



BIOGRAPHICAL MEMOIRS

RICHARD DALE ALEXANDER

November 18, 1929–August 20, 2018

Elected to the NAS, 1974

*A Biographical Memoir by Joan E. Strassmann
and David C. Queller*

RICHARD D. ALEXANDER was the T. H. Hubbell Distinguished University Professor of Biology at the University of Michigan and Curator of Insects at the Museum of Zoology. His long career had three stages. As a graduate student, he wielded a newly developed field tape recorder to pioneer the use of distinctive sounds alongside morphology to discover a wealth of new cricket species. This foundational work grounded the first stage: the importance of behavior, particularly communicative behavior, to speciation and evolution. His second stage turned to the evolution of social behavior, an area where he had important insights on how group living and cooperation evolve. Legendary from this stage was his prediction of what attributes a mammal with sterile castes would have, predictions tested and verified in the naked mole rat. In his third stage, he leveraged his behavioral and social insights and his formidable intellect to solve the complex problem of how to understand human behavior from an evolutionary perspective, focusing on adaptation. Important achievements in his research on humans include his recognition that cultural variation stems from phenotypic plasticity and reflects human reproductive striving. He developed the theory of indirect reciprocity, in which he described networks of cooperators for whom the social glue is reputation. He pioneered the concept that moral systems are systems of indirect reciprocity, thereby showing that biology is critical to understanding human cooperation. He was fascinated by the unique traits of humans and asked questions that had never been asked before, such as why humans are unique among



Figure 1 Richard D. Alexander on his horse. Photo provided by Nancy Alexander.

mammals in concealing ovulation. Throughout his career, Alexander mentored many students, spending considerable time with each and helping them to become the best scientists they could be.

EARLY LIFE AND EDUCATION

Richard Dale Alexander was born on November 18, 1929, in White Heath, Illinois, about 15 miles west of Champaign. His parents were Archie Dale Alexander and Katherine Elizabeth Heath Alexander. Both attended college but did not complete degrees and both taught in one-room schools before turning to farming. Alexander had an older





Figure 2 Dick and Lorrie Alexander. Photo provided by Nancy Alexander.

sister, Nell Beardles, and a younger brother, Noel. The family share-cropped on 151 acres, where they grew feed for the chickens, cows, and pigs they raised. Alexander attended a one-room school before going to nearby Monticello High School. He explored the forests along the Sangamon River, cared for his animals, and made toys like darts from corncobs and feathers.¹

Alexander had not planned to go to college, instead imagining his life would be dedicated to farming like that of his father. But his high school academic advisor, Helen Burgoyne, stopped him in the hall one day and showed him his scores on various college entrance exams, which had previously meant nothing to him. He did not think his family could afford college for him because his sister was going to attend. Burgoyne told him that Blackburn College had a work-study plan and cost \$250 for the year, including room and board. So when he was sixteen years old, Dick went to Blackburn in Carlinville, Illinois, 150 miles away, living in a basement converted to a forty-eight-man dorm. He began in the fall of 1946 and stayed for five semesters. He remembered those days fondly and described many practical jokes in a memoir from that time.² Blackburn only allowed students to work fifteen hours a week, but Alexander discovered he could work more hours if he transferred to Illinois State Normal College (now Illinois State University). He completed a bachelor of science degree in biology education in August 1950 with a plan to teach high school science in southern Illinois. That same year, Dick married Lorraine “Lorrie” Kearnes on August 19, 1950, whom he met as an undergraduate at Blackburn. They would have two daughters: Susan Dale, born in 1953, and Nancy Lorraine, born in 1955.

Alexander’s plans changed when two of his professors at Illinois State, who recognized his talent, urged him to consider graduate school. They contacted academic friends, and before he knew it, Dick had teaching fellowship offers at

both Cornell University and the Ohio State University. He accepted the latter because it was closer to home and his ailing father. Alexander received his master’s degree in 1951, working under noted entomologist Alvah Peterson, and then served in the U.S. Army until 1953 as an entomologist in the Medical Service Corps. He completed his Ph.D. in 1956 under entomologist and bioacoustics pioneer Donald J. Borror and then remained at Ohio State as a postdoctoral fellow until 1957, with funding from the Rockefeller Foundation. From there he went straight to a faculty position as an instructor at the University of Michigan in 1958.³ In 1974, Dick and Laurie fulfilled their dream of owning a farm and bought eighty acres on Bethel Church Road southwest of Ann Arbor.

Alexander rose through the ranks at Michigan. In addition to his faculty position, he was named Curator of Insects in 1959 and continued in that role until his retirement in 2001, and he served as director of the Museum of Zoology from 1993 to 1998. During his teaching career, he was awarded three named faculty positions: Collegiate Professor, Donald W. Tinkle Collegiate Professor, and finally Theodore H. Hubbell Distinguished University Professor. After retirement, he continued writing academic and popular books, articles, songs, and poetry.

A TAPE RECORDER CHANGES EVERYTHING

In his autobiography, Dick said he walked into Donald J. Borror’s office in 1953 after serving in the army, and Borror handed him a “new Magnemite battery-operated tape recorder with a hand-cranked spring-powered motor, and D cell batteries powering the recording apparatus.”⁴ It was new technology acquired from the Germans after World War II. Borror told him to go out and see what he could learn about singing insects. Dick did so and managed to record all of the singing crickets, katydids, and cicadas near Columbus, Ohio, that summer.

Alexander’s recording work resulted in his first publication in the August 1955 issue of *Magnetic Film and Tape Recording Magazine*.⁵ In it, there is a photograph of Alexander with the reel-to-reel deck about the size of a briefcase on a strap across his shoulder and a microphone that fed into a kitchen funnel pointed into the bushes. Alexander’s careful observation skills were already clear in this first article. He was well aware of all the soft singing beetles, treehoppers, and spittle bugs, but recommended that amateurs turn to the louder crickets, grasshoppers, and katydids, even bringing them inside for better recording. He also noted what he called dialects or regional accents, as in the common true katydid, *Pterophylla camellifolia*, which makes a different sound in the South. This was a preamble to his discovery of how many cryptic species there are of many singing insects.

In 1957, Alexander published the heart of his 527-page dissertation in a pathbreaking paper on the taxonomy of field crickets in the eastern United States. It showed that seemingly indistinguishable crickets can belong to different species separated not by morphology so much as by their life cycle and song type.⁶ Crickets that get a head start by overwintering as nymphs emerge before those that overwinter as eggs, and therefore the two types will not encounter each other for mating. This was a revolutionary discovery in an age when it was widely believed that such reproductive separation and speciation could not occur between such “sympatric” (co-occurring) populations, but would require geographic separation (allopatry). Alexander further confirmed the importance of reproductive isolation: with few exceptions, the five different species usually cannot produce viable offspring except by mating with their own species. He showed that about a third of the singing insects in central and southeastern Ohio had not been recognized as different species.⁷ This statistic included an amazing half of the insects singing right on the OSU campus. This discovery was big news and confounded the taxonomists who had been sorting their crickets into species from dead specimens alone. Alexander pioneered the notion that behavior can be as important as morphology for understanding speciation and species boundaries.

A paper published by Alexander in 1962 is still perhaps the best summary of the importance of behavior in systematics.⁸ This transformative article focused on crickets and argued that morphological data alone are insufficient for assigning species. It was a foundational paper, for which Alexander received the AAAS Prize from the American Association for the Advancement of Science, now called the Newcomb Cleveland Prize and awarded only to publications in their journal, *Science*. Alexander concluded his remarkable paper by writing: “...the evolution of animals is typified by nothing quite so clearly as it is by the elaboration and combination of behavioral characteristics.” In 1971, Alexander received the National Academy of Sciences Daniel Giraud Elliot Medal for “his outstanding fundamental work on the systematics, evolution, and behavior of crickets.” This work was characterized by a careful assessment of multiple hypotheses and subsequent consideration of the sort of information necessary to choose among them.

Another puzzle drew Alexander’s attention in the early years: the periodical cicadas.⁹ He applied the same kind of painstaking observation and listening to them that he applied to his crickets. Early on, Alexander reasoned that there was a life-history relationship between seventeen- and thirteen-year cicadas and predicted that for each of the former there should be a species of the latter. Within *Magicicada*, there were at least eighteen distinct broods: thirteen seventeen-year ones and five thirteen-year ones. Pleistocene glaciation was probably

involved in the formation of some of the broods. The 1962 paper is a magnificent study showing the geographic distributions of the different species and broods, variation in songs and the timing of chorusing, and even mating experiments.

THE AUSTRALIA EXPEDITION WITH DAN OTTE

Great field biologists often have one trip that stands out above all others, a career-defining voyage. Darwin’s trip on the HMS *Beagle* comes to mind of course. For Dick Alexander and Dan Otte, it was their year-long trip in 1968-69 to Australia, begun when Dick was thirty-eight and Dan was twenty-nine, having just completed his Ph.D. thesis on grasshoppers. The adventure was challenging to organize and funds were tight, ultimately coming from the National Science Foundation, a Guggenheim Fellowship to Dick, and the University of Michigan. They worked incessantly, camping out of a Land Rover pulling a cart and often following nearly non-existent roads.

Why did they undertake this monumental work? In one of his memoirs, Dick says that it was the absence of character displacement—greater divergence in characters in zones of overlap—in singing insects in the United States that first motivated him.¹⁰ Would Australia be an independent and huge data set to address this provocative question? For the majority of Australian species, Alexander and Otte found a lack of character displacement along with sympatric existence between species without hybridization, just as they had in the United States.

From June 1968 to June 1969, Alexander and Otte covered over 46,000 miles all across and around Australia, listening for and then collecting crickets at 905 places and collecting 492 species, including 376 new species.^{11,12} Their wives and daughters came along, staying in Melbourne, Townsville, and Perth while Dick and Dan collected nearby.

Besides covering the continent looking for crickets, Alexander and Otte visited the universities and museums where crickets were curated, both in Australia and elsewhere. This monumental project took more than a decade after the field work was over and resulted in a publication of 477 pages.¹³ Alexander also wrote a companion travel narrative of the trip for non-cricket specialists.¹⁴ Compelling anecdotes abound in this story of meeting colorful characters, collecting crickets until the early morning hours, fearing snakes, and never giving up.

The Australia cricket project would have been career defining for most scientists, but for Alexander it was just a stepping stone to other problems, and Dan Otte did most of the taxonomic work from the trip.¹⁵ Yet Alexander’s fascination with singing insects never really ended. As late as 2013, he published a paper on *Magiciada* with two of his later graduate students, John Cooley and David Marshall.¹⁶ According

to Alexander's CV, he collected about 10,000 specimens and 10,000 separate tape recordings of more than 1,000 different insects and other animals. His work resulted in descriptions of over 425 new species.

THE EVOLUTION OF SOCIAL BEHAVIOR

Richard Alexander was elected to the National Academy of Sciences in 1974, entirely on his work on the importance of behavior, particularly singing behavior in insects, to systematics, even before the Australia work had been published. But there were already hints of the new directions his curious mind would take, and his most influential work was still to come. Most memorable is a paper on social behavior.¹⁷ There was also a paper that presaged the topic that would occupy Alexander for the rest of his career: "The Search for an Evolutionary Philosophy of Man," which came out of a talk Dick gave while on the Australia trip.¹⁸ It was an indication that even then he was thinking about humans as he collected crickets. After all, if behavior was a missing element in the study of crickets, could it not also be one in the study of humans?

Alexander argued that living in a group causes nearly universal costs to individuals. These are increased competition for resources and reproductive partners and increased transmission of diseases and parasites. Grouping must therefore have benefits that outweigh these costs, and he viewed protection from predators as a primary one. Alexander built upon the work of William D. Hamilton and George C. Williams in taking a clear individual selection perspective on adaptation.^{19,20,21} He argued that social behavior could be explained by kin selection and reciprocity. His emphasis on conflict between groups became a major theme in social evolution research.

A EUSOCIAL MAMMAL PREDICTED: NAKED MOLE-RATS

In thinking about the evolution of eusociality, Alexander reasoned that eusocial vertebrates would be functionally more like termites than like eusocial ants, bees, or wasps. He imagined a hypothetical eusocial vertebrate and postulated a list of specific, falsifiable attributes. This list was not published immediately, but he discussed his hypothetical eusocial vertebrate in terms of a rodent that would live safely under hard ground to avoid predation by snakes in tropical Africa and would feed on large tubers or roots.²² He presented this hypothesis in a guest lecture at Northern Arizona University in Flagstaff, Arizona, in 1976. After the lecture, Terry Vaughan, an author of several textbooks and many articles on mammals, told Alexander that he had precisely described the naked mole-rat, *Heterocephalus glaber*. Little was known about naked mole-rats at the time, but when Alexander



Figure 3 At home with a cane he whittled. Photo provided by Nancy Alexander.

contacted South African environmental physiologist Jennifer Jarvis, she confirmed that colonies were very large and that she was having a great deal of trouble with her laboratory colonies because only one pair would breed. Alexander immediately and excitedly realized that this could be his eusocial mammal. Publications by Alexander and his students include the standard reference on naked mole-rats (co-edited by Sherman, Jarvis, and Alexander),²³ a new volume on fossorial rodents edited by Alexander's student Eileen Lacey,²⁴ and several hundred other articles on topics ranging from the demography and population genetics of naked mole-rats, their social structure, breeding habits, counter-shaded coloration, ecology, and interspecific competition with ants. This kind of prediction is all too rare in behavioral evolution. Alexander's anticipation of the discovery of a eusocial vertebrate in 1976 was said to be a brilliant insight comparable to the prediction of the existence of the planets Neptune by Le Verrier or Pluto by Lowell.^{25,26}

AN EVOLUTIONARY UNDERSTANDING OF HUMANS

Alexander's insights into humans have transformed our understanding of what we do and why we do it in ways that fundamentally change disciplines such as psychology,



Figure 4 Dick and Lorrie Alexander. Photo provided by Nancy Alexander.

philosophy, and human biology. An earlier obituary focused on this area,²⁷ and we draw partly on that account. Alexander left no area of human endeavor unexplored. He probed kinship, care of the young, parent-offspring conflict, childhood, concealed ovulation, culture, morality, humor, religion, art, intelligence, intergroup competition, intragroup cooperation, and indirect reciprocity.²⁸

In a series of articles and two books, *Darwinism and Human Affairs* and *The Biology of Moral Systems*, Alexander argued that our very best traits (such as extreme cooperation and intelligence) evolved in tandem with our very worst trait of between-group warfare.^{29,30,31} The logic begins with humans achieving ecological dominance, which made groups of humans each other's main competitors.³² This meant that the natural conflicts among individuals in a group need to be controlled when the group finds itself in conflict with another group. The more intense the between-group conflict, the more within-group cooperation is favored, though within-group competition is also always present.

Alexander attributed much of what makes us human to the tension between directly selfish actions and those that benefit the group in an environment of competing groups. He viewed social competition as selecting for intelligence, most importantly because it facilitated foresight, reasoning, language, scenario-building, and even traits we view as cultural, including art and religion. Intelligence is of particular importance in humans because the groups humans live in have many levels with different possibilities for conflict and cooperation. These groups can be small groups of families, nomadic groups, or permanent small or large groups of settlements, each with liaisons to other nearby groups to which they may or may not be related.³³ Scenario building is of particular importance in interacting with others in different groups in order to predict their actions and the outcomes of those actions.

As social cognition and complex interactions in and between groups became more and more central to the

evolution of humans, family structure also evolved. Increased intelligence required extended parental care and family structures that could provide it. Alexander postulated that concealed ovulation is important in keeping men close to their partners and better able to participate in caring for the young.³⁴

A natural consequence of competition within groups is dominance, where some members acquire more resources than others. But this can be detrimental to group cohesion, so societies have developed many ways to control excess selfishness. This includes punishment by other group members, most drastically leading to execution or expulsion from the group. Selfish behavior can also be suppressed before it happens by moral systems. For example, Alexander argued that monogamy was important for motivating subordinate men to defend the group and coined the term "socially imposed monogamy."

Central to the way that Alexander envisioned human cooperation and its moral underpinning is the concept of indirect reciprocity. Robert Trivers and Alexander both had earlier developed the concept that Trivers called reciprocal altruism and Alexander called reciprocity.^{35,36} Alexander extended this concept to cover benefits that are not directly reciprocal but instead come from another who is aware of the actor's altruistic actions.³⁷

Alexander was revolutionary in his vision of the importance of social arms races as key to social evolution. He viewed the human mind as necessarily extremely flexible because of these arms races. Under his view of human sociality, human cognition, consciousness, moral understanding, language, art, and religion have evolved for people to thrive in complex multi-level societies where others judge and decide whether to cooperate or not. As Kyle Summers and his coauthors argue in their 2019 obituary, Alexander's revolutionary ideas explain human behavior, and there is no other logically consistent theory of human morality placed in the framework of human life history.³⁸

A TEACHER AND MENTOR

Alexander was an inspiring, caring teacher and mentor. His lecture course in behavior and evolution was legendary and earned him multiple teaching awards. He loved to argue, and he developed arguments as part of his teaching that appeared in copious course handouts long before they were published. His students ran with those ideas, studying coloniality, territoriality, kin selection, communication, parental behavior, mating systems, and sexual selection. In addition to the singing insects and rodents already mentioned, they worked in organisms as diverse as plants, cicadas, wasps, thrips, damselflies, bower birds, bluebirds, frogs, ground squirrels, naked mole-rats, dolphins, and humans.

He sometimes secretly funded graduate research, telling students to apply for university research awards that he funded personally. He also gave that most precious gift to all of us: his time. He commented copiously on manuscripts, often suggesting entirely new approaches and rarely asked to be included as a co-author on them. Richard Alexander was an example of the very best kind of professor and scholar for his intense curiosity and deep questioning, his ability to pivot to new topics and use new tools, and perhaps above all else, his tireless attention to his students. Richard died on August 20, 2018, three months shy of his eighty-ninth birthday.

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REFERENCES

- 1 Alexander, R. D. 2010. Understanding ourselves. In: *Leaders in Animal Behavior: The Second Generation*, eds. L. C. Drickhamer and D. A. Dewsbury, pp. 1–37. New York: Cambridge University Press.
- 2 Alexander, R. D. 2001. *Club 48: A Personal Account of Blackburn College and the Men of Butler Basement. 1946–48*. Manchester, Mich.: Woodlane Farm Books.
- 3 Alexander, R. D. 1988. Moving my family to Michigan. Unpublished manuscript, available at <https://rdalexander.commons.gc.cuny.edu/writings/nonprofessional-works/books-essays/>.
- 4 Alexander, R. D. 2010.
- 5 Alexander, R. D. 1955. Capturing the melodies of insect singers. *Magn. Film Tape Rec.* 2:34–37.
- 6 Alexander, R. D. 1957. The taxonomy of the field crickets of the eastern United States (Orthoptera: Gryllidae: Acheta). *Ann. Entomol. Soc. Am.* 50:584–602.
- 7 Alexander, R. D. 1957.
- 8 Alexander, R. D. 1962. The role of behavioral study in cricket classification. *Syst. Zool.* 11:53–72.
- 9 Alexander, R. D., and T. E. Moore. 1962. *The Evolutionary Relationships of 17-Year and 13-Year Cicadas with Three New Species* (Homoptera: Cicadidae: Magicicada). Miscellaneous Publications of the Museum of Zoology 121. Ann Arbor, Mich.: University of Michigan Press.
- 10 Alexander, R. D. 2010.
- 11 Alexander, R. D. 2010.
- 12 Otte, D., and R. D. Alexander. 1983. *The Australian Crickets: (Orthoptera: Gryllidae)*. Philadelphia: Philadelphia Academy of Natural Sciences.
- 13 Otte, D., and R. D. Alexander. 1983.
- 14 Alexander, R. D. 2016. *White Man's Fire: Tales of Two American Cricket Collectors in Australia: 1968–1969*. Manchester, Mich.: Woodlane Farm Books.
- 15 Otte, D., and R. D. Alexander. 1983.
- 16 Cooley, J. R., et al. 2013. The distribution of periodical cicada Brood III in 1997, with special emphasis on Illinois (Hemiptera: *Magicicada* spp.). *Am. Entomol.* 59:9–14.
- 17 Alexander, R. D. 1974. The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 4:325–383.
- 18 Alexander, R. D. 1971. The search for an evolutionary philosophy of man. *Proc. Roy. Soc. Victoria* 84(1):99–119.
- 19 Hamilton, W. D. 1964. The genetical evolution of social behaviour. I. *J. Theor. Biol.* 7:1–16.
- 20 Hamilton, W. D. 1964. The genetical evolution of social behaviour. II. *J. Theor. Biol.* 7:17–52.
- 21 Williams, G. C. 1966. *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought*. Princeton, N.J.: Princeton University Press.
- 22 Alexander, R. D., K. M. Noonan, and B. J. Crespi. 1991. The evolution of eusociality. In: *The Biology of the Naked Mole-Rat*, eds. P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander, pp. 3–44. Princeton, N.J.: Princeton University Press.
- 23 Cooley, J. R., et al. 2013.
- 24 Lacey, E. A., J. L. Patton, and G. N. Cameron, eds. 2000. *Life underground: the biology of subterranean rodents*. Chicago, I.L.: University of Chicago Press.
- 25 Reaves, G. 1997. The prediction and discoveries of Pluto and Charon. In: *Pluto and Charon*, eds. S. A. Stern and D. J. Tholen, pp. 3–26. Tuscon: University of Arizona Press.
- 26 Galle, J. 1846. Account of the discovery of Le Verrier's planet Neptune, at Berlin, Sept. 23, 1846. *Mon. Not. R. Astron. Soc.* 7:153.
- 27 Summers, K., et al. 2019. Obituary: The nine lives of Richard D. Alexander. *Evol. Hum. Behav.* 40:133–139.
- 28 Summers, K., and B. Crespi. 2013. *Human Social Evolution: The Foundational Works of Richard D. Alexander*. New York: Oxford University Press.
- 29 Alexander, R. D. 1971.
- 30 Alexander, R. D. 1979. *Darwinism and Human Affairs*. Seattle, Wash.: University of Washington Press.
- 31 Alexander, R. D. 1987. *The Biology of Moral Systems*. Hawthorne, N.Y.: Aldine de Gruyter.
- 32 Summers, K., et al. 2019.
- 33 Summers, K., et al. 2019.
- 34 Alexander, R. D., and K. M. Noonan. 1979. Concealment of ovulation, parental care, and human social evolution. In: *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*, eds. N. A. Chagnon and W. G. Irons, pp. 436–453. North Scituate, Mass.: Duxbury Press.
- 35 Alexander, R. D. 1974.
- 36 Trivers, R. L. 1971. The evolution of reciprocal altruism. *Q. Rev. Biol.* 46:35–47.
- 37 Alexander, R. D. 1987.
- 38 Summers, K., et al. 2019.

SELECTED BIBLIOGRAPHY

- 1960 With R. S. Bigelow. Allochronic speciation in field crickets and a new species, *Acheta veletis*. *Evolution* 14:334–346.
- 1962 With T. E. Moore. *The Evolutionary Relationships of 17-Year and 13-Year Cicadas with Three New Species* (Homoptera: Cicadidae: Magicicada). Miscellaneous Publications of the Museum of Zoology 121. Ann Arbor, Mich.: University of Michigan Press.
- The role of behavioral study in cricket classification. *Syst. Zool.* 11:53–72.
- 1968 Life origins, speciation and related phenomena in crickets. *Quart. Rev. Biol.* 43:1–41.
- 1971 The search for an evolutionary philosophy of man. *Proc. Roy. Soc. Victoria* 84(1):99–119.
- 1974 The evolution of social behavior. *Annu. Rev. Ecol. Syst.* 4:325–383.
- 1978 With G. Borgia. Group selection, altruism and the hierarchical organization of life. *Annu. Rev. Ecol. Syst.* 9:449–474.
- 1979 *Darwinism and Human Affairs*. Seattle: University of Washington Press.
- 1983 With D. Otte. *The Australian Crickets: (Orthoptera: Gryllidae)*. Philadelphia: Philadelphia Academy of Natural Sciences.
- 1987 *The Biology of Moral Systems*. Hawthorne, N.Y.: Aldine de Gruyter.
- 1991 With K. M. Noonan and B. J. Crespi. The evolution of eusociality. In: *The Biology of the Naked Mole-Rat*, eds. P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander, pp. 3–44. Princeton, N.J.: Princeton.
- With P. W. Sherman and J. U. Jarvis. *Biology of the Naked Mole-Rat*. Princeton, N.J.: Princeton University Press.