Behavioural Ecology in Traditional Societies

Monique Borgerhoff Mulder

Can models from behavioural ecology explain cultural diversity in human populations? Studies of variation in reproductive and productive behaviour, both within and between traditional societies, are beginning to show that specific predictions from sexual selection and optimal foraging theory can be developed and tested with human data. Greatest success has been in the study of foraging; whereas attempts to understand patterns of marriage and parental investment have been most convincing in those cases where behaviour is related to specific ecological and social conditions. The aim of human behavioural ecologists in the future will be to determine the constraints that the dual goals of reproduction and production place on individuals.

Over the last fifteen years, an exciting new field known variously as 'human sociobiology', 'evolutionary biological anthropology' and 'human behavioural ecology' has been growing fast. Under its first name, human sociobiology has often been equated with the explicit genetically based model of kin selection; but such characterization is incorrect. This new field is concerned with much more than the study of nepotism in traditional populations. In essence, it aims to develop and test specific models that account for behavioural variability observed within and between different human populations, on the assumption that people learn to adopt different behavioural patterns in different ecological and social contexts such that their behaviour maximizes their inclusive fitness. From the outset, then, concepts from optimal foraging theory and sexual selection have played as critical a role in developing hypotheses as have those from the theory of kin selection; specifically, the study of life history variation, reciprocal altruism, sex-biased inheritance, co-operative breeding and evolutionary stable strategy are emerging as key foci of interest.

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In this review, I document the growth and scope of behavioural ecology in its application to human behaviour and suggest where the future of this exciting new approach to the study of human culture may lie. I focus exclusively on research conducted in traditional and historical populations in relatively underdeveloped parts of the world, since studies of adaptation in modern industrial contexts entail a number of assumptions that are difficult to meet[1]. I concentrate on sound empirical research rather than dwell on weaker speculative work, for which detailed conceptual and methodological critiques have already appeared[2,3].

The rate at which empirical papers have appeared is shown in Fig. 1; they now amount to 163 publications. Two highly influential volumes appearing in 1979 and 1981, by Chagnon and Irons[4] and Winterhalder and Smith[5] respectively, sparked off an interest among anthropologists in the relevance of natural selection to the study of human behaviour. Among these studies a principal distinction can be drawn between studies of reproduction and those of foraging (Table 1), with the former growing primarily from evolutionary genetics and the latter from evolutionary ecology[6]. Although studies of reproduction are more numerous (113) than those of foraging (50), both fields have been central to the growth of human behavioural ecology. If analyses of archaeological and paleontological material were included, studies of foraging (and related issues of spatial organization and food sharing) would equal those of reproduction[7,8].

Reproductive competition in men and women

Although many different areas of human reproductive behaviour have been examined from an evolutionary perspective, intra-male competition has been most studied (Table 1). Individual differences in wealth, power, religious position, hunting skill, violence and conformity have all been shown to con-

tribute to high male reproductive success in different societies, largely through enhanced access to mates[9-11]. In my own work with Kipsigis, agro-pastoralists of Kenya, men are shown to be concerned with not only the quantity[12] but also the quality of their mates, in that they make particularly high marriage payments for brides of high reproductive value, as measured by a woman's age at menarche[13]. Intense intra-male competition is now well documented and has generated interesting predictions about sex-specific inheritance in historical[14,15] and traditional societies[16].

Reproductive competition among women has been studied less, but intense conflict can occur. For example, in rural Trinidad, Flinn finds that women in households in which two reproductive-aged women (generally mother and daughter) co-reside have lower fertility than women in households containing single reproductive females; some evidence suggests this may be linked to high agonistic interactions among women within households[17]. Evidence that labour stress may limit women's reproduction comes from Turke's study on Ifaluk, a Micronesian atoll. There, as in many traditional societies, daughters help their mothers considerably in child care, with the result that mothers who produce *daughters* first enjoy longer and more successful reproductive careers than those who produce *sons* first[18], suggesting an element of 'cooperative breeding'[19]. In other societies, such as the Kipsigis, access to resources is more critical to successful reproduction than is access to labour[20]; I found that women appear to choose their spouses with respect to the man's wealth rather than his current marital status[21], as the polygyny threshold model would predict[22] (Fig. 2).

Reproductive strategy and variability in human breeding systems

A salient question to arise from empirical studies such as these is what accounts for the ethnographic diversity, only hinted at here, in breeding patterns. For example, what are the direct ecological correlates of the intensity of male competition? In 1979 Dickemann pro-

posed that extreme environmental instability (drought, famine, war, plague and all the social upheavals thereby engendered) is associated with high levels of polygyny[23]. There has been no systematic test of this hypothesis yet, although there is a significant relationship between unpredictability of rainfall and the cross-cultural occurrence of polygyny (B. Low, unpublished). Betzig suggests that large harems may be particularly prevalent in populations that are circumscribed by geographic or social barriers (mountains or warring enemies), because men who fail to find wives are unable to leave physically and start a family elsewhere[10]; why subordinate males tolerate such reproductive inequality remains unanswered. To date, however, the strongest support for the importance of ecological constraints on human breeding systems is Crook and Crook's description of how polyandry may be directly contingent on the scarcity of cultivable land in the arid Himalayan valleys of Ladakh; the only option for a second son is to share his brother's wife[24].

Evolutionary biological anthropologists more commonly stress the *social* rather than the *ecological* correlates of polygyny[25]. For example, the number of relatives a man can call his allies, his manipulative skills and his reputation can be critical in successful fights or negotiations over women, as Chagnon carefully describes for the largely horticultural Yanomamo Indians of Venezuela[26]. Emphasis on the importance of competition with conspecifics should not, however, detract attention from the role of ecological factors in structuring breeding systems. Indeed it is perhaps only the richness of the Yanomamo environment that enables a man to support large groups of co-resident kin with whom to raid and fight for women[27]. Furthermore, in more labour-intensive productive systems, as among the K'echi Indian agriculturalists of southern Belize, Berte attributes the positive association between a man's reproductive success and the number of his non-descendant kin in the local community to his success in swidden cultivation of maize, which is

itself shown to be directly dependent on cooperative labour exchange among kin[28]. In short, while there are no systematic analyses of the incidence of polygyny across human cultures, resource distributions that enable some men to monopolize resources and/or labour for their own reproductive benefit are likely to be a key factor as in many other species[29].

Foraging strategy

Behavioural ecological anthropologists have begun to investigate diet breadth and group size, primarily among hunter-trapper-fishers, hunter-gatherers and horticulturalists of the Americas. They adopt the models and methods of optimal foraging theorists, working from the assumption that humans select among behavioural alternatives so as to maximize net energy capture per unit time, measuring the costs and benefits in time and calories respectively[30]. Efficiency in energy capture is assumed to correlate with fitness[31], as in all optimal foraging studies, although there has been some debate over whether humans are energy maximizers or time minimizers.

Foraging and optimal diet breadth

Which resources should an efficient forager harvest? The optimal diet breadth model states that, if resources are randomly encountered, an item will be taken only if the net energy return per unit handling time is greater than the average return rate, including search time, of all prey types of higher rank[32]. For the Ache, Hawkes and her collaborators show that resource choice can be predicted from this model: all sixteen food resources exploited by men and women foragers during a four-
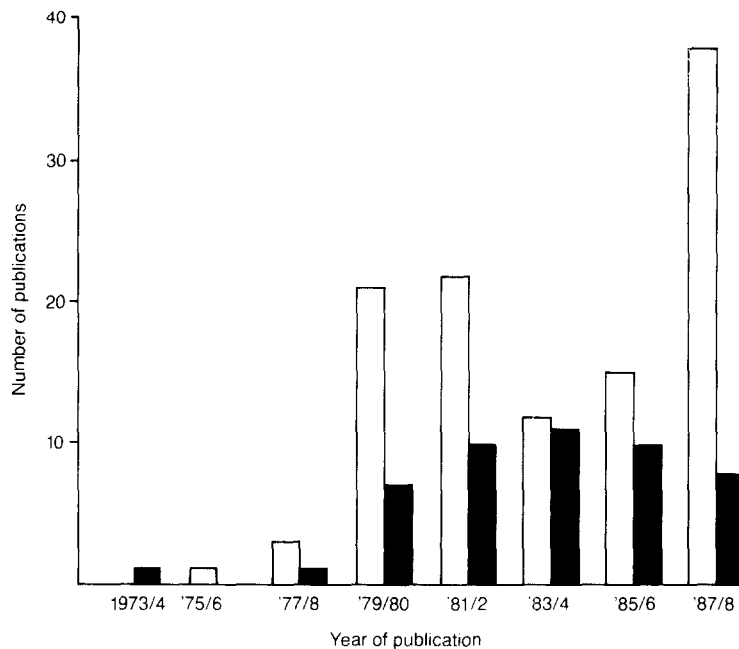

Fig. 1. Number of studies published in two year periods. White bars denote studies of reproduction, black bars studies of foraging. Data include all the empirical, quantitative studies I could find that explicitly address theories derived from evolutionary biological theory with data from traditional and historical societies in relatively underdeveloped regions. Review articles (such as this one) and authored books are omitted, unless containing new analyses of quantitative data. Articles with confirmed 1988 publication dates are included. Bibliography can be obtained from the author.

month period were characterized by higher returns after encounter than overall Ache foraging returns[33]. Diet breadth and patch size models, the latter not assuming a random distribution of prey, also predict the resources taken by the Alyawara Aborigines of Australia, including the recent exclusion of seeds from their diet[34].

Hames and Vickers examine how

Table 1. Studies by central topic

Topic	Number of Publications[a]
Reproductive strategy and mating systems	113
Male competition	36
Investment in offspring	27
Kin selection	15
Parental care	14
Life history studies	11
Female fitness determinants	5
Sexual dimorphism	5
Foraging studies	50
Diet breadth	33
Spatial organization and group size	12
Food sharing and reciprocity	5

[a]Sources of data as in Fig. 1.

Fig. 2. Does the polygyny threshold model apply to pastoralists of East Africa? Polygynously-married wives collecting water: the Tatog of Tanzania. *Photo by Monique Borgerhoff Mulder.*

the effects of hunting technology on diet breadth will depend on prey distributions, how they are hunted and the relative importance of search to pursuit time in hunting[35,36]. Anthropologists are now beginning to examine other factors associated with resource choice: sex differences in resource-gathering efficiency and opportunity costs[31,38], the costs of tool maintenance[34], the optimal strategies of others (K. Hawkes, unpublished), specific nutrient needs[31] and risk aversion (B. Winterhalder, unpublished). Issues still largely unsolved include the tabooing of certain game items and the distribution of hunting technology, such as blowpipes and bows in the Amazon.

game depletion and technology affect species' ranking, and hence what is taken[35]. Diet breadth increases in relation to settlement age among the Siona-Secoya In-

dians of Amazonian Equador, as the high-ranked species become scarce and difficult to hunt and hunters become less specialized; furthermore efficiency increases and diet breadth declines, as people hunt further from their settlements, as shown for the Siona-Secoya, the Yanomamo and their Ye'kwana neighbours[35]. Winterhalder shows how technological innovations that decrease search time constrict diet breadth: with snowmobiles, the boreal forest Cree Indians of northern Ontario can afford to ignore lower-ranked game and specialize on moose, beaver, hare and fish[36] (Fig. 3). Finally, guns that increase the pursuit efficiency of some Ache men, lead to lower-ranked species such as monkeys being disregarded[37], although not among the Yanomamo and Ye'kwana[35]. Clearly

Foraging, group size and settlement patterns

Why do humans invariably live in groups larger than the nuclear family? Behavioural ecologists are starting to determine the selective factors operating on group formation and size. Focusing on hunting, Smith's study of the Inuit Indians of Hudson Bay shows that observed pursuit groups in different types of hunts (e.g. goose, beluga whales, ptarmigan) are generally larger than that which would maximize *individual* returns and smaller than that which would maximize *group* returns[39]. Similarly, Ache hunters call for help after encountering monkeys and coatis, even though individual returns are greater when hunting these species alone[37]. Clearly, pursuit groups are not of optimal size, as measured by energy returns either to the individual or to the group. In an innovative attempt to tackle the unsolved question of optimal pursuit group size, Smith assesses some of the *social* constraints on pursuit group formation, such as relatedness, rules for sharing the kill and conflicts among 'members' and 'joiners' using Inuit data[6]. The importance of constraints on movement and information-sharing remain largely unexamined, as in other species.

Pursuit efficiency seems only to set the *lower* size limits of residential groupings. Blurton Jones[40] proposes one reason why food sharing groups may be larger than the optimal pursuit group size, in-
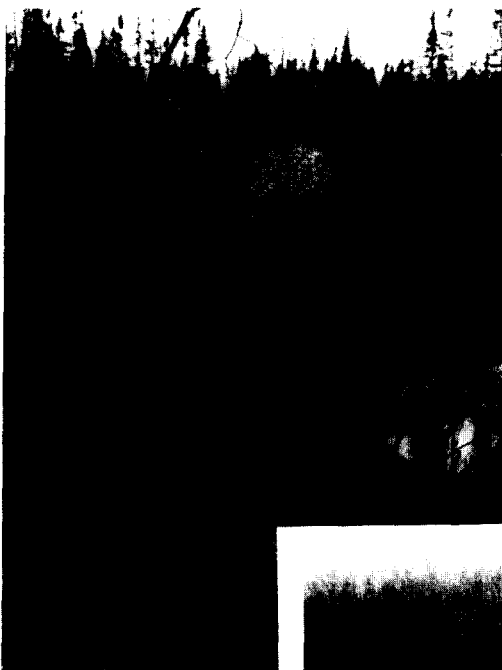

Fig. 3. Cree foragers in the Canadian subarctic use modern technology in the quest for food, but their hunting and tactics date from earlier periods and often match those predicted by foraging theory models. *Photos by Bruce Winterhalder.*

troducing the concept of 'tolerated theft': he suggests that the costs of continued defense of a food resource with a diminishing fitness return curve will far exceed the benefits, leading (under some conditions) to the formation of larger groups than required for efficient food acquisition. Physical defense may be another important factor: the largest Yanomamo villages are found in areas where there is most inter-village warfare[41].

Finally, in less bellicose societies, residential units may be maintained by the need for communal labour in seasonal or fluctuating environments and in economies of scale where individual efficiency is greater in a group than alone[42]. Although there are some exciting comparative studies of the effects of resource predictability and density on human patterns of settlement and exchange[43–45], testing models for the distribution of territoriality[46] and central place foraging[47], little is yet known of the determinants of the size and stability of human settlements. This is a question that deserves priority of investigation, given modern nations' interference with traditional land rights and the effects on subsistence, ranging and settlement.

Integrating studies of subsistence and reproduction

Suddenly a wealth of empirical evidence is pouring into a field once characterized as idle speculation and 'just-so' story telling. The future of behavioural ecology of traditional societies must lie in an integration of studies of reproduction and foraging[6,29,31]. Since the ultimate 'goal' of any organism is to maximize fitness, it becomes necessary in studies of foraging to determine the fitness consequences of energy capture. Similarly, studies of reproduction must assess the fitness gains associated with reproductive and social activities that compete with foraging for an individual's time.

Rather remarkably, studies in human behavioural ecology are at the forefront in investigating such trade-offs between production and reproduction, perhaps because with advanced technology humans are less critically energy-limited than many other species. As evolutionary biological anthropologists

recognize that variations in time allocated to different activities in different subsistence types probably reflect differences in *fitness benefits* and *opportunity costs* as much as in *net energy returns*, they are starting to examine the constraints of foraging (essentially food production) on reproduction (and vice versa) and how different trade-offs between these activities are reached. Thus, for example, Hawkes, Hill and Kaplan's finding that good Ache hunters hunt for *more* hours than do poor hunters and still consume significantly *less* of their own meat than do others seemed anomalous until the reproductive benefits (extramarital matings) of being a reliable meat provider were shown[48]. In a similar vein, Bailey argues that specialization in foraging for honey and meat among male Efe pygmies of the Ituri Forest in Zaire is primarily a strategy for forming important political liaisons with their agricultural Lese neighbours[49].

Trade-offs between foraging and reproduction have also been determined for women. Blurton Jones examines how the birth intervals of !Kung women, who carry their babies while gathering mongongo nuts over large daily ranges in the intense heat of the Kalahari, vary according to parity, family size and degree of dependence on gathered foods. A quantitative model shows that spacing births at 4-year intervals precisely reduces a woman's nut and baby load to that which will support the family without threatening women with thermal exhaustion[50]. Among the Ache, where foraging is less energetically demanding, women have shorter birth intervals (Fig. 4); furthermore, Ache women with dependent unweaned offspring can reduce their foraging effort compared with that of other women[38], perhaps because men supply nearly 90% of the calories eaten by the whole group[33,48]. Such studies of the ecology of reproduction and parental care should play a pivotal role in future studies of human behavioural adaptation, as suggested by Irons[51]. Clearly however, for human behavioural ecology to rival that of non-humans, many more studies are needed: this review was based on work conducted in just sixteen traditional societies.

Fig. 4. Ache woman forages with her child (Paraguay). Photo by Department of Anthropology, University of Utah.

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Projection Matrices In Population Biology

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Projection matrix models are widely used in population biology to project the present state of a population into the future, either as an attempt to forecast population dynamics, or as a way to evaluate life history hypotheses. These models are flexible and mathematically relatively easy. They have been applied to a broad range of plants and animals. The asymptotic properties of projection matrices have clearly defined biological interpretations, and the analysis of the effects of perturbations on these asymptotic properties offers new possibilities for comparative life history analysis. The connection between projection matrix models and the secondary theorem of natural selection opens life cycle phenomena to evolutionary interpretation.

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Projection matrix models are an increasingly popular tool for describing population dynamics. They have been applied to a wide array of demographic problems (vegetative propagation[1], predator–prey interactions[2], competition[3], two-sex populations[4], weed control[5], patch dynamics[6], bud dynamics on trees[7], density dependence[8]) for a variety of species ranging from mites[2] to whales[9]. Projection matrix models serve two main scientific purposes. First, they can be used in attempts to forecast population dynamics (e.g. of pest organisms[2,10]). Second, because properties of the model correspond to life history characteristics such as fitness and reproductive value, they can be used to evaluate the long term consequences of hypothetical changes in the life cycle. Our review focuses on the latter application.

The simplest projection matrix models are discrete, linear, time invariant functions that map the

state of a structured population from one time to the next. The transition into the next state is assumed to depend only on the current state of the population. The entries in population projection matrix contain all necessary dynamical information, summarizing the ways in which survival, growth, development and reproduction change the composition of the population from one time to the next. In matrix notation this can be expressed as a simple multiplication:

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t) \qquad (1)$$

Here $\mathbf{n}$ is a state vector whose elements are the numbers of individuals in each recognized category, and $\mathbf{A}$ is a square, non-negative matrix.

Part of the success of projection matrices is due to the flexibility of their mathematical formulation. One can choose almost any set of categories in which to classify individuals, any time step over which to evaluate transitions, and almost any complexity in transition pattern[11]. Data from which to estimate the parameters of the model are at least conceptually straight-