

Ngongas and ecology: on having a worldview

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Ngongas provide a metaphor for some of the opportunities and challenges facing the science of ecology and evolution. Ngongas, the traditional healers of the Shona culture, Zimbabwe, fail in the delivery of quality health by today's standards. Their outdated worldview makes most health related issues seem more complicated and more multi-factorial than when viewed through the worldviews of modern medicine. With the wrong worldview, one can work very hard, be very bright and dedicated, and still be ineffective. With the right worldview, one can work much less hard and still be extremely effective. As ecologists, we should be opinionated and possess clearly articulated worldviews for filtering and interpreting information. As ecologists, we are also a bit like ngongas – we often fail to provide answers for society's ecological questions and problems, and we excuse ourselves with a belief that ecological systems are too complex and have too many factors. Unlike ngongas, this invites us to pay a lot of attention to promoting and assessing competing worldviews. We should be open-minded to the anomalies in our worldview and the successes of alternative viewpoints. As an admitted ecological ngonga, I discuss the worldview I use in my own research: the Optimization Research Program, a Darwinian research program that uses game theory to conceptualize and understand ecological systems. I use it to illustrate how worldviews can synthesize disparate ideas. (I use kin selection and reciprocal altruism as examples.) I use it to show how new ideas and predictions can be generated. (I use root competition in plants and the possibility that increased crop yield may be forthcoming from knowledge of this game.)

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Ngongas and worldviews

The ngongas swirled and danced on the steps of the hospital welcoming back a member of the professional community, my Dad. To me, a sixteen year old, these traditional medicine men of the Shona culture looked marvelous, dressed sometimes in leopard skins, crowned with feathered hats and toting bags filled with bones, horns, python skins and muti (medicinal ointments). A clash of worldviews underpinned the pomp of the ngongas and my father's discomfiture. They were reminding Dad of their presence. Dad, a surgeon, serviced health in two hospitals and outlying clinics in Zimbabwe (then Rhodesia). The ngongas serviced health in the villages and from their kraals.

A detailed study of the achievements of the ngonga's "traditional" and Dad's "modern" medicine would be instructive and merited. But, in its absence, it is probably fair to say, that by late 20th century standards, Dad and his compatriots were successes and the ngongas were much less so. The hospitals effectively treated and vaccinated against measles with few second thoughts. The ngongas fretted about measles as some of their patients died and quite a few survivors remained blind. Why the differences in success?

Was it always so? Probably not. Preference might be given to an ngonga over a blood-letting physician of Europe in the Middle Ages.

Is it intelligence? Even adjusting for my biases, Dad is an extremely bright person. But, indubitably there are even smarter persons among the ngongas.

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Is it dedication? Dad in volunteering time to mission hospitals is highly dedicated. But, again, there must be some ngongas that have even more drive to cure and tend to the health problems of their communities.

Is it intensity of training? Dad often pointed out his numerous years of post-graduate education. Yet, many ngongas had been apprenticing since they were children and their training could continue well into their thirties.

Is it the ability to do science? Probably not. Ngongas likely experiment and share results. An ngonga may deviate in his treatment of a child's measles. He notices and reports a small but significant decline in blindness by shaking the bones first, leading the family counter clockwise around the kraal, appealing to the ancestors, and applying muti last. In time this may become the new norm of practice.

Is it worldview? Yes! Dad's core assumptions regarding physiology, anatomy and infectious diseases lead to a course of action and a set of conceptual and methodological tools that yield success. And they differ greatly from the tools and practices emanating just as logically from the ngonga's core assumptions regarding health. These core assumptions comprise a worldview. The ngongas worldview conflates anatomy, disease, physiology, metaphysical processes, ancestors, and social fabrics in a manner that complicates and obscures most ailments. Through the spectacles of Dad's worldview, health is rendered simpler and more transparent.

So here's the rub. A bright, dedicated person receiving education under the ngonga's worldview is doomed to work hard and achieve much less than a lazier, less bright, and less dedicated person who practices "modern" medicine's worldview. (A council of ngongas recently applied their worldview and concluded that treating AIDS should include killing infant orphans.)

Here are the messages of this paper for students of evolutionary ecology. First, I am going to argue that we are currently a bit of an ngonga science. Yes, I am an ecological ngonga (whew! good to have that confession off my chest!). And, being at this stage of scientific understanding is okay. It offers certain exciting opportunities and challenges.

Second, it should be obvious that worldviews matter. Get your worldview wrong (relative to other views) and you are doomed to work hard, view nature as overly complex and confusing, and achieve less in a lifetime of science. Get your worldview right and you can work much less hard and still achieve much more. In summary, we should pay a lot more attention to our own and to others' worldviews than we usually do.

Third, to illustrate the formalizing of a worldview, I will discuss the worldview that drives my own perspectives and research. And then illustrate, with somewhat parsed examples, how a worldview serves the two purposes of: 1) simplifying and synthesizing existing ideas and knowledge, and 2) directing research and application.

Worldviews and research programs

Following a philosophy of science outlined by Lakatos (1978) a research program or paradigm (Kuhn 1970) consists of a series of hard-core hypotheses. From inside the worldview, the hard core serves as axioms that are not directly tested. As axioms they limit and channel the logical deductions and predictions that emerge from making observations and hypotheses regarding natural phenomena. The hypotheses that emerge when applying a worldview to a specific scenario or context are referred to as auxiliary hypotheses. When conducting research, the scientist is generally testing these auxiliary hypotheses rather than the hard core.

As a quick example, consider foraging theory. The hard-core assumptions view feeding behaviors as adaptations shaped by natural selection to maximize fitness. Application of the theory requires hypothesizing an environmental context, a set of constraints that define the aptitudes and choices available to the feeding animal, and an objective that relates measures of feeding performance to fitness. For instance, let us consider how long a feeding animal should remain depleting a food patch before moving onto another. We hypothesize that the animal is trying to maximize its net rate of energy gain and that the animal has excellent knowledge of the patch's resource abundances and its harvest rate within the patch. We test the theory and discover that the animal does not harvest the patch as thoroughly as theory predicts.

Our compound hypothesis has failed, but, which of the constituent hypotheses is wrong? 1) Does the animal not forage optimally? Perhaps the assumption of optimality is incorrect. 2) Is the forager not as smart as we thought? Perhaps we have misidentified constraints on the animal's information state or repertoire of feasible behaviors. 3) Or, is the animal attempting to maximize something other than net energy gain? Perhaps we have postulated the wrong objective function. In applying a worldview or research program, one generally opts for the latter two possibilities rather than the first. The first is a hard-core assumption, the latter two are auxiliary hypotheses. To be vibrant, failure of a prediction should quickly and effectively lead to refutations of auxiliary hypotheses. These refutations should then lead to new hypotheses and insights that expand the scope of the research program rather than ad hoc explanations for each test's failure.

For instance, animals may not have perfect information regarding patch quality and harvest rates. This has led to novel theories (Oaten 1977, Iwasa et al. 1981, McNamara and Houston 1987) and tests (Valone and Brown 1989, Valone and Giraldeau 1993, Olsson and Holmgren 1998). Or, animals may include considerations of food and safety when maximizing fitness. This has led to an entire subfield of foraging based around

feeding under predation risk (Sih 1980, Gilliam and Fraser 1987, Brown 1988, Houston et al. 1993, Lima 1998). A worldview and its resulting research program becomes degenerate when explanations for failed tests become excuses that offer little in the way of new insights, applications or hypotheses.

Worldviews: turnover and replacement

Relative to ngonga-ism, modern medicine is a vibrant worldview and ngonga-ism is currently degenerate. How can a practitioner of one of these worldviews recognize this? Based on the hierarchy of hypotheses presented above, a scientist, ngonga or otherwise, will respond to failures by rearranging auxiliary hypotheses rather than questioning the hard-core hypotheses of the worldview itself. Yes. But the ngongas should, as the reception for my father showed, keep an eye on the competition. This should not be my Dad per se, but his worldview and its application. By keeping an eye on the scope and successes of competing worldviews, and by acknowledging the accumulation of anomalous results emanating from one's own worldview, a scientist can judge vibrancy and degeneracy.

The turnover and replacement of hypotheses within a research program proceeds relative to their position in the hierarchy of the worldview. The worldview turns over slowest, while highly specific hypotheses, narrower in scope and application, can turnover very quickly. However, the speed and effectiveness at which an individual scientist replaces hypotheses depends on her/his temperament with respect to ego, motive, personal goals, pride, etc. Some are willing to replace auxiliary and/or hard-core hypotheses more or less quickly than others, and in a fashion that is more or less productive to the scientific progress.

Consider the following "typology of a scientist" with respect to evaluating data and willingness to change views and hypotheses accordingly (Table 1). People can be opinionated or un-opinionated. The former quickly draw conclusions and interpretations from available information, and these facts quickly become theory-laden and packaged into a somewhat inseparable mixture of actual phenomena and worldview. The latter people recognize the facts or phenomena but do not integrate them into a worldview, or they try to keep them distinct from interpretations. People can be close-

Table 1. Typology of a scientist based on all combinations of persons being opinionated vs unopinionated and close-minded vs open-minded.

	Close-minded	Open-minded
Unopinionated	Cynical	Wishy-washy
Opinionated	Stubbornly know-it-all	Constructive

minded or open-minded. The former much prefer to question and reject new and contrary facts than to accept that a favored hypothesis is wrong. The latter prefer to alter hypotheses and views relatively quickly in light of new information or facts.

The possibility of being any combination of opinionated vs unopinionated and close-minded vs open-minded offers four types of scientists (Table 1). I am sure you can recognize yourself and some others in the four boxes. Sometimes, we as individuals operate according to one box or another depending upon the circumstances and issues. However, for whatever reasons, certain combinations occur more naturally than others. For instance, people who are opinionated are generally close-minded. People who are open-minded more often than not are also un-opinionated. In fact, we often associate growing older as scientists with a process of moving from being open-minded and un-opinionated to being close-minded and opinionated.

I would like to suggest that for the workings of a worldview, for the productive turnover of hypotheses, and for progress in science (Oh no! A worldview of worldviews), we must fight against natural tendencies and strive to be at once open-minded and opinionated. Here is why. Being open-minded insures a productive and fair evaluation of information in a manner that can matter. New information and views are welcomed as opportunity and progress rather than as threat and complication. Being opinionated means having a worldview and hierarchy of hypotheses from which to evaluate, interpret and apply information rather than having no means to integrate, synthesize and use available information. The constructive scientist has a strong worldview whose auxiliary hypotheses and ultimately whose hardcore hypotheses can and must be challenged and allowed to turnover. He or she has interest in the progress and application of other competing worldviews. The constructive scientist values the process more than the views and hypotheses themselves. In short, the constructive scientist brings about the turnover and replacement of auxiliary and hard-core hypotheses.

In any field of science, some hard-core hypotheses turn over relatively quickly while others endure, prove useful and become relatively unassailable. These hypotheses become Laws (see Turchin 2001). As a field accumulates more and more Laws it tends to become increasingly successful at identifying and answering questions and problems of concern to people in general. Such a field has a fertile worldview, and much activity goes into formalizing its application, clarifying details and refining auxiliary hypotheses – much like modern medicine in regard to infectious diseases. When societal questions remain unanswered, when solutions seem exceedingly complex, and refining auxiliary hypotheses achieves little in terms of societal goals, then a field of science should be more willing to replace worldviews,

more willing to reject hard-core hypotheses and less interested in auxiliary hypotheses for their own sake. A scientist of the ngonga's worldview should be as interested in whether the rattling of bones is even necessary, as in better ways of rattling bones.

What of all this for the science of ecology and evolution?

Questions and worldviews in ecology and evolution

Our field has several big questions that then devolve into more practical questions of managing and changing our environment. 1) Fit of form and function: How is it that organisms possess characteristics that make them ideal for dealing with the challenges and opportunities of their environment? 2) Diversity of Life: Why are there so many kinds of different living organisms? 3) Procession of Life: Despite the huge variety of life forms, why does life seem connected according to certain common design rules and hierarchies of complexity? 4) Distribution and Abundance: What regulates the abundances of different organisms. Then there are the practical questions of society regarding the control of pests, the success of valued species, the preservation of biodiversity, the management of natural areas, and the creation or restoration of ecosystems that please in terms of aesthetics, education, production of physical commodities, and/or the regulation of ecosystem processes.

Our field has made great progress in the last century and a half. We know a lot and can certainly enjoy and celebrate achievements (see Oksanen 1991, Rosenzweig 1992). Yet we hold to a lot of unsupported ideas, almost to the point of superstition (Slobodkin 2001, kindly refers to these as "reifications"). We are not wholly successful at providing solutions for even fairly modest requests from society to design parks, sustain yields of natural resources, save species, and manage the functioning and composition of ecological communities. Consider each of the big questions.

The fit of form and function we know to be evolution by natural selection. But, much debate revolves around the role of genetics in allowing us to model and understand evolution by natural selection (Willis et al. 1991). Must evolution by natural selection be understood and managed as a historical process or can the products of evolution be studied ahistorically by their present function and the forces that maintain their present state? We know that as we change habitats and environments species will evolve (witness antibiotic resistant strains of bacteria, pesticide resistance in invertebrates, weed ecotypes that invade and respond to our agricultural practices, and the shrinking in size at first reproduction of commercially valuable species such as cod, Law 2000).

We are less successful at predicting how much, how fast, and in what direction species will evolve. Under present worldviews and knowledge, it is deemed too complicated with too many factors!

The diversity of life has not produced many general and widely accepted hard-core assumptions. Populations can grow exponentially under ideal conditions and will eventually face limits to growth in response to resources, space and biotic interactions (Turchin 2001). But how much these processes, operating locally or regionally, contribute to diversity is cause for much debate and numerous theories. Speciation is the evolutionary process producing diversity. But, whether speciation emerges adaptively or non-adaptively, occurs to fill available ecological opportunities or occurs haphazardly remains contentious. The interplay between ecological and evolutionary processes, and local and regional scales are known to influence biodiversity. But, we are less successful at predicting how to manage biodiversity, prevent extinctions, and maintain and support communities with particular characteristics and compositions.

The procession of life has inspired large advances in the past thirty years. Techniques of phylogenetic analysis combined with molecular genetics has produced increasingly reliable pictures of how life is related and when important events occurred. We are obtaining better and better views of the temporal and spatial patterns of the procession. But, while we have the states, we do not have a good handle on the actual evolutionary, abiotic and biotic forces that produce the patterns. A bit of ancestor worship can creep into historical approaches occupied with establishing phylogenetic independence for studies of evolutionary ecology (Brooks and McLennan 1991). Is macroevolution merely microevolution writ large, or are their hierarchies of forces (i.e., species selection above the level of populations and individuals) producing a hierarchy of life? How quickly does diversity recover from a mass extinction? Are mass extinctions irregular or cyclic, due to endogenous or exogenous factors? Is there progress in the procession or merely contingency and mixtures of good and bad luck? Has diversity plateaued or has it been generally increasing? To us right now, it all seems very complicated with too many factors to sort out.

Are we ngongas? In two senses, yes. Society would like to balance conflicting demands for development, human welfare and nature. We shake our bones, remark on the great complexity of nature, note the intractable inter-connectedness of life, and then keep our fingers crossed when agencies actually take our advice. We fear that we may be wrong and that our suggestions may not work. "More research is needed" is a favorite hedge for admitting our ignorance or lack of confidence. I am exaggerating. We have been successful at bringing some species back from the brink. Agriculture, silviculture and epidemiology all represent

vibrant and successful applications of ecological and evolutionary principles. Collapses of fisheries and losses of biodiversity often emerge from a lack of social, political or economic will, rather than bad ecology. But, when the will is there, we often have answers that place unacceptably wide margins of uncertainty on the amount of land required, the likelihood of species extinction, the likely ecosystem functions, and the prescriptions for ridding undesirable species. The ecological and evolutionary consequences of global climate change offer perhaps our most interesting challenge. Can we predict and prescribe, or will we explain events after the fact or play sideline Cassandras (Aarssen 1997, Lawton 1999, Murray 2000)?

We are also ngongas when we apply worldviews and prescriptions far beyond their bounds of application or long after they have been discredited. Reified ideas held on faith rather than scientific support (Slobodkin 2001) provide some examples: diversity and complexity beget stability (Hutchinson 1959), species-diversity gradients (Rosenzweig 1992, 1999), the “airplane rivet” perspective on communities where species loss necessarily threatens the community’s collapse (Bazzaz et al. 1998), and the need to preserve genetic variability as a means of preserving the ability of a population to respond to natural selection. Conservation genetics emphasizes the dire consequences of inbreeding, loss of heterosis, and loss of coadapted gene complexes for causing extinctions. These factors can matter (Lacy 1987) and can be of conservation importance (e.g., Florida panther, O’Brien et al. 1990). Yet, most extinctions result from over-exploitation, competitive exclusion, or habitat loss and degradation. A priority on genetics in species recovery plans and population viability analyses leads us to re-arrange genetical deck-chairs on an ecological Titanic (Brown 1994).

We are ngongas in a very exciting sense. We do not yet have very satisfactory worldviews. We should welcome competing worldviews. While it is well worth arguing worldviews, we should encourage ecologists to pursue their worldviews in ways challenging to their own and to the worldviews of others. We should do the same with our own worldview. We can be opinionated and evaluate information and motivate our own scientific inquiries through the lens of a well-formulated worldview. And, we can be open-minded and admire and learn from the successes and applications of other worldviews. Furthermore, because there are numerous ecological scenarios for which answers and prescriptions are still debatable and equivocal, we can use conservation and restoration as opportunities to experiment and compare competing hypotheses and worldviews (Bradshaw and Chadwick 1980, Jordan et al. 1987). We are invited to worry less about fine-tuning hypotheses within a worldview, and to worry more about modifying our worldview.

The optimization Research Program

My worldview follows the Optimization Research Program as described by Mitchell and Valone (1990). It places an emphasis on using the ecology and evolution embedded within Darwin’s theory of natural selection to understand individuals, populations, and communities (Orians 1962). The hard-core assumptions of this Darwinian approach lie in three axioms. It differs from what most of us think of in terms of modern evolutionary theory in that the theory is framed within the logic of game theory rather than population genetics or quantitative genetics. I subscribe to a “strategy” rather than “genetic” approach to evolutionary ecology (see Vincent and Brown 1988). This does not mean that the optimization approach disavows or ignores genetics. The subtle but important difference between a genetical and an optimization approach to studying evolution by natural selection is that in the former genetics is part of the hard-core assumptions whereas in the latter it forms part of the auxiliary hypotheses. In an optimization approach the details of genetics may or may not be necessary. As Grinnell (1924: 225) noted when referring to evolution:

“Evolution [by natural selection] is not variation, nor is it inheritance, nor gene-mutation, nor hormone production, nor any other quality of feature or process, though each and all of these may be vital to the existence and persistence of living beings.”

Games have players, strategies, payoffs and rules. Life as a game recognizes individual organisms as the players, their heritable phenotypes as their strategies, their expected per capita growth rates (= fitness) as payoffs, and the ecological and physical factors determining fitness as the rules. Darwin’s postulates of 1) heritable variation, 2) struggle for existence, and 3) variation influences the struggle can be translated into a game.

Heritable variation: Organisms are comprised of heritable phenotypes, u , that are drawn from some set of evolutionarily feasible strategies, $u \in U$. Heritable means that like tends to beget like. The offspring of individuals with strategy u will likely have offspring with the same strategy. However, variation means that novel strategies from the strategy set do occur either as invasions from elsewhere, breeding among individuals, or mutations of strategies that occur from parent to offspring. The emphasis is on strategies not genes. While genes are the fundamental unit of inheritance they are not always the fundamental constraint on strategy sets. Genes, along with chemical and physical processes, contribute to the nature and boundaries of the strategy set. Genes are exceedingly important as the recipe of inheritance, but they are not the strategies of the Darwinian game. (Caveat: there are times when the genes are the individuals of the game and times when the heritable structure and operation of the genome is the strategy under selection.)

Struggle for existence: Organisms via their births and deaths have fitness. The struggle emerges from conjoining two Laws of Ecology (Lotka 1925, Murray 2000, Turchin 2001): 1) All populations have the capacity to grow exponentially under ideal conditions, and 2) No population can grow exponentially forever, there are limits to growth. Let G denote fitness (per capita growth rate) and N population size. The struggle for existence recognizes three things: under ideal conditions $G > 0$, population size can influence fitness, and at sufficiently high population sizes fitness declines with N and $\partial G/\partial N < 0$.

Variation influences the struggle: Fitness, G , is influenced by the individual's strategy, u , the strategies of others (denoted by the vector of extant strategies $\mathbf{u} = (u_1, \dots, u_n)$ where n is the number of different strategies currently found in the population), the frequency distribution of strategies among individuals (denoted by the vector $\mathbf{p} = (p_1, \dots, p_n)$ where p_i gives the frequency of strategy u_i within the population), and population size, N . Fitness is described by $G(u, \mathbf{u}, \mathbf{p}, N)$, where u denotes the strategy of the focal individual. The strategies of others, \mathbf{u} , their frequencies in the population, \mathbf{p} , and population size, N , represent the individual's biotic environment. This is a fitness generating function (Vincent and Brown 1984, Brown and Vincent 1987). The expected fitness to an individual using a particular strategy, u_i , can be found by setting $u = u_i$. In this way, the variable u in G allows one to generate fitness functions for each strategy currently in the population or for any strategy that might be evolutionarily feasible.

The three hardcore assumptions given above generate evolution by natural selection. The fitness generating function gives changes in population size:

$$\partial N/\partial t = N\bar{G}$$

where \bar{G} refers to average fitness: $\bar{G} = \sum p_i G(u_i, \mathbf{u}, \mathbf{p}, N)$.

The frequency of strategies among the existing strategies will change according to:

$$\partial p_i/\partial N = p_i G(u_i, \mathbf{u}, \mathbf{p}, N)/\bar{G}$$

The fitness generating function produces both population dynamics and evolution. Evolution can be defined as change in strategy frequency. But, in this strategic approach, evolution actually emerges from differences in the population growth rates of individuals with different strategies.

One can derive evolutionary dynamics that are analogous to dynamics from genetical models. For a group of interbreeding individuals, the change in their mean strategy value will be in the direction of and proportional to the fitness gradient. The following adaptive dynamic (Metz et al. 1996) applies to situations in which there is either a fixed variance of strategy values around the population's mean (Charlesworth

1990, Abrams et al. 1993, Vincent et al. 1993), or when new strategies arise by mutation near the population's mean (Diekmann and Law 1996, Hammerstein 1996, Kisdi and Geritz 1999):

$$\partial u_i/\partial t \propto \partial G/\partial u|_{u=u_i}$$

This game theoretic formulation of natural selection produces both ecological and evolutionary dynamics. Often, these dynamics take the evolving populations and species to combinations of strategies that are evolutionarily stable strategies (ESS, Maynard Smith and Price 1973, Maynard-Smith 1982). An ESS is resistant to invasion by rare alternative strategies and convergent stable in the sense that adaptive dynamics will return to the ESS when strategy values are near the ESS (Cohen et al. 1999). Evolutionary game theory has grown considerably in the past decade (Abrams and Matsuda 1996, Geritz et al. 1998, Hofbauer and Sigmund 1998).

Within a population genetics or quantitative genetics worldview, the optimization research program seems like an unrealistic, short-cut approach to solving problems with frequency-dependent selection. As a worldview in its own right, however, the underlying genetics become one of several important constraints that influence the set of evolutionarily feasible strategies and the possible directions of adaptive dynamics. From the perspective of evolutionary ecology, melding the genes of evolutionary dynamics with the individuals of ecological dynamics is cumbersome and often uninformative. However, the strategies of evolutionary game theory provide a seamless and transparent connection between ecological and evolutionary dynamics.

Simplicity and synthesis: kin selection and reciprocal altruism

Kin selection and the concept of inclusive fitness has advanced our understanding of natural selection (Hamilton 1963). It solved a lingering puzzle. In the dog eat dog world of natural selection, how is it that so many organisms behave altruistically and cooperatively with each other? So long as the cost-benefit ratio of cooperating is less than the relatedness among individuals ($r > c/b$) then a cooperative gene can spread through the population. From a genetic perspective, be nice to relatives because they share some of your genes. Inclusive fitness becomes a concept that adjusts individual fitness for the effects that an individual has on relatives weighted by their relatedness.

An alternative hypothesis for cooperative behavior is reciprocal altruism by which an individual uses some form of tit-for-tat to reward individuals that behave cooperatively and punish those that do not (Trivers 1971, Axelrod and Hamilton 1981). For reciprocal al-

Table 2. A form of the Prisoner's dilemma written as a game of cooperation in which the Cooperate strategy bestows benefit b on its partner and incurs cost c to itself while the Defect strategy bestows no benefit and incurs no cost. The matrix entries represent the payoff to an individual using a row strategy when partnered with an individual using a column strategy.

	Cooperate	Defect
Cooperate	$b - c$	$-c$
Defect	b	0

truism to evolve, individuals must have some knowledge of their opponents' behavioral proclivities. This knowledge comes via previous iterations of the game. Individuals play the game repeatedly.

A game theoretic perspective allows us to simplify and combine kin selection and reciprocal altruism into a single general model of kin selection and reciprocal altruism (see also Wilson and Dugatkin 1991, I thank Cathy Geraghty for contributing to the following analyses). The paradox of cooperation begins with the Prisoner's dilemma shown in one of its forms in Table 2.

In the game of cooperation, individuals can bestow benefits to each other (b) while incurring a cost (c) of providing these benefits. When two cooperators interact, each of them receives the benefit and pays the cost ($b - c$). For cooperation to be collectively worthwhile, the net benefit of cooperating must be greater than 0, which is the payoff that two defectors obtain from interacting. But, if interactions occur at random and if the game is played but once it is always best to defect.

We will relax both of these assumptions by considering non-random interactions and an iterative game by which individuals can gain information about others' predispositions. As an iterative game, we assume that each player plays the game many times. For simplicity, consider three strategies: always cooperate (All-C), always defect (All-D), and tit-for-tat (TFT). TFT individuals cooperate unless an individual is known to be All-D (Axelrod and Hamilton 1981, and see Dugatkin 1998). Assume that r is the probability of non-random interactions of like interacting with like (independent of the frequency of the strategy in the population). Assume that k is the probability that an individual knows the strategy of its opponent based on prior knowledge or experience. These adjustments to the Prisoner's dilemma yield a new payoff matrix shown in Table 3.

The new game is quite different from the one-play, random interaction Prisoner's dilemma. Notice that the entries in the payoff matrix represent expected payoffs to pairs of strategies. Furthermore, the payoffs have been adjusted for the fact that following many interactions a portion r occur with a like individual and only the portion $1 - r$ occur with the randomly selected individual represented by the column strategy. Consider

an All-C's interaction with an All-D individual. Only $1 - r$ of the time does the interaction actually take place (generating a payoff of $-c$) and the rest of the time All-C interacts with All-C. In other words, the payoffs in each cell of Table 3 already account for the statistical distribution of non-random and random encounters. (This is a useful accounting device, and there are other ways of obtaining the same result by writing a simpler payoff matrix and later incorporating the effects of r into a strategy's expected payoff.) In the case of the TFT strategy, the cells already account for the probability of recognizing the other player.

The All-D loses some of its advantage because of the assortative interactions and because the TFT individuals sometimes recognize the All-D individual for who it is. Similarly, the All-C and TFT individuals get cheated less in the face of All-D individuals.

We can examine the various ESSs of the model. All-C cannot be invaded by All-D so long as (Grafen 1979) All-C played against All-D yields higher rewards than All-D played against All-D:

$$b - c > (1 - r)b \Rightarrow r > c/b$$

This form of Hamilton's rule does not require genetic relatedness. All it requires is that an individual has a probability r of interacting with an individual with the same strategy. Interactions among relatives generates a positive r , but it is not necessary. From a strategic modeling approach, kin selection is too narrow a term. Kin selection is a form of cooperative behavior that can evolve when individuals interact non-randomly with respect to strategy.

TFT cannot be invaded by All-D so long as TFT played against TFT serves better than All-D played against TFT:

$$b - c > (1 - r)(1 - k)b \Rightarrow k > (c - rb)/b(1 - r)$$

It is easier for TFT to be an ESS than it is for All-C. TFT can benefit both from non-random interactions, r , and from having an iterative game that provides knowledge of others, k . If there are no non-random interactions ($r = 0$), TFT can still be an ESS so long as the

Table 3. Payoff matrix for an interactive Prisoner's dilemma with non-random interactions and described by three strategies: All-C means cooperate on all interactions, All-D means defect on all interactions, and TFT means only defect with individuals known to be All-D. The terms of the matrix have been adjusted for the probability of like interacting with like, r , and the probability that an individual recognizes its partners strategy, k (see text for further explanation).

	All-C	TFT	All-D
All-C	$b - c$	$b - c$	$r(b - c) + (1 - r)(-c)$
TFT	$b - c$	$b - c$	$r(b - c) + (1 - r)(1 - k)(-c)$
All-D	$(1 - r)b$	$(1 - r)(1 - k)b$	0

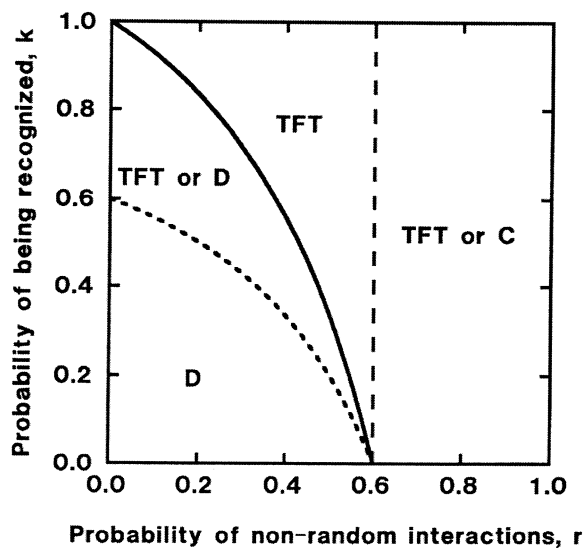


Fig. 1. The combinations of r and k that permit the evolution of cooperation. The term r represents the probability of non-random interactions in which like interacts with like (the coefficient of relatedness from genetical models of kin selection is a special case). The term k represents the probability that an individual knows the behavioral strategy of an individual during a play of the game ($k > 0$ for iterative games of reciprocal altruism). The likelihood of cooperation being an ESS increases with both r and k . "D" indicates the regions where always defect is an ESS. "TFT" indicates where a tit-for-tat strategy is an ESS. "C" indicates the regions where always cooperate can be an ESS.

probability of recognizing others is greater than the cost-benefit ratio: $k > c/b$ (Brown et al. 1982).

All-D cannot be invaded by TFT (and hence All-C) so long as All-D played against All-D serves better than TFT played against All-D:

$$0 > r(b - c) + (1 - r)(1 - k)(-c)$$

$$\Rightarrow k < (c - rb)/c(1 - r)$$

Decreasing either k or r increases the likelihood that All-D is an ESS. In fact, if there are no non-random interactions ($r = 0$) then All-D is always an ESS, even when TFT is also an ESS.

It is now possible to consider all combinations of non-random interactions and foreknowledge of others that permit cooperation to evolve (Fig. 1). Allowing both r and k to vary at values greater than zero, increases the range over which cooperation can evolve and reduces the likelihood that All-D will be an ESS. Values of r , $k > 0$ also permit cooperation where kin selection or classic reciprocal altruism would seem to fail. Rather than alternative hypotheses for the evolution of cooperation, kin selection and reciprocal altruism can be considered jointly (Wilson and Dugatkin 1991).

Research and application: root competition in crop plants

I would now like to consider an application of game theory to root competition that recently generated novel predictions, motivated experimental studies, and revealed phenomena in crop plants that might facilitate breeding for higher yields (Gersani et al. in press, Maina et al. unpubl.). Plants are known to adjust root production in response to nutrient availability and competition from other plants (Campbell and Grime 1989, Friend et al. 1990, Caldwell 1994, De Kroon and Hutchings 1995, Gersani et al. 1998). Consider an annual plant that must "decide" how to allocate roots between two soil habitats. Consider two scenarios. Under the fence-sitter scenario, two plants each share two habitats by virtue of having roots in each. Under the owner scenario two plants each have their own habitat. Each scenario has two plants and two habitats.

To generate predictions, assume that the total rate of nutrient uptake, H , increases at a diminishing rate with the total root mass in a habitat. Assume that fitness or fruit production increases monotonically with net nutrient uptake, where some nutrients are lost to the maintenance of roots and shoots. Finally, assume that plants sharing the same habitat acquire resources in proportion to their root mass. Hence, the net uptake rate, G , of the two scenarios are given by:

$$\text{Owner: } G = H(u) - C(u)$$

Each of two fence-sitters:

$$G = u_1^A H_1 / (u_1^A + u_1^B) + u_2^A H_2 / (u_2^A + u_2^B) - C(u_1^A + u_1^A)$$

where u refers to the root production of an individual within a habitat, the superscripts A and B refer to different plants when there are more than one plant sharing a habitat, the subscripts 1 and 2 refer to different habitats when a plant occupies more than one habitat, and the function C (in units of H) gives the cost of maintaining roots and their associated above-ground shoots and leaves. The above model assumes that either above-ground competition is negligible or that competition for light remains relatively constant with rooting strategy.

The owners represent a single player game in that the success of an individual does not depend upon the root allocation of another. The two fence-sitters represent a two-player game in that the fitness of one individual is influenced by the presence and root allocation strategy of the other. In the following analyses, I will keep the quality of the two habitats of the fence-sitters equal.

Applying the techniques of evolutionary game theory and the ESS maximum principle (Vincent and Brown 1988), the ESS amount of root production per individual plant, u^* must satisfy:

Owner: $\partial H/\partial u = \partial C/\partial u$

Fence-sitter: $(\partial H/\partial u + H/u)/2 = \partial C/\partial u$

As a game, the ESS root allocation of an individual under the owner scenario is less than that of an individual under the fence-sitter scenario (Gersani et al. in press). This is because the marginal rate of nutrient uptake, $\partial H/\partial u$, is less than the average rate of nutrient uptake, H/u . Hence, the value of root production that satisfies the necessary condition for the owner leaves the right-hand side of the fence-sitter's condition too large. Furthermore, the overproduction of roots by the fence-sitters in response to inter-plant root competition results in reduced fruit production relative to the owners. The reason for this has to do with intra-plant and inter-plant competition for nutrients. For the owner, each increment of roots provides the plant with additional nutrients but some of this increase comes at the expense of the plant's existing roots. In response to this intra-plant competition, the plant should appropriately moderate root growth. For the fence-sitters, each increment of roots provides additional nutrients, some of which come at the expense of the other plant's roots. This inter-specific competition among roots encourages each plant to continue producing roots. Unless the plants can come to a cooperative solution, analogous to the root allocation by an owner, two fence-sitters' ESS results in a tragedy of the commons (Hardin 1968): both plants lose yield to the overproduction of roots.

Colleagues and I have tested the model's predictions with peas, soybeans and a Kenyan variety of bean (Gersani et al. in press). Plants were grown either as owners (one plant per pot) or as fence-sitters (two plants sharing two pots). In all cases, the owners produced 20–30% more yield per individual, and the fence-sitters produced 30–90% more roots. Even with extensive plant breeding, cultivars may over-proliferate roots beyond that which would maximize the farmer's yield. Without knowledge of the game being played by plants underground, it may not be possible to recognize the potential for breeding more “docile” plants that produce roots cooperatively under conditions of inter-plant root competition. Knowledge of this game may in time lead to the breeding of docile root cultivars that permit increased yield without any concomitant increase in fertilizers, space, or pesticides (much like the breeding of cultivars with shorter stems facilitated the green revolution by making plants more “docile” with respect to competition for light).

Discussion

As evolutionary ecologists we recognize that our science is not yet “predictive” (Lawton 1999), falls short of

providing answers to societal questions (Aarssen 1997), and may lack the Laws associated with sciences such as physics and chemistry (Turchin 2001). Is this a problem in a normative sense? No. It represents the state of scientific advancement of the field. It makes us *ngongas* in the sense that we have not yet solidified an entirely effective worldview. Phenomena seem unassailably complex with too many interacting factors. An effective worldview would render most of these phenomena simpler and more transparent. Of course, it may be that ecology is uniquely complex and different from other “hard” sciences. I do not think so. We just have a way to go. Our emphasis should concentrate more on promoting competing worldviews than on fine-tuning current worldviews. We do not want to be *ngongas* in the sense of squelching alternative worldviews before they have a chance to develop. Rather than putting down other worldviews, we should be pushing our own to the limit.

To achieve the above we must, as scientists within the field of evolutionary ecology, have a well-formulated worldview. We should be opinionated. When asked what our worldview is, we should be able to articulate it clearly to a broad audience. This includes discussing and separating ones hard-core hypotheses from the currently useful and important auxiliary hypotheses. We should be open-minded at two levels. As new information and experiments become available, we should be willing to turn over our auxiliary hypotheses rapidly and efficiently. At another level, we should be constructively critical of our own and other worldviews. We can then recognize the anomalies in our own worldview and the unique contributions and successes of competing worldviews.

The Optimization Research Program (Mitchell and Valone 1990) provides the worldview that motivates the questions of interest to me. It is conventional in one sense. It embraces the ecological and evolutionary processes embodied in Darwin's theory of natural selection. It is less orthodox in that it focuses on heritable phenotypes and game theory to formulate hypotheses, both hard-core and auxiliary ones. Genetics holds a special place as the recipe of inheritance, but it is only one of several factors constraining the set of evolutionarily feasible strategies. The emphasis is on revealing the consequences of natural selection for individuals, populations and communities. The defining principle for our field, under this worldview, is an optimization principle rather than the conservation principles of physics. This principle is embodied in the ESS concept where evolutionary dynamics on the fitness generating function lead to strategies that maximize G with respect to the individual's focal strategy, u . This worldview holds that insights from natural selection will simplify and synthesize our understanding of ecological systems.

A worldview succeeds when it synthesizes and simplifies concepts or phenomena that seem more complex

or inaccessible to alternative views. A game theoretic approach to the evolution of cooperation provides such an example. Genetical models of kin selection (cooperation among relatives) or reciprocal altruism (tit-for-tat style behaviors) can be quite complex. The two avenues for cooperation seem quite distinct and may even be viewed as occurring along different levels of selection (kin selection being group selection at the family level, and reciprocal altruism at the individual level). Under the Optimization Research Program, kin selection is just a special case of non-random interactions among strategies where like is more likely to interact with like, and reciprocal altruism represents iterative games where players gain knowledge of others' strategies through their actions. Both avenues can be synthesized into a single, simple conceptual approach to cooperation.

A worldview succeeds when it predicts new phenomena that may or may not have ever been measured or observed. A game theoretic approach to inter-plant root competition shows that at the ESS annual plants may engage in a tragedy of the commons. Because of the benefits derived from "stealing" nutrients from neighbors, plants must over-produce roots beyond the level that maximizes collective seed or fruit yield. If this ESS is still present in crop cultivars, then knowledge of the game should direct breeding programs that could increase yields by encouraging plants with "cooperative" or "docile" rooting strategies. Initial experiments suggest that crops such as beans, peas and soybeans are not yet docile.

Worldviews matter. Our current worldviews in ecology and evolution leave us a bit like the ngongas. But, progress within and turnover of worldviews should be rapid, efficient, and constructive. We may be ngongas, but not for long. What is your worldview?

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