Cooperation, Competition and Economic Rent:
A Natural History Perspective

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All species cooperate, generating a shared surplus, or economic rent. Rent provokes competition between groups and between individuals within groups for a greater share of the rent. Competition in turn both dissipates rent and spurs innovation. Among territorial species, holders of superior territories have incentives to practice "imperialism"—controlling larger territories than necessary. Among non-territorial species, intense competition may promote rapid speciation.

In the beginning, there was cooperation. The earth is about 4.5 billion years old. The earliest known fossils are stromatolites, dating back some 3.5 billion years. These are remains of sticky mats of photosynthetic cyanobacteria (" blue-green algae"), clinging to rocks in ancient shallow seas, trapping sediment, and building up layer upon layer. By releasing oxygen, cyanobacteria created the atmosphere that made possible organisms that use oxygen to obtain energy. Non-photosynthetic bacteria, then and now, collect by the billions to form "bacterial slimes" on surfaces. Within the slimes, bacteria engineer the chemical environment to better digest a food source (which could be a mineral) or resist desiccation or environmental toxins.

Over two billion years ago, eukaryotic cells evolved. Unlike the simple cells of bacteria, eukaryotic cells have a nucleus and are packed with tiny "organelles." At least two of these, the mitochondria or "energy packs" and the chloroplasts of green plants, originated as "endosymbionts." These in turn descended from once-independent primitive bacteria. So eukaryotes themselves are cooperatives.

About half a billion years ago, eukaryotes gave rise to multicellular animals and plants, true cellular cooperatives. Cells of some plants and simple animals, like sponges, can survive on their own and regenerate the whole organism. Cells from more sophisticated organisms perish if separated.

Modern organisms quite visibly cooperate. On land, birds and mammals live in flocks or herds or packs. In water, whales swim in pods, fish in schools, and colonies of corals form vast reefs, building on the limestone skeletons of their ancestors. Plants cooperate too; a cluster of plants facilitates reproduction, and binds the soil, making the neighborhood more congenial to their kind.

Areas of Cooperation

How do organisms cooperate? They cooperate to feed, to protect themselves and to reproduce.

Feeding. As noted, bacterial colonies release chemicals to digest a substrate. Dinoflagellates in a "red tide" release toxins that kill fish, providing nutrients. Predators like starfish, orcas, wolves or lions hunt in packs. Social insects carry cooperation to its most sophisticated non-human level. For example, leaf-cutter ants cultivate edible fungi in vast underground farms. Many ant species herd aphids, which they "milk" for honeydew. Not only do bees collect, process and store honey and pollen, but individual bees "dance" to direct hive-mates to good sources of nectar. After a night's hunt, vampire bats regurgitate blood to share with less successful roostmates.

Protection from enemies and from the elements. Social insects cooperate to build nests—often emerging in a stinging fury when disturbed. Tropical termites build huge earthen towers with an "air conditioning" system of tunnels and vents to maintain a cool even temperature within. At the microscopic level, fungal colonies in the soil release "antibiotics" to inhibit bacteria. Schools of squid or herring, flocks of crows, herds of antelope, troops of monkeys—hang together to increase the group's ability to spot and dodge a predator. Groups, such as lions or baboons, also cooperate to seize or defend territory against other groups of the same species.

Reproduction. Reproduction requires cooperation. Even organisms like bacteria and many plants that reproduce asexually most of the time, must on occasion mate—exchange or combine genetic material with others. Coral animals (hydra) cooperate in spectacular fashion: every year, at the same hour of the same night, all the corals on a reef pour eggs and sperm into the water, thus maximizing the chance that eggs will be fertilized, and overwhelming predators with sheer volume. Social insects share care of the young, as do group-living mammals like wolves or meercats, and many species of birds including some weavers, woodpeckers and parrots. Often the offspring from one year hang around to help out with the next generation. The emperor penguins, made famous by the March of the Penguins film, huddle together in large groups through the icy Antarctic winter, keeping warm the single egg laid by each pair.

Patterns of Cooperation

In his *Principles*, John Stuart Mill distinguishes "simple" cooperation and "complex" cooperation, the first being where the cooperators all perform the same function the second where they specialize. (John Stuart Mill 1870).

Most cooperation among organisms is simple, such as hanging together for food and protection. Single-celled organisms, like bacteria, protozoans or fungi, may cooperate in colonies of millions or billions of genetically identical or closely-related individuals.

Social insects engage in complex cooperation. Several genetically-identical castes of leaf-cutter ants perform specialized tasks within the same nest, ranging from giants who guard the next to tiny ants who tend the underground fungus gardens.

Cooperation for reproduction is often complex. Sexual reproduction requires at least two individuals in complementary roles. Among mammals, birds, some fish and reptiles, and even some insects, parents care for vulnerable offspring. In effect, parents and offspring “cooperate” in preserving the family genes—though obviously it’s not a conscious purpose. From the viewpoint of the offspring, cooperation is a matter of life or death. The parents, however, make an unconscious calculation of costs and benefits; if food is scarce, or infants are weak, they may abandon one or more offspring.

Cooperation varies over the life cycle. Among solitary predators such as tigers, males and females cooperate in mating, and females “cooperate” with young, but otherwise go their own way. “Slime molds”, which are not molds but a kind of amoeba, live separate lives in rotten wood, cow pats, or similar moist habitats. But when food grows scarce, they congregate into huge swarms, which grow stalks with spores. The spores disperse and, if they land in suitable habitat, germinate into new tiny amoebae.

Sometimes cooperation is a tournament, in which low-ranked members wait for an opening in higher ranks—an opening which only a few of them will find. For example in wolf packs, only the “alpha” male and female breed. Other members of the pack, often siblings or older cubs of the alphas, help to raise the alphas’ new cubs. However should something happen to one of the alphas, lower ranked members have an opportunity to fill the vacancy. Many birds follow this pattern, which is common when good nesting sites are rare.

Habitat, Territory and Cooperation

All species require particular types of physical habitat, sometimes narrow and sometimes broad. Suitable habitat determines species' range—humans and rats having among the broadest ranges. This habitat may change over the lifecycle. For example, the malaria-causing plasmodium parasite lives partly in the anopheles mosquito, and partly in humans. Some creatures, like fleas on a dog's back or bot larvae in a zebra's gut, occupy mobile habitats. A safe place to raise young is often the most valuable part of a habitat—a water-filled leaf for a tree frog, a hollow tree for a pair of parrots, or a remote island beach for seals. In fact, it's difficult to describe cooperation without specifying cooperators' habitat, be it a spot on a rock, an acid bog, the underside of an ice flow or half an ocean.

In some species, individuals, pairs or families stake out a particular territory or "turf" within the species' habitat. Some, such as social insects and many land predators, hold territories year round. Others, including most birds, hold territories only for the breeding season. The territory may be so critical that an individual or group spends substantial time patrolling or looking for opportunities to expand into a neighbor's territory. Nevertheless, even the most solitary animals, such as tigers, share their territory at least part of the time with mates or young.

Economics of Cooperation

Why do species cooperate? They cooperate because they gain from cooperation. They could not even survive without cooperation for reproduction.

What does cooperation mean in economic terms? An individual seeking to cooperate with another individual, or with a group, faces a simple question: do marginal benefits exceed marginal costs compared to going it alone? An individual or a group deciding whether to accept an additional individual faces the reverse decision: at the margin, does the additional member contribute more than it costs? For example, one more bird in a flock of crows adds another pair of eyes to watch for predators, but also another mouth to eat the local corn.

Cooperation generates economic rent

Cooperation generates a surplus not clearly attributable to the efforts of individual cooperators. It is a joint product, a net benefit beyond the net marginal product of each individual. The whole is greater than the sum of the parts. Cooperation generates "economic rent."

For species of organisms, rent means health and even survival in the short run, and reproductive success in the long run. (Biologists sometimes measure a species' success by "biomass", by which criterion bacteria rank first by orders of magnitude.) Rent means health and reproductive success to subgroups within a species as well, and of individuals within the subgroups. However, the interests of the species, subgroups and individuals do not always coincide.

Economic Rent Generates Competition for Rent

Where there is rent, there must be rent-seeking and rent-defending. In other words, there must be *competition for shares of rent*. That competition occurs between subgroups of a species, within subgroups, and between individuals. (It even occurs within individuals, if you think of cancer cells as competing for an individual's resources.) Competition accounts for much of the complex behavior of organisms in the natural world.

Competition dissipates rent.

Competition for shares of rent necessarily dissipates rent. That dissipation is especially obvious during reproduction. A single anchovy female can produce between 20,000 and 30,000 eggs a year. An apple tree may produce a hundred pounds of fruit each year, to have on average one seed survive to maturity.

Among non-monogamous animals, competition between males notoriously wastes resources and impairs fitness. Male sea lions and gorillas grow gargantuan compared to females, in order to fight other males for control of harems. (Robert Frank 2005) Male deer grow huge heavy antlers for the mating season, and then shed them. And then there’s the male peacock’s tail, which clearly makes the bird more vulnerable to predators. Bright colors make males of many bird species more vulnerable to predation.

As I will elaborate later, among territorial species, competition dissipates rent by motivating individuals and groups to claim and defend territories larger than necessary to protect a food supply.

Competition spurs innovation.

While dissipating rent, competition simultaneously spurs innovation. There is innovation to better capture rent—the wasteful mechanisms just noted arose to help rent capture. Then there is innovation to better protect rent from capture. Finally there is innovation that avoids competition by doing something really different—exploiting different resources or old resources differently. This is innovation by splitting off a new species from an existing one—at once reducing competition and increasing efficient use of resources. Evolution itself can be seen as innovation driven by competition for rent.

Limiting rent dissipation by controlling population.

To sustain rent, groups of cooperating organisms must avoid the Malthusian trap. Since such groups necessarily share a habitat this amounts to avoiding what Garrett Hardin famously called the “tragedy of the commons.” (Garrett Hardin 1968). The “tragedy” is not “ruin” as Hardin feared, but simply the point where excess population reduces average product to average cost, and rent is totally dissipated. The solitary anchovy gains no more security in joining the hungry school than it loses in sharing their slim pickings—and in fact the school will disperse.

To maintain rent, cooperating organisms must exclude outsiders and prevent excessive multiplication of insiders. If they cannot do so, they become truly marginal, vulnerable to extinction from the slightest deterioration in their environment.

Species may pursue two broad population control strategies: Strategies that rely on controlling territory, and those that do not. Territorial strategies range from controlling a territory year-round, to controlling it only during a key period, normally the breeding season. Two primary non-territorial strategies are “hit-and-run” and “perfect timing.” The territorial strategy merges into the non-territorial where territory is held only for a brief instant.

Territorial strategies for population control.

Territorial species exclude others of the same species from their territories, while limiting reproduction within their territories. This is perfectly obvious with species where individuals, or pairs hold territories. The size of a territory held by, say, a pair of robins, depends both on food density and on time and energy needed to defend the territory. Divide suitable robin habitat by the average robin territory, and there’s the population limit. Chicks hatched each year must hang around the fringes until established robins die or can be driven out. Population control is more subtle where family groups control territory, for example, a turkey gobbler and his ten or fifteen hens. But the basic pattern is the same: the group excludes outsiders of the same species. It either evicts young adults, or forces them to wait for reproductive opportunity until dominant adults die or are defeated.

Social insects like ants, bees and termites all stake out territory and defend it year round. There may be millions of ants in a leaf-cutter nest, but they have no problem identifying and excluding outsiders, because members of each nest have a characteristic smell. Population control is not a problem either, because the members of a given colony are all offspring of one or a few queens, and themselves sterile. When times are bad, workers cut back on the number of grubs they raise. When times are good, they may raise extra queens, and send them forth, sometimes with their own complement of workers. Social insects may compete, colony against colony, but not within colonies.

Group-living predators like wolves and lions hold year-round territories. So do chimpanzees, gorillas, baboons, and many species of monkeys. Among other communal animals, such as horses, or elephants, several related groups may share a range. Both types of communal animals control numbers by evicting juveniles—sometimes males, sometimes females, sometimes both—after they reach a certain age. The juveniles then wander around, sometimes in loose groups of their own, such as “bachelor elephants,” until they can join a new group. Mortality is high among such juveniles.

Sometimes, males cooperate to attract females to a common breeding territory, or “lek.” Birds, such as the north American prairie grouse and the south American manikin, "dance" on the lek. The males jump up in the air, calling and displaying. Females watch from the sidelines, eventually choosing a mate (usually one of two or three that dominate the lek), copulating, and leaving to nest by themselves. Even more spectacular, certain southeast Asian fireflies congregate by the thousands in particular trees, where they flash in synchrony—a beacon to every female in miles. The deafening chorus of bullfrogs around a pond likewise summons the females. Competition for space in the lek, or in the tree, or around the pond serves to limit reproduction.

Many shallow water fish compete for mates, pair up and stake out breeding territories on the bottom. This is typical of ocean reef fish. Another ocean fish, salmon, swim up freshwater streams where they aggressively compete for mates and for spawning spots on the gravel stream beds. Salmon live at the border between territorial and non-territorial; they hold territories only for hours, and rely primarily on timing.

Non-territorial strategies for population control.

Hit-and-run. All members of bacterial, slime mold or fungal colonies can reproduce by simply dividing in two, which would seem a recipe for a self-destructive population explosion. However, bacteria and their ilk avoid disaster by pursuing a feast-and-famine hit-and-run strategy. Consider anthrax. A cow out on the range inhales spores from the soil while grazing. The cow dies, and the bacteria, no longer infective, proliferate in the carrion—pieces of which may be dragged around by scavengers. When the food starts to run out, that signals the anthrax bacteria to come together to form deadly spores, often exchanging genetic material in the process. The spores may wait in the soil for thousands of years until the next victim inhales them. Food shortage as a breeding and sporulation signal works for bacteria, because most members of a colony are genetically identical and hence not in competition for resources.

Perfect timing. Many species reproduce only at highly limited times and places. This goes by definition for species that hold territories only for the breeding season. But it goes *a fortiori* for communal breeders, who simply assemble at a set time and place. Sometimes, like frogs croaking around a pond, the males compete for females. In other cases, such as coral animals, males and females simultaneously let loose sperm and eggs. The less a species relies on territory to control population, the greater the reliance on exquisitely-timed simultaneous breeding.

Reproducing in the same space-time spot often enables species to overwhelm predators with more offspring than they can devour in a short period—a strategy known as "predator saturation." For example, baby seals and sea lions entering the water for the first time must run a gauntlet of sharks and killer whales. Elk in Yellowstone Park calve simultaneously; grizzlies feast on the calves for three weeks, until the calves grow too fast to catch. Oak and hazelnut trees overwhelm squirrels and jays with a nut bounty.

But there's a broader evolutionary logic to dependence on very specific times and places for reproduction, a logic that suggests such dependence is itself an adaptation for population control in non-territorial species. Imagine a species occupying a particular habitat. Terrain is never quite uniform, neither is weather. Inevitably, a space-time spot within the range is optimal for reproduction. The individuals that breed within those optimal spots leave more offspring. But that in turn creates a natural selection process for individuals that both seek out the optimal spot and are better adapted to breeding there. There is a positive feedback loop, leading to increasing adaptation of the species to the optimal spot—and increasing competition for access to the spot. Crowding into preferred space-time spots in turn serves to limit population.

The worst possible situation for population control is an open commons with communal breeding. This is the case with many species of open ocean fish, which travel and spawn in huge schools. There's no possibility of excluding outsiders; in fact fish often forage in mixed species schools of similar size—juveniles of big fish alongside adults of smaller fish. However, open ocean fish spawn at specific times of the year—often a one or two day window—in very specific spots, with males and females simultaneously releasing milt and eggs. For example, Atlantic bluefin tuna, which can grow to over 1000 pounds, begin life as microscopic fry. Even though they range over thousands of miles of ocean, the tuna breed only in a handful of "hot spots" in the Caribbean and in the eastern Mediterranean, where upwelling nutrients favor the fry's survival. Noone has actually witnessed tuna spawning; the evidence comes from hooked fish. But one can speculate that mature tuna crowd into the hot spots at the right time, excluding smaller and weaker fish, or causing them sufficient stress that they don't attempt to breed.

Competition for Rent Between and Within Groups

Competition for rent is universal. Males compete with females, siblings compete with each other. Among eagles and other predatory birds, older chicks may peck younger siblings to death, a practice known as "cainism."

Competition between groups of the same species takes the form of territorial wars. Under shallow water, mobile packs of sea urchins, starfish, or limpets may engage in slow-motion shoving matches with same-species packs. On land, groups holding year-round territories—such as wolves, lions, or chimpanzees—may raid neighbors' territories, killing vulnerable individuals. Occasionally they may wipe out the entire neighboring group, and take over their territory.

Competition within groups commonly leads to dominance hierarchies or, among fowl, "pecking orders." A small subgroup of aggressive males and females intimidate lower ranking animals in the group. The dominant subgroup hogs the best food, and enjoys the greatest breeding success. Subordinate animals may experience so much stress that they do not breed at all; in effect the stress response keeps them from wasting resources on futile reproduction. Among chimpanzees and porpoises a pair and sometimes a trio of brothers may dominate the group, intimidating the females and leading raids on neighboring groups.

It gets worse. When younger males successfully challenge dominant males and take over a group—the first thing they do is kill the infants. That brings the females into estrous sooner. (Female chimpanzees and porpoises normally care for an infant three or four years before producing another.) Females respond to this threat by promiscuous mating—to the extent they can manage behind the back of the dominant males—so that males can't be sure they aren't killing their own offspring. Sometimes dominant females also kill the offspring of subordinate females.

Territorial Quality, Competition and Imperialism

Some species, notably mammalian predators and social insects, defend territories year round against competitors. Other species, birds especially, defend territories only part of the year. Defending a territory dissipates rent; it requires time and energy patrolling, howling or singing, and occasionally fighting with neighbors.

Within the range of any species, there must inevitably be locations that are superior for feeding, for protection, and for reproduction. Consequently, among territorial species, some individuals or groups hold richer territories than others.

In this fact, that some territories are richer than others, lies a further stimulus to rent dissipation which I will call “imperialism.” Imperialism occurs when occupants of superior locations use their resources to claim extra large territories. Why might this happen?

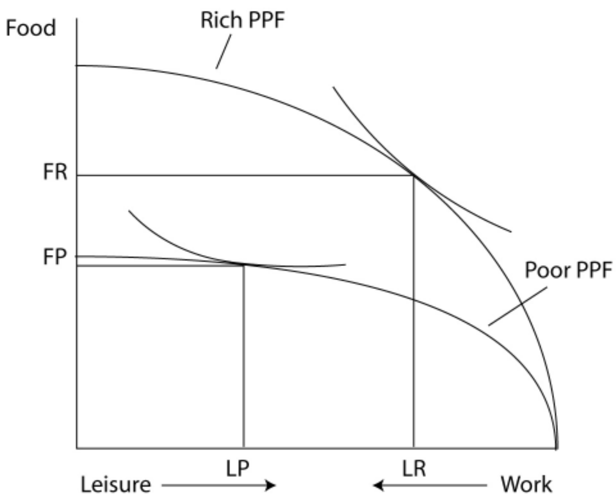

Figure 1

Occupant(s) of rich territory consume food FR and leisure LR.
Occupant(s) of poor territory consume food FP and leisure LP.

Imagine a species occupying a range that varies in the availability of food. And imagine that the range is divided up into territories, held by individuals (such as tigers) or groups (such as chimpanzees). All else being equal, will richer territories be larger or smaller than poorer territories?

Assume an individual or group splits its time between foraging for food, patrolling the boundaries of its territory, and simply relaxing—and, for a group, socializing. The larger the territory, the more patrolling required. (Assuming most patrolling occurs around the perimeter, patrolling time logically rises with the square root of the territory’s area.) Patrolling of course costs energy and takes time from foraging and relaxing. There must be an optimal territory size, where marginal costs equal marginal benefits.

If patrolling serves only to assure the food supply, then richer territories should be smaller than poorer territories. Logically, why work any harder than necessary to assure an ample food supply? To put it more formally, assume owners of a territory have a production possibility frontier along which they can trade off food for leisure. In a richer territory, territory owners can enjoy more food, but maximum leisure remains constant—the total time in a day. Assuming leisure is a superior good to food, they will logically choose both more food and more leisure. (Ie the income effect outweighs the substitution effect.) See Figure 1. But—assuming the marginal product of effort in foraging equals the marginal product of effort in patrolling a territory—more leisure means less foraging *and* patrolling, which means a smaller territory.

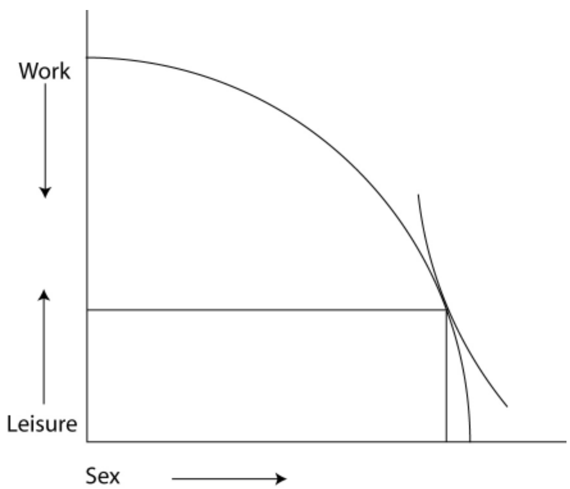

Figure 2
Given a choice of leisure and sex, individuals choose less leisure and more sex.

If there's an additional consideration, like sex, then the calculation changes. Presumably, sex is a superior good to leisure, as depicted in Figure 2. Consider the dominant males of a chimpanzee tribe. Holding more territory may enable them to maintain a larger harem and to keep rival males further away from females and vulnerable offspring. In a richer territory, it takes less time to gather the same amount of food, leaving more time and energy for patrolling against intruders. It follows that richer territories may be larger than poorer territories—or at least not as small as they would be were food the only consideration. To put it another way, in richer territories the shape of the production possibility frontier between

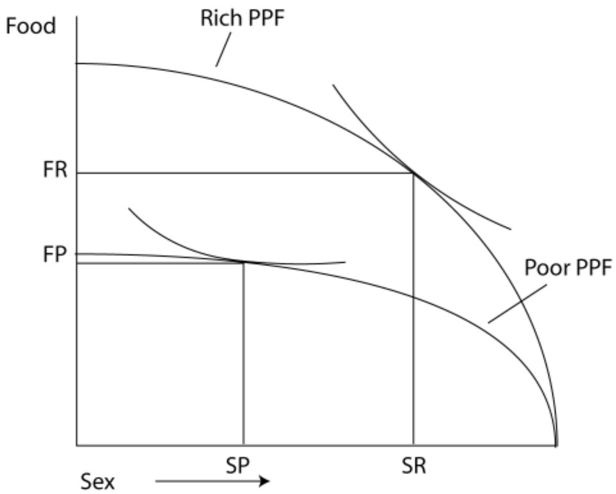

Figure 3

Occupant(s) of rich territory consume food FR and sex SR.
Occupant(s) of poor territory consume food FP and sex SP.

food and sex is different, lowering the relative cost of keeping away outside males. See Figure 3.

The net effect is that occupants of richer terrain may behave more aggressively towards neighbors and act in a more expansionist manner than occupants of poorer territories. There's a general equilibrium implication here too: the greater the inequality of resources over the range of a species, the more aggressive and expansionist the behavior of the occupants of the richest locations—at the expense of the species as a whole. In effect, the occupants of the richest locations, in seeking their own advantage, dissipate rent for the species as a whole.

(I am not yet sufficiently familiar with the literature to know if this predicted relationship between territory richness and size has been observed. But it is an eminently testable proposition: How does the size of territories in the richer parts of a species' range compare with the size in poorer parts? Are rich territories smaller or larger? How does the food supply per capita in a rich territory compare with that in a poor territory? How does the time spent on foraging and other activities compare between rich and poor territories?)

The same argument holds within a group hierarchy. If the only issue is food, then the dominant animals content themselves with first pick of the food and otherwise take it easy. Most of the time, dominant male lions snooze, leaving the hunting to the females, and only showing up at mealtime. But when there's a female in estrous, watch out! Dominant male baboons, never very nice in the first place, turn positively vicious, chasing and biting subordinates almost at random. In other words, the dominant animals within a group are in the same position as the occupants of a superior territory; when there's sex at stake as well as food they forsake leisure for tyranny. Again, such behavior dissipates rent.

Open Competition and Innovation

At the opposite end of the spectrum from territorial animals are species whose lifestyles do not permit them to claim territories. As noted above, they must engage in communal breeding in very narrow space-time slots. These species include open water fish and some migratory birds and grazing mammals. These also include the famous emperor penguins, who huddle together in groups through the Antarctic winter to raise a single chick per pair.

Competition dissipates rent and stimulates innovation. Where species cannot establish territories within a range, intense competition may induce rapid innovation, that is, the formation of new species. There is in fact an ongoing discussion in the ecological literature on "sympatric speciation," which means that a single species splits in two within a shared range. The issue is no longer whether it happens, but how often it happens and by what mechanisms.

For example, in the 1930s and 1940s, sockeye salmon were introduced into Lake Washington in Washington State, which is fed by the Cedar River. Within some thirteen generations, the sockeye had split into two distinct populations: one is adapted to breeding in the cold, rapid-flowing river, and the other to breeding along a sandy beach in the lake. The fish have become strikingly different in body size and shape. Yet outside breeding season, both populations mingle in the lake (Jonathan Weiner 2005). This is just one of many examples of rapid speciation of lake fish.

The conventional scenario for origin of new species depends on geographical isolation: two populations of a species become isolated from each other, for example on different islands like the Galapagos finches. They evolve by adapting to slightly different environments, and/or by simple genetic drift. When they come together again, they are too different to interbreed. What's remarkable about the sockeye and other fish is that they can speciate rapidly without any obvious barriers to allow subgroups to evolve in isolation.

I suggest that the following happens. As I noted above, animals that reproduce in open competition adapt to breed cooperatively at very specific times and locations. They become tightly adapted to this time and location. At the same time, this tight adaptation makes the breeding success rate of any individual very low. At some point, the probability of success breeding in a different time-space spot exceeds that of breeding in the preferred spot. A few mutant fish manage to breed in a new location—and they're off and swimming to start a new species.[1] Dieckmann & Doebeli have developed sophisticated mathematical models of sympatric speciation; they suggest that rather than being an oddity, sympatric speciation may be more the norm. Their models depend on the reasonable assumption of assortive mating. That is, within the normal variation of a population, males and females tend to pair with similar males and females.

[1] This explanation makes sense for fish, but I have trouble with the penguins. The emperors breed in about 40 different groups of several hundred birds each, scattered around the Antarctic. Since the penguins need large groups for warmth, how could a few pioneers start a new group miles from the original group?

(Mathematically, the models look suspiciously like economic models of product differentiation!)

Pressures for sympatric speciation also apply to territorial species, but with perhaps less force. Territorial species feel less pressure to breed simultaneously; and by definition their breeding locations are more spread out—in fact spread over their entire range for year-round territorial species. Hence, there's less opportunity to do something really different from the mainstream. "Imperialism," as described above, keeps down population size and keeps rents up, at least for dominant animals—who may be the only breeders. These factors, I suggest, reduce the likelihood and speed of sympatric speciation. The most numerous examples in the literature are fish.

Implications for Human Societies.

Humans are of course animals. Humans cooperate and compete. They monopolize territories. They dissipate rent in territorial wars. And they innovate. But there's an important difference between humans and "lower" animals: "lower" animals take their environment much as they find it, while humans can construct their environments, physical and institutional.

Human institutions to varying degrees foster cooperation and moderate destructive competition. A primary institution, dating at least to the stone age, is religion. In *The Science of Good and Evil* Michael Shermer defines religion as "a social institution that evolved as an integral mechanism of human culture to encourage altruism and reciprocal altruism, to discourage selfishness and greed, and to reveal the level of commitment to cooperate and reciprocate among members of the community." (Michael Shermer 2004).

Institutions like government by kings or dictators or wealthy oligarchs establish and protect extreme inequality in ownership of territory. Such governments tend to dissipate rent by extravagant projects, like pyramids, or by foreign aggression.

Implications for Economic Theory.

Cooperation, competition and economic rent each figure prominently in the work of the classical economists. Adam Smith laid out how cooperation enhances productivity on a small scale—the famous pin factory—and large scale through the market. He denounced obstacles to competition, including barriers to free trade. (Adam Smith 2000). David Ricardo explained how, once land and other natural resources are "appropriated" ("privatized" in modern language), economic rent accrues to holders of superior quality property. (David Ricardo 1996). Henry George emphasized the superior capacity of urban land in fostering productive cooperation, a superior capacity reflected in high urban land values. (Henry George 1879).

Neoclassical economic theory downplays cooperation and ignores rent, to focus almost exclusively on competition. However, substitute the word "profit" for "economic rent" and the natural history model becomes recognizable in the theory of the firm. Firms cooperate legally in trade and illegally in cartels. They compete if they must. They try to control territories, real and in "product space." Competition dissipates potential profits, as evident in the old complaint that "half of all advertising is wasted; the question is, which half?" CEO's of big firms engage in "empire-building" efforts to increase market share at the expense of profits. However competition presses firms to innovate by developing new products and new methods; the more intense the competition, the greater the pressure.

Small firms, including inventors in garages, are the source of virtually all major innovations.

Implications for the Theory of Cooperative Enterprises

The theory of cooperative enterprises holds that when the stakeholders in an enterprise share ownership and control in a democratic manner, the organization functions more productively. The incentives of stakeholders are better aligned. More effort goes into producing value, and less into tussling over shares of that value.

A sophisticated theory of cooperatives must address economic rent. If cooperatives build up or acquires a rent-yielding resource, then there arises pressure to exclude new members or force high admission fee, to allow old members one way or another to extract their share on retirement—and even to sell out altogether. A successful cooperative must specify rules for rent-sharing that provide the best incentives, --in full recognition that no arrangement can be perfect. In the real world, cooperatives often seem to function better in marginal circumstances—perhaps because there's less rent to quarrel over.

Conclusion.

There's an underlying logic to seeking a natural history perspective on the economic concepts of cooperation, competition and rent: Humans like all other species engage in optimization within constraints of time and space. The mathematics of economics and ecology are identical. We should expect the same patterns to appear, and they do, sometimes with a twist! The natural history perspective reassures us that indeed public policies should encourage cooperation and channel competition towards innovation instead of monopoly. It also suggests we should discourage rent-seeking behavior by sharing rents, whether within a cooperative firm, or within society at large by means of taxes. That is the thrust of Henry George's proposal: collect the rent by a tax on resource values, and use it for the common good.

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