

Continuous Evolutionary Game Theory

The following represents a brief summary of continuous games. Discrete games are those where each player can only choose from a finite set of strategies (for example fight or run). Continuous games deal with cases where each player can choose from an infinite set of strategies by varying the strategy over some range. A common example is body size. On the assumption that the type of food consumed is proportionate to body size, coevolution of competition is often modeled by assuming the players (in this case species) vary body size or some measure of body size as a strategy to escape competition (e.g. Roughgarden's *Anolis* lizards or Peter Grant's *Geospiza* finches). Body size is a continuous strategy since it can take on any value over some reasonable range. Note that these games are played over many generations. Each individual is only playing one strategy for its life-time. However, over evolutionary time, a game is being played (assuming that the trait is heritable).

There are three types of factors that influence the fitness of an organism as a function of its strategy:

- Frequency dependent - my fitness depends on what other individuals are doing (what strategy they are playing). In competition for example if everybody else has a beak size of 1.5cm and I come along as the only player with a beak size of 0.75cm I will be able to access food that no else can, but if everybody else also has a beak size of 0.75, I will be at a disadvantage. Hence the fitness of beak size is "frequency dependent"
- Density dependent - my fitness depends on population size. Sometimes this is quite overlapping with frequency dependency. However, think of density dependency as those cases where my fitness depends on the absolute magnitude of individuals, not the percentage of individuals with my strategy. Classic population models (e.g. logistic) all have density dependent fitness built in (i.e. fitness decreases as population size increases). Density dependent selection may also be important on say clutch size - larger clutches are better with low densities, but smaller clutches are better with high densities.
- Intrinsic - i.e. fitness varies purely as a function of physiology, development, and the environment. In other words this is the catchall for fitness that is not frequency or density dependent. It often also includes the cost side of a strategy. Bigger horns than anybody else are better for fighting (a form of frequency dependence), but they also have a cost that is independent of the size of anybody else's horns.

Throughout continuous game theory, the concept of fitness used is absolute (not relative). It is equivalent to the Malthusian notion of fitness. I.e. the number of individuals produced in the next generation for a discrete model or the instantaneous rate of reproduction (i.e. r) for the continuous model. This can also be derived from population dynamics models as $\frac{1}{N} \frac{dN}{dt}$ yielding for example $r(1-N/K)$ from the logistic. Note

that this means that if you have a population dynamics model (dN/dt) you automatically have a fitness function and it contains density dependence and intrinsic fitness (for the parameters such as r and K in the logistic equation). However, it does not have any frequency dependence built into it.

This fitness then is a function of the strategy played, as well as the frequency and density. You will see a variety of notations for this fitness including $F()$ and $G()$, but I will use $W()$ here. As we just discussed, fitness is a function of the strategy, the frequency of other strategies, and the density. In short we have fully specified the fitness function as $W(u, U, N)$ where u is my strategy, U is the strategy of the rest of the population, and N is the density (size) of the population. The description of U (the strategy of the species) can be complicated as different individuals in the species can be using different strategies. Thus U can be represented either as a vector of # of individuals playing various strategies or as a probability density (e.g. normal with mean μ and standard deviation σ). However, in most cases, you will see U being modeled under the assumption that the rest of the population is all playing one strategy, in which case U is a scalar. This system is readily extendible to coevolution of two species ($W_1(u, U, V, N_{1,t}, N_{2,t})$ gives the fitness of species 1 for an individual playing u with the population of species 1 playing U , while the population of species 2 is playing strategy V).

The evolution and population dynamics are then fully determined by $W()$ as follows:

$$(1a) \quad N_{t+1} = N_t W(u, U, N_t)$$

$$(1b) \quad \Delta U = k \frac{\partial}{\partial u} W(u, U, N_t) \text{ evaluated at } u=U \text{ where } k \text{ is a constant often } h^2$$

Equation 1a gives the population dynamics and equation 1b gives the change of strategy (i.e. evolution in the trait). Equation 1a is identical to most population models in existence and is not considered to need justification. Equation 1b can be justified on the basis of Wright's adaptive landscape, quantitative genetics, replicator dynamics of haploid asexual populations, or more sophisticated approaches such as Hammerstein's streetcar theory of evolution (see reference listed below).

There is considerable controversy in the early literature as W was originally defined as $W(U, N_t)$. In short the concept of fitness of an individual with strategy u vs. a population with strategy U was eliminated. This ends up being equivalent to a group selection argument. It works if there is no frequency dependent selection, but if there is frequency dependent selection (and there always is in multispecies coevolution models), it produces incorrect results.

Under the dynamics given in equations 1, if the system is to be an ESS equilibrium U^*, N^* then the following must hold:

$$(2a) \quad \frac{\partial}{\partial u} W(u, U, N_t) = 0 \text{ at } U^*, N^* \text{ (remember, } u \text{ is also set to } U^* \text{ after taking the derivative)}$$

$$(2b) \quad W(U^*, U^*, N^*) = 1$$

Equation 2a means that U has evolved to a critical point either a maximum or a minimum (and hence $\Delta U = 0$ and evolution has stopped). Equation 2b means that the population dynamics are at a stable equilibrium point (i.e. $\Delta N = 0$). Early analysis called this an ESS if U^* was a maximum (determined by showing

$$\frac{\partial^2}{\partial u^2} W(U^*, U^*, N^*) < 0$$

The reasoning was simple. The essence of an ESS is noninvasability. If the population is playing strategy U^* and a mutant shows up playing u , then if u necessarily dies out it, U^* is an ESS. If u grows and flourishes, U^* is not an ESS. By making U^* occur at a maximum in fitness, this implied fitness of any strategy other than U^* was lower than the fitness of U^* and hence could not invade.

More sophisticated analysis has required that an ESS meet at least one additional criteria: that the dynamics of the system given by (1) cause the system to evolve to the ESS point. In other words equation 2 guarantees that if a population is at the ESS strategy U^* , then it can't be beat but it does not show that a population could ever evolve to this strategy given that it started at some other random point. Without density dependence and frequency dependence these two concepts (stable once there, evolve to get there) are identical but they are not necessarily the same with frequency/density dependence. The system will evolve to the point U^* if and only if either:

$$3a) \quad \frac{\partial^2}{\partial u^2} W(u, U, N) + \frac{\partial^2}{\partial u \partial U} W(u, U, N) < 0$$

or

$$3b) \quad \frac{\partial^2}{\partial u^2} W(u, U, N) - \frac{\partial^2}{\partial U^2} W(u, U, N) < 0$$

Equations 3a and 3b are mathematically equivalent. So equation 2 implies noninvasability, equation 3 implies that the equilibrium is an attractor (that evolution will evolve to that point) under the dynamics of equations 1. Thus a more appropriate definition of an ESS requires:

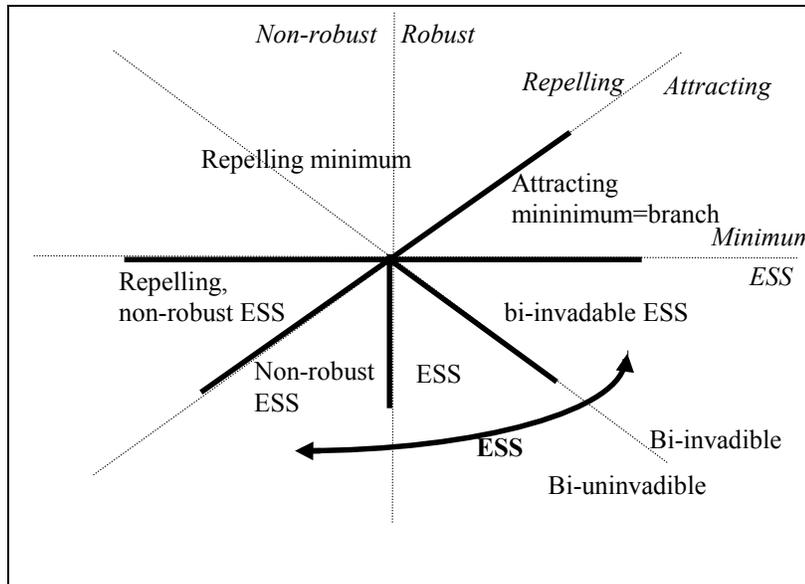
- Equations 2 be met - i.e. it is a stable point
- Fitness is at a maximum (i.e. $\frac{\partial^2}{\partial u^2} W(U^*, U^*, N^*) < 0$)
- The stable point is an attractor (i.e equations 3)

However, points that are of interest sometimes only meet two of the above three criteria. This results in the following surprising result. With frequency dependence we can have any of the following:

- An ESS maximum that is an attractor (meets all 3 criteria)
- An ESS maximum that is unstable (it will never be reached, and will be quickly evolved away from if the "hand of god" should start the system there) (meets first 2 criteria)
- An ESS minimum (the system will go there, but it will minimize fitness) (meets 1st and 3rd criteria)

Having already complicated the ESS definition by not only requiring non-invasibility (i.e. a fitness maximum) and the ability to get there (i.e. an attractor), some authors have identified additional criteria that might be necessary for a meaningful ESS.

Geritz et al define two additional traits relevant to analyzing an ESS besides the common attractor/non-attractor and ESS (maximum)/minimum. One is whether the ESS strategy can invade nearby strategies when the strategy itself is rare (called here “robust”). It is unclear how important this trait really is and many authors ignore it (see Kisdi and Meszina referenced below for one discussion). The final trait is whether an ESS (which is by definition uninvadable by a mutant) can be simultaneously invaded by two mutants - one on either side - in a sort of pincer effect (called here bi-invasible). Geritz et al conclude that this factor only matters at stable minimum, in which case it can be a mechanism of speciation. Thus Geritz et al define 4 traits of a candidate ESS (= a critical point of the fitness function). These traits are not totally



independent, so instead of $2^4=16$ possible categories, we only have 8. Geritz et al arrange these traits nicely in a circle as shown above where being to one side of a dotted line indicates presence of the trait (indicated in italics) and to the other side of the dotted line indicates absence (or the opposite) of the trait. The solid black lines indicate divisions between biologically meaningful categories. Thus the 6 conceivably biologically meaningful categories are:

- **Attracting minimum** - a minimum that is actually achievable. Because it is always bi-invadable it may serve as a branching point for speciation! Note that it is also necessarily robust. Geritz et al describe this in detail.
- **Repelling minimum** - evolution should never end up here
- **Repelling ESS** - never achieved even though it is an ESS - the cautionary tale of why you have to worry about whether you can get there, not just whether it is an optimum. Note that it is also necessarily non-robust and bi-uninvadable
- **ESS** - the purest ESS - it is not invadable (since it is a maximum), is an attractor, and is robust. Hence we will always get there. It is also bi-uninvadable
- **Bi-invadable ESS** - this is an attracting, robust ESS. As an ESS it is a fitness maxima and hence is uninvadable by a mutant with a different value. However, two mutants, one on each side can invade. However, evolution will push them back to the ESS strategy. Thus Geritz et al conclude (correctly in my opinion) that this doesn't matter. In short this should really be treated like an ordinary ESS. Thus bi-invasibility really only matters at a minimum.
- **Non-robust ESS** - this is an attracting, uninvadable, bi-uninvadable ESS that is not robust - i.e. it can not invade nearby strategies when it itself is rare. There is some debate of how important this is. See Kisdi and Meszina for an example. In my opinion this is unimportant. The non-robustness might imply that it takes slightly longer to get to the ESS, but in the end it is an achievable, non-invadable ESS and should be treated like a pure ESS.

In short there are really only four meaningful categories, the 1st three above plus an attracting ESS which combines the last 3 categories.

Finally, it is possible that the final state will not be a single ESS point but rather will be a cycle or strange attractor. In this case the trait undergoes continuous evolution, also causing population sizes to fluctuate. This has been found in models of both predator prey dynamics and of asymmetric competition. In either case this is called a Red Queen scenario. The phenomenon of evolutionary limit cycles have been observed in nature including taxon cycles in *Anolis* lizards, predator prey-red queen systems, and the rock-scissors-paper nature of a trimorphic lizard population studied by Sinervo.

Shortcomings and my two cents

In my opinion, four shortcomings of current continuous game theory are:

- lack of stochasticity - many of the conditions of an ESS are specifically designed to protect against stochasticity. In particular the idea of an attracting ESS assures us that a population at the ESS will return after any sort of small perturbation. However, the question of what an ESS is if the payoffs fluctuate (due to so variable rainfall favoring different germination strategies) has been given a mathematical answer (so called invasion exponents) that is not entirely satisfying to me. Invasion exponents take an average over an infinite period of time and consequently ignore streaks of unusually good or bad luck (e.g. the drought that led to the Dust Bowl in the 30's). Some who agree with this assessment conclude that this means there will be a large variety of coexisting phenotypes and nothing more can be said (see the concept of an ECS listed below), which is equally unsatisfying. Also meaningful study of how close to the ESS we can expect the population to be given various stochastic disturbance patterns has not been answered.
- assumption of fixed population dynamics - most models assume that populations have a constant size - or in other words that population dynamics are much faster than evolutionary dynamics, an assumption often not justified, and definitely not justified in the case of a stochastic environment where there is year to year variation in the environment and yearly reproduction.
- ignoring of multiple ESS's - some games will have multiple alternative ESS's. Exploration of what the basins of attraction are for each ESS should be done in this case. If there is only one ESS it should be demonstrated by showing that the ESS is a global maximum, not just a local maximum. Authors rarely bother. This is usually done by graphing the fitness function (derivatives alone can not ascertain whether is a maximum is local or global).
- monomorphic population - most models assume that the established population plays a single strategy. In fact the established population may be polymorphic. The monomorphic assumption can be justified by saying fitness is a function of the rare mutant vs. the average population (hence reducing a polymorphic population to a monomorphic one). This may be valid for some traits, but for other traits, averaging is a poor approach.

Some very interesting work has been done recently by mathematical economists who have adopted evolutionary game theory back from biologists. They have been studying the effect of stochasticity in a context of multiple ESS's. They have found that stochasticity can simply mean that any ESS is achievable regardless of initial conditions, but they have also found that under the right conditions (in particular the presence of mutation), stochasticity can guarantee that the highest peak is always obtained regardless of initial conditions! This work has only been applied to discrete games to date and it would be interesting to formally apply it to continuous games.

There has been a lot of polemics about Roughgarden's initial 1977 formulation and lack of intra-specific frequency dependence. While to ignore this is wrong in many now well-documented cases, there are cases where ignoring it is legitimate and the tools Roughgarden developed to analyze these situations are much more powerful than those currently available for the intra-specific frequency dependence case - we shouldn't throw out the baby with the bath water.

With regard to attracting minima serving as speciation machines, the point has not been proved in my opinion. There is no debate that the dynamics cause disruptive selection leading to a drive towards phenotypic splitting. One must be careful, however, because without the evolution of assortative mating, the

branching is meaningless - interbreeding will constantly eliminate the branching. While it is true that hybrid individuals will have lower fitness this does not automatically guarantee that assortative mating will occur. In my opinion whether assortative mating will occur depends a lot on the trait. If intermediate body sizes are less fit, it seems conceivable that assortative mating might develop because this is a highly observable trait, but if the trait being modelled is dispersal rates, it is harder to imagine a scenario in which assortative mating develops.

Finally, much of the analysis presented above of an ESS consists of taking a derivative and evaluating it at the ESS. This gives you information only for a very small interval around that point. Finding techniques to get more global analysis seems desirable. If you start far away, will it take a million years to achieve the ESS? Will a boundary absorb you instead? Will you be attracted to another ESS instead? Will the population dynamics go haywire every time the trait is bumped moderately far from its ESS value?

References

Best recent summaries:

- Abrams PA, Matsuda H, Harada Y "Evolutionary unstable fitness maxima and stable fitness minima of continuous traits" in *Evolutionary Ecology* 1993, 7, 465-487
- Geritz SAH, Kisdi E, Meszina G, and Metz JAJ, "Evolutionary singular strategies and the adaptive growth and branching of the evolutionary tree" in *Evolutionary Ecology* 1998, 12, 35-57
- Hammerstein P, "Darwinian adaptation, population genetics and the streetcar theory of evolution" in *Journal of Mathematical Biology* 1996, 34, 511-532 (this issue consists entirely of articles on adaptive dynamics, many of which are quite good)
- Kisdi E, Meszina G, "Life histories with lottery competition in a stochastic environment: ESSs which do not prevail" in *Theoretical Population Biology* 1995, 47, 191-211
- Ellner S, Hairston NG, "Role of overlapping generations in maintaining genetic variation in a fluctuating environment" in *The American Naturalist* 1994, 403-417

Namers:

The concept of an ESS has inspired many tweekers who have added minor additions to the basic non-invasible criteria. The following lists papers that first defined these extensions. See the cheat sheet at the end for definitions of these terms.

- ESS=Smith & Price 1973, Maynard Smith 1982
- ESS State - Reichard and Hammerstein 1983 - possibly earlier
- CSS - Eshel and Motro 1981, Eshel 1983
- convergence stability - Christiansen 1991
- stable ESS Max/unstable ESS max/stable ESS min - Abrams et al 1993
- internally/externally stable - Feldman et al 1991, Lessard 1990
- short/long term evolution - Eshel 1996, Hammerstein 1996 (earlier?)
- δ/m stable - Taylor 1989, Christiansen 1991
- ECS - Cohen & Levin 1991, Ludwig & Levin 1991
- EAST/PEAST/MEAST - Christiansen 1991
- anti-ESS - Uyenoyama and Bengtsson 1982
- EGS - Eshel & Feldman 1982, 1984
- EGS = Any new mutation from an internally stable must be favored if closer to the EGS. Differs (??) from CSS in cases such as sex linked control of sex ratio, linkage limited control of crossover rates.

Justifiers:

The following are papers which have attempted to justify the use of the dynamics equation 1b above. The justifications are based on various preexisting population genetics methods.

based on quantitative genetics

Charlesworth 1990, Taper & Case 1992, Abrams et al 1993 (listed in Geritz et al 1998)

based on allelic genetics

Eshel & Feldman 1982, 1984; Eshel 1983, 1991, 1996; Hammerstein & Selten 1996; Matessi & Di Pasquale 1996; Weisseing 1996 (listed in Gertiz et al 1998)

based on mutations as a stochastic process

Diekmann and Law 1996, Hammerstein 1996, Eshel 1996

based on learning

Abrams et al 1993

Complications

The following papers address some of the issues mentioned in the “shortcomings and my two cents” section

stochastic non-invasability

Turelli 1978, Turelli & Petry 1980, Chesson & Warner 1981, Ellner and Hairston 1994, Haccou & Iwasa 1995

Variable population

Turelli & Petry 1980, Ferriere and Gatto 1995

Polymorphic resident populations

Brown & Vincent 1987, Vincent & Brown 1988 (use a polymorphic population), Taper and Case 1992 (use a probability distribution of traits)

Two or more traits evolving simultaneously

Abrams et al 1993, Matessi & Di Pasquale 1996 (conclusions are similar even though they don't appear to be at first glance)

Stochasticity and multiple ESS

Foster & Young 1990, Fudenberg & Harris 1992 (in Journal of Economic Theory)

ESS cheat sheet for continuous traits - Brian McGill June 1998

Note: $W(u,U,N)$ can always be found from a population dynamics equation by $W(u,U,N) = \frac{1}{N} \frac{dN}{dt}$. Notation: u is individual strategy (makes individual selection, can drop if no freq dep), U is population strategy (assumed monomorphic, gives frequency dependence), N is population size (giving density dependence). W is also called $F()$, $G()$, $\rho()$ etc.

Trait	Adjective	Description	Form 1*	Form 2*
1 Non-invadable	ESS	The ESS trait can not be invaded by any other nearby mutant - in short when the population is at U , U is a maximum. IE it can handle a new mutant.	$\frac{\partial}{\partial u} W(u,U,N)=0$ $\frac{\partial^2}{\partial u^2} W(u,U,N)<0$	NA
2 Evolvable	attracting	The population will evolve to U . In dynamical terms U is an attractor. IE it can handle the whole population being bumped. If no frequency dependence or U linear in u then $1 \Rightarrow 2$	$\frac{\partial^2}{\partial u^2} W(u,U,N) + \frac{\partial^2}{\partial u \partial U} W(u,U,N) < 0$	$\frac{\partial^2}{\partial u^2} W(u,U,N) - \frac{\partial^2}{\partial U^2} W(u,U,N) < 0$
3 Invades when rare	robust	The trait U can invade <i>nearby</i> populations when U is rare. Note if 1+2 true approaches asymptotically anyway, however crucial if stochastic	$\frac{\partial}{\partial U^2} W(u,U,N) > 0$	NA
4 Population size stable		The population has a stable equilibrium point at the ESS	$W(u,U,N)=1$ (0 if continuous)	

In all cases the terms are evaluated at $u=U=U^$ and $N=N^*$ - i.e. take the derivatives and then substitute the equilibrium values U^* for u & U , N^* for N

Names

Name	Criteria
ESS, δ -stable	1+4 = uninvadable
convergence stable, m-stable, EGS (Evol genetic stability), EAST (evol attainable stable trait)	2 (+4 assumed) = attractor
stable ESS maximum, CSS (continuously stable strategy), MEAST (monomorphic EAST)	1+2 (+4 assumed) = uninvadable attractor
internally or short term stable	at genetic stability assuming no new mutants ($\Delta p=0$) (4 assumed)
external or long term stable	1+2+4 = uninvadable attractor
Unstable ESS maximum,	1 but not 2 (+4 assumed) = unattainable, uninvadable
Stable ESS minimum, PEAST (polymorphic EAST), anti-ESS	2 but not 1 (+4 assumed) (must \Rightarrow 3)
ECS (Evol compatible strategy)	3+not 1 (+4 assumed) = invades & invaded by any strategy

Variations

- If at stable ESS minimum (2+4+not 1) or ECS (3+4+not 1) must have $\frac{\partial^2}{\partial U^2} W(u,U,N) + \frac{\partial^2}{\partial u^2} W(u,U,N) > 0$ and hence the ESS is subject to invasion by a dimorphic population - stable ESS minimum is an attractor and therefore leads to direct branching after going to equilibria point vs. ECS has no attractor and simply has many mutations successful
- Can have cycling - i.e. the evolution (and hence population dynamics) does a periodic cycle instead of a stable point (e.g. taxon cycles, Red Queen). Chaos also possible
- Can have more than one ESS in which case can either have polymorphisms or which ESS is reached depends on where you start. Which of these happens depends.
- If the population is subject to stochastic fluctuations, then replace $W(u,U,N)$ with $E[\ln W(u,U,N)]$ and meeting 3 becomes important. Would also like to have $\frac{\partial^2}{\partial N \partial u} = 0$
- Similarly if the population undergoes cycles or chaos replace with limit as t approaches ∞ of $E[\ln W(u,U,N_t)]$

Dynamics

Evolution: $\Delta u = \sigma_p^2 h^2 \frac{\partial}{\partial u} W(u,U,N)$

Ecology: $\Delta N_t = N_{t-1} W(u,U,N_t)$ all evaluated at $u=U=U_t$