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Nonmaternal care: a half-century of research

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ABSTRACT

This paper aims to serve three purposes, providing: 1. a half-century retrospective on research in on nonmaternal care of the young, with an emphasis on key advances; 2. a commentary on the research papers in this special issue on nonmaternal care; and 3. a summary of nonmaternal care among hunting-and-gathering cultures—representing the human Environments of Evolutionary Adaptedness (EEAs)—in the broader context of human evolution. While the research being done now is excellent and uses appropriate evolutionary theory and cutting-edge methods ranging across behavioral biology (field and laboratory observational studies, controlled experiments, careful behavioral measures, energetics, neurotransmitter function, neuroendocrinology, neuroimaging, and genetics, among others), it is difficult to make generalizations beyond stating that nonmaternal care is a multifaceted evolved function in some species, which usually contributes to the reproductive success of the mother and the survival of the young. Why it evolved when and where it did is not an impenetrable question, but needs further research. The same is true for the mechanistic biology of various types of allomaternal care. I conclude with some observations on historical changes in non-maternal care since the hunting-gathering era, including in industrial and postindustrial cultures. It is evident that in the human species at least, many arrangements for care of the young are possible and adaptive.

1. Introduction

It is my happy but challenging task to comment on the papers collected in this special issue of *Physiology and Behavior* devoted to nonmaternal care of the young, also known as allomaternal care, or allocare for short. (Some authors object to this abbreviation on etymological grounds, but it seems useful and acceptable to me.) This commentary will of course not permit me to do justice to all 16 of these fine studies, which focus variously on voles, mole rats, meerkats, cooperatively breeding carnivores, lemurs, callitrichids, colobines, gorillas, bonobos, and humans—in Poland, Israel, the Philippines, Vanuatu, among the Tsimane, Pume, Maya, and in gay and heterosexual fathers in the U.S.

All are rich and precise in their measurement and analysis of behavior. Some look at hormones as possible causes or effects of nonmaternal care, others at brain activity. Some are based in wild populations, others in laboratory settings, some in traditional, some in modern cultures. There are also comparative papers exploring the endocrinology of alloparental care broadly across animal taxa and on the role such care may have played in primate brain evolution. But before turning to them, I will try to offer some historical perspective—one which is inevitably also personal. After commenting on them, I will briefly summarize some findings in my own field of hunter-gatherer childhood, in evolutionary and cross-cultural perspective.

2. A partly personal history

I can date my interest in the evolution of behavior, and of care of the young in particular, to 1965, when a professor of mine at Brooklyn College handed me a copy of Irven DeVore's just-published collection, *Primate Behavior: Field Studies of Monkeys and Apes* [7]. It tried to fulfill the promise of its subtitle by bringing together most of the people engaged in such studies, ranging widely over ecology and behavior. No book at that time could have focused a collection on a “narrow” topic like nonmaternal care.

There was another classic collection, *Behavior and Evolution,* edited by Anne Roe and G.G. Simpson, that pointed the way toward considering behavior as an appropriate subject for evolutionary biology [57]. Both these books helped introduce European ethology to Americans, who typically studied behavior without evolutionary perspectives or models, and with a focus on laboratory learning in only a few species. Studies of brain activity were crude, neither hormones nor genes were measurable in field settings, and any application of biology to behavior was offensive to many academics. Mentioning nonhuman and human behavior in the same paragraph could endanger your career.

But the world was about to change. “Gene” was still a four-letter word, and the specter of Social Darwinism, eugenics, and racism was often raised by it. But models such as kin selection [11], reciprocal altruism [64], and a vigorous revival of Darwinian sexual selection [63]

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were about to make a large impact on anthropology, ecology, ethology, and psychology in a combination of approaches variously referred to as neo-Darwinian theory, behavioral ecology, sociobiology, and evolutionary psychology [6,30,70] Meanwhile, hunter-gatherer studies were reestablished on a new foundation, with a strong influence of ecology, archeology, and evolution rather than being based simply on traditional ethnography [41,42].

The papers collected here assume all that and much more, as they should. It is sometimes said that one of the main reasons for the progress of science is the arrogance of graduate students, and their tendency to care about the future, not the past; but my role here is to remind us of the past, so we can better appreciate the present. Here are some things these authors and you, their readers, might take for granted, but we never would have then:

1. Genetic paternity and other relatedness determinations, as well as hormone analysis, are now part of the state of the art; biobehavioral and biocultural models are ubiquitous;
2. Long-term longitudinal studies are increasingly the norm, with teams of fieldworkers continuously monitoring known individuals in known wild populations;
3. Kin selection and other neodarwinian models are routinely accepted as valuable heuristic devices, even when they are not confirmed;
4. Very large numbers of excellent people are working on these problems, and most of them are women;
5. Everyone in this and related fields takes evolution as given—the context without which, to paraphrase Theodosius Dobzhansky, nothing in biology or behavior makes sense.

It was evident half a century ago that maternal care would be logical grist for the mills of physiological psychology, comparative ethology, and evolutionary theory, but nonmaternal care was much less common in nature and much less studied. Still, some of us were starting to pay attention to it, not just in field work but in broad comparative perspectives.

Jane Lancaster looked at “play-mothering,” suggesting benefits for the infant, the mother, and the juvenile providing care [40]. Sarah Hrdy published a wide-ranging review of allomaternal “care and exploitation”, making the vitally important point that some kinds of nonmaternal care benefit the “carer” more than the infant or juvenile; the latter may even be harmed [1]. James McKenna, in comprehensive comparative reviews, considered allocare as well as maternal care [49,50]. I wrote on relations among infants and juveniles, including care, with a focus on San hunter-gatherers but in a comparative perspective [33]. Others focused on nonmaternal care more generally among Pygmy hunter-gatherers [19,66].

The grip of psychoanalytic theory, with its emphasis on the mother-infant bond as the source of all other relationships, was waning. Konrad Lorenz had long since defined different, largely independent, categories of relationships among birds [43], and Harry Harlow did something similar for monkeys [12,15]. In fact, he and his colleagues showed that peers could be as or more important than mothers for normal social development, and that slightly younger juveniles could uniquely promote recovery from maternal deprivation [13,14]. No one knew much about the neurobiology of relationships, but many of us began to think that different kinds of relationships probably had overlapping but separate circuitry rather than all being derived from one original relationship—partly because they evolved for different purposes.

In more recent decades, a leading investigator of cooperative breeding in birds, Stephen Emlen, developed an evolutionary theory also applicable to humans, about the conditions in which extended families will and will not be stable [9]. Kristen Hawkes, beginning with her work on Hadza hunter-gatherers, emphasized the role of grandmothers as alloparents [17], while Barry Hewlett [19,20], Kim Hill and Magdalena Hurtado emphasized the role of adult males [21], and Karen Kramer the role of older siblings and other children [36,37]. Probably the most comprehensive model of cooperative breeding in human evolution was that of Sarah Hrdy in her classic, *Mothers and Others* [24]. Meanwhile, on the neurobiological side, Thomas Insel, Larry Young, James Rilling, and others made major contributions to our understanding of how the brain generates paternal behavior in species from prairie voles to humans [25,56].

3. Studies in this special issue

Four or five decades after serious interest in non-maternal care began, the studies in this issue confirm its importance as distinct from maternal care, and underscore its adaptive value and partial physiological independence. As a very broad overview, here are the top ten generalizations I have gotten out of this excellent collection:

1. Paternal care is common in fishes and extremely common in birds, but is quite unusual in mammals.
2. Primates have more allomaternal care, and more male care in particular, than mammals generally.
3. Paternal involvement is associated with low testosterone (T) in both non-human and human primates, with at least one exception—higher T is associated with fathering in red-bellied lemurs; this exception should be studied further.
4. Contrary to expectations, genetic paternity does not seem to be a consistent predictor of male involvement.
5. Variations within species are clearly important and need to be studied further, including among humans; controlled comparisons, such as that between Tsimane and Vanuatu fathers, could prove especially valuable;
6. Maternal primacy in the care of the very young remains true except in some humans; coupled gay fathers have a particularly important role to play in research, since they are a sort of “pure culture” of fathering.
7. The special role of the young in allocare may be important in understanding the evolution of the long human childhood and the short human inter-birth interval (compared to apes), so crucial to our success.
8. The same is true of the special role of grandmothers.
9. Studying oxytocin (OT) is a challenging but very important future path; studies of vasopressin (VP) will also be important. Unfortunately peripheral measures of these may not reflect very well what they are doing in the brain. Measuring genotypic polymorphisms in OT and VP receptors and their promoters is promising.
10. Brain activation studies are increasingly defining social circuitry, and nonmaternal caregivers may have activation of overlapping but to some extent distinct subsets of the general social circuitry

Let me now briefly comment on the individual studies.

Wang and colleagues focus on paternal behavior in mandarin voles, a socially monogamous species of the genus (*Microtus*), which has taught us so much about the physiology of parenting. Compared to first-time fathers, experienced ones showed more active paternal behavior such as licking, retrievals and nest building. Knowing from studies of maternal behavior that the nucleus accumbens and medial amygdala are important, the group looked at OT and dopamine (type 2) receptors in those structures. New fathers had more OT receptors but fewer D2 receptors in the accumbens only. We might speculate that their behavior needed more of a boost but that the fathering experience was less rewarding. OT and D2 receptors in both brain locations changed in interesting ways as pups matured. All in all, there was a “dynamic interplay between the fathering experiences and brain biology” (p. 000).

Together with their relatives the naked mole-rats, Damaraland mole-rats are of almost unique interest among mammals because they are inbred and therefore “eusocial”—highly cooperative, almost like bees, with some individuals in a colony suppressing breeding to be