 2011), although its genetic bases remain to be investigated.

Large-scale gains and losses of X chromosome material in humans manifest most prominently in Turner syndrome among females (XO, or partial deletion of the Xp chromosome arm) and Klinefelter syndrome among males (usually XXY). Females with Turner syndrome exhibit selective deficits in social behavior (which is normally better-developed in females than males) as well as a diverse set of other male-biased physical and cognitive phenotypes (Crespi 2008). Klinefelter syndrome also engenders social abnormalities, but they manifest as high rates of schizophrenia and related conditions in adulthood and relatively poor verbal skills (Crespi et al. 2009); as infants, they have been described as “easy” babies, and as children, they are notably shy and reserved (Schoenstadt 2006). These findings generally corroborate important roles of X-linked genes in social-behavioral and other cognitive traits, as well as reproduction.

Finally, X-chromosomal genes show strong, differential effects on risk and expression of premature ovarian failure (POF) (Cordts et al. 2011; Jiao et al. 2012), defined clinically as loss of ovarian function at an early age (40 years or younger) owing to loss or depletion of oocytes (Skillern and Rajkovic 2008; Reddy et al. 2009; Persani et al. 2010). Premature ovarian failure represents the extreme of continuous age-based variation in ovarian function, with normality being represented by menopause at around age 50 (Reddy et al. 2009; He et al. 2010; Persani et al. 2010). As such, many or most cases of POF represent “pathologically” early menopause. Like age at menopause, POF is highly heritable; moreover, some POF genes and pathways are also implicated in menopause age within the normal range, and with aging itself (Monget et al. 2012; Qin et al. 2012; Semeiks and Grishin 2012). Turner syndrome shows very high rates of POF (Skillern and Rajkovic 2008; Persani et al. 2010), as does fragile X syndrome (caused by reduction or loss of function for the X-linked FMR1 gene; Sullivan et al. 2011) and heterozygous loss of function in the tumor-suppressor gene PTEN (Reddy et al. 2009). All three of these important causes of POF are also associated with autism spectrum disorders (Miles et al. 2003), suggesting pleiotropic molecular-developmental links between reproduction and social cognition.

The X in Human Extramaternal Care

The social-insect haplodiploidy hypothesis was originally set in a hymenopteran pedigree contextualized for helping of mother by sets of her offspring that are full sisters. Let us situate the X chromosome (and autosomes) in a patrilocal pedigree of humans (Fig. 2) and presume, based on the theory and evidence described above, that it influences social-behavioral-reproductive interactions that impact inclusive-fitness maximizing by the parties involved. With regard to extramaternal care, salient differences from diploidy include higher relatedness (3/4) among full sisters but lower relatedness of sisters to brothers (1/4) and higher relatedness (1/2) of paternal grandmothers to granddaughters but lower relatedness to grandsons (0).

High full-sister relatedness could, in theory and under some sex-allocation scenarios, facilitate daughters helping their mother by investing differentially in their sisters, as suggested originally for Hymenoptera. The efficacy of this scenario should be constrained, however, by the long, slow human childhood, such that females must presumably be at

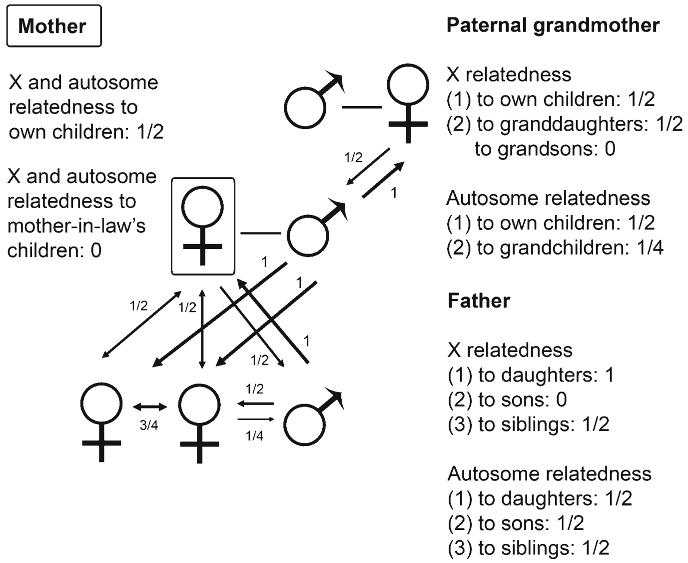

Fig. 2 X chromosomal relatedness, compared with autosomal relatedness, for a human three-generation pedigree with patrilocal residence. X chromosomal relatedness is either the same in both directions (*double-headed arrows*) or different according to direction (*single-headed arrows*). Autosomal first-degree relatedness (not shown on the pedigree itself) are all 1/2

least 8–10 years of age to provide much help to younger sisters—an age when helping would begin to more and more strongly impact their future personal reproduction. Moreover, the brood would need to consist of the correct sexes at appropriate age ranges, and daughters of all preadult ages would also still be competing among themselves for forms of maternal investment—reducing X-chromosome allele success without mechanisms to reduce local resource competition, as for autosomes (Johnstone and Cant 2010; Strassmann and Garrard 2011; Mace and Alvergne 2012). Although, for alleles on the X, daughters should thus be nicer to sisters than to brothers (see Rice et al. 2010), such supportive behavior would not be likely to translate into substantial extramaternal help.

Stronger positive effects of paternal grandmothers on granddaughters ($r=1/2$) than on grandsons ($r=0$) have been implicated by human comparative data (Fox et al. 2010; Wilder 2010), which provides convergent evidence supporting a role for X-chromosome effects on care, cooperation, and help in reproduction (see also Jamison et al. 2002; Tanskanen et al. 2011). These relatedness effects are embedded in a pedigree framework (Fig. 2) in which the focal female is unrelated to her mother-in-law but related by 1/2 to her own offspring (for a relatedness difference of 1/2). In such a family situation, mothers-in-law prefer to produce and care for their own daughters over their grandchildren, but to a lesser degree ($r=1/2$ compared with 1/4, for a relatedness difference of 1/4) (Cant and Johnstone 2008). These relatedness disparities represent strong variation in the magnitude of selection for helping versus reproducing, which should tend to tip the balance toward menopause and paternal-grandmother care (Cant and Johnstone 2008; Cant et al. 2009).

Because she is younger, a focal female (Fig. 2) will also be more fecund and produce children with fewer *de novo* mutations and better overall health (te Velde and Pearson 2002; Kong et al. 2012; Myrskylä and Fenelon 2012), and her mate should tend to prefer own offspring over additional (full or half) sibs, especially if his mother will assist with their care (Crespi 2009). Increased investment overall in daughters—by mothers and grandmothers—may also be favored by the X, given that under patrilocality females disperse, reducing local competition for reproductive resources among sisters (Strassmann and Garrard 2011; see also Haig 2006). This daughter-biased sex-investment ratio effect may additionally favor paternal-grandmother help—and make humans similar to some social insects in an additional vein (Cronin et al. 2013). Finally, Fig. 2 also shows that, curiously, only the focal female shows a lack of intragenomic X versus autosome conflict (owing to a lack of relatedness asymmetries), which should presumably benefit both these individuals and their descendant kin.

Among hymenopteran and thysanopteran insects, the hypothesized facilitating impacts of haplodiploidy on the evolution of eusociality are limited predominantly by selection for sex-allocation ratio balancing (Gardner et al. 2012). However, sex ratios with biases that are "split" between families can sustain local, more or less conditional female biases that may favor helping (Gardner et al. 2012). Among human families, split sex-investment ratios may arise naturally owing to variation in whether the paternal (or other) grandmother is alive and present. Moreover, granddaughters may differentially seek out, and benefit from, paternal grandmaternal care because of their high relatedness to these potential helpers for the X chromosome and the more general, relatively pronounced benefits from transmission of cultural information from especially old to especially young females. Rice et al. (2010) describe and analyze recent evidence for increased care devoted to granddaughters compared with grandsons by both paternal and maternal grandmothers, and Holden et al. (2003) show how daughter-biased investment by parents and grandparents can favor the evolution of matrilinial inheritance patterns.

The haplodiploidy hypothesis for human extramaternal care is meant less as an overarching driver for the evolution of grandmaternal help than as a synergistic or auxiliary factor, which may be important in getting this form of care started and in structuring patterns of care among populations, societies, and extended families. Moreover, despite the extraordinary evolutionary powers vested in the X, it still competes with a powerful autosomal cabal. Further analysis of this genetic facet of insectan apes requires inclusive-fitness modeling and collection of anthropological data targeting the key assumptions and predictions.

The Essential Difference

I have focused so far on convergent similarities of social insects and humans with regard to morphology, ecology, life history, behavior, and genetic relatedness. These convergences are notable but must be considered in the context of a fundamental difference: the general absence in humans of reproductive division of labor (castes). Unlike social-insect females, human females typically reproduce, barring early death or disease. Among other animals, the evolution of reproductive division of labor involving alternative, exclusive life-history trajectories is determined by the benefits and costs of reproductive suppression (by dominant reproductives) and the benefits and costs of being suppressed and self-suppressing (among subordinate helpers) in the context of relatedness, ability to dominate, and especially the costs to dominants of subordinate reproduction (Clutton-Brock et al. 2010). These costs and benefits accrue to both individuals and their social group—to the extent that group success mediates individual inclusive fitness, as it certainly does in humans and social insects.

How and why has human evolution avoided a eusocial system of dystopian reproductive castes, or cooperative breeding, among fertile-age females? The simplest hypothesis is that benefits from lifelong female helping, in terms of additional offspring produced by relatives, are too low to overcome the large personal reproductive costs. Such benefits are low, in turn, mainly owing to severe limitations on increases to female fecundity, which follow inevitably from the high energetic costs of producing large, and large-brained, offspring (Cant and Johnstone 1999; Isler and van Schaik 2012). Augmentation effects, whereby mothers as well as social groups increase fitness from larger group sizes (at least to some point; Quinlan and Flinn 2005) would also favor reproduction by all reproductively capable females (Fig. 1).

Alternatively, what about decreases to fecundity falling differentially on socially subordinate females (Nichols et al. 2012)? Under relatively strong ecological constraints, which presumably have not been unusual during human evolution, energy available to a human group may fall below requirements for maintaining all reproductive-age females at energetic levels required for sustaining pregnancy and lactation. In such circumstances, socially dominant females should, to the extent they can, tend to more or less monopolize reproductive resources and breed, while less-dominant females may still contribute to group, family, and personal benefit but forgo reproduction via amenorrhea or high rates of early miscarriage, until energetic conditions improve. Lahdenperä et al. (2012) indeed suggest, based on data from preindustrial Finns and an inclusive fitness model, that ecological resource scarcity has mediated the evolution of menopause, in the context of mothers competing with mothers-in-law.

This social-ecological system, which represents a form of cooperative breeding but with relatively low reproductive skew, is characteristic of banded mongooses (Bell et al. 2012) and asexual *Pristomyrmex* ants (where it has been invaded by less-helpful cheaters; Dobata et al. 2009)—is it also found among hunter-gatherer humans? Do the unique human-female propensities to delay first reproduction, sequester gluteofemoral fat, advertise fertility, and minimize daily energy invested in pregnancy and lactation (Ellison 2003; Leonetti and Chabot-Hanowell 2011) follow from such considerations? And might such highly facultative, ecologically driven cooperative breeding provide group-level benefits by maximizing overall offspring production across highly temporally variable levels of resources? By contrast, an egalitarian, non-cooperatively-breeding "solution," which may be more favored by most males in the group and better sustain groupwide cooperation, would involve more equal allocation to females of reproductive resources but result in increased mean and variance for offspring and mother mortality. Data salient to testing these hypotheses, which determine the degree to which humans resemble cooperatively breeding and eusocial insects as regards reproductive division of labor, presumably exist in the anthropological literature, or await collection.

Insectan Human Nature

The main goal of this paper has been to motivate consideration of human social-reproductive phenotypes in the light of insect cooperative breeding and eusociality. Three primary implications ensue.

First, the broad swath of human convergences with social insects described here compels the inference that common selective pressures have driven human and social-insect evolution. As such, explanatory frameworks and theory can usefully be transferred from one domain and research tradition to the other. The worldwide ecological and demographic "success" of both humans and social insects also appears to follow from comparable social and reproductive adaptations, although in humans the behavioral components of such traits are, of course, much more facultative and sophisticated. Considering human hunter-gatherer groups as "colonies" (e.g., Kramer and Ellison 2010) should lead to additional comparative insights into both human and social-insect evolution.

Second, development of a "haplodiploidy hypothesis" for human social cooperation and its logical consequences leads to novel predictions concerning the potential role of the X chromosome in the evolution of human extramaternal care. This hypothesis also draws needed attention to genetically based proximate mechanisms for the evolution of female reproduction, menopause, long human lifespans, and human social cognition and behavior, which should dovetail with ultimate causes as well as directing data collection along promising new paths.

Finally, conceptualizing humans as insectan apes further highlights the tremendous diversity among human groups with regard to ecological and social traits that impact upon local forms of extramaternal care (Valeggia 2009; Kramer 2007, 2010; Sear and

Mace 2008; Strassmann 2011). Such variation parallels the substantial sociodiversity among cooperatively breeding and eusocial insects and implies that understanding human extramaternal care systems requires linking of ecology, demography, and sociality with female reproductive behavior strictly on a population-by-population basis. How and why humans and social insects originally evolved extramaternal care remains a deeply challenging question, but analyses of convergence provide important clues concerning the selective underpinnings of the extraordinary results.

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