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Understanding ourselves

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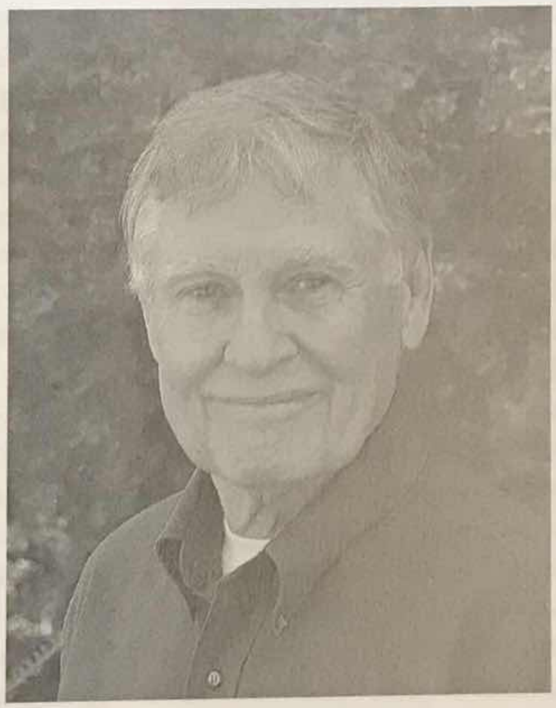

Biographies, as generally written, are not only misleading but false. The author makes a wonderful hero of his subjects; he magnifies his perfections, if he has any, and suppresses his imperfections. History is not history unless it is the truth.

Abraham Lincoln

Myth does not mean an absence of truth but a concentration of truths.

Doris Lessing

Would that all of our autobiographical myths could be concentrations of truths!

Autobiographies are trickier than biographies. Stanley Elkin (1993) has suggested that everyone has a worthwhile life story to tell about herself or himself, but no one is likely

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to tell it completely and accurately. Part of the reason for these failures, said Elkin, is that we never reveal everything in the darkest corners of the basements of our lives (his actual phrase was the "nasty hoard" in the "secret cellar"). Another part is that, sometimes, we simply cannot recall and interpret accurately, even if honestly, what really happened, when, and why.

When autobiographies are requested in scientific contexts, the accounts are probably expected to center around the scientific work of the author. This may or may not be the author's first choice in autobiographic materials. But such a focus surely eases the first reason for imperfection, though not eliminating it entirely. All scientists are likely to have at least a few too-dark secrets in the basements of their professional performances, especially in the sociality and ancillary responsibilities of their science. The focus on science also retains difficulties with regard to recalling and interpreting honestly, because all of us so-called scientists have gradually but certainly adjusted and re-adjusted our views of the tendrils of understanding and influence that were generated during the earliest stages of our budding careers, and that have contributed to our becoming what we are. We cling to our interpretations of the steps in our development and performance because they seem to make sense to us, and they are likely to exalt us more than the alternatives; and also because, as is surely healthy in moderation, we tend to like our own versions of ourselves. The saving grace is that, if the connecting aspects of our grown-up version of how we, as we might think, "came to be famous" were put together early enough in our careers, they may actually have influenced significant portions of our life's itinerary.

There is likely a parallel to all of this in the evident reluctance of people in general, including at least most biologists, to accept ourselves – meaning all humanity – as having evolved through a process of differential reproduction, an acceptance that necessarily calls for submitting to a thorough revealing of how we have evolved and what we are evolved to be, and to do. Even universal darkest corners of basements – and *a fortiori* those who publicize them carelessly – can be difficult to tolerate.

When I was invited to provide an autobiography for the first volume, I rejected the idea because, at age 52, I still held the fond belief that I had scarcely begun. Now, on the verge of age 80, thinking otherwise seems a little easier. As might be expected, I have sometimes favored information and activities not represented in my published work, or obscurely represented there. Because the different topics that held my attention across the past 70 years or so did not appear in a simple non-overlapping sequence, the reader will find me returning to earlier dates each time the subject changes. My professional attention to human behavior and evolution did not develop until the mid-1960s, but its origins, I realized belatedly, were older than any of my other academic interests.

Early life

I was born, and lived during the first 16 years of my life, in a modest farmhouse in Sangamon Township, Piatt County, Illinois. Our farm was not far from the north branch of the Sangamon River, and the extensive wooded areas along the river became my principal boyhood haunt. My family made its living from a 151-acre general-purpose farm operated "on the shares" with the landlord, a high school classmate of my parents. We grew corn, oats, clover, alfalfa, and pastures, all as livestock feed – no cash crops. We bred, raised, and marketed hogs and beef calves, and sold cream from several milk cows and eggs from a large flock of hens. We relied heavily on chickens for our own meat because a chicken was the appropriate size for one meal so that there was little or no need for an icebox. Virtually all of the meat, eggs, and milk products that we consumed came from our own animals, and most of our vegetables and fruit came from our two large gardens. We separated cream and skim milk with a hand-cranked separator kept in the kitchen, and made butter with a small hand-cranked churn. Skimmed milk (today's "no fat" milk) was fed to the hogs. My mother preserved meat, vegetables, and fruit enough to last the winter, nearly all that we needed – at first in Mason jars, later with a hand-cranked home-canning machine. Her cook stove was fueled initially with wood, later with coal. She used a hand-operated washing machine and wringer at first, then acquired a used machine operated by a step-start gasoline engine. Our house was heated by two free-standing oil stoves, one in the living room and one in the dining room.

My home environment those first 16 years was a rich one, full of hard work and the incessant demands of a complicated livestock operation. All of our farm work was done with horses until I was 13, the same year that electric lines reached our farm. The independent play and exploration of farm kids in those less complicated days, when there were virtually no "No Trespassing" signs and a higher proportion of unsupervised and unrestricted activities, now seem to me to have been unusually conducive to development of a creative and imaginative approach to life (cf. Alexander 1991b, 2001a, 2004, 2005b, 2006b, mss. 1–3, 5)

I have two siblings: an older sister, Nell Beadles (dentist's wife and homemaker), and a younger brother, Noel (farmer). Both of my parents, Archie Dale Alexander and Katherine Elizabeth Heath Alexander, attended college briefly, and each taught in a one-room country grade school for a few years before changing to farming. I attended a one-room country school for seven years, starting at age five. The second year I was boosted by my teacher, Mrs. Edna Williams, to third grade, the same grade as my older sister (this same sequence occurred for my mother, my father, and my aunt Ruth; other than my father, Ruth was the only one of her eight siblings to complete high school). My school was elegantly spare, with no library other than an 8-volume set of *Compton's Pictured Encyclopedia*. When I was in seventh grade, an 8-volume set of *Book Trails* was added. In seventh and eighth grades, we were required at the end of the school year to spend a day at the county seat, taking written examinations constructed by Charles MacIntosh, the county superintendent of schools, to verify that we were qualified to proceed into high school.

My high school graduated 46 students in my class of 1946. I had spent six years in 4-H and four in the Future Farmers of America. I was chosen by the local Rotary Club as the "outstanding boy" in my high school class, but I graduated fifth or so, behind a slate of scholarly girls. I never won an athletic letter, a failure that has always bothered me. I did win "outstanding student" awards in art and agriculture, and a blue ribbon in a saxophone quartet at a state band contest; and I achieved State Farmer status in the Future Farmers of America, boyhood haunt. My family made its living from a 151-acre general-purpose farm operated "on the shares" with the landlord, a high school classmate of my parents. We grew corn, oats, clover, alfalfa, and pastures, all as livestock feed – no cash crops. We bred, raised, and marketed hogs and beef calves, and sold cream from several milk cows and eggs from a large flock of hens. We relied heavily on chickens for our own meat because a chicken was the appropriate size for one meal so that there was little or no need for an icebox. Virtually all of the meat, eggs, and milk products that we consumed came from our own animals, and most of our vegetables and fruit came from our two large gardens. We separated cream and skim milk with a hand-cranked separator kept in the kitchen, and made butter with a small hand-cranked churn. Skimmed milk (today's "no fat" milk) was fed to the hogs. My mother preserved meat, vegetables, and fruit enough to last the winter, nearly all that we needed – at first in Mason jars, later with a hand-cranked home-canning machine. Her cook stove was fueled initially with wood, later with coal. She used a hand-operated washing machine and wringer at first, then acquired a used machine operated by a step-start gasoline engine. Our house was heated by two free-standing oil stoves, one in the living room and one in the dining room.

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My favorite course in high school was English, with an emphasis on poetry. The use of language, in all of its aspects, never stopped being a passion, and I always regarded it as my second choice in teaching. It occurred to me long ago that even such a seemingly simple source as a dictionary can be used to extract broadly interesting and deeply significant information about ourselves as members of the human species.

I remember a serious discussion with our English teacher, Miss Katharine Turner, about Robert Frost's intended meaning for his poem *Mending Wall.* Miss Turner suggested to the class that the poem showed that farmers are generally too set in their ways to change in accord with newer times. Sensitive about the sometimes tense interactions of my father and his neighbor, who each held responsibility for half of the livestock fence between their two farms, I argued to her that the poem reflected Frost's belief that for neighbors to cooperate in repairing that no longer essential stone wall between their properties helped maintain their friendship and cordiality. I liked Frost's, "Good fences make good neighbors." But I haven't forgotten his question to someone who asked him to explain one of his poems. He is reported to have sat in silence for a moment, before he said, "What do you want me to do, say it in a worser way?"

In 2001, I was inducted into the Monticello Community High School Hall of Fame – a delightful experience that included riding with Lorrie, my best friend now of 61 years, and wife of 58 years, and with some of the grandchildren of my brother (our own four grandchildren were attending school in California). On the afternoon of Homecoming day we traveled slowly in a broad circle through the town of Monticello, in the lead car of the parade, with a huge sign on the door with my name on it. During the entire ride we called back and forth with friends, relatives, and classmates among the crowds that lined the parade route, some of whom I hadn't seen in more than 60 years.

In the fall of 1945, Helen Burgoyne, a teacher of Latin, whom I had not even known was my high school advisor, walked past my girlfriend and me in the hallway and paused to ask if I intended to go to college in the fall. I said I didn't know, and wondered aloud why she had asked. She looked at me for a moment and said, "Come with me." She took me to the school office and showed me my scores on college entrance examinations and other tests, all of previously unknown significance to me. I was dumbfounded, by her interest, by the existence of the tests, and by the scores she showed me. When I explained that my family had no funds to send two offspring to college at the same time, she told me about Blackburn College, a southern Illinois school with a student work plan and a total expense of US$250 for the entire year, including room and board. That was, of course, a time when a farm hand's pay was approximately a dollar a day, and room and board; and when a new Ford V-8 sedan cost a little over US$700.

After five semesters at Blackburn (described in detail in Alexander 2001b), I transferred to the Illinois State Normal College (now Illinois State University), where I majored in education in biology, graduating in August 1950. I had decided I needed courses not given at Blackburn, and also realized I could work more hours outside classes there, earning my way completely by attending classes and retaining jobs 12 months of the year (Blackburn restricted students to 15 hours of work each week). Because of this schedule, and my indecision about professions, I accumulated over 150 semester hours of coursework. Without my being conscious of the reasons then, most of my optional courses were human-oriented, on such topics as introductory and educational psychology, abnormal sociology, philosophy, history, economic geography, and others.

During undergraduate years my interests progressed through a sequence of perhaps predictable changes in anticipated and desired professions: dairy farmer, veterinarian, county farm advisor, chemist, teacher, biologist, and finally entomologist. Two of these dreams failed for specific reasons. My necessarily out-of-state application to veterinary school, when I was a sophomore with a single course in biology, was rejected. I also discovered that the severe headaches that frustrated me in chemistry laboratories were a reaction to nitric acid fumes.

My "off-the-farm" work began at age 14 or 15, when I detassled seed corn. A year or so later, as a result of the World War II shortage of metal for repairing combines, I "ran a rack" (loaded and drove a wagon transporting bundles of oats to the thresher) with a team of horses, across 2–3 weeks and many miles, on the last old-time threshing run in Piatt County, Illinois (Alexander ms 2). At ages 15 and 16, I worked parts of two summers on a neighboring farmer's commercial hay baler (Alexander ms 2), and spent much of one summer mowing fencerows with a hand scythe on a neighboring farm – a half mile a day. During two summers, 17 and 18, I worked in a gravel quarry, first as clay-picker on a rock-crusher, and later as grease monkey on the gravel washing plant. For a short time I worked 60 feet above the ground helping construct overhead bins for sand and gravel, a stint that earned me the union wages of a high steel worker. I also went through the initial steps of learning to weld and to operate a dragline crane and a bulldozer (Alexander ms 2). At Blackburn I fired furnaces, tended the lawn, felled trees, hauled garbage, painted interiors and exteriors of buildings (dorms, offices, and a chapel), janitored classrooms, and helped tear out and remove an old railroad. At Normal I worked at several jobs simultaneously: handyman for multiple families, washing dishes and glassware in a restaurant and a chemistry department, and serving as biology department teaching assistant and stockroom clerk. As a graduate student at Ohio State University I was of course a teaching assistant. During the first summer break I bottled milk at the university dairy and later made illustrations for an entomology textbook being authored by two professors: my eventual doctoral advisor, Donald J. Borror, and Dwight M. Delong.

My roommate, across nearly all four years of undergraduate work, and ultimately my 60-year closest and most influential male friend, was the late Dr Carl Walter Campbell. He was, like me, an Illinois farm kid. As a University of Florida professor, he came to be regarded as the first-ranked tropical fruit horticulturist in the world and one of the three most important of all time. As students, Carl and I worked at the same jobs, took almost all the same courses, sang together in choirs, glee clubs, and quartets, and for nearly two years cooked most of our meals in basement kitchens. Among other things we learned how to make a meal of bread and milk-and-flour gravy that included half a pound of pig liver, the last item costing seven cents. Carl and I thrived on thinking of ourselves as deep and profound thinkers, and serious critics of all that surrounded us. No topic was outside our limits. While undergraduates, we generated a strong interest in American folk music and occasionally performed together. As a result I learned to play, rudimentarily and left-handed, guitar, fiddle, harmonica, and five-string banjo, and I searched out and saved a few nineteenth century local songs, known only to one or two of the then oldest people in the farming community of my childhood (Alexander ms 2). Carl, who died in 2006, was an extraordinary intellectual influence across my entire adult life, but especially during our undergraduate years. In 2006, he and I received honorary doctorates in science from Blackburn College at the same podium on the same day without the then Blackburn officials knowing beforehand of our relationship. As well, only two years apart, we received the inaugural lifetime achievement awards of our most appropriate but quite different scientific societies. We each had a hand in starting one of those now international societies, dealing, respectively, with tropical fruit horticulture and human behavior and evolution.

Although I rejected a career in agriculture after only one year in college, I never lost my attachment to farming as a way of life. As a result, Lorrie and I have operated an 80-acre farm continuously for 35 years. We have raised mostly hay, and maintained several pastures; continuously bred and raised horses and cattle; and started and trained riding horses. Our major operation has been maintaining breeding herds of horses to support my effort to understand and write about horse social behavior and the horse–human interaction (Alexander 2001a, 2006b, ms 3). Included among our crops were our hard-working, hard-thinking daughters, Susan and Nancy, now school teachers in California, and, more recently, four diverse, exceptional, and dear grandchildren who continue to visit us regularly: Alex and Lydia Turner, Morgan Johnson, and Winona Johnson-Alexander.

I always liked school, but I sometimes had trouble staying with its specific projects. If I had been in elementary school more recently, I might have been diagnosed as a victim of one of the now widely discussed short-attention-span afflictions. As a freshman in college, having to study hard for the first time in my life, I realized that, compared with fellow students in my study hall, I had difficulty continuing an assignment until it was finished. I contemplated this problem seriously, until I generated the conscious strategy of continuing an intellectual activity only until my interest began to lag, then changing immediately to the most attractive alternative and repeating, returning to the temporarily abandoned projects one by one – over and over if necessary – until all were completed. I think I eventually learned to follow this procedure without conscious effort. It has made me an insufferably frustrating co-author and caused my working spaces to be cluttered to the point of being intolerable to others. But, even though I may have taken the strategy to extremes, it seems to have worked reasonably well. Several years ago a publisher's representative sat down with me at a meeting of the Human Behavior and Evolution Society, noted that her company had recently published the autobiography of a certain prominent evolutionary biologist, and suggested that I might also write an autobiography for them. I replied that I hoped to write an autobiography someday, but it was not an immediate goal. I said I had a number of partly finished book manuscripts on my computer that I regarded as more pressing. After a moment she asked how many book manuscripts I had on my computer. I answered immediately and truthfully, "Fifty-five." After a significant period of silence (or a period of significant silence!), she rose and said, "Thank you," as she departed without looking back. I still have about 40 of those manuscripts to go, so I have little hope of reversing her opinion that I am stark raving mad.

In the fall of 1949, as a college senior, I applied for a high school science teaching job in southern Illinois, was interviewed, and accepted the position. While the contract was in the mail, two professors, Ernest M. R. Lamkey (bacteriologist) and Donald T. Ries (entomologist), heard about my prospective job and phoned me repeatedly, urging me instead to consider graduate school. I told them I knew nothing about graduate school, and, because of my father's serious (soon to be terminal) illness, neither my parents nor I had funds for such a purpose. As a result, each of these two thoughtful professors secured a teaching fellowship for me, by communicating with old friends, Ries with Howard Evans at Cornell and Lamkey with Alvah Peterson at Ohio State. I chose Ohio State because it was closer to my home in Illinois (thus, to my ill father), and entomology over botany and zoology, because of how well I had liked Ries's undergraduate entomology course. Otherwise, according to Howard Evans, I would have been his first doctoral student at Cornell. I likely would have studied wasp behavior because I was already attracted to it. Instead I became the first doctoral student of Donald J. Borror and studied, across the first phase of my professional life, speciation, acoustical behavior, sexual behavior, and aggression in the singing insects, and the evolution of life history patterns in crickets. My Master's advisor at OSU was Lamkey's old college roommate, Alvah Peterson.

A week after I obtained the B.Sc., Lorraine Kearnes, whom I met at Blackburn, and I were married and left immediately for Columbus, Ohio. On my first day at OSU, before classes had commenced, I talked with Dr Peterson about courses. One of them, we decided, would be an independent research course on dragonflies, an insect group that had fascinated me while I was amassing an insect collection for an undergraduate entomology course. I thought of dragonflies as the dinosaurs of the insect world. I had first paid close attention to them in an abandoned and partly flooded gravel pit in Normal, Illinois. When I left Peterson's office that afternoon I went directly to the Olentangy River, carrying an aquatic net and jars, and began to collect dragonfly and damselfly juveniles. By the end of the term I had distinguished the juveniles of all of the local species, and matched all but one of them to the known adults in the area. That one may have been a new species with cryptic adults. I never found out. But I had become permanently imprinted on the Odonata, and I have continued across many years an effort to explain their unique – perhaps uniquely bizarre – copulatory behavior, in conjunction with my interest in the origin of insect wings and the phylogeny of mating behavior in the Arthropoda (Alexander 1961, 1967a, ms. 4; Alexander *et al.* 1997; Carle 1982).

After the first term at OSU, I nearly dropped out of graduate school because of a B− grade in Donald J. Borror's course on insect systematics, which I regarded as my most important course. I studied alone that first term, knew virtually nothing about graduate school or the department, and believed (erroneously) that Borror couldn't possibly expect us to learn "all that stuff." Lorrie earnestly talked me into continuing one more term, during which I managed to elevate my almost defunct self-respect by obtaining the highest grade in the second term of Borror's (to me, and to many others) all-important course.

In August 1951, I completed a master's degree with a thesis on the biology of arthropods living inside shelf fungi. I collected fungi everywhere I could within about 100 miles of the University, placing them in paper bags and watering the fungi at intervals, saving some immatures for illustration, and allowing the rest to become adults so that I could identify them. The entomology graduate students at Ohio State then were a wonderful group. Regardless of the nature of their thesis work, nearly every one had chosen a particular group of insects to study, biologically and systematically. Carloads of entomology graduate students traveled to unglaciated southeastern Ohio on weekends, often sleeping overnight in the woods. It was an exhilarating and rewarding time that I believe had a strong influence on my later scientific activities.

During the last part of that summer I completed 50 or 60 drawings for Borror's entomology text (including a drawing of a male ant used on the cover spine) before entering the Army in September. Most of my drawings are still in that remarkable textbook, which may have set a record by being continuously in print, and in classroom use, for 54 years; it is currently a text in the introductory entomology course at the University of Michigan. Imagine my pleasure when, for the most recent (7th) edition of what is now called *Borror's Biology of Insects*, I received a request from Charles A. Triplehorn, one of the current authors, and a close friend and graduate student colleague, 1950–51, for use of two of my more recent drawings.

In the fall of 1951, I was drafted into the Army – probably because my conscience, from having experienced the extreme patriotism of WWII, prevented me from completing the examination that determined whether or not a graduate student could be drafted. It was later explained to me in front of the Monticello, Illinois, courthouse and all the other departing inductees, that I was drafted out of graduate school because the fellow who otherwise would have gone had to stay home and help his father harvest corn. I accepted this decision with a faint humor but without resentment. In Chicago I was invited to apply for a direct commission. When I realized I would have to serve three years instead of two, plus the six months before the commission could be approved, I discarded the application, enabling me to return to Ohio State in the fall of 1953. Luckily for me, the war was formally ended less than two weeks before I was scheduled to be shipped to Korea as an infantry rifleman, one of the most dangerous roles in an extremely dangerous war. After basic training I became an entomologist in the Medical Service Corps at Fort Knox, Kentucky, in the winter inspecting mess halls and in the summer locating potential malaria-carrying mosquito breeding sites for the pest control unit. I was assigned to the latter job because of the concern that returning soldiers might bring Korean malaria back with them. During that time I also explored the caves of Fort Knox with a fellow soldier, became interested in speciation in the blind cave beetles there, and hoped for a while to do my doctoral research on that problem at the

University of Chicago, with Allee and Emerson, until I learned that both had retired. In 1960, Emerson served on the committee that awarded me the AAAS Prize.

Career stage 1: the singing insects

While in the Army I successfully sought to work with Donald J. Borror when I returned to OSU. When I walked into his office he handed me a new Magnemite battery-operated tape recorder with a hand-cranked spring-powered motor, and D cell batteries powering the recording apparatus. It was one of the first battery-operated tape recorders made following American acquisition of tape recording technology from the Germans after winning the war. Borror simply said to me, "Why don't you take this out in the field and see what you can learn about the singing insects." I did that, and by late summer I had managed to tape-record, collect, and identify all of the species of crickets, katydids, and cicadas in the vicinity of Columbus, Ohio. Included were many undescribed and misidentified species. Dr Edward S. Thomas, an astute and kind lawyer and natural historian curating insects in the Ohio State Museum, who knew most of the singing insects of Ohio well, took me under his wing. I also wrote for advice to Bentley B. Fulton, then a professor at North Carolina State. He sent me a wonderful letter welcoming me to the study of singing insects, and telling me exactly how he would proceed in my situation. Later I visited him, and we became good friends. When he died, I was invited to honor him by lecturing to the general session of the North Carolina Academy of Science. I titled my talk *Dr Bentley B. Fulton and the Singing Insects.*

Among other things, Fulton was the first to hybridize different species of crickets and show, by using ingenious devices he constructed himself, that the songs of the hybrids were distinctive, and never heard in nature despite micro-geographic intermixing of individuals of the species involved. Though he didn't mention it, his (1933) experiments also showed that species differences, as well as "complex organs" within species, are due to a history of what Darwin called "numerous, slight, successive modifications" (see also Alexander 1968b, 1978, 1979, ms 1). Fulton thus demonstrated that species differences can be explained by micro-evolution, and that, at least in this case, so-called macro-evolution is simply micro-evolution extended. The relevant one of Darwin's several remarkable challenges was: "If it could be demonstrated that any complex organ existed, which could not possibly have been formed by numerous, successive, slight modifications, my theory would absolutely break down." (Darwin 1859, p. 189; for other challenges, see Alexander 1979, ms. 1). Needless to say, not this challenge, nor perhaps any of Darwin's other challenges, has been met. This particular challenge of Darwin's, and Fulton's extension of it to species differences, nullifies a major argument of those who think "intelligent design" is necessary to explain species differences (see also Alexander 1978, 1979, 2008, ms 1).

My first contribution to science was a paper delivered in 1954 at the Ohio Academy of Science meetings in Athens, Ohio. The title was *Songs of the House Cricket*. It was an effort to analyze and explain functionally the array of stridulatory signals made by the introduced European House Cricket, *Acheta domesticus* Linnaeus, using the tape recorders acquired by Borror, and the only OSU audiospectrograph, made available by Joseph Hynek (later director of the UFO project) in the astronomy observatory. The talk was something of a disaster. I had ambitiously – and recklessly – planned to synchronize slides of audiospectrographs of songs with tape recordings of the same songs. Perhaps this had never been attempted before, at least publicly. Unknown to me, the OSU professor, Carl Reese, who agreed to show the slides for me, had opened his car door into the street during the noon hour, just before my talk, and a passing motorist had slammed the car door around against the side of his car. The poor man came in late, still traumatized, and immediately got my slides irreversibly out of synchrony with the tapes. As a result the talk was hopelessly confusing and ran well over its time. In charge of the session was Alvah Peterson, a rigid taskmaster with respect to time-keeping in scientific meetings. He was known for responding to pleas for a little more time by calling for a vote from the audience on whether the speaker should be allowed to continue. No one wanted to run that gauntlet, and Peterson was not lenient just because I had been his master's student. Somehow I struggled through that first talk at a scientific meeting, but at the end there was considerably more laughter than clapping.

In 1955, I delivered two talks on my research at the Cincinnati meetings of the Entomological Society of America. One of the sessions, a symposium on systematics, was hosted by Professor Theodore H. Hubbell, then Director of the Museum of Zoology at the University of Michigan. Hubbell and I had a mild disagreement in the discussion following my talk, and I uncompromisingly expressed a strong view. He thought I was describing species without having located any morphological differences between them, although I hadn't actually done that – yet. He ducked his head, in what I would later learn was his politely humble manner, and asked, "What about the poor curator who cannot distinguish specimens of the different species?" I replied – I'm not sure how much defensively and how much arrogantly – "Well – if I were a curator I would rather label a specimen *Gryllus* sp., and know it was correct, than label it *Gryllus assimilis* and know it was wrong." At that time I "knew" I would never be a curator because I had declared more than once that I would not take such a job; nor did I know that Hubbell had labeled virtually all U.S. *Gryllus* specimens in the University of Michigan Museum of Zoology as *Gryllus assimilis*, and of course added on each label: "det. T. H. Hubbell."

Some time later, I learned that Hubbell and Delong had subsequently been on an ESA committee together, and had discussed me as a possible job candidate at the University of Michigan. As a result, even though the Museum of Zoology had hired a second entomologist in 1956, an unprecedented third position was established, and I was invited to give a job seminar. After my seminar, in a five-minute encounter in the darkness of the back porch of Hubbell's home, the chair of the Zoology Department, Dugald E. S. Brown, a molecular biologist, hired me half-time in each of the two units with a verbal offer of US$5200 for a 12-month position. There were no other candidates. This whole event is one of several I have described in this essay that probably can no longer occur "legitimately" in academia in America.

In August 1957, Lorrie and I moved our family to the University of Michigan, and I began as Instructor in Zoology and Curator of Insects. Almost 44 years later, following a five-year period as Director of the Museum of Zoology, I retired, delighted to be the Theodore H. Hubbell Distinguished University Professor Emeritus of Evolutionary Biology and Curator Emeritus of Insects. Some time before the retirement I asked Dr Hubbell, then in his late 80s, why he had hired me after what I remembered as my smart alec performance in our long-ago interaction in Cincinnati. True to his "Prince of a Man" nature (as he was designated by his friend and colleague, Dr Irving J. Cantrall), Dr. Hubbell replied simply, "I respected your opinion."

I have always regarded my student life as a series of accidents and last-minute assists from perceptive people, mainly teachers. If Helen Burgoyne had not paused in a hallway in the fall of 1945, and asked me if I was going to college, I may not have gone. If Professors Lamkey and Ries had not invested considerable time and effort in encouraging and enabling me to start graduate school, I almost certainly would never have done it. At the end of my first semester as a graduate student, if Lorrie had not pleaded for me to try one more term, I definitely would have dropped out. If Dwight DeLong had not secured a truly last-minute 15-month Rockefeller Foundation postdoctoral position for me when I failed to obtain a suitable position after graduating, I likely would not have remained in academia. If Donald Borror had not passed on to me his own invitation to speak on singing insects at that 1955 Entomological Society of America symposium on systematics, if Theodore H. Hubbell had not been the chair of that symposium, and if Hubbell had not subsequently been on that ESA committee with DeLong, a position would not have been created for me at the University of Michigan. It is difficult to imagine what might have happened. I had been offered a temporary position by the chair of the entomology department at the University of Illinois, but I have always believed that I would have gone back to Illinois as a farmer.

Despite the spur-of-the-moment nature of my choice of entomology for graduate work (rather than zoology or botany), I never regretted it, largely because of three truly outstanding entomology professors at the Ohio State University, whose memories I revere: Alvah E. Peterson, Donald J. Borror, and Dwight M. Delong. They and Theodore H. Hubbell primed the pumps of whatever success I have realized. Borror started me on a wonderful set of problems when he handed me one of his Magnemite tape recorders. He also turned out to be the kind of advisor who demonstrates continually how to get important things done and lets his students conduct their own projects. There could not have been a better advisor for me.

By the time I had completed my doctoral thesis I had shown that nearly a third of the species of singing insects in central and southeastern Ohio were as yet unrecognized, and others were recognized but wrongly classified, wrongly understood, or wrongly named. I was astonished that almost half of the singing insects on the OSU campus were undescribed. I had become fascinated by several special problems in crickets, including mating behavior, male aggression and territoriality (Alexander 1961), the evolution of life history variations (Alexander 1968a), and a new method of speciation that Robert S. Bigelow and I later called allochronic speciation (Alexander and Bigelow 1960). A more appropriate adjective would have been allohoric – referring to seasonal separation of adults – but we didn't like its sound, or the possible confusion that might have been engendered, involving gradual sympatric seasonal divergence in the seasonal mating period, which is not likely to result in speciation.

In 1959 Bigelow and I presented the speciation paper at the Darwin Centennial meeting of the Society for the Study of Evolution at the University of Chicago, and later published it in *Evolution* (Alexander and Bigelow 1960). Neither of us doubted that we were correct, despite significant skepticism and subsequent molecular information convincing others that it could not have happened as we said (Mayr 1963; Harrison 1979). We knew that species which overwinter in two different life stages, so widely separated on the life cycle that they breed non-overlappingly in their brief adult seasons, are subject to speciation via accidental and more or less sudden seasonal separation of adults (Alexander 1968a). We knew that there are several pairs of sister species of Orthoptera with this particular difference. A third species that we regarded from the first as having some of the relevant attributes of the ancestor of the two allochronic but phenotypically, ecologically, and geographically almost identical species turned out to be able to produce both life cycles among the offspring of a single female (Walker 1980; Masaki and Walker 1987; R. D. Alexander, unpublished). We also realized that the strongly divergent selection resulting from the dramatic shift between the two life cycles could possibly result in genetic happenstances that could confuse the effort to place the speciation event temporally, or on a phylogenetic tree of *Gryllus* species. The only questions seem to be how anciently and how often such speciation has taken place. We came to understand the difficulty in verifying precisely how even "ordinary" instances of speciation take place, difficulties that restrict biologists to understanding speciation mainly from broadly comparative study – including representations of all the stages of speciation by combining multiple instances of speciation, rather than being able to view all stages of speciation in single cases. These difficulties cause biologists to withdraw from unusual or unique forms of speciation, in particular when such cases require learning obscure or unfamiliar details of the biology of the organisms involved (Alexander 1967c).

My work with cricket biology eventually resulted in an effort to compare the evolution of mating behavior in all arthropods (Alexander 1967a) and generated the theory, still unfalsified, I think, that insect wings were courtship devices prior to their becoming flying organs (Alexander and Brown 1963), whether or not they actually began with still another function (cf. Kukalova-Peck 1978, 1983). This suggestion correlated with the discovery that primitively wingless hexapods do not copulate directly, and that the earliest copulations were almost certainly luring acts in which the female mounted the male. As with modern crickets and some others that copulate female-above, the female is stimulated to mount and remain mounted by a wide variety of glands and other stimuli on the male's back, usually exposed by the male lifting and vibrating the wings, and sometimes including the female eating the male's wings (Alexander 1967a; Alexander and Otte 1967).

The area I was covering in my field work on singing insects kept expanding outside Ohio, and because of a Rockefeller Foundation postdoctoral grant I was able to work in most of the eastern United States. After moving to Michigan in 1957, I began to include all of the U.S., and Mexico down to Cuernavaca. Eventually I was able to distinguish the songs of nearly 1000 species of mostly North American crickets, katydids, and cicadas. Once a song has been learned, the geographic and ecological distribution, abundance, seasonality, and diurnal activity of that species can be learned perhaps more quickly than can be accomplished with any other kind of organism; and locating and collecting individuals is also much quicker and easier. The reason is that among sympatric and synchronic species, each species has a unique song, and the songs can not only be used to locate and approach individuals, but also are distinguishable while one is driving, sometimes at speeds of 30–40 mph. Some insect songs can be recorded continuously with a microphone in a parabola held in the window of a slow-moving vehicle, thereby capturing the songs of all singing males in a transect along the road, demonstrating continuous changes in songs, for example, across hybrid zones (for extensive data from a long and complicated hybrid zone, see Alexander 1968b). On many occasions my students and I have been able to capture the only individual heard singing across hundreds of miles, even though it was often singing in a hidden location, or in the top of a tall tree. I learned that the field crickets (*Gryllus* spp.), said by James A. G. Rehn and Morgan Hebard in 1919 to be a single species all over the New World (a conclusion repeatedly maintained by Rehn), included a large number of different species. Three decades ago, as my primary interests were changing, I turned over all of my *Gryllus* specimens and records, including scatterdiagrams of songs and morphology, to Dr David Weismann, who presently estimates there are at least 50 U.S. species in the genus (personal communication). I also made all of my singing insect materials available to Dr Thomas J. Walker.

One of the discoveries that puzzled me, in studying the singing insects, was the absence of character displacement (Alexander 1969). I could not convince myself that this paradox had been resolved by anyone. Eventually I decided it was important to work on a different continent and compare the two faunas with regard to this and other questions. Daniel Otte, my third doctoral student (following Kenneth C. Shaw and Mary Jane West), and I took our families and flew to Australia in 1968, using funds from National Science Foundation and Guggenheim grants, and from the University of Michigan, which allowed me to take a six month sabbatical leave followed by nine months of off-campus duty. Otte and I traveled 46,000 miles in 12 months in Australia, in a Land Rover, and discovered approximately 376 new cricket species, and 492 species in all (Otte and Alexander 1983). We also came away with recorded songs of approximately 35 cricket species that we were never able to collect, chiefly because they lived in the tops of tall trees in jungles where the trees could not be felled because of density and vines.

As in the U.S., we found no obvious cases of character displacement. Using songs, we were able to develop better maps of distribution of even the most commonplace species than could have been accomplished by using all of the Australian specimens in all of the collections of the world. On our first trip north in Australia we predicted, and then were able to demonstrate, that two species of *Teleogryllus* – being used in a large experiment in Melbourne, and expected to cause field hybridization that would produce sterile or out-of-season hybrids and interfere with rangeland depredation by field crickets – were living in sympatry without hybridizing. When we reported this to the experimenters, from a region none of them had inspected, they checked what we had said, and abandoned their experiment. We also discovered that what was regarded as two or three cricket species depredating the outback rangelands was actually many times that, thus an enormously more difficult proposition. I have always believed that these discoveries alone more than justified the financial cost of our work in Australia, scoffed at by the media (e.g. Paul Harvey), as well as Indiana's U.S. Representative Richard Roudebush. The eventual result was a confrontation between the Director of the National Science Foundation and the Congress regarding two grants, mine and that of Gordon Orians for biological work on red-winged blackbirds.

Since our monograph on Australian crickets was published (Otte and Alexander 1983), Dan Otte has gone on to become the world's all-time outstanding cricket systematist, doubling the known world species of crickets while also expanding his thesis work on grasshoppers in comprehensive and superbly illustrated monographs of the North American fauna. When I once asked him why he turned to crickets rather than continuing solely with the grasshoppers with which he had worked as a graduate student, he said simply, "Australia."

One of the most amazing groups of insects, studied by Thomas E. Moore and me primarily in the 1950s and 1960s, comprises the 17- and 13-year cicadas. Among other things we discovered that, rather than the one or two species generally accepted, this group included three 13-year species and three 17-year species, each species with a sister species having the other life cycle. Subsequently, two of my students, John Cooley and David Marshall, in 1997, discovered a seventh species, evidently derived from a 17-year population in the area where the sets of species with the two life cycles meet. This peripheral population had evidently changed its life cycle from 17 years to 13 years and eventually spread well into the 13-year species' geographic range, and as a result was still undergoing character displacement in song (Cooley *et al.* 2001; Marshall & Cooley 2000). This ongoing case of character displacement, in species with such long life cycles, and the necessarily infrequent encounters between species, fuels the speculation that one reason character displacement is so rarely observed is that it typically quickly reaches the stage at which selection is no longer favoring divergence in the relevant traits, and that condition spreads rapidly throughout its range. The details of the life histories, speciation, and acoustical communication of the periodical cicadas have made it one of the insect wonders of the world (Alexander and Moore 1962; Alexander 1967c, 1968b; Cooley *et al.* 2001).

The first time I participated in a discussion of how my lifetime interest in biology might have been generated was at a faculty lunch with several biologists at the University of Michigan 50 years ago. I was surprised to learn there that many of my colleagues had been youthful natural historians, or insect collectors, some preparing scientific papers while they were still in high school. As with Sewell Wright, some of them spoke of reading Darwin at early ages. Excepting my rambling explorations in the local woods and along the Sangamon River, and my efforts to make pets of a large number of local mammals and birds (raccoons, possums, a gray fox, 13-lined ground squirrels, white-footed mice, a hawk, a crow, pigeons, starlings, and betsy beetles), I had little experience with such things. I did have an older first cousin (one among 34) who, while in high school, netted butterflies, ran strings lengthwise through their bodies, and used them to decorate his room. On this account I regarded him as perverse, and still do; perhaps he was, because he became a daredevil pilot rather than an entomologist, eventually dying in a crop-dusting accident in Georgia, caused by a wing-dipping greeting to a Georgia farmer, which unfortunately contacted a power line.

During approximately half of my time concentrating on the singing insects, evolutionary biologists were largely restricted to studies of evolutionary pattern: fossils, and comparative studies derived from phylogenies of species. Attention to adaptations was so limited and general as to be largely trivial. It was a time when evolution was often defined, perhaps timorously, as change across time. Population genetics seemed to be flourishing, but, owing to the manner in which fitness was represented in equations, it was for decades typically practiced in such a way that the effect of differential reproduction was seen as maximizing the fitness of populations. Eventually the fallacious argument was made that rapid evolution constitutes a threat to the survival of a population because rare new beneficial mutations automatically lower the fitness of the abundant alleles already present (Brues (1964) explained the error; cf. Alexander 1988). Serious studies of evolutionary processes, especially efforts to understand evolutionary adaptation in detail, began to flourish following George Williams's 1966 book *Adaptation and Natural Selection*.

Career stage 2: evolutionary adaptation, social behavior, and the evolution of eusociality

In 1955, while I was a postdoc, and program chairman of the Columbus Entomological Society, Donald R. Meyer (an OSU psychologist) and I cooperated to bring Theodore C. Schneirla to the OSU campus to discuss European ethology, and to speak to the entomologists about army ants and to the psychologists on the ontogeny of emotions in higher mammals. As a result Schneirla became a good friend who stopped in to visit me at Michigan whenever he came to see Norman R. F. Maier, his friend and co-author on one of the earliest American texts on animal behavior. Maier, a behavioral and later industrial psychologist, was at that time the only U-M person who had received what was then referred to as the AAAS Prize (now known as the Newcomb Cleveland Prize and given for a different kind of contribution). These two men happened to be among the first people I told in 1961 – proudly, if I remember correctly(!) – that I had just won that prize. The three of us were having lunch together in downtown Ann Arbor.

When I decided to dedicate *Darwinism and Human Affairs* to the great teachers in my life, I realized with a shock that I would have to include Don Meyer. His course discussing European ethology, using Tinbergen's *The Study of Instinct* as the text (criticized severely in the course), frustrated me so that I spent most of the time between sessions figuring out how to demonstrate to him what I regarded as the error of his ways. I wasn't entirely enthusiastic about European ethology, mostly because of some of its theoretical assumptions; but I had soft spots for several of its suggestions, such as seeking to work out the entire behavioral repertoires (ethograms) of species in evolutionary terms. I also regarded Meyer as terribly lazy because he consistently came to class saying he had lost his notes, or was unprepared. He would walk into his classroom with nothing in his hands, sit on his desk facing us, tell us he had lost his notes – or something else of the same nature – and ask us what we would like to discuss. Long afterward I realized that because such behavior had kept me stirred up and angry, he had (accidentally, I thought then) taught me an immense amount. I spent most of my time between his class periods trying to find ways to thwart his arguments. Forty years after taking Meyer's course, and 17 years after including him in the dedication of my book, at a used book sale in Ypsilanti, Michigan, I found a symposium volume that included a paper of his on rhesus monkeys. In it I read with astonishment his contention that he had deliberately conducted his classes in the way that he did because he regarded formal lectures as an imperfect way to teach. There is no doubt that Donald R. Meyer and Theodore C. Schneirla influenced my life significantly, even if in directions neither of them would necessarily favor.

I think it is accurate to say that the second phase of my career as an evolutionary biologist was evidenced by a growing interest in social behavior (Alexander 1974), and that the experiences I have just described were instrumental. This interest actually began in 1954, not only from my studies of crickets, but from wondering how what is now called eusociality (societies with queens and sterile workers and soldiers) could have evolved.

Between 1954 and 1958, I was impressed by the work of Charles Michener and Howard Evans, who, in the analytical methods of that day, were approaching the problem of eusociality by matching the phylogenies of bees and wasps, respectively, with comparative studies of their behaviors that are associated with eusocial life. But I was more interested in termites than in the Hymenoptera, and eventually more interested in the effects of the process of evolution than in tracing long-term patterns. I generated the idea then that the main precursor of eusociality might be the tending of offspring until they reached either adulthood or a juvenile stage at which they could assist in the rearing of younger offspring. I searched for instances in which offspring were indeed reared to adulthood while remaining in direct association with parent(s). I was at first surprised that such a situation seemed extremely rare, except in eusocial forms, causing me to wonder whether that situation led to most or all cases of the evolution of eusociality. This question remained in my mind across several decades, as a manuscript was slowly generating, starting in the mid-1970s, in which I sought to develop this idea. I realized that if offspring were reared to adulthood, the rearing situation would have to be relatively safe. Termites were my model, and I understood that the dead logs in which many termites live are expansible fortresses made of food. It seemed to me that a newly adult offspring reared in such a safe place, particularly where successive generations of offspring could be reared successfully, might well gain genetically sometimes, by remaining in the nest and tending younger offspring, as juvenile termites do. The alternative of setting out to start a new nest would sometimes be less successful than helping in the existing nest. I had not developed the idea quite this far when I first encountered Bill Hamilton's (1964) intimidating papers quantifying the benefits of assisting close relatives. As a result, the paper that had been generating for so long, titled *The evolution of eusociality*, was not completed until 1991, as the first chapter in *The Biology of Naked Mole Rats*, and co-authored by two of my doctoral students, Katherine M. Noonan and Bernie Crespi (Alexander, Noonan, and Crespi, 1991). Noonan worked on eusocial paper wasps, and

Crespi, who was Bill Hamilton's student until Bill returned from the U-M to Oxford as a Royal Society Research Professor, was a student of Thysanoptera, in which he had discovered eusocial forms (Crespi *et al.* 2004).

My efforts to understand eusociality were greatly enhanced by my long-time association with a beetle in the family Passalidae that lived in a forest near my family's farm. As a boy I carried these "betsy beetles" in my pocket in penny matchboxes, and I made wagons and other vehicles such that I could hitch the beetles up in teams, by tying threads of "harness" to their anterior horns. I carried them to school, and to church, for times when the proceedings seemed too absolutely boring. In church I toyed at length with the temptation to allow a betsy beetle to climb the dress of some girl – any girl – who happened to be sitting in front of me. Luckily, I never was bold enough to allow a climbing beetle to reach bare skin.

I have since admired passalids, and I watched their behavior in terraria in my office across decades. In the 1970s I wrote and published a laboratory exercise for introductory zoology, and used them in that course, which was enrolling *c.* 525 U-M students each term, for the several years that I taught the course (Alexander 1967b). The passalids I used have a rich repertoire of stridulations, including acoustical exchanges with their larvae, which evolved their stridulatory device independently of that used by their parents. A tongue and groove fastener keeps the adult's thick, tough, black, polished forewings together (passalids are also called "patent leather" beetles). When the forewings are pried apart, and their complexly folded yellowish translucent underwings are extended, the dorsal surface of the abdomen is revealed to be as clear as Cellophane, so that the movements and structural features of the internal organs of the beetles can be watched as long as is desired. When the beetles are eventually released, they carefully fold their underwings, snap together the elytra, and walk off undamaged, ready to repeat everything for the next student.

As an added attraction, these passalids carry up to 30 or more species of mites on their external surface, many of them specific to particular locations on the beetle. But I eventually realized that using them in large zoology classes has the potential for extinguishing the North American species. They are already gone from two of the habitat niches in which I initially found them, one in Illinois, the other in Michigan. Luckily, those who followed me in teaching the behavior labs in introductory biology at Michigan were not as entranced with passalids as I was, and dropped that exercise when I stopped teaching the introductory course. They also dropped my exercise on cricket behavior (Alexander 1972a) and another of my design that consisted of bringing in dozens of fragments of "habitats" in appropriate containers so that the 525 students (in laboratory groups of 25–35) could have two-hour indoor "field trips" in which they could sort and distinguish large numbers of species (and contemplate the concept as well as the diversity). They could also see various life stages in metamorphosis, and directly observe predation, parasitism, mutualism, and other biological phenomena, involving members of nearly all animal phyla, alive in fragments of their "natural" habitats (Alexander 1972b).

My fondness for passalids, coupled with a 1947 *Scientific Monthly* paper by Clarence Hamilton Kennedy (then an OSU professor emeritus), titled *Child labor of the termite society versus adult labor of the ant society*, were instrumental in generating the questions

I raised about eusociality in the early 1950s, leading me eventually to argue that Hamilton may not have been correct in his rather tentative suggestion that haplodiploid sex determination, and the resulting closer genetic relationship of full sister workers in the Hymenoptera (3/4 rather than 1/2 genetic overlap), might explain why the Hymenoptera evolved eusociality 13 or so times and the rest of the insects only once (termites). Noonan, Crespi, and I argued instead that the chief precursor of eusociality was life in a relatively safe location coupled with parental care up to either adulthood in the offspring, or to some earlier life stage that enabled the offspring to take on duties within the nest that benefited younger siblings, or aided the reproductive adults in other ways (Crespi has since labeled this, "Alexander's Factory-Fortress Model" for the evolution of eusociality. We argued that the degree of risk in starting a new family, weighed against the safety of the parental nest, the possibility of aiding close relatives, and the potential for expansion of the nest (allowing sizable increases in family or colony size), could be the appropriate variables. Beyond the mere plausibility of this argument, we used what we thought to be the best comparisons available, the abundance of extensive parental care among extant non-eusocial species closely related to the eusocial Hymenoptera (extensive, but not lasting until the offspring achieved adulthood while actually associating with their mother), and the rarity of continuous direct parental care to adulthood in the absence of eusociality (meaning that hymenopteran females that merely stock with food items and then close the nest and leave it are not as likely to give rise to eusocial descendants as females that feed offspring directly to adulthood and perhaps as well continue to defend the nest until the offspring are mature).

From the ancestors of probably tens of thousands of non-eusocial extensively parental Hymenoptera there had evolved 13 or so cases of eusociality, compared (when we began these considerations) to one case in all other insects (termites). Among all other insects, there were then known only a handful of cases of parental care lasting to or near adulthood of the offspring, and a few hundred with somewhat less extensive parental care. We concluded that the termites, perhaps more than the Hymenoptera, had crucial special advantages. First, they live in expansible fortresses made of their food (dead logs and trees), enabling them to be relatively safe at all times – even sufficiently as to favor neoteny – and to evolve step-by-step increasingly effective defensive structures and behavior. Second, insects with gradual rather than complete metamorphosis not only can produce opportunities for older juvenile offspring to aid younger juveniles, but can also allow juvenile stages to evolve gradually, to become increasingly better helpers as they move toward adulthood. We noted that entomologists had long referred to termite workers as "permanent juveniles" that have evolved to senesce and die without assuming the usual attributes of adults. Hymenoptera could become significant helpers only as adults, after a (typically) non-helping, almost entirely dependent larval stage followed by a non-helping pupal stage. Moreover, neither hymenopteran juvenile stage is of a nature that – as with gradual metamorphosis – facilitates a step-by-step improvement in helpership features as the juvenile grows and matures.

Long after I had generated most of these arguments, I realized that my hypothesis was vulnerable. A great many mammals and birds rear offspring to suitable stages for offspring helping, and have gradual metamorphosis, but at that time none were described as being eusocial. I could have argued that mammals and birds haven't been around, or parental, long enough, but that seemed a lame proposition. In the expansible food-filled fortresses of termite-like insects, new adults or late juveniles might not have as much impetus to leave the parents' nest immediately. But most birds and mammals don't live in such long-term safe and expansible hideaways. Indeed, the altriciality of songbirds has been attributed to the importance of rapid growth and development, facilitating earlier departure from the increasingly unsafe nest (Ricklefs 1983; cf. Alexander 1990b).

I decided that the best way to explain my argument was to generate an elaborate description of a hypothetical vertebrate, which, if it existed, would be eusocial. Starting around 1976, I did this, and presented the argument, including 15 or 20 predicted attributes of the hypothetical species, in a series of six lectures given in North Carolina, Michigan, Colorado, and Arizona (3 lectures). At Northern Arizona University, Terry Vaughn, a mammalogist who had recently been on sabbatical leave in Africa, introduced me to naked mole rats (NMRs) after telling me enthusiastically that the hypothetical eusocial vertebrate I had just described in my lecture was "a perfect description of the naked mole rat of Kenya!" At that time no one seemed to be entertaining notions of eusociality in any vertebrate. I had never heard of naked mole rats. I asked Terry Vaughn what was known about them, and he said nothing much except that they live underground in groups. I asked him if anyone was working on them and he told me about Jennifer Jarvis, a professor at Capetown University in South Africa, previously at the University in Nairobi, Kenya. He said that, along with some others, she was interested in their physiology because of their virtual hairlessness and their lack of control of body temperature. I wrote to Jenny, explained my hypothesis, and asked a series of questions designed to tell me whether or not NMRs are eusocial. Her prompt replies virtually demonstrated that they are. At the time I was completing *Darwinism and Human Affairs*, and I decided I could not go to Africa until that book was in press. I asked my former doctoral student, John Hoogland, if he and his wife, Judy, would like to go with Lorrie and me to visit Jenny and get her to go with us to Kenya to study and capture some NMRs. John decided not to go because he wanted to remain concentrated on his studies of prairie dogs. I approved of that decision, and the world can see from John's magnificent work on prairie dogs that it was a good one (e.g. Hoogland 1995). I then asked two other former students, Paul Sherman and Cynthia Kagarise Sherman, if they would like to participate in the study. They were enthusiastic, and the four of us went to South Africa in December 1979. When we arrived, Jenny presented me with a manuscript arguing that NMRs are eusocial. I cannot deny that I felt a twinge of proprietorship about the seminal idea, but fortunately I elected simply to help her with the paper, and spent most of that first night sitting on the cover of the toilet seat in the bathroom of Lorrie's and my hotel room, working on it while Lorrie slept. I suggested a more direct title, and worked over the entire paper, handing it back to her the next morning. We asked her to come to Kenya with us and offered to cover her travel expenses and food. She could not come with us immediately, so we went on ahead and waited in Nairobi for her to arrive. There she arranged for us to rent a Land Rover. The five of us went to Mtito Andei, between the game parks Tsavo East and Tsavo West. There we engaged the services of a local Kikuyu man, Anthony Simon N'Dalinga Chondo, who had previously helped Jenny capture NMRs. With Jenny's and N'Dalinga's help we collected about 120 individuals, placing them in two sizable flat tin containers, and carried them by plane back to the University of Michigan and Cornell University.

Jenny brought with her to Kenya her manuscript, which she had reworked to reflect my comments. Paul and I both read it this time and commented critically. Some time after we had returned to the U.S., Jenny sent me the final version of the paper, telling me that *Science* had rejected it and asking what I thought she should do. I worked through the paper again, reducing it substantively without, I believed, removing anything crucial, and advised her to resubmit it, behaving as if the editor had invited her to improve it for possible publication. Then I contacted the *Science* editor, arguing that the paper was the most important mammal discovery of the twenteith century, that it certainly would be published, and that it should be published in *Science*. This time it was accepted (Jarvis 1981). It was surely no accident that the paper was initially rejected. It was in need of further editing, but, more importantly, as with perhaps most biologists then, the reviewers must have found incredible the notion of a mammal with queens and workers. They could well have supposed that Jenny had been influenced by unnecessarily exuberant or even mentally aberrant entomologists! Across the next few years, the team of NMR enthusiasts agreed to work on their separate projects, meeting for discussion at least once in Ann Arbor, cooperating in wonderful good humor, and holding off separate publications until the volume on the biology of naked mole rats was finally produced (Sherman *et al.* 1991).

My former doctoral student, Stanton Braude, who has now devoted more than a quarter of a century to the field study of NMRs in Kenya, published a list of my predictions about vertebrate eusociality (Braude 1998). Although I (sadly!) did not predict either hairlessness or heterothermy, the set of predictions I used in my lectures in the 1970s almost certainly matched no species in the world except the naked mole rat. I was delighted when, concerning those eusociality predictions, the Austrian mathematical ecologist Karl Sigmund, in his 1993 book on mathematical ecology, wrote (p. 118) that, "This splendid feat of theoretical biology ranks with the prediction of the planet Neptune by astronomers." Later I transmitted to him, via one of his colleagues, my contention that predicting eusociality in one animal species among at least tens of millions is surely incredibly more difficult than predicting one more planet in a "puny" group of eight. I cautioned the messenger to explain that I was grinning mischievously when I gave him the message. He assured me with a smile of his own that, "Karl will understand completely!"

Passalid beetles are not yet absent from the still developing theater concerning the evolution of eusociality. More than 30 years ago, the late botanist Laura Berkeley, and subsequently her husband, Jack Schuster, carried out with me undergraduate research projects on the North American passalid species I had been watching in terraria in my office. When Jack asked my advice about continuing to work on passalids in graduate school, I recommended that he work in Florida with my Ohio State graduate student colleague, Thomas J. Walker, a superb scholar studying mainly singing insects. Jack did that, and among other things became one of the foremost students of the world fauna of

Passalidae. In March 2007 he came from Guatemala City to the University of Michigan to examine Passalidae in the Museum of Zoology collection. There I peppered him with questions regarding whether any of the 600 or so world species of Passalidae tend their offspring in such a fashion as to fit my model of incipient eusociality, and might have become fully eusocial. To be fair, searching for eusociality has not been a central theme in Jack's life work as a passalid systematist (but see Schuster and Schuster 1997). It is also possible that, as the variety of eusocial species continues to grow, we will have to generalize and perhaps simplify or expand the definition of eusociality. Jack and Laura Schuster have reported that most Passalidae live in family groups, including both parents, larvae, pupae, and teneral mature offspring. Young passalids "must eat the feces of the mature adults" (inoculated with bacteria and fungi from the digestive tract of adults). "Larvae and adults cooperate in pupal case construction and teneral adults repair pupal cases of siblings." These kinds of interactions qualify as "complex subsociality" or incipient eusociality and seem to support the "factory-fortress" hypothesis (see above). I continue to regard passalid beetles as an important frontier yet to be crossed in the study of eusociality. This transition may, however, be much more unlikely for Passalidae than for termites, because Passalidae suffer from the handicaps of all holometabolous insects with respect to generating helpers among their juveniles.

Career stage 3: evolution and human behavior

Until I entered graduate school I had never been exposed to even the possibility of taking a course in evolution. I have no memory of any undergraduate or graduate course teaching me anything significant about the evolutionary process. Unlike my colleagues at Michigan I had not read Darwin, or any other documents that caused me to think about evolution. As a doctoral student I tried to understand Sir Ronald A. Fisher's 1930 book, but I was studying species and started with that chapter. I too hastily decided that Fisher didn't understand species and speciation, and neglected the rest of his book until I co-taught evolutionary ecology at Michigan with Don Tinkle. Beginning with that course, Fisher's essays on topics such as allelic dominance, sex ratio selection, heroism, runaway sexual selection, and the first quantification of kin selection – involving bright color in poisonous caterpillars moving in sibling groups – began the process of making him one of my biological heroes for his contributions to adaptive behavior. It is telling that modern biologists took so long to understand Darwin's various challenges, and as well to understand Fisher's adaptive hypotheses.

Although there was one course in evolution taught at Ohio State in the 1950s, I don't think I ever knew a graduate student who had taken it. Instead we went *en masse* to the geology department and fulfilled the evolution requirement by taking a course in paleontology. We sacrificed process for pattern because we knew, in a vague way, that evolution courses based on process tended then to be fuzzy and often simply wrong. Even population genetics was generally regarded as frustrating; and of course we were correct in being skeptical because there was little thought of assessing levels at which selection operated most strongly, therefore no way to predict or understand directions of selection. Williams's arguments provided the basic understanding that allowed biologists and others to begin to examine organisms in light of the evolutionary process confidently and effectively.

Unfortunately, the human-oriented social sciences, medical sciences, political sciences, and some other formal activities had already generated answers to their various questions and established research languages and strategies in the late nineteenth century and early twentieth century. Religion, of course, had done so long before. Along with negative views about the ethics or fairness of some human adaptations, and too-frequent oversimplifications of their developmental backgrounds – both made more evident by increased attention to how the evolutionary process works – this situation created a general tendency to doubt, avoid, and derogate virtually all "adaptationist" approaches. It did not help that some senior and distinguished evolutionary biologists, who did not wish to go back and straighten out their now revealed errors, as well as others with political and ideological stances, also took up the cudgels against Williams's arguments. This widespread negative attitude toward efforts to explain human adaptations has by no means disappeared, but it has certainly waned, at least in some circles.

Because biologists did not soon enough provide a way for budding social and medical scientists, and others, to incorporate the evolutionary process into their newly organizing societies, attitudes toward accepting such a ponderous and seemingly intrusive paradigm would probably have been skeptical from the start. Biologists have been just as reluctant to incorporate studies of humans into their own departments. As a result, biology and all the other disciplines that were trying to understand the human species have tended to remain on separate paths. This situation has surely been a significant force in delaying the study of evolutionary adaptations of the human species and for that reason, perhaps, delayed as well our ability to act on the acute global problems that are beginning to be frightening to thoughtful people. They are unprecedented both in their topics and in that they require global agreement to be solved (Alexander ms 1).

In 1949, when I was waiting to take my turn as a new 19-year old student teacher, I was appalled at the difficulty the student teacher who preceded me was having with the class. I had not been sufficiently aware of the possibility of disciplinary problems. I began to search frantically for a way to begin that would enable me instantly to capture the interest of the class. In a newspaper I read about a species of kittiwake that unlike related kittiwake species laid its eggs on cliff ledges. Its eggs, the article said, were more triangular than those laid in nests on the ground. I told this story to the class the first day and asked them how they thought this had come about. Two hands shot into the air, one of a boy from a nearby orphanage, whose goal was to become a veterinarian, and one of a girl whose father was a professor (and who later informed me that a B+ grade I had just given her was the only grade other than an A she had ever received). I allowed the boy to speak first and he said (paraphrased), "As the egg is being laid, the female kittiwake squeezes the reproductive tract while the shell is being formed, in a way that causes the egg to take a triangular form." Without commenting I turned to the girl. She exclaimed, "That's not it at all! The eggs of ledge-nesting kittiwakes at first varied in how triangular they were, and the less triangular ones rolled off the cliff more often. This eventually caused all the surviving eggs of the cliff-nesters to be triangular." I explained how both answers could be correct, and not in conflict, though only the latter one explained why the cliff-nesting kittiwake alone laid triangular eggs. Not until much later did I realize that, in the very first student comments in my very first class meeting, two high school kids had described what came to be widely understood as the proximate mechanism and ultimate function by which adaptive traits can be described and understood. I wished I had been astute enough to compliment them sufficiently, and explain fully the beauty of their two answers combined, as well as explore the possibility of alternative explanations. Teaching that high school course became my introduction to the evolutionary process and hypothesizing about adaptation.

How and why did I make the transition, initiated around 1967, from studying the singing insects as a systematist and behaviorist to eventually writing some 50 articles and two books about how evolution applies to humans and, in particular, human behavior? I decided in 1954, the day after I passed the written and oral preliminary examinations for the doctorate, that I wanted to be an *evolutionary* biologist. A few years later I realized I would like to think of myself (grandly!) as trying to falsify the hypothesis that everything about life is a result of evolution, in the successions of environments that have occurred across the history of life (evolution, after all, is a simple process; it is the accumulated effects of the almost endless changing successions of environments, large and small in their influence, external and internal to the organism, that have caused life, and the developmental and other processes across the lifetime, to be diverse and almost unbelievably complicated – and, indeed, somewhat jerry-rigged.)

The approach I set for myself would require that I proceed eventually to the most difficult of all traits (behavior) and the most difficult of all species (humans). I was delighted with this thought because I had realized by then that I had long been interested in where humans had come from, what they are like, and how they had gotten to be the way they are. I believed by then that such interests were the reasons I had taken a number of special optional courses about humans and their activities. I also understood that, if I followed my intent, I would eventually have to try to understand, in evolutionary terms, the human behaviors most difficult to understand – for example, social behavior, culture, morality, religion, humor, music, and the arts. If I could not solve those problems I could not generate a strong likelihood that the implication in my falsification effort was reasonable. I also realized that to fail completely with any human topic would be, at least for my grand goal, a disaster. This is why I have published on all of the above topics, even when I knew that I had not yet achieved unique and unassailable theory (Alexander 1974–1991a, 1993, 1998, 2005a, 2006a, 2008). I felt that revealing even incomplete and unsatisfactory results might assist others in continuing to more satisfactory conclusions.

Some time after I had decided I would become an evolutionary biologist, I realized I knew of no individual in evolutionary biology that I could accept as a bona fide, complete, and satisfactory hero. For some reason I felt then that everyone should have a hero in his own field. Several evolutionary biologists had qualities that I appreciated very much, but none completely filled the bill. To me, then, Charles Darwin seemed a remote figure, as did Fisher, although I eventually recognized both as true intellectual giants (Darwin in particular – cf. Alexander ms 1). So I decided, quite consciously, to create for myself a composite hero from contemporary biologists. The people who made up that composite hero were Howard Evans (because of his strong and effective devotion to field work), Ernst Mayr (because of his determination, his persistence, and his enthusiasm for eschewing wishy-washy-ness and continually giving the students of the world something concrete to shoot at), Donald J. Borror (because of his constant devotion to his work and his unpretentious passion for getting things straight), Alvah Peterson (because of his common sense, his almost regal kindness, and his scholarly approach to everything), and George Gaylord Simpson (because he seemed to me one of the most brilliant, serious, and unapologetic students of the evolutionary process).

As an instructor, my initial duties at Michigan were teaching laboratories in introductory biology. After a year or two I offered a course in insect behavior, which was taken by only two students, both undergraduates. Both became academic biologists. Mary Jane West-Eberhard is a member of the National Academy of Sciences, who became a student of social wasps and a close friend and co-author with Howard Evans. Bruce Goldman is a professor at the University of Connecticut, who has studied the physiology and behavior of naked mole rats.

Around 1960 I asked the biology department head, the molecular biologist Dugald E. S. Brown, if I could initiate a new course for upper undergraduates and graduate students, which I would title *Animal Behavior and Evolution*. I was skeptical of my chances, and prepared to leave Michigan if the request was denied. At the time there was no course on animal behavior and no course on evolution in the U-M biology department. Some evolution was taught in an ecology course, and it was discussed minimally in courses such as entomology and vertebrate natural history. But the large introductory course in zoology was based on an almost ridiculous caricature of evolution. My questions about evolution and behavior, submitted for the written doctoral examinations in biology, were often treated by colleagues as jokes (e.g. "Why female coyness?"), and almost never accepted on the examinations. To my surprise, however, Brown acted as though he was wondering why I hadn't asked for a new course before. He proceeded to give me good advice and strong support. I went on to teach some version of animal behavior and evolution to classes, eventually of 100–200 graduates and undergraduates, for almost 40 years. For a few years I co-taught a new course, evolutionary ecology, with Donald Tinkle. I also taught seminars on animal and human behavior and evolution nearly every term for the 44 years of my tenure at Michigan. It would be folly for me to try to list all of the distinguished ecologists, systematists, behaviorists, physicians, anthropologists, psychologists, and others who happened to be in Tinkle's and my courses. Two of them have autobiographies in this volume. Several are members of the National Academy of Sciences.

Approximately 12 years before my retirement in 2001, I changed the title of my course to *Evolution and Human Behavior*. I took up the human species the same way I took up the study of other species – as a systematist, and in the particular way that systematics was seen in the middle of the twentieth century. That is, I began to explore the biology of the human species when, as I said in *The Biology of Moral Systems*, "biology" means everything about the life and natural history of the group or species in question, through the eyes of an evolutionary biologist (Alexander 1987). After my retirement, the anthropology course taught by my former student Beverly Strassmann, currently U-M Associate Professor of Anthropology, became the U-M's central course in human behavior and evolution.

In early 1949, when I transferred to Normal as a second semester junior, I saw in the catalogue a course called philosophy. I read the abstract and was exhilarated. I believed I had finally found the course that I had always wanted to take. I have no memory of ever having known there were courses called anthropology, in any school I attended, until I took the job at Michigan in 1957. Philosophy at Illinois State Normal proved a huge disappointment. At the beginning of the course we were assigned to read a set of philosophical "classics." I was exuberant about this task when I began it. Every night at eight when my evening work washing dishes in a downtown restaurant was finished, I would run several hundred yards to the library reading room and read until the library closed at eleven. But I quickly began to feel that I was reading material within which I could find statements that I liked, or that intrigued me, and others that made no sense, or had no basis. There was no scientific backing, and thus no real distinction between the two categories. Because I could find no way to establish one view over another, or to detect errors, I felt as though I was being cheated, left – indeed, encouraged – to choose the statements I thought were reasonable and then treat them as factual. I never finished reading a single one of those assigned classics. Eventually I simply gave up. On the last night that I walked out into the darkness and away from that assignment, as the library was closing, I muttered out loud to myself, "Philosophers are no better off than theologians: they have no decent theory." Today that seems a surprising statement, certainly for a 19-year old version of myself; but it is exactly what I said, under those exact circumstances. I held no ill feeling toward the philosophy professor, an excellent teacher named Francis Belcher. I thought enough of him that almost a year after I had left for graduate school I sent him an essay titled *Biology for Survival*, and explained in an accompanying letter that I felt I had done a poor job of answering when he deliberately challenged me in class with the excellent question, "Why would *anyone ever* want to become a *biologist!*"

As my interest in pursuing questions about evolution and human behavior grew, I began to recall the effect during my childhood of my family's faithful attendance at the United Methodist Church in a tiny ghost town in Piatt County, Illinois. I remembered being puzzled because so much of what was discussed in that church involved causes and effects – events – that I never had experienced in everyday life outside the church. I recalled sitting in the church on Easter mornings and wondering what it meant for the preacher to say that a man had risen from the dead and ascended into Heaven to sit at the right hand of God the Father Almighty. I developed a habit of sitting in the back of the church so that I could watch the backs of the necks of the farmers I knew well. I wanted to know if they squirmed in their seats, or if their necks became a little redder, or if anything else indicated discomfort with assertions and claims that seemed to me to be unlikely, or even outlandish. I never perceived any such response. This caused me eventually to realize that I was in some sense on the outside of this local community, looking in. I never forgot that. But years later, when I was contemplating studying the human species in evolutionary terms, my undergraduate preoccupation with courses in the social sciences and history and the arts and philosophy seemed finally to make sense. I knew I would have to start with simple questions about humans but continue on a gradual course toward tackling the most difficult questions imaginable, at least about living creatures. I believed that such questions would be the most severe tests of possible falsification of evolution as the explanation of all life.

At some time during the later stages of my formal schooling I became aware that I had known, since high school days, that the only place the questions I wanted to answer about humans were raised was in that little country church. In retrospect I believe that I have wished to have this truly important set of questions answered since I was a child. Probably, I was interested because I found it difficult or impossible to accept much of what was said in the church; perhaps the principal reason was a certain difficulty in thinking metaphorically. Nowhere outside that church do I recall receiving even a smidgeon of an answer to my questions about humans: not in school, from elementary school all through undergraduate school, not from my parents, not from any teacher, not in any publication. Eventually I asked my mother why we had never discussed the questions of where humans came from, what they are really like, and how they got to be that way. She did not answer for a while, and then, without looking at me, said, "We didn't have time." I objected, noting that in our family we discussed all kinds of other questions. I pointed out that there is always time on a farm to discuss such things because so many of our tasks could be carried out while thinking hard about something entirely different. She did not respond, and in a brief bout of sympathy I asked if she thought it might be because we had no reasonable theory. After another period of silence she said in a subdued voice, "That might have been part of it." My mother was devoted to her church, even if in a social way more than a narrowly religious one. I understood I would not receive additional help from her with that question.

In the mid-1960s Professor Emmet T. Hooper asked me if I would take over from him the job of reviewing Robert Ardrey's *The Territorial Imperative*. I declined. Undaunted, he somehow entered my office when I was not there and left the materials involved on my desk. I kept looking at them and finally decided, after all, to review Ardrey's book, and to include in the review Konrad Lorenz's O*n Aggression*. Eventually I asked Don Tinkle to co-author the essay (Alexander and Tinkle 1968a).

In early 1968, the Alexander and Otte families – four adults, two teenage girls, and two 1½ year old twin girls – left together for Australia to monograph the crickets of that continent. In Melbourne, Professor Murray Littlejohn asked me to speak to the Royal Society of Victoria on human behavior and evolution. I declined, saying I knew nothing except what I had written in the Ardrey–Lorenz review. He suggested I talk on that topic, but I didn't want to do that. The cricket expedition left shortly afterward, in a new Land Rover towing a two-wheeled trailer, to spend several months in northern Queensland. When we returned to Melbourne, Murray had scheduled the talk he had asked me to give. Neither he nor I remembers whether I eventually agreed to do it, or if he simply put me down for it. In any case, everything was in good humor, and I gave the talk, titled *The Search for an*

Evolutionary Philosophy of Man. During parts of the lecture the audience was deathly quiet. As Murray and I walked down the street afterward, he said thoughtfully, "The clerical robes and collars were not there; but their ghosts were!" I decided to turn the lecture into an essay and spent many hours on the project in the University of Melbourne library (Alexander 1971).

By the time I returned from Australia I had discovered a statement by the University of Chicago anthropologist David Schneider that the asymmetrical treatment of cousins in many pre-technological societies could not be explained by "biology." That use of the term "biology," I had come to realize, was mostly restricted to social scientists and philosophers, and roughly meant "genetics and physiology." I felt that it was a way of referring to what many people call "hard-wired," "innate," or "instinctive" traits, thinking that such adjectives contribute to an understanding of how humans acquire their traits – falsely, I believe, or at least clumsily and imperfectly. The events between the zygote and the organism, during which all of the genetic elements in the genome are necessarily selected in the direction of cooperating completely with their fellow units within the genome (even if they never achieve it), are too numerous and complex to be so labeled (Alexander 1990a, 1991a). In my opinion, the "genetic and physiological" definition of "biology" has had a broadly significant negative effect, hindering progress in the study of not only evolutionary adaptation, particularly as applied to humans, but our understanding of development (ontogeny), learning, and all related biological problems. It happened because the human-oriented disciplines developed before serious study of human adaptation was possible, and because ontogeny is so complex that we are reduced to manufacturing terms to use when we are really too ignorant to have much of an idea about what is actually involved (West-Eberhard 2003).

It seemed to me that if evolution can explain all aspects of all life – including learning and culture – society-wide patterns of culture should not be frequently or significantly contrary to a history of natural selection, even if they are learned (Alexander 1979; Flinn and Alexander 1982); otherwise the capacity for the cumulative learning of culture could not continue to evolve. I set out to find as many statements like that of Schneider as I could, so that I could see whether they actually were inconsistent with a history of natural selection. I supposed that such patterns were learned, but I felt that the relevant learning capabilities and tendencies had surely been patterned by natural selection, such that Schneider's kind of statement would at least be misleading. I was willing to work from the assumption that our main problem is to find out more about how learning has evolved, and how it works, rather than accept that culture is independent of changes saved as a result of differential reproduction for reasons other than massive and rapid alterations of the human environment.

It was not easy to locate statements such as Schneider's. I went through the journals article by article, sometimes page by page. Most articles in anthropology journals then gave little clue of such topics or conclusions in their titles or abstracts. I did find two other examples that seemed to me important. (1) The avunculate, or mother's brother phenomenon, which had also been examined in detail by Schneider and his co-author Kathleen Gough (1961). These terms refer to situations in which men show a great deal of attention to their sister's children, sometimes more attention than to their spouses' children. (2) Asymmetry in cousin marriages. I set out to discover whether these different phenomena had features consistent with a history of natural selection. Every case of that sort that I eventually discovered did indeed turn out to have an evolutionarily consistent solution. Eventually I brought most of the solutions together in *Darwinism and Human Affairs* (1979; see also Alexander 1998, 2006a).

In the mid-1960s I was examining a paper that seemed to show that the human brain cavity continued to expand well after it had exceeded the brain cavities of related primates, and may even have increased its rate of expansion afterward. I pondered for a long time what hostile forces of nature could be responsible for the continuing growth of an organ as calorically expensive as the human brain. Eventually I decided that the only qualifier has to be humans themselves. It seemed to me immediately that this could only happen if humans lived in groups and had as their most important "enemies" other groups of humans. I pursued this idea and eventually argued that humans had become sufficiently ecologically dominant that all of Darwin's "Hostile forces of nature" – predators, parasites, diseases, food shortage, climate, and weather – had been reduced, or changed in relative importance, in a fashion that caused human groups to use a greater proportion of their calories in being directly and acutely competitive with other human groups for certain special resources, including mates. Thus, internecine battles could become efforts not only to displace but to destroy other humans (typically men and boys) but also to gain other humans as resources (typically women and girls). I argued that this is the reason for the continuing prevalence of different forms and magnitudes of warfare (and its relatives), and that the alternation of intense and organized cooperation within groups and adversarial relations between groups sets up a perpetual favoring of genes that improve the ability and tendency of humans to further the subtlety and complexity of their sociality and all its mechanisms, and to change quickly to meet the immediate circumstances. I referred to the result of all this as an endless Balance-of-Power Race. Some authors have suggested that it should have been termed an imbalance-of-power race, but maintenance of multiple groups can occur only if groups continue to remain balanced in ways that prevent wholesale annihilation. Weak groups may disappear, but stronger groups must continue to fill in the spaces if multiple competitive groups are to persist. I believe that the most intense and frequent efforts would typically be on the part of slightly weakened groups that needed to continually re-establish balances that would lower the likelihood of all-out contests. Because the members of a single species behaving this way are bound to exchange genes continually (or repeatedly), evolutionary selection can continue indefinitely to favor those who are able to form and live in groups that can protect themselves. It is difficult to imagine the kinds of environmental and situational changes that could halt the ensuing evolutionary races in brain size and function and their consequences.

I have argued (Alexander 1990–2008) that (1) the combination of the uniquely large and complex human (primate) brain, and its middle and late life social (kin group) functioning across much of the adult lifetime, is responsible for (2) the doubling of the human lifetime compared to all our extant ape relatives, and by extension, (3) the long juvenile life and learning period, and the altriciality of the human baby, as preparation and enhancement of later learning and use of knowledge, facilitated by (4) the unique ability of humans to learn the relative genetic overlap among virtually their entire kin groups, owing to (5) concealment of ovulation, which allowed accurate knowledge of genetic relationships of different kin in even multi-male groups and thereby enabling virtually all of the uniquely social human traits (Alexander 2008), and (6) menopause, as transfer of effort from offspring production to support of up to the entire kin group midway through the adult lifetime of women.

How have humans accomplished this? They do not grow continually. They are not armored or surrounded by individuals sufficiently devoted to protecting them. We need only consider a set of human traits that menopause also demonstrates: living in kin groups under conditions that have spawned the huge brain that causes the human baby's head to be the limiting factor in successful birth, and to become the most calorically expensive – and the most remarkable – organ of the human body. … The human brain and all of its correlates in learning, cognition, consciousness, extensive and elaborate scenario-building, memory, and other intellectual features enable human individuals to increase their reproductive output via kin help and make evolution of longer lifetimes adaptive. The collection of mental adaptations in humans – and their continued elaboration late in life – can be so significant that individuals that have become seriously senescent in physical attributes can nevertheless remain important, or even essential, to the survival of families and kin groups. … It is obviously possible to evolve a longer adult life if the rate of reproduction can be sufficiently increased as to delay or reverse senescent trends caused by late-acting deleterious pleiotropic effects of genes that have their advantageous effects primarily in earlier life (Williams 1957). … It is thus not surprising that age is so often venerated, and that some kinds of leaders are desired or required to be as old as, or older than, the usual age of death in non-human primates. Although there have been suggestions that the altriciality of the human baby is responsible for the extension of the adult human lifetime, and its intelligence (e.g., Hutchinson 1965, Williams 1992), the reverse – or some kind of successive reinforcement – also seems possible: that selection favoring the collection of mental capabilities of adults may have caused those capabilities to be further enhanced by beginning and increasing their elaborateness and the earliness of [learning and] development in the human juvenile

(Alexander 2008).

I consider the evolution of the combination of Ecological Dominance and the related Balance-of-Power Race among human groups to be the most general and most important adaptation of the human species (Alexander 2008). By this I mean that virtually all of the unusual or unique traits of humans are molded around this combination of traits. The resulting amity–enmity axis – the extreme cooperativeness within the local unit of competition and its correlated ability to marshal against other local units of competition – is currently the world's greatest problem, and this has some possibility of being true indefinitely. Because of this unique set of adaptations, the traits of humans are often decidedly different from, or even opposite to, those of related species – or, in some cases, opposite to all such traits in all species. To me it seemed that, in attempting to analyze adaptations, one has to consider the human species as an *N* of one. As a result I developed an approach to the analysis of humans that I called the Jigsaw Puzzle Method (Alexander 1990b). I considered different traits as if they were pieces of a jigsaw puzzle that can only be completed by discovering how all of the pieces (traits) are related functionally. Some time after I generated this idea, I realized that theoretical physicists must similarly examine the only physical universe available to them. My thought that this approach resembled that of the theoretical physicists trying to assemble all of the functions of the universe was confirmed by Professor Gordon Kane, a U-M Professor of Physics, who assured me, "You are doing exactly what we are doing."

I have had great difficulty seeking to solve what I see as the four most difficult aspects of human behavior to understand thoroughly: music, humor, the arts, and religion. Twice I have literally "copped out" while giving lectures on the arts to large numbers of people. The first time I was delivering a special lecture sponsored by the U-M College of Literature, Science, and the Arts. The second involved an international symposium on human behavior and evolution in Stockholm, Sweden. In the first of these two lectures I stopped short, at the end of a 50-minute talk, because I suddenly realized that the theory I was developing was not worthy. In Stockholm, on the night before my lecture, I could not convince myself that I could justify lecturing as though I could describe and support a satisfactory theory of the arts. So I gave a general lecture on human evolutionary adaptation instead. I rationalized to the audience that no such lecture had been given in the series, and that one was needed. At the end of my lecture I delivered a ten-minute condensed version of my original topic, the arts. The best published version I have yet been able to muster as an explanation of the arts, including humor, music, and religion, appear in *Darwinism and Human Affairs* (Alexander 1979), and in my chapter in the volume *Darwinism and Philosophy* (Alexander 2005a). I had already published a long paper on humor in *Ethology and Sociobiology* (1986a) and an important addendum on humor concerning social-intellectual play in *The evolution of the human psyche* (Alexander 1989). My hypotheses about music were summarized in an abstract of a talk delivered to the Human Behavior and Evolution Society 14 March 1988. The abstract was published in the program of the meeting. A more elaborate discussion of the evolutionary background of music appeared in a course text, titled *Understanding Humanity*, printed and distributed in Ann Arbor, 1997–98, for my course in Evolution and Human Behavior.

I think there is sometimes confusion about the different approaches of researchers, and what they are trying to accomplish, in adopting an evolutionary approach to understanding the human species. Paleontologists and archaeologists are tracing patterns of change through evolutionary time, as by examining and dating fossils, tools, weapons, and other relicts. Such investigators are primarily seeking to explain where humans have been, when they were there, their long-term movements, and what they did at different times and in different places. Others are using molecular information, sometimes taken from fossils, sometimes from comparative study of extant humans around the globe, to reconstruct approximately the same aspects of long-term human history. My own primary effort, since 1967, has been to use knowledge of how the evolutionary process – differential reproduction – works, and how it has through its cumulative effects resulted in humans being what they are today. Obviously, in the end, all of these different approaches to patterns of change and the cumulative processes of change must necessarily be combined and synthesized repeatedly to continue generating the most accurate overall picture of human nature and history. We are surely in a position to understand ourselves profoundly, as we will need to be if we are to begin to solve, for the first time, the succession of global problems that are descending upon us.

My graduate students and postdoctoral associates

Anything and everything that I may have accomplished as a biologist after moving to Michigan has been facilitated by the 33 doctoral students whose committees I have chaired between 1958 and the present, and almost as many postdoctoral fellows and other doctoral students who have worked more or less directly with me. There is no way to measure the importance of the hours we sat in Rooms 2009, 2080, and the Faculty Conference Room in the University of Michigan Museum of Zoology, arguing, lunching, and laughing over all of the topics mentioned in this essay, and many more. Those former students and postdocs are all splendid people, and keen observers and analysts of the world and its inhabitants.

I was fortunate to become enamored with the evolutionary study of social behavior at a time when students were beginning to show the same interest, and at a time at Michigan when biology graduate students were admitted on the basis of their application qualifications, as determined by a department-wide committee, rather than to fill slots in particular fields or in the laboratories of particular faculty members. They were assured of financial support for five years via teaching assistantships, and they were given a little over a year to complete a preliminary qualifying examination and select a sub-discipline and a doctoral chair. These arrangements made the biology doctoral students at Michigan financially and otherwise more independent than is often the case. This is why so little of the student research described in this essay was done, or published, in a formally cooperative way with me. Our interactions were virtually all informally cooperative, and my students typically wrote doctoral theses based entirely on their own independent research, more often than not funded by their own research grants.

Starting in 1966 (Williams 1966), my students and I recognized that it is parsimonious to assume that evolutionary selection is typically (but not always, of course: cf. Alexander 1974, 1993; Alexander and Borgia 1978) most effective at the lowest levels of organization of life – meaning it is the best hypothesis to entertain at the start. As a result of their beginning with this hypothesis, my doctoral students were among the first investigators to realize and demonstrate the importance of recognizing individuals in field studies of adaptiveness in the social behavior of organisms such as milkweeds, damselflies, aphids, social wasps, acacia ants, field crickets, grasshoppers, true katydids, meadow katydids, thrips, dung flies, leopard frogs, Sierra toads, bullfrogs, bank swallows, cockatoos, mountain bluebirds, prairie dogs, ground squirrels, dolphins, cicadas, field mice, naked mole rats, white-tailed deer, and humans.

Concluding reflections

In January 2001, I retired with the intent of writing children's books, books about horses and horse people, poems, songs, and articles and books of local historical interest. I have done these things, and am doing them still, to the best of my ability; and I continue to enjoy every minute. The beginnings of some of these writings took place more than 60 years ago, but my more than a half century as a professional biologist seems to have trained me in precisely the wrong directions for significant contributions to literature or the arts. Perhaps my efforts to reverse such training are somehow part of my continuing striving to understand in evolutionary terms the arts and such related human activities as music and humor. Perhaps I am simply not talented in the appropriate directions. I continue, however, to feel strongly that those of us trained in evolutionary biology – indeed, in systematics, and in accounts and syntheses of all the life attributes of individual species – have a special kind of knowledge and skill, which includes a responsibility to build toward a profoundly more penetrating understanding of ourselves, as individuals and as part of the cooperating and competing collective of humanity. In the end, regardless of how reductionistically we begin, we must understand ourselves, and indeed all life, as whole organisms. Despite the most dramatic and valuable starts with the genetic materials, the almost unbelievable complexity of development, owing to the nearly complete cooperation of genes in genomes (Alexander 1993, 2005a; West-Eberhard 2003; Burt and Trivers 2006), will prevent a fully ontogenetic exposing of ourselves from being possible for a very long time. Theodosius Dobzhansky (1961) summarized the basic reasons almost a half century ago:

Heredity is particulate, but development is unitary. Everything in the organism is the result of the interactions of all genes, subject to the environment to which they are exposed. What genes determine is not characters, but rather the ways in which the developing organism responds to the environment it encounters.

Recently, an evolutionary biologist was quoted as saying, "Science doesn't answer questions about the meaning of life." The same person also said, "To say that just because something is terribly complex it needs a supernatural explanation is to give up on the scientific enterprise." Taken together, these two statements, from the same person in the same article, highlight the reluctance of biologists to speak plainly about evolution as an explanation of human life and human traits, as well as all life and its traits, including religion. Assuming that a supernatural is not to be invoked, what approach other than science exists to take over when "terribly complex" questions such as the meaning of life are contemplated? On what basis can an evolutionary biologist argue that science cannot analyze something, such as the meaning of life, necessarily derived in some fashion, however indirectly, from the evolutionary past of the human species? All of the attributes we engage to even pose questions such as the meaning of life are somehow results of the evolutionary process. The science of biology does not hesitate to seek the answers to all questions about other living creatures, including the "meaning" of all aspects of nonhuman life (their evolved significance as well as their personal meanings for humans). I regard it as unfortunate that we humans withdraw from at least hypothesizing that every aspect, every trait, every result of change in life has to be an outcome of the cumulative process of evolution as it has occurred in the dauntingly extensive and intricate successions of environments across history.

At the risk of being judged a hopeless megalomaniac, I will say here that it is my greatest regret, so late in my lifetime of thought and research, that I have been inadequate in my attempts to discover and explain how people everywhere can understand themselves sufficiently better from knowledge of evolution as to change the sociality of global humanity in a positive way. Regardless of the pace of technological and other scientific advances, understanding of ourselves in evolutionary terms – understanding sufficiently profound that it requires at least a temporary ability to withdraw slightly and judge ourselves as if we were aliens, or members of a different species – may always be necessary if we are to recognize and accept the most important sources and reasons for change in the social life of humans. I regret my inability to identify confidently even the first steps of a solution to the long-standing central problem of humanity that derives from the prevalence, throughout our history, of uniquely ferocious and frequent inter-group competitions within our own species.

A hydrogen bomb is an example of mankind's enormous capacity for friendly cooperation. Its construction requires an intricate network of human teams, all working with single-minded devotion toward a common goal. Let us pause and savor the glow of self-congratulation we deserve for belonging to such an intelligent and sociable species.

(Robert S. Bigelow, 1969. The Dawn Warriors*)*

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Leaders in **Animal Behavior**

The Second Generation

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Lee Drickamer and
Donald Dewsbury

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