

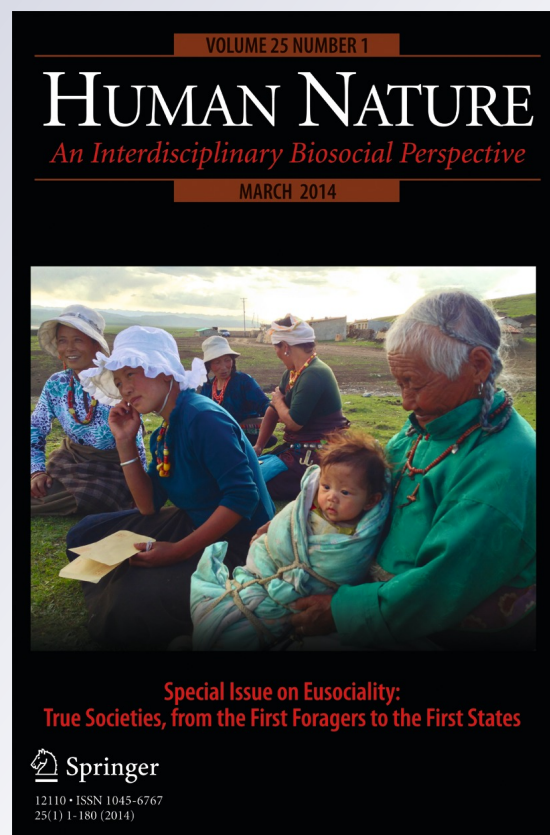
Eusociality: From the First Foragers to the First States

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Eusociality: From the First Foragers to the First States

Introduction to the Special Issue

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Abstract People have always been social. Ethnographic evidence suggests that transfers of food and labor are common among contemporary hunter-gatherers, and they probably were common in Paleolithic groups. Archaeological evidence suggests that cooperative breeding went up as we settled down: as territory defenders became more successful breeders, their helpers' fertility would have been delayed or depressed. And written evidence from the Neolithic suggests that the first civilizations were often eusocial; emperors fathered hundreds of children, who were provided for and protected by workers in sterile castes. Papers in this issue of *Human Nature* look at helpers and workers across the eusociality continuum—from hardworking grandmothers and grandfathers, to celibate sisters and brothers, to castrated civil servants—from the first foragers to the first states.

Keywords Eusociality · Cooperative breeding · Human evolution · Reproductive variance

Most parents care for their own young, but some parents get help. In a variety of arthropods, in roughly 9% of bird species, and in at least 3% of all mammals, dependents are fed and protected by alloparents—that is, by animals who put off or give up on raising their own young in order to raise other group members' sons and daughters (Hrdy 2009; Wilson 1975). Incurring that cost, in part, defines *eusocial*, or “truly social,” groups.

In any species—from arthropods to birds to mammals—wherever good habitats are scarce, animals are reluctant to disperse. Instead they stay in a territory and help others to reproduce (Emlen 1982, 1995; Vehrencamp 1983). Where ecological constraints are relatively low, direct reproduction is often delayed, and nonbreeders become helpers-at-the-nest (Brown 1987; Skutch 1935). And where ecological constraints are relatively high, direct reproduction is denied, and nonbreeders become parts of a sterile caste (Batra 1966; Wilson 1971).

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People have always been social. Sometime toward the end of the 7–8 Ma since our lineage split off from a last common ancestor (Langergraber et al. 2012), our life histories diverged from other apes' in several ways (Smith 2013). Hunter-gatherers give birth after an interval of just over 3 years, roughly half as long as the almost-6-year interval in wild chimpanzees (Alvarez 2000; Thompson et al. 2007). And though most men, women, and chimps stop reproducing by around age 45, some hunter-gatherers become fathers at age 70 and beyond (Gurven and Kaplan 2007; Kaplan et al. 2010; Tuljapurkar, Puleston and Gurven 2007). Our interbirth intervals became shorter, and our lifespans became longer—as recently as over the past few hundred thousand years (Austin et al. 2013; Lee 2012).

Both trends would have been facilitated by alloparents. Children in contemporary natural-fertility, natural-mortality societies usually have a number of caretakers. Mothers on average provide about half of direct childcare, and less than half of all calories, so most children get contributions from their same-generation, parent-generation, or grandparent-generation kin (reviews in Kaplan et al. 2000; Kramer 2010; Sear and Mace 2008; Strassmann and Garrard 2011). Sometimes—*unlike* most other social species—*H sapiens* helps down the generations: grandmothers, in particular, help their children to raise babies (Hawkes et al. 1998; Kim et al. 2012). And other times—*like* most other social species—*H sapiens* helps up the generations: daughters, in particular, help their parents to reproduce (Kramer 2011; Turke 1988). Children are fed, foraged for, carried, and cared for by their siblings and grandmothers.

Both kinds of cooperation would have increased with sedentism. These days, most hunter-gatherers live on the margins. They forage in the deserts of Africa and Australia, in equatorial forests, in parts of the Arctic. And foragers in more marginal habitats—away from coastal strips and inland waterways, on territories where subsistence is spotty and climates vary—are more mobile than other foragers (Keeley 1988; Keen 2006; Kelly 2013; cf. Hölldobler and Wilson 2009: chap. 1). As Richard Lee noted, famously, about the Kalahari Desert Ju/'hoansi: "People get on each other's nerves. . . . Conflict usually results in one or both parties splitting off to seek greener pastures. . . . Foragers have a great deal of latitude to vote with their feet" (Lee 1979:367). And egalitarianism follows. Contemporary foragers seldom have more than a dozen children, and their reproductive variance is often restricted to single digits (Betzig 2012). Most people become mothers and fathers.

In the Pleistocene, their habitats would have been better. And wherever their resources were available year round, and rich, foragers would have been apt to stay put. There is some archaeological evidence of sedentism for almost as long as we've been human. Post holes and stone hearths from the Middle Stone Age in Africa are suggestive of a more settled life (Barham and Mitchell 2008; McBrearty and Brooks 2000), and there are burials, with associated grave goods, from around 100,000 years ago in the Levant (Bar-Yosef 2002; Mellars et al. 2007). Staying put should have facilitated transfers both up and down generations: grandparents and older siblings would have been more likely to live in the same area (Hill et al. 2011), and to pass on material wealth (Borgerhoff Mulder et al. 2009). And inequality would have increased. As in contemporary semi-sedentary societies, reproductive variance would have risen to double digits, and some fathers would have had dozens of children (Betzig 2012). More people would have been childless—but willing to help.

After the Neolithic Revolution, we settled into permanent groups. There were houses with stone foundations, and communally built walls, towers, and other forms of public architecture (Childe 1936); by as early as 10,000 years ago, the first written records and accounts were being kept (Schmandt-Besserat 1996). In some of the first histories, kings put up bronze and cedar palaces that held up to a thousand women, and fathered as many as 70 sons (1 Kings 11:3, 2 Kings 10:1, 2 Chronicles 11:21; Halpern 1988). Across ancient civilizations, some men had hundreds of children, and many helpers and workers were facultatively or obligately sterile as a result (Betzig 2012).

From the beginning of human evolution to the beginning of history, *H. sapiens* has spanned the eusociality continuum (see Sherman et al. 1995; cf. Crespi 2005). At the low end of the continuum, we've been cooperative breeders. Helpers have included our sisters and brothers, who occasionally put off starting their own families in order to help their parents reproduce. And at the high end of the continuum, we've been eusocial, or "truly" social. Sterile workers—from postreproductive grandmothers in the first foraging societies (Foster and Ratneiks 2005) to castrated civil servants in the first states (Betzig 2013)—have fed and defended other people's daughters and sons.

Papers in this issue of *Human Nature* look at sociality across the human spectrum—from help offered by all other group members toward the children of 20- to 35-year-old "queens" (Crespi 2014), to help from children's sisters or brothers (Kramer 2014), to help from their grandmothers or grandfathers (Hawkes 2014), to help from their unmarried, or celibate, uncles and aunts (Ji et al. 2014), to help from the hundreds of thousands of eunuchs that, across ancient civilizations, made up sterile castes (Betzig 2014).

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