

Population Regulation and the Life History Studies of LaMont Cole

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ABSTRACT – Transformative changes marked the growth of mid-twentieth century American ecology. This included redirection of the scholarly focus of the discipline, especially on the role evolutionary theory and “levels of selection,” and increased visibility of ecologist as public figures in the environmental movement with special knowledge of how natural systems work. Cornell ecologist LaMont Cole is an important figure to examine both of these trends. Like many of his contemporaries, Cole was devoted to a perspective on natural selection operating at levels *above* the individual. However, because of his influential mathematical treatment of animal demography he has been historically subsumed into a group of scholars that views the events in the life course as adaptations to the maximization of individual fitness – life history theory. Cole’s popular writings and lectures, which consumed his later career, extend his scholarly portrayal of natural populations as tending toward stable and homoeostatic equilibrium, with the goal of drawing contrasts with the deviance of rapid human population growth. In both regards, Cole serves as a topical and temporal extension of the well-documented and analyzed ecology of his mentors – Alfred Emerson, Thomas Park, and Warder Allee – in the University of Chicago Zoology Department.

KEYWORDS – Life history theory, demography, ecology, evolution, group selection.

Introduction

Biological thought was transformed by the modern synthesis of population genetics. However, establishing the primacy of natural selection in explaining biological patterns was a contentious process (Kimler 1986; Collins 1986; Gould 1983). While many researchers were comfortable with narratives drawing on the importance of many evolutionary processes through the 1950s, by the mid-1960s a controversy over the “levels of selection” debated the relative importance of selection operating within and between populations (Williams 1966a; Wynne-Edwards 1962). These arguments often focused on demographic processes; that

is, rates of birth and death occurring in natural populations. One side of this debate, which maintained *individual* fitness is maximized by selection operating within populations (intrademic selection), produced a basic body of theory in evolutionary ecology dealing with the adaptive structuring of events in the individual life course including birth, growth and development, maturation, reproduction, senescence, and death, commonly called life history theory (Stearns 1992; Roff 2002). The other, which proposed populations are regulated by individuals curbing their reproduction to the benefit of the *group*, was quickly silenced, and branded as “heretical” (Hagen 1992, Ch. 8).

Life history theory was historically conjoined with individual or intrademic selection in its development during the 1950s and 1960s. However, theoretical development was necessarily heterodox through much of this period. Some unity between life history theory and intrademic selection was personal; the same individuals were vocal proponents of both ideas, such as George Williams (Williams 1957; 1966a; 1966b). Other scholars underwent personal “conversions”, stuttering away from group or interdemic explanations, like Peter Medawar.¹ Still other researchers who contributed to the development of life history theory were staunchly “group selectionists.” LaMont Cole, the subject of this paper, falls into this category.

Though Cole is widely known for only a handful of scholarly publications in the 1950s, his case is instructive for several reasons. First, it illustrates how scientific orthodoxy can be established. Cole himself was inflexible in his devotion to group-based evolutionary scenarios but he has been thoroughly reinterpreted in recent texts. Furthermore, as group selection fell out of favor, Cole’s scientific publications ended as he devoted himself to administrative endeavors and public outreach. These public contacts included a willingness to extend his ostensibly scientific and objective work to human population control and environmentalism. This is anticipated by similar activities of his mentors in the University of Chicago Zoology Department. As these are well documented and contextualized, Cole can be explored as an historical and topical extension of the “aggregation ethics” espoused in Chicago by Warder Allee and Alfred Emerson prior to mid-century (Mitman 1992).

¹ Contrast his views in Medawar (1946) and Medawar (1952).

Cole at Chicago

LaMont Cole was born in 1916 to a pair of famous anthropologists, Fay-Cooper Cole and Mabel Cook Cole. He entered the University of Chicago in 1934 as an undergraduate, majoring in physics with minors in astronomy and mathematics. Summer breaks were spent as chief herpetologist for Rainbow Bridge, Monument-Valley Expeditions (1934–1937) gathering specimens for various American museum collections.² After graduating in 1938, he went to the University of Utah to work on a master's degree in zoology under Angus Woodbury, Walter Cottam, and Seville Flowers. Cole's thesis, completed in 1939, explored the relationship of temperature and humidity resistance to protective coloration in desert lizards (Cole 1943). In the same year, he returned to the University of Chicago to pursue a doctoral degree in zoology.

Chicago zoology in the 1940s was one of few major departments in the United States with an active program in ecology. The core of the ecological faculty was Warder Allee, Thomas Park, and Alfred Emerson.³ Allee and Emerson offered a vision of animal ecology focused on the origins, development, and structure of cooperating groups ranging from the population to the community. Allee had spent much of his career documenting evidence for the beneficial effects of group living, benefits he believed to be phylogenetically ancient and thus at the core of all animal life. Emerson devoted much of his research to the evolution and taxonomy of termites, a group noted for complex social organization and cooperative behavior. For Emerson, the ecologist most interested in evolution at Chicago, populations, species, and communities moved toward greater integration among parts through feedback loops that established system-wide *homeostasis* within this superorganism (Emerson 1939; 1943). Park, a former student of Allee, returned to Chicago from a fellowship with Raymond Pearl.⁴ This formed the basis for a research program aimed at understanding the dynamics of taxonomically or genetically heterogeneous insect populations carried out in the laboratory under controlled conditions. Park also brought with him mathematical inclinations, in his case they were demographic, that ecologists at Chicago typically avoided, or relied on the authority of their colleague Sewall Wright. Allee, Park, and Emerson worked over a decade in writing a

² It was during these expeditions that Cole met Woodbury and decided to become an ecologist (Cole, n.d.).

³ See Mitman's (1992) *The State of Nature* for a detailed intellectual and social history of Chicago zoology.

⁴ See Kingsland (1995) for an account of Pearl's research.

weighty textbook *Principles of Animal Ecology*, published in 1949.⁵ The volume was constructed in an encyclopedic fashion with evolutionary topics reserved for the final section which Emerson wrote. His homeostatic and superorganic views were clear:

The existence of complex internal adaptation between parts of an organism or population, with division of labor and integration with the whole system, is explicable only through the action of selection upon the whole units from lowest to the highest. Conversely, these integrated levels would not exist as entities unless selection acted upon each whole system. (Allee *et al.* 1949, 684)

Wright's "shifting balance" theory was an important foil for Emerson and Allee in arguing for group and community selection (Wright 1945). This was a formal model for how a trait that is beneficial to the group but harmful to the individual can increase in frequency through the differential survival of groups (interdemic selection). The details of the argument were unimportant for Allee and Emerson;⁶ it was a license to emphasize evolution at levels beyond the individual and discount the importance of competition within groups. Cole's commitment to the Chicago brand of evolutionary theory was clear in 1950 when he favorably reviewed *Principles of Animal Ecology*. Referring to Emerson's chapters on evolution, Cole wrote, "[t]he emphasis of this section is on natural selection acting upon biological units which may commonly be more than individual organisms. The approach is convincing, even uncontestable" (Cole 1950, 155).

Though he applied to work with Allee, Cole was accepted as one of the first graduate students of Park (Park 1988, 219). Cole completed his doctoral thesis in early 1944, describing numbers and distribution of "cryptic fauna" living under boards in a woodland tract owned by his family in rural Illinois (Cole 1946a). This work dealt with the important question of what factors led to the distinctive assemblages of species found in different environments. Were species integrated parts of a superorganic, homeostatic community, or simply the result of shared tolerances among species for temperature, light, moisture, chemicals, and other abiotic factors? Cole portrayed these assemblages as unintegrated groups of organisms which had only their abiotic tolerances in common. This was a break from Emerson and Allee's view but Cole diplomati-

⁵ Two other authors contributed to the volume – Park's brother Orlando from Northwestern University and Karl Schmidt from the Field Museum of Natural History. (Allee *et al.*, 1949) Cole used the textbook in classes (Cole 1950).

⁶ The details are critically important in more recent models of group selection (Wilson 1975; Agrawal *et al.*, 2001).

cally avoided generalization noting, “[t]he evidence that the cryptozoic fauna... is held together primarily by common habitat requirements and tolerances of the constituent species suggests a qualitative distinction from...highly integrated animal communities” (Cole 1946a, 84). There were many other cases in which species’ assemblages might form tightly integrated communities as his advisors supposed, Cole had simply identified one which was not. Cole’s doctoral work highlights several trends in much of his life’s work: a reliance on a whole-hearted empiricism, a statistically underwritten devotion to parsimony and testing of null hypotheses, and consequent tendency toward reductionism and analysis of what were perceived as simple phenomena. However, these trends were tempered by the avowedly holistic training of Chicago zoology, which impressed a view of populations as organic entities with their own distinct properties that Cole was unwilling to abandon throughout his career.

Association, Oscillation, & Life Histories

Upon leaving Chicago with his Ph.D. in 1944, Cole was commissioned into the U.S. Public Health Service where he worked until discharged in 1946. His health service work allowed for further investigation of interspecific animal associations as he tracked the abundance of rats and their ectoparasite loads in an effort to control typhus outbreaks in the American South and Hawaii (Cole and Koepke 1946; 1947; Cole 1945a). These and other publications from this period focused on the statistical question of how accurately to describe the pairwise association or co-occurrence of species.⁷ The articles were technical and offered only limited discussion of how measuring interspecific association related to the larger question of community structure.

After spending a short time as an instructor at the University of Indiana, Cole was hired at Cornell University in 1948, where he stayed for the remainder of his career.⁸ In the early 1950s, Cole was stimulated, in part, by Palmgren (1949) to embark on a related research program on the cycling of animal population sizes (Cole, 1951, 1954b, 1957a). Cole took a statistical approach to the problem of population fluctua-

⁷ Cole attempts to relate species co-occurrence due to a single external factor – a third species or some abiotic cause. (1945b, 1946a; 1946b; 1949; 1957)

⁸ With his arrival at Cornell, Cole’s redirection into studies of life histories and population cycles is not surprising. A departmental project report for 1948–1949 lists “Life histories, behavior, economic status, relations to land use, and management of birds” and “Investigations on the cyclic nature of small mammal populations.” Cornell Department of Zoology Records Box 3 Folder 2.

tion. He tested the null hypothesis of random fluctuation by comparing the few existing records of animal population sizes with tables of random numbers. As in his dealing with species co-occurrence, Cole found no evidence that animal populations went through regular cycles.⁹ Cole did not take this to indicate that population size fluctuated in an entirely haphazard manner but that it was separately influenced by such a variety of environmental factors that it merely appeared to be random. Having questioned an external environmental “governor” of population oscillations, Cole looked elsewhere, to the internal properties of populations.

He recognized the relative numbers of the sexes and age classes along with the life history features (age at maturity, longevity, and fecundity) of population members either allowed or prevented populations from increasing rapidly to take advantage of favorable environmental conditions.

A species in which each female produces only one or two offspring per year will ordinarily have a high rate of survival and cannot be expected to greatly exceed its usual performance in response to one or two favorable years while species with higher reproductive potentials can exhibit dramatic increase in the course of a single exceptional season. Consequently we might expect that more or less fixed life history features such as fecundity, longevity, and age at reproductive maturity would determine a minimum period for any population oscillation. (Cole 1951, 250)

Furthermore, population sizes in successive years are not independent because of carry-over from previous years. This carry-over includes the composition of the population and its effect on the environment in depleting resources (Cole 1954b).

Underlying Cole’s interest in population cycles was an understanding compatible with, if not derived from, Emerson’s emphasis on homeostasis that populations were naturally at equilibrium. If populations fluctuated randomly, then a long-term equilibrium size existed and was the dominant feature of the population. As he put it for the lay reader of *Scientific Monthly*:

[T]here is for each species and population some stable or average equilibrium size toward which the population is trending. A population that is growing or shrinking is in a temporary and unstable state. If we wish to understand population phenomena we must consider the population in its equilibrium condition. (Cole 1948)

However, equilibrium was not just an empirical description of population size but a metric of group survival and thus success over the

⁹ *Journal of Wildlife Management* published a symposium issue devoted to this idea. See Cole 1954b.

long chronology of evolutionary time. The ability to maintain a standing population and perpetuate the species was the criterion and functional role of life history traits. Populations "efficient" in accomplishing this task persisted. For Cole, evolution within populations was secondary to establishing population efficiency and the long-term maintenance of stable equilibrium size (Cole 1948, 338).

Here, then, are the ingredients for Cole's inquiry into life histories: a general interest shared with most all of his peers in the broad ecological question of what factors control the distribution and abundance of animals, a particular understanding of fluctuations in population size as being modulated by internal properties of the population concomitant with an acceptance that populations were organic entities rather than simply collections of individuals, a belief that populations can be characterized by and studied at an equilibrium condition, and a predilection toward casting group efficiency as the criterion by which natural selection operates.

Population Consequences of Life History Phenomena

Around the same time his work on population cycles was published in the early 1950s, Cole began exploring simplified mathematical models of life histories (Cole 1952). The result of this work was a widely cited and generally misunderstood article published in the *Quarterly Review of Biology* (Cole 1954a). The paper was important for several reasons. First, Cole demonstrated that the mathematical tools of demography could be meaningfully applied to ecological questions of describing and predicting population structure and dynamics, with only limited information on the animals in question. Second, Cole emphasized that life histories should be viewed as strategic adaptations, though he inferred they were adaptations for group survival and efficiency not individual fitness as assumed in life history theory. Finally, Cole formulated much of his exploration in terms of the impact of small changes in the life history on the population intrinsic rate of increase, r , a commonly used fitness measure in later life history theory. It did not, however, provide any further insight on population fluctuations.

Important in his dealing with life histories was Cole's discussion of a 1931 paper by W. R. Thompson that offered a precise way to predict population growth based on knowledge of only a few attributes of the average individual: age at sexual maturity, the number of offspring per reproductive event, and the number of reproductive events (Thompson

1931).¹⁰ Like Cole, Thompson was mostly interested in how changes in life history traits affected the composition and immediate growth of populations. However, Thompson had taken a particularly harsh stand in the article against the life-table methods of Lotka that were becoming more commonly used among ecologists.¹¹ Additionally, by the time Cole came to addressing Thompson's arguments, Thompson was arguing against the use of mathematical models in biology at all, particularly the population genetic arguments fueling the modern synthesis (Kingsland 1986).

Cole attacked Thompson's dismissal of life-table methods by directly demonstrating the equivalence of Thompson's simple life cycle model with one Cole developed from the Euler-Lotka equation – a fundamental relation in life table methods used in ecology and life history theory.¹²

$$1 = e^{-r} + b e^{-r} - b e^{-r(n+a)} \quad (2)$$

In Cole's model, like Thompson's, all one need know about an animal is its age at maturity (a), average birth rate (b), and number of reproductive events in a lifetime (n) to calculate the rate of population increase (r).¹³ That Cole took this task seriously is evidenced by his devoting eight of the article's 34 pages to dealing with Thompson's objections and reconciling Thompson's model with his own.

Cole's model included a number of shortcuts for convenience. In particular, one need not know anything about survivorship, as Cole allowed for individuals to live to their maximum age before dying. Furthermore, reproduction was set at a constant rate of b offspring per time interval.¹⁴ In short, Cole's model would allow ecologists to attack population phe-

¹⁰ See Kingsland 1986, 1995 for an analysis of Thompson's work.

¹¹ For examples see Leslie and Ranson (1940); Deevey (1947); Birch (1948); Leslie and Park (1949). Leslie had apparently discovered Lotka's work in a literature search in the early 1930s (Caswell 18, 2001). Leslie's boss, Charles Elton, recognized Lotka by hanging a picture of him in the Bureau of Animal Populations library (Kingsland 1995, 133).

¹² The Euler-Lotka equation is given in various forms. Cole developed his model from a summation form popularized by Birch (1948). It is

$$1 = \sum_{x=a}^w e^{-rx} l_x b_x \quad (1)$$

where x is age, l_x and b_x are the survivorship and fertility functions of x , respectively, a the age at maturity, and w the age of last reproduction or maximum lifespan. See the text for definition of r and e .

¹³ e is the base of the natural logarithm ~ 2.71828 .

¹⁴ Cole had difficulty in fitting real data into the model, particularly with b which he maintained should be equal for all organisms that typically produce singleton offspring. That b must be measured over the same time interval as a and n did not occur to him. This led to inaccurate depictions, such as his Figure 5.

nomena much like a physiologist. A few representative animals could be studied in the laboratory, pertinent information could be recorded, and comparisons could then be made with other species or populations.¹⁵

Cole accepted that natural selection produces adaptations. As shown above, his evolutionary training at Chicago from Emerson positioned him such that the ultimate criterion for selection was group persistence. Focusing on species, Cole maintained that long-term persistence resulted from efficient turnover of members through death and reproduction. Competition *among species* could play an important role as a selective force.

If it is to survive every species must possess reproductive capacities sufficient to replace the existing species population by the time this population has disappeared.... It also seems obvious that a species which diverts too large a proportion of its available energies into unnecessary, and therefore wasteful, reproduction would be at a disadvantage in competition with other species. (Cole 1954a, 104)

For Cole, life history adaptations include factors that integrate populations, like feedback loops that lead to homeostasis. Mammary glands exist to integrate parent and offspring, and fish species over-produce offspring as a cannibalistic form of maternal provisioning (Cole 1957c, 1954a).¹⁶

Cole's mathematical simulations of changes in his life cycle can also be viewed as explorations of population integration. While later intellectual generations read these as intrademic selective scenarios, Cole was demonstrating how life histories are complete strategies in which each parameter's value to population growth and composition were dependent on one another (Kingsland 1995, 174). In outlining what has become known as "Cole's paradox", he was, in fact, demonstrating how the relative benefit of reproducing a single or multiple times in the lifetime depends upon age at maturity.¹⁷ He summarized the section stating, "Our

¹⁵ Cole had a background in physiology and much of the work in ecology at Chicago was physiological, carried out in the laboratory. See Kingsland 1995 for more on the movement toward laboratory methods in ecology and Mitman 1992 for the particulars of Chicago. In the late 1940s and early 1950s, Cole was working with water fleas (cladocerans) in the lab, but apparently never gathered results worth publishing (Cole n.d.).

¹⁶ Emerson was regularly singled out in the "levels of selection" debate, but Cole was also implicated for repeating some of Emerson's arguments: "[Cole and Emerson] have stated that one cannot explain the existence of mammary glands on the basis of selection for individual fitness because they contribute to the nutrition of another individual. The mammary glands are directly involved in a female mammal's attempts to increase her 'currency of offspring.' What could be a clearer example of a character that contributes to individual fitness?" (Williams 1966a, 159).

¹⁷ "Cole's paradox" became famous in its apparent solution in the early 1970s (Gadgil and Bossert 1970; Bryant 1971; Charnov and Schaffer 1973). See Brommer (2000) and Roff (2002) for recent his-

general conclusion was that the relative importance of changes in litter size and changes in the number of litters produced depends on the rate of maturation” (Cole 1954a, 122). The analysis which followed demonstrated further connections among life history features and importantly to population attributes of crude birth rate, age distribution, and rate of increase. For Cole, individuals within populations follow strategies that maximize the long-term stability and “good” of the population. Life histories are adaptations for maintaining group numbers around an optimal equilibrium.

The intrinsic rate of increase, r , calculated from the Euler-Lotka equation or a simplification of it, is currently a commonly used measure of fitness in evolutionary ecology (Roff 2002; Stearns 1992). However, it was *not* fitness to Cole. His interest in this parameter was directly related to population fluctuation as it is undeniably a metric of potential growth rate. Species, or other groups, with high r are likely to fluctuate more than those with low r . At points, Cole, notably in his *Quarterly Review* article, allows r to indicate a “selective pressure,” equating r with fitness, but these are prefaced by statements that limit selection to be for an increase in the intrinsic rate of increase. These are only special cases for Cole and “presumably...[r] is not always, or even commonly, the maximum that could conceivably be achieved by selecting for this ability alone”. Group selection would eliminate populations with such wasteful over-production. This view contrasts markedly with work on life history evolution in the following decade and which has remained dominant today.¹⁸ Indeed, r is a ubiquitous mathematical parameter in theoretical population ecology. However, because Cole was primarily interested in population equilibrium or steady-state properties, the r appearing in the case of unlimited growth described by the Euler-Lotka equation was of less interest than that of the logistic or its extensions in the interspecific competition and predator-prey systems of Lotka and Volterra.¹⁹

torical treatments by practitioners of life history theory. One can easily connect Cole’s interest in these two kinds of life history with wanting to understand population fluctuation. Animals reproducing over many seasons should have populations showing stronger correlations in size from year to year than those in which animals reproduce and immediately die.

¹⁸ See in particular Lewontin 1965; Williams 1966b; Gadgil and Bossert 1970.

¹⁹ The logistic equation

$$\frac{dN}{dt} = rN \left(\frac{K - N}{K} \right) \quad (3)$$

is a simple expression of population dynamics when there is a maximum population size or “carrying capacity” (K) given the environmental circumstances. As population size (N) approaches K the rate of growth (dN/dt) slows to 0 and final population size equals K . Lotka and Volterra independently extended the logistic equation by allowing members of one population to be counted proportionally

While I have argued that Cole's primary interest in life histories was to explain population fluctuations through their internal properties, it seems his inquiry was ultimately a failure on this account. His 1954 article on population cycles offers only a short section on carry-over effects between years and no subsequent work deals with the issue (Cole 1954b, 14). I suspect Cole found the internal properties of populations to be as potentially complex as the external environmental influences he believed were so varied they could be modeled with random numbers. As he concluded one section in his *Quarterly Review* article "there is an interaction of life-history phenomena such that the importance of any conceivable change can only be evaluated through consideration of the total life-history pattern" (Cole 1954a, 122). There was no clear way to join his life history model with population fluctuations; despite its simplicity there were too many variables and too many relationships among them.

Cole's interest in explaining population fluctuations or regulation through the internal properties of populations had much in common with his contemporaries' interest in "density-dependent" factors that control population size. These contrast with researchers favoring "density-independent" factors of the environment such as temperature, humidity, chemical concentrations, and light.²⁰ The British ornithologist David Lack is a particularly useful contrast in this regard. In the same year Cole's *Quarterly Review* article was published, Lack outlined how "density-dependent" processes in a variety of taxa could regulate population size through competition for limited resources (Lack 1954, Ch. 1–5). Like Cole, Lack took an explicitly evolutionary view of population regulation and life history traits, but he only dealt with competition *within* populations. Extending earlier studies on clutch size in birds, Lack emphasized that an intermediate number of offspring was most common because this trait was under stabilizing selection (Lack 1947; 1948). Hereditary variations for small litters were eliminated from populations because they were numerically overwhelmed in future generations but excessive litter sizes were also held in check by a lack of food for offspring to reach maturity (or ability to provision through

as members of a second and predicting the respective growth, decline, or stable coexistence of the two competing populations. Kingsland (1995) provides a detailed account of the development and controversial role of these equations in early theoretical ecology. See pages 107 and 133 in Cole (1954a) for discussion of r beyond the Euler-Lotka equation. See also Slobodkin (1961) for a textbook treatment of modeling populations by one of Cole's contemporaries and close friends.

²⁰ See Andrewartha and Birch (1954) for a "density-independent" view and Lack (1954) for "density-dependent." Cole was not allied to either camp in this debate but, as has been shown, was open to factors external and internal to the population that could control its size.

parental care). For Lack, the “efficiency” of populations resulted from internal processes in the population but they were evolutionary results of selection in changing its *genetic* composition rather than sex ratio or age structure. Life histories were adaptations but only to the benefit of the individuals bearing them. These perspectives coexisted into the early 1960s but only Lack’s would survive the “levels of selection” controversy of that decade (Wynne-Edwards 1962; Williams 1966a).

Human Population Control

Ecology in the 1960s was a discipline growing in numbers and changing in its theoretical and empirical core.²¹ Such growth encouraged disciplinary specialization and sometimes radical reconsideration of what ecology should be (Gould 1983, 147; Kimler 1986, 147; Collins 1986, 147; Hagen 1992, 147). Collins identifies three important trends in this period. First, influential articles by Mayr and Orians distinguished between functional or proximate explanations for phenomena and ultimate or evolutionary ones (Collins 1986; Mayr 1961; Orians 1962). Questions of causality can be answered on separate levels, such as a bird migrates on a particular date because of proximate cues (food shortage, light sensitivity, temperature drop) or ultimate causes (a selective history favoring genotypes that promote migration). The implication being that evolutionary ecologists should, of course, focus on ultimate causes once the functional-proximate mechanisms were understood.²² Second, scholars developed a greater awareness of the importance of genetic variation and microevolution to ecological questions of population size and interspecific relationships. Particularly important in this regard was the recognition that the speed at which evolution can proceed was not dissimilar from that of ecological processes. The long chronology of “evolutionary time” was telescoped into the readily observable “ecological time.” Finally, there was a narrowing of acceptable levels of selection to the gene or individual at the expense of larger groups of organization. Williams (1966a, 9) logically argued for a definition of function and adaptation tied exclusively to selection and therefore ultimate causation (Hagen 1992, 156). Parsimony dictated evolutionary cause (selection)

²¹ The major society in Britain and the United States both tripled between 1940 and 1960. See British Ecological Society (1964); Burgess (1977).

²² Textbooks were built around evolutionary theory rather than simply including it as another possible explanation for animal diversity and distribution. It became the explanation.

and effect (adaptation) be cast at the level of the individual, and only involve groups when individual explanations failed.

The 1960s was a period of transition for Cole as well. His research largely ended as he took on administrative tasks as department chair at Cornell (1964–1967), vice president and then president of the Ecological Society of America (1964, and 1967–1968), and various executive and advisory positions in the American Institute of Biological Sciences, National Science Foundation, and National Health Institute (Cole n.d.). Cole maintained an interest in population processes but it was focused nearly exclusively on one, the global human population and its remarkable growth.²³

Cole's scientific publications end around 1960 with an acrimonious exchange over competitive exclusion with Leigh Van Valen in *Science* (Cole 1960a; 1960b; Van Valen 1960).²⁴ Competitive exclusion is the notion that only one species may occupy an ecological niche which it prevents others from occupying and, in turn, is prevented from occupying the niche of any other species. The exchange focused on the strength and nature of competition. Cole maintained that competition was ubiquitous and that balance between inter- and intraspecific competition maintained populations at equilibrium levels and allowed for long term persistence of competing species.²⁵ Van Valen, in contrast, supposed competition is rare because one species is quickly replaced.²⁶ Just what competition could be to Cole, a typically population-level concept, came in his reply:

I will concede that the individual organism is 'harmed' by the predator that totally consumes it or by the competitor that causes it to starve to death, but this does not necessarily harm the population to which the individual belongs. At this level the activities of other species in holding down numbers may be important influences favoring survival. (Cole 1960b, 1676)²⁷

Cole was an outsider in a changing field. He endowed competitors

²³ Cole's scholarly activities were deemed sufficient for election to the National Academy of Sciences. However, he was never elected because academy members took issue with some of his popular writing and lectures (Walsh 1971).

²⁴ Cole's only other scientific publications after 1960 are on design of experiments (Cole 1962b) and a book chapter reviewing his unchanged ideas on population cycles and life histories (Cole 1965).

²⁵ This idea is anticipated in his research on population cycles where he lays out three possible sets of factors: external abiotic environment, internal population attributes, and relationships with other species (Cole 1951, 250).

²⁶ Latent in these arguments is the contemporary development of niche theory (Hutchinson 1957).

²⁷ This is a distinctively Chicago-zoology view of competition as both cooperative and disoperative.

with functional and ultimate roles in regulating the size of opponent populations and argued about population processes without reference to their genetic composition.²⁸ Although the reasons for his decision are undocumented,²⁹ Cole's next notable publication signaled the direction the remainder of his career would take. It was a book review of Rachel Carson's *Silent Spring* (Cole 1962a).

Though it was an attack on widespread pesticide use, *Silent Spring* helped to spark a public awareness of environmental issues throughout the world by identifying connections between human activities, the health of wild plants and animals, and reciprocal effects on human well-being. Cole had already expressed concern over human population growth but public appetite for such material that related human activities to environmental degradation was suddenly much greater (Cole 1955; 1958). Pesticide use and pest control, in general, were of secondary importance to Cole; he wanted to get to the root cause, too many people consuming too much of the Earth's resources, and disrupting otherwise balanced, homeostatic ecological systems in the process (Cole 1964; 1968; 1969a). Cole contended that there were too many people based on very general calculations of how much energy humans were consuming out of the total energy budget of the planet. Coupled with these numerical arguments were speculative narratives of human prehistory leading up to the recent removal of regulative forces that held the global human population in check.

What then to do about over-population? In an illuminating public lecture at Cornell in 1972 on the "Ecological Hazards in the Third World," Cole offered "austerity measures."

Any food shipped to India or Bangladesh, by keeping additional people alive and breeding, will only make the day of reckoning worse when it comes... maybe the best thing could happen to India is if that cholera outbreak took hold... We are doing a disservice to a country – I think it's immoral – to go into a country and tamper with their death rate, unless we are going to tamper with their birth rate also. (Cole 1972)

But the overpopulation problem was more complex than just numbers of people and was certainly not limited to developing nations.

²⁸ See note 16.

²⁹ It may simply be coincidence that Cole became more active in department and society administration, public lectures, and popular writing as his views on selection became heretical.

In term of the length of time he will live, the resources he will consume and the pollution he will cause... I estimate 1 American is the equivalent of 80 Indians. Others have estimated this figure as low as 25 or as high as 200. (Cole n.d.)³⁰

There is clear carry-over in Cole's public advocacy on human overpopulation from his earlier scientific publications. One finds continued understanding of populations as integrated units with feedback mechanisms that should promote long-term stability or equilibrium. Human population growth was so shocking because it appeared all limiting factors had been removed, at least temporarily. Solutions to global population increase necessarily involve balancing birth and death rates.³¹ Governments as integrative institutions of society are the prime avenue through which this demographic balance can be achieved. Individual choice and liberty are subordinate to the will and "good" of the population.

Cole's ideas have roots in a controversy around the time of the Second World War, in which paleontologist G.G. Simpson noted the totalitarian implications of such a biological philosophy writ social by Cole's mentors at Chicago (Simpson 1941).³² None of the Chicago zoologists had political outlooks of fascist, socialist, or communist flavors. Emerson, for example, was committed to democratic capitalism with some strong social controls that promoted cooperation, consensus, planning, and group consciousness (Mitman 1992, 164). While Emerson's reasoning was analogical and directed toward establishing a biological basis for ethical and political positions, Cole's was contrastive and abstract. Modern humans, unlike natural populations, did not balance reproduction and death nor did they find a stable rate at which to consume resources. The environmental crisis was the result of these broken integrative processes. Humans were an aberration in a natural order that only temporarily fluctuates around stable equilibria at many levels of organization. This is a common world-view among ecologists and laypeople that nature is capricious but ultimately beneficent and functions harmoniously through relationships among its many constituent biotic and abiotic elements, often expressed through aphorisms such as "balance of nature" or "mother nature" (Edgerton 1973; Pimm 1991; Jelinski 2005).³³

³⁰ From a press release dated March 31, 1972. See also Cole 1970b

³¹ Cole inferred steady-state populations should be paralleled by steady-state economies and decried the "obsession with growth" of most politicians, planners, and economists (Cole, 1972).

³² Simpson only attacked Ralph Gerard directly, a neurobiologist in the department of physiology at Chicago, in the article, but made frequent reference to studies of social insects that were certainly aimed at Emerson. See also Gerard 1940.

³³ Pickett *et al.* (1994, Ch. 9) suggest replacement of these ideas for communicating with laypeople through a "flux of nature" metaphor that emphasizes lack of equilibrium.

While Emerson offered biologically grounded hope for a world at war, Cole used scientific arguments about populations as a millennial call to destabilize accepted notions of progress and hope for the future (Cole 1969a; 1969b). Cole thus continues the social tradition of Chicago zoology of placing ethical positions upon biological bases of the systems they apply to, but divorces it from faith in the inevitability of movement toward greater integration, regulation, cooperation, and homeostasis (Mitman 1992, Ch. 7). For Cole, natural order can only be restored through active participation in the control of a globally deviant human population.³⁴

In this way, Cole blurs the distinction between the healing and engineering metaphors used to contrast ecologists in the pre- and post-Second World War eras (Mitman 1992, Ch. 1 and 9). As healers, Allee and Emerson looked to nature for fundamental principles governing social behavior and evolution that were “a therapeutic for curing social ills.” This image was replaced in the post-war era by ecologists mechanistically focused on practical management of natural systems through the common currency of energy cycling through biotic and abiotic vessels – ecologists became environmental engineers. Cole’s position in this dichotomy is difficult. He maintains a biological humanism, inferring human populations should be regulated and stable, just like wild animals. However, the healing message is gone. Instead, Cole offers practical solutions to regulate, or engineer, the human rather than the natural.³⁵ In this sense healing, both environmental and social, comes from engineering a proper balance of the global human population with its resources.

It is difficult to know whether Cole’s socio-political views on population control preceded or motivated his ecological interest. There is some suggestion simply from the chronology of publications that he had a growing interest in population processes, with overtly social implications, in the late 1940s and was impassioned enough to part ways with an old friend and advisor over how to address the “population problem” in the mid-1950s (Cole 1948; 1955).³⁶ However, there is no record of Cole ever

³⁴ There is nothing particularly novel in this position within the environmentalism of the late 1960s and 1970s. For example, see Ehrlich (1968); Ehrlich and Ehrlich (1970) and the Zero Population Growth movement (renamed Population Connection) or the Club of Rome’s Limits to Growth.

³⁵ Cole (1968) and Cole (1970a) contain some suggestions of how to do this: delay marriage, legalize abortion, disseminate contraceptives, offer cheap or free sterilization, and institute financial rewards for women who choose not to have children. He usually leaves the particulars up to a hypothetical multidisciplinary body of experts who would decide the sustainable number of people for the planet and design a strategy to implement it.

³⁶ Norton (1983) offers a similar analysis of R.A. Fisher’s interest in genetics and selection with his participation in the eugenics movement.

joining any organization devoted to political action on environmental or population problems. The organizations Cole chose to work through were all scholarly and decidedly “establishment.”³⁷

Conclusion

In the 1960s much of evolutionary ecology followed the lead of a new generation of scholars focusing on selection operating on the genetic composition of populations. Cole, while initially clashing with this new group of ecologists, ultimately diverted his attentions to raising public awareness about the ecological impact of a growing human population. Group selection, loosely applied as it was by Cole and his mentors, was cast into disrepute. Population efficiency no longer merited interest in a field focused on individual reproductive decision-making optimized by intrademic selection. Nevertheless, Cole's orphaned mathematical explorations, which included the ubiquitous parameter r , were later adopted (coopted?) by evolutionary ecologists and reformulated as “selection favors those genotypes that have the highest rates of increase” (Roff 2002, 3).³⁸

Cole's public endeavors, however, continued a tradition of treating the population as a distinct level of organization, rather than merely a collection of individuals. Furthermore, Cole drew upon commonly held views of nature as ordered – tending toward stability and equilibrium, but he accomplished this through contrasting the aberrant modern human with the normative natural. While Emerson and Allee offered hopeful visions grounded in biological “facts” for a world troubled by depression and war, Cole, like many other environmentalists, was a prophet of doom in an age of affluence – a human population engineer for the healing of environmental wounds.

³⁷ See page 505 for organizations Cole was active in. He seems to have been uneasy about many of his peers in the environmental movement. One notable connection is the short-lived but influential radical journal *Concerned Demography* that was briefly published at Cornell. In it, Cole's position, that poverty and environmental degradation are the result of over-population, is attacked as imperialist, racist, and contributing to maintenance of the status quo (Greenhalgh 1996).

³⁸ This is in direct reference to the impact of Cole's 1954 *Quarterly Review* article.

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