

Letters to the Editor

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Evolution Versus Invention

THE PAPERS BY R. GELMAN AND C. R. GALLISTEL (“Language and the origin of numerical concepts,” *Viewpoint*, p. 441), P. Pica *et al.* (“Exact and approximate arithmetic in an Amazonian indigene group,” *Report*, p. 499), and P. Gordon (“Numerical cognition without words: evidence from Amazonia,” *Report*, p. 496) in the Special Issue on Cognition and Behavior (15 Oct. 2004), taken jointly, establish two key points: Animals as well as humans have an analog system for representing numeracy. The analog system, although yielding only approximate answers, supports complex numerical computations including comparison, addition, and subtraction.

Hunter-gatherer groups, whose languages contain only a few number words (“one, two, many” in one case; “one” to “five” in another), pose a problem. Despite having number words, they perform only approximate numerical calculations, even when problems contain only numbers for which they have words.

Despite their interest and clarity, we suggest that the above-mentioned papers overlook two key points. First, hunter-gatherer number words are not comparable to our own. Even the smattering of data reported by these authors indicates that hunter-gatherer number words name approximate magnitudes, not exact sets of objects as ours do. There is then no paradox in the fact that hunter-gatherers perform only approximate numerical calculations.

Second, it is not language per se that is critical for understanding the transition from analog to digital numeracy, but the change from foraging that did not require exact numbers to technologies that did. Humans, as hunter-gatherers, evolved a system for analog numeracy [(1), p. 29]. When forced to adopt new technologies—pastoralism, gardening, trade or barter, and ultimately full-time farming—they then invented systems for representing exact numeracy: dots, bars, and a shell standing for zero (Mayan) (2); ropes and knots (Incas) (3); fingers and fists (sub-Saharan

tribes) (4); the abacus (Chinese) (5); Roman and Arabic numerals; and so forth. The systems are all combinatorial: The use of a base (e.g., 5, 10, 20) permits forming new numbers by combining existing numbers. They are also recursive: New numbers are formed by adding one. Both recursion and a combinatorial approach are longstanding human capacities evident in, for example, both language and (to a lesser extent) social behavior.

Conceivably, the same contingencies led both to the invention of written language and to exact numeracy. Writing arose as a belated consequence of the transition from foraging to agriculture. Farming resulted in surplus goods, necessitating a system for marking the goods, identifying ownership of casks of oil and the like [(1), p. 8].

Although hunter-gatherers had little need for exact numbers, one can imagine that no owner of stored goods would wish to receive three casks of oil when he had stored four, nor would the individual who had stored the goods wish to return five casks when he had stored four.

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References

1. D. Premack, A. Premack, *Original Intelligence* (McGraw-Hill, New York, 2003).
2. M. D. Coe, *Breaking the Maya Code* (Thames & Hudson, London, 1999).
3. M. Ascher, R. Ascher, *Code of the Quip: A Study in Media, Mathematics, and Culture* (Univ. of Michigan, Ann Arbor, MI, 1981).
4. P. Gerdes, *Historia Math.* **21**, 345 (1994).
5. Y. Li, S. Ran Du, *Chinese Mathematics, a Concise History*, translated by J. N. Grossly, A. W. C. Lun (Clarendon Press, Oxford, UK, 1987).

Elephants, Ecology, and Nonequilibrium?

ELEPHANTS AND THRIPS MAY HAVE SOMETHING in common: It has been proposed that elephants in Africa do not reach carrying capacity because they inhabit “nonequilibrium” ecosystems with highly variable rainfall (“Space—the final frontier for economists and elephants,” E. Bulte *et al.*, *Perspectives*, 15 Oct., p. 420). Similarly, it has been proposed that thrips in Australia do not reach a carrying capacity because of climatic fluctuations (1). The nonequilibrium (density-independent) ideas of the 1950s are being reworked as “state-of-the-art” ecological theory by Bulte *et al.* We should remember, however, that a more sophisticated analysis (2) of the same thrip

populations revealed strongly density-dependent population change and hence a carrying capacity.

The suggestion that multispecies systems are unlikely to show density dependence is erroneous. In contrast, evidence is emerging of the very widespread occurrence of density dependence (3), even in complex marine systems (4, 5). Detection of such effects typically takes over four generations (6); well over a hundred years might be needed to detect density dependence in an elephant population.



The application of nonequilibrium hypotheses to savannah has been challenged on theoretical and empirical grounds. Models indicate that herbivores in semi-arid areas are in long-term equilibrium with a subset of their resources (7). Competitive regulation is now very clear in a number of species of large herbivores in Africa, including wildebeest (8). A review (9) concluded there was no evidence of a paradigm shift to a nonequilibrium perspective among those researching grasslands. Large species are unlikely to exhibit metapopulation dynamics (10).

The harvesting of elephants is, rightly, controversial. We suggest that the nonequilibrium perspective is unlikely to clarify how their populations might respond to management.

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References

1. H. G. Andrewartha, L. C. Birch, *The Distribution and Abundance of Animals* (Univ. of Chicago Press, Chicago, IL, 1954).
2. F. E. Smith, *Ecology* **42**, 403 (1961).
3. R. Lande *et al.*, *Am. Nat.* **159**, 321 (2002).
4. M. S. Webster, *Ecology* **85**, 986 (2004).
5. J. S. Shima, *Oecologia* **126**, 58 (2001).
6. P. Rothery, in *Insect Populations in Theory and Practice*, P. J. Dempster, I. F. G. McLean, Eds. (Kluwer Academic, Dordrecht, 1998), pp. 97–133.

7. A. W. Illius, T. G. O'Connor, *Oikos* **89**, 283 (2000).
8. A. R. E. Sinclair, C. J. Krebs, in *Wildlife Population Growth Rates*, R. M. Sibly, J. Hone, T. H. Clutton-Brock, Eds. (Cambridge Univ. Press, Cambridge, 2003), pp. 127–147.
9. D. D. Briske, S. D. Fuhlendorf, F. E. Smeins, *J. Appl. Ecol.* **40**, 610 (2003).
10. S. Harrison, in *Large-Scale Ecology and Conservation Biology*, P. J. Edwards, R. M. May, N. R. Webb, Eds. (Blackwell Scientific Publications, Oxford, UK, 1994), pp. 111–128.

IT IS A PLEASURE TO SEE ECONOMISTS BORROWING from ecology (“Space—the final frontier for economists and elephants,” E. Bulte *et al.*, *Perspectives*, 15 Oct., p. 420) because the traffic has usually been in the other direction. But Bulte *et al.* are surely throwing the elephant out with the bathwater when they assert that equilibrium ideas in population ecology are often false. We know that temporal environmental variation prevents plant-herbivore systems from reaching a stable equilibrium, but we also know what to do about it, in theory, if our aim is to harvest such populations sustainably (I). “Nonequilibrium,” on the other hand, is a shibboleth often used to invoke some mysterious dynamical regime in which herbivores are somehow not coupled to the dynamics of their resources (2). The reality is simpler and more conventional than that. Spatial environmental variation results in a patchwork of resources that vary in quality and accessibility. A subset, the key resources (3), is what the herbivore population depends on to get through the dry season, when mortality threatens. Modeling shows that, despite short-term fluctuation due to temporal stochasticity, the herbivore population is in long-term equilibrium with these key resources. In other words, herbivore population size depends largely on the environment’s endowment of key resources and hardly at all on the remaining parts of the habitat (4). Space may be the final frontier, but the challenge is to identify and manage the key resource, or equilibrial, parts of the system, rather than to worry about the irrelevant nonequilibrium remainder. By characterizing the entire system as nonequilibrium, and failing to make the distinction between types of resources, the nonequilibrium paradigm suffers from the problem of not seeing the trees for the wood.

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References

1. R. Lande *et al.*, *Ecology* **78**, 1341 (1997).
2. A. W. Illius, T. G. O'Connor, *Ecol. Applic.* **9**, 798 (1999).
3. I. Scoones, *J. Arid Envir.* **9**, 221 (1995).
4. A. W. Illius, T. G. O'Connor, *Oikos* **89**, 283 (2000).

Response

WE AGREE WITH ILLIUS AND HAMBLER *ET AL.* that density-dependent effects are important in the population dynamics of many

species but differ with their interpretation of the term “nonequilibrium.” A more important point, however, is that the simplistic bioeconomic models that we criticized in our Perspective do not acknowledge the many other, complex interactions, apart from density dependence, that can also influence population size, nor the fact that density-dependent effects are only dominant at certain spatial scales (I).

We used the term “nonequilibrium” in its broadest sense to mean “not-at-equilibrium,” rather than to imply that equilibrating, density-dependent processes are not important. It is well recognized in the ecological literature that environmental stochasticity can affect population size (I), but it is only a very small subset of nonequilibrium theories—those termed “disequilibrium”—that assert that environmental variability can completely override the effects of biotic interactions. Rangeland ecologists, for example, have argued that herbivore population density is largely determined by extreme events like drought, which in semi-arid savannas are frequent enough to keep populations at levels that are too low for density-dependent effects like competition to operate (2).

This disequilibrium viewpoint is extreme, however, and most authors now agree that both density-dependent and environmental variables affect population size (3). Although density-dependent effects might cause populations to tend toward an equilibrium, it is likely that the position of the equilibrium will change over time and that factors such as rainfall, fire, disease, or human influence deflect populations away from a possible equilibrium or “carrying capacity.” Rather, population size may be envisaged as varying around an equilibrium point (perhaps more usefully termed an “attractor”) and can move between two or more domains of attraction.

The debate in nonequilibrium ecology has thus moved beyond the question of whether density-dependent or environmental variables are most important. Since the early 1990s, discussion has focused on identifying the scales at which different processes predominate, and how to combine this knowledge in ways that are ecologically meaningful (4). Recent advances in hierarchical modeling, for example, integrate nested processes in a spatially explicit, hierarchical framework (5). Advances like these may provide the basis for spatially defined—and more ecologically realistic—bioeconomic models in the future.

In the meantime, equilibrium models with density-dependent factors can provide an approximation of reality at certain (species specific) spatial scales. The challenge is for economists and ecologists to work together to develop models that not

only are theoretically rigorous but also incorporate appropriate spatial and temporal complexities of changing environments.

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References

1. D. L. DeAngelis, J. C. Waterhouse, *Ecol. Monogr.* **57**, 1 (1987).
2. R. H. Behne Jr., I. Scoones, C. Kerven, *Range Ecology at Disequilibrium: New Models of Natural Variability and Pastoral Adaptation in African Savannas* (Overseas Development Institute, London, 1993).
3. J. Wu, O. L. Loucks, *Q. Rev. Biol.* **70**, 439 (1995).
4. S. Levin, *Ecology* **73**, 1943 (1992).
5. J. Wu, J. L. David, *Ecol. Model.* **153**, 7 (2002).

National Environmental Policy Act at 35

1 JANUARY 2005 WAS THE 35TH ANNIVERSARY of the signing into law of the U.S. National Environmental Policy Act (NEPA). It has since been copied and enacted in many local U.S. jurisdictions and around the world, so we believe this is the proper time to list some of its accomplishments and continuing problems.

First, the existence of the statute and its implementing regulations have required U.S. agencies to at least acknowledge that there are environmental consequences of their actions. Second, the existence and publication of NEPA Environmental Analyses (EA) or Environmental Impact Statements (EIS) have provided for much more public input into decision-making.

But NEPA was designed to do more. It was meant to force agencies to “insure the integrated use of the natural and social sciences... in planning and decision-making.” The U.S. Council on Environmental Quality (CEQ) regulations for NEPA implementation say that “NEPA’s purpose is not to generate paperwork—even excellent paperwork—but to foster excellent action,” and to lead agencies toward “actions that protect, restore, and enhance the environment” (I). That goal is frequently lost in the admittedly difficult process of producing an EA or EIS.

In 1996, the average EIS was 570 pages, although the CEQ regulations state it should be only 150 pages, or 300 for complex projects (I , 2). This mass of paper is frequently unnecessary, as it is no more than the description of the existing environment (3).

There are an enormous amount of environmental data already gathered on almost all of the United States. If these data were collected in one or more depositories, they could be reused and reduce the time and effort devoted to writing EISs (4) and could serve as a quality control mechanism for the statement produced.

NEPA explicitly states that agencies are to use an interdisciplinary approach to their work, but this is not apparent in current EISs. The problem is that, despite years of effort and the development of university programs that claim to teach interdisciplinary environmental research, the ability to perform it in the real world of deadlines and finite resources does not yet exist. Another problem is the separation of “social” impacts from “environmental” impacts in EISs. The underlying principle of NEPA is that all impacts of a project are eventually social, as they ultimately affect people. Evaluation of the cumulative effects of several projects is also missing from most EISs, which devote the majority of their analysis to the current project (5).

Over the past 35 years, NEPA has greatly improved the quality of U.S. governmental decisions regarding the environment and enhanced public participation in

the process, but there are still aspects that need research and implementation if NEPA is to achieve its objectives.

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References

1. 50 C.F.R. § 1500.1.
2. B. C. Karkkainen, *Columbia Law Rev.* **102**, 903 (2002).
3. D. Bear, *Nat. Resour. J.* **43**, 4 (2003).
4. J. F. DiMento, H. Ingram, *Nat. Resour. J.*, in press.
5. N. N. Mccold, J. W. Saulsbury, *Environ. Manage.* **20** (no. 5), 767 (1996).

TECHNICAL COMMENT ABSTRACTS
COMMENT ON “Long-Lived *Drosophila* with Overexpressed dFOXO in Adult Fat Body”

Marc Tatar

Giannakou *et al.* (Brevia, 16 July 2004, p. 361) reported that dFOXO overexpression extends *Drosophila* life-span. However, mortality was similar among experimental and control groups in replicate trials, except for one week when there were many deaths in control adults. This early event reduces the control survivorship and is mistaken for evidence that aging is retarded by overexpression of dFOXO.

Full text at www.sciencemag.org/cgi/content/full/307/5710/675a

RESPONSE TO COMMENT ON “Long-Lived *Drosophila* with Overexpressed dFOXO in Adult Fat Body”

Maria E. Giannakou, Martin Gross, Martin A. Junger, Ernst Hafen, Sally J. Leever, Linda Partridge

Tatar suggests that the conclusions of our study are erroneous due to excessive mortality in young control flies. We show that, both in our published results and in other results we had at the time of publication, there is a highly reproducible increase in overall survival and maximum life-span of females with dFOXO overexpression in fat body.

Full text at www.sciencemag.org/cgi/content/full/307/5710/675b