

- GELLNER, E. 1982. "Relativism and universals," in *Rationality and relativism*. Edited by M. Hollis and S. Lukes. London: Blackwell.
- GEORGESCU-ROEGEN, N. 1971. *The entropy law and the economic process*. Cambridge: Harvard University Press.
- GREGORY, C. 1982. *Gifts and commodities*. London and New York: Academic Press.
- JORION, P. 1986. Reprendre à zéro. *L'Homme* 26:305.
- LÉVI-STRAUSS, C. 1949. *Les structures élémentaires de la parenté*. Paris: Presses Universitaires de France.
- . 1955. *Tristes tropiques*. Paris: Plon.
- . 1958a (1945). "L'analyse structurale en linguistique et en anthropologie," in *Anthropologie structurale*. Paris: Plon.
- . 1958b (1945). "Le redoublement de la représentation dans les arts d l'Asie et de l'Amérique," in *Anthropologie structurale*. Paris: Plon.
- . 1958c (1955). "La structure des mythes," in *Anthropologie structurale*. Paris: Plon.
- . 1962. *La pensée sauvage*. Paris: Plon.
- . 1971. *L'homme nu*. Paris: Plon.
- . 1973a. "Réflexions sur l'atome de parenté," in *Anthropologie structurale deux*. Paris: Plon.
- . 1973b (1960). "Sens et usage de la notion de modèle," in *Anthropologie structurale deux*. Paris: Plon.
- . 1973c (1952). "Race et histoire," in *Anthropologie structurale deux*. Paris: Plon.
- . 1983 (1971). "Race et culture," in *Le regard éloigné*. Paris: Plon.
- . 1985. *La potière jalouse*. Paris: Plon.
- OSORIO DE ALMEIDA, M. 1988. *Hamiltonian systems: Chaos and quantization*. Cambridge: Cambridge University Press.
- PIAGET, J. 1970. *L'épistémologie génétique*. Paris: Presses Universitaires de France.
- PRIGOGINE, I., AND I. STENGERS. 1985. *Order out of chaos*. London: Fontana Paperbacks.
- . 1988. *Entre le temps et l'éternité*. Paris: Fayard.
- ROEMER, J. 1981. *Analytical foundations of Marxism*. Cambridge: Cambridge University Press.
- SHUBNIKOV, A. V., AND V. A. KOPTSIK. 1974. *Symmetry in science and art*. New York and London: Plenum Press.
- TURNER, T. 1990. On structure and entropy: Theoretical pastiche and the contradictions of "structuralism." *CURRENT ANTHROPOLOGY* 31:563-68.
- VAN FRAASSEN, B. C. 1989. *Laws and symmetry*. Oxford: Oxford University Press.
- WASHBURN, D. K., AND D. W. CROWE. 1988. *Symmetries of culture: Theory and practice of plane pattern analysis*. Seattle and London: University of Washington Press.
- WEIL, ANDRÉ. 1949. "Appendix mathématique," in *Les structures élémentaires de la parenté*, by C. Lévi-Strauss. Paris: Presses Universitaires de France.
- WEYL, H. 1946 (1939). *The classical groups*. Princeton: Princeton University Press.
- WIENER, N. 1961 (1948). 2d edition. *Cybernetics*. Cambridge: M.I.T. Press.

On Optimal Foraging Models and Subsistence Transitions¹

K. HAWKES AND J. O'CONNELL

Department of Anthropology, University of Utah,
Salt Lake City, Utah 84112, U.S.A. I IX 91

Layton, Foley, and Williams (CA 32:255-74) are right: "progress" doesn't explain transitions from hunting and

1. We thank Duncan Metcalfe for his good advice.

gathering to agriculture, but theory and models from behavioral ecology might. The "diet-breadth" model could be especially useful, but Layton et al. confuse key terms and important implications. We review the distinction between search and handling costs, discuss the implications for resource domestication and population growth, and summarize pertinent work on gender and foraging strategies.

The diet-breadth model (MacArthur and Pianka 1966, Emlen 1966, Charnov and Orians 1973) is one of the classics in foraging theory (Stephens and Krebs 1986). It deals with the decisions foragers make whenever they encounter something they might eat—whether to "handle" the item (i.e., pursue, capture, process, and consume it) or continue searching for something else. The decision that maximizes the mean rate of gain depends on which alternative is likely to give the higher return.

The difference between handling a resource and specializing in it (i.e., searching for and handling *only* that resource) can be very great. Layton et al. confuse this by talking about returns in "kilocalories per hour spent *searching for and processing*" resources [our emphasis] but listing *only handling returns* to illustrate these rates. For example, they cite Hawkes, Hill, and O'Connell (1982:table 3) as reporting a return rate of 65,000 kilocalories per hour for collared peccaries. This suggests that a hunter could meet >20 person-days of caloric requirements in 60 minutes' work! If this were so, food acquisition would be a trivial matter. As our paper actually indicates, in both text and figure (p. 390), this is the rate to be earned *after* a herd of peccaries has been found. It does not count the considerable cost of search. Any forager who took *only* peccaries would spend so much time looking for them that his average foraging returns would be <150 kilocalories per hour—less than he needed to survive.

The distinction between search and handling is directly relevant to predictions about changing resource abundances. Resources can be ranked by benefits gained from consumption relative to costs of handling. Foragers seeking to maximize their mean rate of gain should always stop searching to take high-ranked resources. The choice to take low-ranked resources depends on the chance of finding something higher-ranked. Counterintuitively, low-ranked resources will be included in the diet independent of their own abundance and entirely as a function of the encounter rate for higher-ranked prey. Low-ranked resources may be common, but foragers should exploit them only when they cannot expect a higher return from searching for and handling something better. If encounters with higher-ranked items are sufficiently frequent, foragers should ignore those of lower rank. Resources with handling return rates below the mean rate available for searching for and handling higher-ranked items should never be taken. If encounters with high-ranked prey decline in frequency, foragers will at some point do better by investing less in searching for them and more in handling lower-ranked resources.

Two implications follow: First, given the goal of re-

turn rate maximization, high-ranked resources should never drop out of the diet. Foragers will always do better to pursue them whenever encountered, no matter how rarely. Layton et al.'s prediction that as "a population of hunter-gatherers increases in density, high-ranking resources will be over-exploited, and the resulting shift to the exploitation of lower-ranking resources will allow higher-ranking ones to regenerate" (p. 256) cannot be derived from the diet-breadth model. Second, as more kinds of resources are added to the diet, search time declines, approaching the point at which all foraging time is devoted to handling. Thus, Layton et al.'s prediction of "increased mobility in search of food sources which yield a lower return" (p. 256) also does not flow from the model. In fact, it predicts just the reverse: smaller foraging radii associated with greater diet breadth (e.g., Cane 1989).

The link between diet breadth and proportion of foraging time devoted to search versus handling has implications for subsistence transitions, including plant and animal domestication. Where the optimal diet is relatively narrow and search represents a large part of foraging costs, increased search efficiency could have a large effect on overall efficiency, yet a similar increase in handling efficiency could not. Conversely, where diet is broad and handling represents the bulk of foraging effort, improvements in handling efficiency would have large effects. If seed selection, sowing, and cultivation lead to increased handling efficiency (say, by favoring stiffer rachises, larger seeds, and thinner seed coats), they will make a much larger difference in foraging return rates when most foraging time is spent in handling.

Animal domestication may be related to the same feature of foraging economics. Dogs may reduce search time. If so, their domestication and use will be especially attractive when search is the major cost of foraging. Cattle, sheep, goats, and camels may reduce the handling costs of very low-ranked plants that they turn into milk. These animals will thus become attractive targets for domestication not as substitutes for vanishing game (cf. Foley 1982) but as processors where human diets are already very broad. Russell (1988) marshals several lines of evidence to suggest the probable importance of milk from the earliest stages of ungulate domestication.

Layton et al. argue two points about population growth: (1) that "hunter-gatherer populations have the potential to increase in size more rapidly than they apparently did in the Pleistocene" (p. 259) and (2) that greater use of low-ranked but relatively abundant resources toward the end of the Pleistocene promoted population growth (p. 260). Neither is consistent with the assumptions about fitness maximization they elsewhere adopt. The first is based on the assertion that modern hunter-gatherers, notably the !Kung, curtail population growth through long birth spacing. As Smith (CA 32:268-69) points out, Layton et al. do not cite Blurton Jones's (1986, 1987a; Blurton Jones and Sibly 1978) elegant demonstration that this practice *maximizes* rather than reduces the number of grandchildren !Kung women

leave behind (see also Hawkes and Charnov 1988). The second point is inconsistent with a key assumption of the diet-breadth model: all else being equal, foragers who maximize nutrient return rates enjoy greater reproductive success than those who do not. Increases in diet breadth result from reduced foraging return rates and so lead to *declines* in population growth rates.

Our discussion of handling economics and domestication permits us to carry this farther. Assuming capacities and tendencies to try alternative foraging strategies and to repeat and copy those which give higher rates of gain, foragers accept a broader diet because it allows a higher overall rate than could be earned by more search. In some times and places, foragers will maximize mean return rates by eliminating search entirely (e.g., Hillman 1989). Under these circumstances, innovations that increase handling efficiency will have their greatest effect. In fact, they will be the *only* way to achieve higher food-acquisition rates. If these acquisition rates are linked to reproductive success, population growth rates will respond accordingly. From this perspective, sharper growth should be associated *not* with broader diets but with subsequent increases in handling efficiency associated with practices which result in domestication. From this perspective, population growth rates probably decline with expanding diet breadth in the Mesolithic and then increase with improvements in handling efficiency in the Neolithic.

Layton et al. note that "high-ranking resources are . . . typically animal and low-ranking resources typically plant" (p. 256). It is also the case that men generally hunt and women gather. Gender clearly plays a role in human foraging strategies (Jochim 1988). If men take high-ranked resources and spend most of their time searching for prey, while women target low-ranked foods and spend more time processing, which of them is making the optimal choice? If diet breadth increased markedly at the end of the Pleistocene, was food acquisition mainly men's work in earlier times? and if so, what did women do? Layton et al. avoid these issues by referring to the "average" forager, presumably of "average" sex. (Since we have occasionally been guilty of the same averaging [Hawkes, Hill and O'Connell 1982], this is a criticism of some of our own work as well.)

Gender differences have been investigated among the Ache, where quantitative behavioral observations show a clear falsification of the simple expectation that foragers will maximize their mean rate of energy gain (Hill et al. 1987). The diet-breadth model accurately predicts the range of resources exploited by the "average" Ache forager, but men and women pursue different foraging strategies. In general, women take resources which do not conflict with child care (Hurtado et al. 1985), while men pass up many plant foods which are in the "optimal set" while they hunt. Neither men nor women are maximizing their individual mean rates of energy gain.

The surprising observation that Ache men accept a mean rate of energy gain less than half that they *could* earn has prompted two lines of inquiry, one emphasizing the role of nutrients other than energy in determining

resource choice (Hill 1988, Kaplan, Hill, and Hurtado 1990), the other focusing on potential differences in men's and women's foraging goals (Hawkes 1990, 1991). The latter is especially pertinent to the issues raised by Layton et al.

As indicated above, expectations about diet choice and foraging strategies rest on the assumed relationship between efficient food procurement and reproductive success. Men and women can enhance their reproductive success in different ways. This suggests a link between two common characteristics of human food acquisition: gender differences in foraging and the sharing of food among adults. Both occur among other primates (e.g., Galdikas and Teleki 1981, Boesch and Boesch 1989) but never approach the extremes commonly observed among humans. Among hunter-gatherers, meat is usually acquired by men and is generally shared more widely than vegetable food (Marshall 1961, Kaplan and Hill 1965). Meat acquisition often requires substantial search time. Where search time is relatively great, there will be substantial variance in short-term mean return rates. If daily variance is high (Kaplan and Hill 1985, Hawkes, O'Connell, and Blurton Jones 1991), then widespread sharing of game may result. Though often interpreted as active distribution on the part of the hunter, this can also be read as "tolerated theft" by the recipients (Blurton Jones 1984, 1987b). Either way, hunters can anticipate that their catches will be widely distributed. Their direct consumption gains (and those of their own families) will be only a fraction of any prey they acquire. At the same time, the interest and attention of potential consumers outside the hunter's family may yield other, nonnutritional benefits, including mating opportunities.

Under these circumstances, foragers face another trade-off in addition to search versus handling, this one between the benefits of food they can expect to keep for themselves (and their families) and those that may result from the procurement of food likely to be eaten mostly by others. The fitness costs and benefits may be very different for men and women. Under some circumstances, some foragers, often women, may serve their fitness best by acquiring food that can be kept for themselves and their children. Others, often men, may have more to gain (and less to lose) if they procure resources which do not ensure a steady income but which draw attention from many. In the Ache case, not only do men hunt, thereby choosing resources that go most widely outside their nuclear families, but also they take more of the vegetable foods which are widely shared; women show the reverse preference (Hawkes 1991).

Attending explicitly to gains other than direct consumption, specifically sexual strategies and mating competition, has implications for predictions about population growth. If men gain favorable treatment from choosing "risky" but widely shared resources and if this treatment gives them a better chance at higher fitness than they could expect from taking resources that would go mostly to their wives and children, then provisioning families is a losing strategy. Instead, fitness-maximizing

men should choose to "show off," i.e., pursue the high-risk foraging option (Hawkes 1990, 1991). Under some circumstances, this could result in lower fertility for women than they might have had with provisioning husbands. Where this is so, declines in the abundance of "risky" resources would reduce the frequency of hunters' bonanzas and, by extension, limit the reasons for favorable treatment. As women gave fewer sexual favors to "showoffs," fitness payoffs to provisioning men would increase. In this scenario, expanding diet breadth for men would increase the fertility of women (Hawkes 1990). Layton et al.'s prediction about diet breadth and population growth could follow.

This argument may seem dangerously far from the safer ground of the diet-breadth model, but it serves to underline a central concern in behavioral ecology, namely, identifying the options open to individuals in any given situation and the fitness-related costs and benefits associated with each. The diet-breadth model assumes a choice between continuing to search and stopping to handle resources where the value of alternatives is measured in mean acquisition rates. Other trade-offs may be important as well.

References Cited

- BLURTON JONES, N. 1984. A selfish origin for human food sharing. *Ethology and Sociobiology* 5:1-3.
- . 1986. Bushman birth spacing: A test for optimal interbirth intervals. *Ethology and Sociobiology* 7:91-105.
- . 1987a. Bushman birth spacing: Direct tests of some simple predictions. *Ethology and Sociobiology* 8:183-203.
- . 1987b. Tolerated theft: Suggestions about the ecology and evolution of sharing, hoarding, and scrounging. *Social Science Information* 26:31-54.
- BLURTON JONES, N., AND R. SIBLY. 1978. "Testing adaptiveness of culturally determined behavior: Do Bushman women maximize their reproductive success by spacing births widely and foraging seldom?" in *Society for the Study of Human Behavior symposium 18: Human behavior and adaptation*. London: Taylor and Francis.
- BOESCH, C., AND H. BOESCH. 1989. Hunting behavior of wild chimpanzees in the Tai National Park. *American Journal of Physical Anthropology* 78:547-73.
- CANE, S. 1989. "Australian Aboriginal seed grinding and its archaeological record: A case study from the Western Desert," in *Foraging and farming: The evolution of plant exploitation*. Edited by D. Harris and G. Hillman, pp. 99-119. London: Unwin Hyman.
- CHARNOV, E., AND G. ORIANS. 1973. *Optimal foraging: Some theoretical explorations*. Salt Lake City: Department of Biology, University of Utah.
- EMLEN, J. 1966. The role of time and energy in food preference. *American Naturalist* 100:611-17.
- FOLEY, R. 1982. A reconsideration of the role of large mammal predation in tropical hunter-gatherer adaptation. *Man* 17:393-403.
- GALDIKAS, B., AND G. TELEKI. 1981. Variations in subsistence activities of female and male pongids: New perspectives on the origins of hominid labor division. *CURRENT ANTHROPOLOGY* 22:241-56.
- HAWKES, K. 1990. "Why do men hunt? Benefits for risky choices," in *Risk and uncertainty*. Edited by E. Cashdan, pp. 145-66. Boulder: Westview Press.
- . 1991. Showing off: Tests of an explanatory hypothesis about men's foraging goals. *Ethology and Sociobiology* 12: 29-54.

- HAWKES, K., AND E. CHARNOV. 1988. Human fertility: Individual or group benefit? *CURRENT ANTHROPOLOGY* 29:469–71.
- HAWKES, K., K. HILL, AND J. O'CONNELL. 1982. Why hunters gather: Optimal foraging and the Ache of eastern Paraguay. *American Ethnologist* 10:345–63.
- HAWKES, K., J. O'CONNELL, AND N. BLURTON JONES. 1991. Hunting income patterns among the Hadza: Big game, common goods, foraging goals, and the evolution of the human diet. *Philosophical Transactions of the Royal Society*. In press.
- HILL, K. 1988. Macronutrient modifications of optimal foraging theory: An approach using indifference curves applied to some modern foragers. *Human Ecology* 16:157–97.
- HILL, K., H. KAPLAN, K. HAWKES, AND A. HURTADO. 1987. Foraging decisions among Ache hunter-gatherers: New data and implications for optimal foraging models. *Ethology and Sociobiology* 8:1–36.
- HILLMAN, G. 1989. "Late Paleolithic plant foods from Wadi Kubaniya in Upper Egypt: Dietary diversity, infant weaning, and seasonality in a riverine environment," in *Foraging and farming: The evolution of plant exploitation*. Edited by D. Harris and G. Hillman, pp. 207–39. London: Unwin Hyman.
- HURTADO, A., K. HAWKES, K. HILL, AND H. KAPLAN. 1985. Female subsistence strategies among Ache hunter-gatherers of eastern Paraguay. *Human Ecology* 13:1–28.
- JOCHIM, M. 1988. Optimal foraging and the division of labor. *American Anthropologist* 90:130–36.
- KAPLAN, H., AND K. HILL. 1985. Food sharing among Ache foragers: Tests of explanatory hypotheses. *CURRENT ANTHROPOLOGY* 26:131–33.
- KAPLAN, H., K. HILL, AND A. HURTADO. 1990. "Risk, foraging, and food sharing among the Ache," in *Risk and uncertainty*. Edited by E. Cashdan, pp. 107–43. Boulder: Westview Press.
- LAYTON, R., R. FOLEY, AND E. WILLIAMS. 1991. The transition between hunting and gathering and the specialized husbandry of resources. *CURRENT ANTHROPOLOGY* 32:255–74.
- MACARTHUR, R., AND E. PIANKA. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603–9.
- MARSHALL, L. 1961. Sharing, talking, and giving: Relief of social tensions among !Kung Bushmen. *Africa* 31:231–49.
- RUSSELL, K. 1988. *After Eden: The behavioral ecology of early food production in the Near East and North Africa*. British Archaeological Reports International Series 391.
- STEPHENS, D., AND J. KREBS. 1986. *Foraging theory*. Princeton: Princeton University Press.

Serials

African Studies celebrates its 50th anniversary with a special number, a Festschrift for Philip and Iona Mayer. The journal (formerly *Bantu Studies*) is the main forum for publications on the social anthropology of Southern Africa, and this number, entitled *Tradition and Transition in Southern Africa*, presents a sample of current anthropological writings on the country. Several address Philip Mayer's own particular interest in urbanisation and labour migration in Southern Africa, describing personal "narratives of resistance" produced by labourers in the gold mines, the relationship between male associations and migrant labour in the Transkei, adaptations to town life, including new forms of marriage relationship, and rural responses to migration, including Transkeian rituals and

the apparent spread of "extramarital relations" in Lesotho. Philip Mayer described the divergent identities of "Red" and "School" Xhosa in the sixties, and in perhaps the most striking contribution to the present collection David Webster describes how, in a Kwazulu border community, men present themselves as "Zulu" while women sustain a "Thonga" identity. His recent murder, almost certainly by elements in the security forces, was a terrible loss to South African anthropology. The volume, edited by A. D. Spiegel and P. A. McAllister, also contains a fascinating fragment of joint autobiography from the Mayers. It may be ordered from the Witwatersrand University Press, 1 Jan Smuts Ave., Johannesburg 2001, South Africa.