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REVIEW

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The enemies within: intergenomic conflict, interlocus contest evolution (ICE), and the intraspecific Red Queen

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Abstract Different loci within the genome of a single species can potentially coevolve in a manner that is analogous to the Red Queen process among species. The major factor driving this antagonistic coevolution among loci is intergenomic conflict, i.e., discord between individuals that is mediated by two or more gene products that are derived from different gene loci. We conclude that antagonistic coevolution is common among loci that code for social interactions, and that it has broad evolutionary implications, especially in the context of speciation and sex chromosome evolution.

Key words Red Queen · Coevolution · Counter-adapted gene complexes

Introduction

Species evolve in response to their biotic environment and this can lead to coevolution between species that interact in either a mutualistic or an antagonistic fashion (Futuyma and Slatkin 1983). In the latter case, evidence for the operation of the Red Queen process (i.e., antagonistic coevolution of a species with its enemies – predators, herbivores, competitors, and pathogens; Van Valen 1973), is well documented in both agriculture (Day 1974; Robinson 1976) and natural systems (Parker 1985; Lively 1989). The Red Queen is characterized by an interspecific evolutionary chain reaction: adaptation by species $A \rightarrow$ counter-adaptation by enemy species $B \rightarrow$ counter-adaptation by species $A \rightarrow \ldots$, which can lead to a protracted period of coevolution (Ehrlich and Raven 1964; Vermeij 1983).

A parallel evolutionary chain reaction can occur between non-allelic genes within the genome of a single species. With sexual recombination, alleles residing at one locus have only a transient association with nonhomologous alleles residing at other loci. As a consequence, different gene loci can evolve in a semi-autonomous fashion, and can therefore potentially coevolve in an antagonistic manner.

Intragenomic conflict among genes that reside in the same individual can drive interlocus antagonistic coevolution, and this has been studied extensively in the context of ultraselfish genes and cytoplasmic genetic elements (e.g., Werren 1991; Bull et al. 1992; Hurst 1992). But there is an alternative form of genomic conflict that results from discord between nonallelic genes that reside in different individuals, i.e., conflict between alleles that reside at different gene loci which mediate conflict (e.g., competition) between different individuals. We will refer to such inter-individual genomic conflict as *intergenomic conflict*.

Interlocus contest evolution (ICE)

Intergenomic conflict is a selective agent that can drive antagonistic coevolution between loci within the genome of a single species. We will refer to this process as *interlocus contest evolution* (*ICE*). Consider the case where a gene product, produced in one individual and derived from an arbitrary *A* locus, interacts with a different gene product produced in a different individual and derived from a different, *B* locus. In certain circumstances the gene products of the *A* and *B* loci will mediate contests between the two individuals. In this context the fitness of the alleles at the *A* locus will depend on the identity of the alleles at the *B* locus in the opponent. Thus, like host and parasite, the gene products from the *A* and *B* loci are part of the evolving, biotic environment of one another, and they can potentially coevolve in an antagonistic fashion, via an intraspecific Red Queen process.

A key characteristic of ICE is that it can lead to a self-reinforcing adaptation/counteradaptation chain reaction. That is, it can lead to recurrent, even perpetual,

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gene substitution at antagonistically interacting loci and thereby continually drive genetic and phenotypic divergence among related species or isolated populations. In general terms, ICE speeds the rate of evolution whenever allelic substitution at one locus selects for a new allele at the interacting locus, and vice versa, so that no stable equilibrium can be achieved, or is achieved after many iterations. As a consequence, an increased rate of allelic substitution is a "footprint" left behind by the ICE process. Other factors besides ICE also can lead to rapid evolution at a locus, but this characteristic nonetheless can be used to identify loci where ICE is potentially operating.

Here we explore the domain and ramifications of ICE. Our aim is to unify a broad set of biological phenomena by demonstrating that they are all special cases of the more general ICE process. We hypothesize that ICE, operating at a minority of loci, acts as a sort of evolutionary catalyst in a number of macroevolutionary phenomena including speciation and sex chromosome evolution, and that ICE is the dominant mode of evolution for genes controlling social behavior.

Intersexual conflict

In the absence of strict monogamy, a fundamental conflict arises between the sexes over investment. One sex (hereafter assumed to be male) invests predominately in fertilization opportunities while the other sex invests predominately in offspring (Bateman 1948; Williams 1966; Trivers 1972; Parker 1979). This basic conflict may manifest itself in many traits associated with sexual reproduction (Parker 1979; Rice 1996; Arnqvist 1997).

The opportunity for ICE to mediate male-female conflict is greatest in sex-limited genes, but sex limitation is not necessary. Genes expressed in only one sex are selectively neutral when present in the other sex. Male- and female-limited genes are therefore acted upon separately by selection and will evolve in a semi-autonomous manner. Like different species in a community, sex-limited genes within a genome can coevolve in a mutual or a conflictual manner.

Gametes

Recent molecular studies indicate that some gamete proteins are evolving extremely rapidly (Palumbi and Metz 1991; Vacquier and Lee 1993; Lee et al. 1995; Metz and Palumbi 1996). For example, Vacquier and co-workers have studied lysin, an acrosomal sperm protein of the abalone, for over a decade (reviewed in Vacquier et al. 1995). This protein is released from the anterior portion of the sperm (acrosome) when it encounters an egg. Lysin functions to bore a hole through a glycoprotein matrix that surrounds the egg, and thereby permits the sperm to approach closely enough to fuse with the egg's plasma membrane and initiate fertilization.

Interspecific comparisons indicate that the lysin gene is evolving extremely rapidly. A combination of sequence and crystallography studies demonstrate that most of nucleotide substitutions are nonsynonomous, and are positioned in the region of the lysin protein that directly interacts with the matrix surrounding the egg. Vacquier's group has favored the hypothesis that antagonistic coevolution between unidentified pathogens and the egg has driven this rapid change in the egg matrix, and that lysin is tracking the interspecific Red Queen process between pathogen and egg.

An alternative explanation is that ICE is driving the rapid evolutionary change. Consider the sperm-egg interaction from the lysin gene's perspective. The faster the lysin molecule bores through the egg matrix, the higher its fitness when competitor sperm are present. So, faster is better.

Next consider the genes that codes for the matrix protein and the enzymes that glycosylate this protein. From their evolutionary perspective, rapid sperm passage through the matrix will permit more than one sperm to penetrate the egg before the fast and slow blocks to polyspermy are implemented (yielding polyspermy and/or multiple sperm-entry sites for pathogen infection) and thereby decrease the chance of zygote survival. So, slower is better.

The conflict between the lysin gene and the genes that code for the egg matrix can be expressed by their differing optima for the rate at which the sperm transgress the matrix surrounding the egg. These opposing optima can initiate perpetual antagonistic coevolution: change in lysin → faster sperm → decreased egg survival → change in egg matrix → slower sperm → selection for compensating change in lysin → faster sperm → ... . In this molecular context an evolutionary stalemate seems unlikely. Recent work by Palumbi and co-workers on the bindin gene (Palumbi 1997) and by Vacquier and co-workers on the lysin-like sperm protein in the snail genus *Tegula* (M. Hellberg, personal communication) are also consistent with this general form of an ICE interpretation.

In organisms like the abalone, which broadcast their gametes into the water column, the opportunity for ICE due to male-female conflict is restricted primarily to egg-sperm interactions. Once internal fertilization and paired mating between individuals evolved, the opportunity for ICE increased substantially. Below we first consider ramifications of internal fertilization then courtship.

Internal fertilization and reproductive tracts

Recent studies indicate that reproductive tracts tend to evolve far faster than the rest of the organismal phenotype (see for review Eberhard 1985, 1996; Thomas and Singh 1992; Pitnick and Karr 1996; Rice 1997). For example, Eberhard (1985) compared the rate of phenotypic divergence in male external genitalia between species with internal or external fertilization. Among species with external fertilization, the male genitalia are conserved characters that evolve slowly. Among species with internal fertilization, male genitalia are among the most rapidly evolving organs. A more recent review by Eberhard (1996), surveying hundreds of different studies, demonstrates that the internal anatomy, biochemistry, and physiology of male and female reproductive tracts are also evolving very rapidly. Eberhard's explanation is that cryptic female choice, i.e., female choice that occurs during the time after the onset of mating but prior to fertilization of eggs, is driving the rapid evolution.

An alternative explanation is that this rapid evolution is being driven by ICE. As an example, consider the seminal fluid proteins, a major component of the male reproductive tract, and their targets (tissues within the female and also sperm and seminal fluid proteins from another male). Some seminal fluid proteins have biological activity within the female reproductive tract while others enter her blood stream (reviewed in Eberhard 1996). The function of most seminal fluid proteins is still unknown but some mimic female hormones and others bind to the brain and other tissues and thereby modify female reproductive physiology and mating behavior.

Seminal fluid proteins do a variety of things that are clearly beneficial to males. In *Drosophila* they reduce a female's sexual appetite so that she is less likely to remate (Aigaki et al. 1991), they increase her ovulation rate (Chen 1984), and they appear to mediate sperm competition (Clark et al. 1995; Harshman and Prout 1994). On the other hand, *Drosophila* seminal fluid proteins are toxic to females, so that the more she receives the faster she dies (Fowler and Partridge 1989; Chapman et al. 1995). Interestingly, recent molecular work with *Drosophila* (Aguade et al. 1992; C-I Wu, personal communication) indicates that the two seminal fluid proteins studied to date (*Mst26Aa* and *Mst26Ab*) are evolving very rapidly and the pattern of synonymous to nonsynonymous nucleotide replacement indicates that this rapid evolution is being driven by positive selection rather than genetic drift. This rapid evolution may be the footprint of ICE.

A three-way conflict produces manifest opportunity for ICE to drive rapid antagonistic coevolution among loci controlling male and female reproductive tracts, behavior, and physiology. For example, consider a female's remating rate. From the perspective of those genes controlling female remating, there will be some optimum mating rate that is determined by a compromise between: (a) the frequency of sterile males, the amount of sperm successfully stored from each copulation, and other factors that promote multiple-mating, versus (b) the toxicity of seminal fluid, any adverse effects of seminal fluid pheromones, and other costs of mating such as increased predation risk and venereal disease (Daly 1978; Arnqvist 1997).

Next consider a male who just mated the female. A subset of his genes are selected for "defense," i.e., selected to suppress her remating rate (pheromonally via seminal fluid proteins and/or behaviorally by mate guarding, for instance) and increase ovulation rate and energy allocation per egg to a level that maximizes the females short-term fitness (since offspring produced later in the female's life will likely be sired by another male). Defense genes are also selected to reduce the probability of the male's sperm being displaced when the female ultimately does remate. In sum, the genes mediating male defense are trying to maximize the female's short term fecundity while the female's genes that code for the targets of male defense genes are trying to maximize the female's life-time fecundity.

Lastly, consider a second male that encounters the female after she has mated. A subset of genes in this male are selected for "offense," i.e., to entice the female to remate despite the fact that additional courtship, mating, and seminal fluid may be harmful to her. Offense genes are also selected to replace the extant sperm in the remated female with those of the second male.

To the extent that there are different sets of gene loci coding for offense, defense, and the interacting female characters, there will be opportunity for antagonistic coevolution among these loci. Because many of these interactions are mediated by a match between gene products, e.g., a change in receptor molecule(s) may be followed by a change in the inducer molecule(s), followed by a new compensating change in receptor, ... , perpetual ICE can ensue.

Compared with the simple case of lysin and the egg matrix described above for abalone, internal fertilization generates many new opportunities for intergenomic conflict. The female reproductive tract and behavior can be collectively viewed as the analog of the glycoprotein matrix surrounding the abalone egg, and the male reproductive tract and behavior replaces the simple lysin gene product. Aspects of female behavior and the structure, physiology, and biochemistry of her reproductive tract can restrict sperm access to the egg, while male behavior and the structure, physiology, and biochemistry of his reproductive tract can evolve to overcome such barriers.

Internal fertilization does more than extend the range of opportunity for male-female conflict concerning sperm and egg, however, since it constrains the two sexes to directly interact. To receive sperm a female must also accept seminal fluid proteins, airborne pheromones, and male behavior, all of which can act to modify her behavioral and physiological phenotype in ways that increase male fitness at the expense of female fitness. Mutations expressed in females can be expected to be recruited at many loci which counter such male-induced impediments to female fitness, and thus a greatly expanded arena for ICE is established.

Courtship

Courtship includes any communication between a male and female that influences their probability of mating.

Courtship is surprisingly complex compared to other communication signals. Communication between cooperating individuals is typically characterized by simple, short, and unobtrusive signals (e.g., alarm calls), whereas that between adversaries is characterized by signals of greater magnitude and complexity, consistent with an arms race (Krebs and Dawkins 1984). Courtship signals are among the most conspicuous (Wilson 1975) and rapidly evolving (Mayr 1963; West-Eberhard 1983, 1984), and the evolutionary trend is toward greater elaboration (e.g., size, coloration, odor, calling; Ryan 1990). The rapid evolution and elaboration of courtship suggest that ICE may play a role.

As an example of male-female discord, we focus on the conflict over mating rate. Mating may be costly to females due to: (a) energy loss, injury, predation and parasitism (Daly 1978; Arnqvist 1989; Arnqvist 1997); (b) increased mortality via seminal fluid toxins (Fowler and Partridge 1989; Chapman et al. 1995; Gems and Riddle 1996); and (c) changes in female reproductive behavior and physiology produced by seminal fluid proteins/pheromones (reviewed in Eberhard 1996). Mating also has costs to males (e.g., Partridge and Farquhar 1981), but because males typically invest less parental care and are susceptible to cuckoldry when pair-bonded, they are generally expected to have a higher optimum mating frequency (Parker 1979).

The conflict in mating rate can be mediated by physical coercion (e.g., forced matings; Rowe et al. 1994; Clutton-Brock and Parker 1995) but this behavior is absent or rare in most species. Instead, the sex with lower parental investment persuades the other to mate via courtship displays. Courtship displays have been hypothesized to evolve via four major classes of sexual selection models: self-reinforcing runaway selection, indirect female benefits (good genes), direct female benefits (e.g., resources, parasite avoidance, species recognition, mating synchronization), and sensory exploitation (reviewed in Andersson 1994).

All four of these sexual selection models may operate in nature, and it is clear that direct benefits can play an important role in sexual selection (Kirkpatrick and Ryan 1991). Here we suggest an alternative hypothesis that is motivated by the ICE process. We extend the pioneering work on sensory exploitation – also called sensory drive, traps, and bias (West-Eberhard 1984; Kirkpatrick 1987; Basolo 1990; Endler and McLellan 1988; Ryan 1990; Ryan and Rand 1993; Eberhard 1996; Sinervo and Basolo 1996) into the context of interlocus contest evolution concerning mating rate. The logic motivating the ICE-courtship hypothesis is simple: (a) males and females differ in their optimum mating rate, (b) alleles are favored at one set of loci in males that code for courtship signals that super-stimulate females, i.e., cause females to mate at a rate beyond their optimum, and (c) alleles are favored at female courtship receptor loci (by this we include all other loci that influence female response) that code for sensory system modifications that reduce such super-stimulation. In this ICE-courtship view, many of the conspicuous aspects of courtship are the sensory equivalents of physical coercion (i.e., males super-stimulate rather than coerce females to mate at a rate beyond the female optimum) and thus seduction replaces coercion.

As an example of ICE courtship, consider the case of sensory exploitation in two genera of poecilid fish (*Priapella* and *Xiphophorus*; reviewed in Sinervo and Basolo 1996). Sworded males occur in some *Xiphophorus* spp. but not in *Priapella* (or other related genera), indicating that the sword arose after the divergence of these two genera. *Xiphophorus* spp. females prefer conspecific sworded males; the longer the sword the greater the preference. Remarkably, Basolo also found preference for longer swords (artificially attached to conspecific males) in *Priapella* females, i.e., in the genus where males lack swords.

These data indicate that female preference for sworded males originated as an incidental (pleiotropic) byproduct of their sensory system. While this is consistent with the ICE-courtship hypothesis, it remains to be established whether or not sensory exploitation causes females to mate at a rate beyond their optimum. If so, then female sensitivity to the stimulating male trait should *diminish* after the trait evolves. New data from the laboratory of Alexandra Basolo support this view. A.L. Basolo (personal communication) has recently compared the strength of sword preference in both *Priapella* and *Xiphophorus*. She found that females of the sworded species prefer swords *less* than females of the swordless *P. olmeceae* (i.e., slope of female sword preference vs. sword length was almost 3 times higher in the swordless species).

Another study of a different swordtail fish also supports the ICE courtship hypothesis (Morris et al. 1996). Females of the pygmy swordtail (*X. pygmaeus*) prefer larger, heterospecific males from a related species (*X. nigrensis*) over their own smaller males. Before 1988, all known populations of pigmy swordtails had small males, but then a group of populations containing large males was discovered. In these populations, female preference for large body size was substantially reduced.

In summary, we suggest that many data that have traditionally been interpreted as evidence for the operation of sexual selection via female *preference* may actually reflect the evolution of female *resistance* in the context of self-reinforcing ICE. Male-female conflict in mating rate causes male courtship loci to continually evolve new ways to super-stimulate females, and this causes female receptor loci to evolve abating counter-adaptations.

Parent-offspring conflict

In addition to gamete fusion and mating, parental investment is another major mode of social interaction, and hence an opportunity for ICE. As described by Trivers (1974), a father, mother, and offspring may differ in the optimal resource allocation to the offspring, resulting in a coevolutionary conflict (Parker and Macnair 1979). Consistent with this three-way conflict, the mammalian placenta is evolving at an unusually rapid rate (Haig 1993). Below we briefly outline Haig's work on pregnancy conflict in the context of ICE.

Consider a mating between a male and female that produces an offspring. If the male is unlikely to sire additional offspring by this same female in the future (or if she is multiply inseminated), then any genes that he expresses during spermatogenesis that influence the placenta's phenotype (and other factors such as pheromones which are transferred from fetus to mother) that maximize the female's investment in this particular offspring will benefit the male, no matter what the consequences to the female's later reproduction. We refer to these as the "male-benefit loci."

Genes expressed in the female will be selected to produce a placenta, endometrium, and other physiological factors associated with pregnancy, that maximize her lifetime fitness, as opposed to her fitness through the focal offspring. We use the term "female-benefit loci" to describe those that move the level of resource transfer toward the female's optimum.

Genes expressed in the fetus will be selected to produce a level of resource allocation to the fetus that is intermediate between that of the male-benefit and female-benefit loci, owing to the fact that the fetus shares half its genes with the female and hence gains inclusive fitness by her later reproduction. Any genes that can move the resource transfer level toward the optimum for the fetus we refer to as "offspring-benefit loci."

Genes expressed during spermatogenesis and oogenesis can influence the phenotype of the fetus and placenta by imprinting genes that effect their development. Genes expressed in the female can also evolve to produce physiological mechanisms to counter any characters of the placenta and fetus that are contrary to the female's optimum resource allocation to the fetus. Genes expressed in the fetus can potentially evolve to promote regulatory processes that counter male and female adap-tations that move the resource allocation away from the fetus's optimum. Assuming that at least some unique loci mediate the male-benefit, female-benefit, and offspring-benefit adaptations concerning the rate of resource transfer, a three-way tug-of-war produces opportunity for the ICE process.

A similar three-way conflict arises when parents feed their offspring, as occurs in many birds. Unless there is true monogamy, the optimum feeding rate will differ between the male and female just as it did above but with the additional complication of cuckoldry (Trivers 1985). To the extent that begging and other resource-transfer signals by the offspring are coded by loci other than those affecting reception in the parents, the opportunity for ICE is realized.

Interference competition

An additional opportunity for ICE, outside the context of reproduction, is competition between individuals. Interference, as opposed to scramble, competition is most likely to be associated with opposing sets of genes that determine the outcome of competition between individuals. These opposing sets of genes will code for signal or receiver phenotypes, in the context of threat displays, and offense or defense in the case of combat.

Threat displays

Antagonistic displays within or between the sexes is another social interaction that may lead to the ICE process. Threat displays can rapidly diverge among closely related species (e.g., Ruibal 1965; Carpenter and Ferguson 1977). Theory both supports (Bond 1989; Gardner and Morris 1989; Grafen 1990) and refutes (Maynard Smith and Parker 1976; Dawkins and Krebs 1978; Wiley 1983; Grafen 1990) the conclusion that signals used in the assessment of a rival's fighting ability evolve to be deceiving rather than honest indicators. Several experimental studies, however, support the importance of deceit (Steger and Caldwell 1983; Adams and Caldwell 1990; Wagner 1992) and hence the opportunity for ICE.

As an example of a signal phenotype that has diverged dramatically among related species, consider the case of the northern elephant seal's (*Mirounga angustirostris*) unusually low-pitched threat vocalization (Bartholomew and Collias 1962), which is absent in related species. The elephant seal's enormous nose may have evolved as a resonating device to amplify low frequencies (Bartholomew and Collias 1962), but critical tests of this hypothesis are lacking (B.J. Le Boeuf, personal communication). When male elephant seals encounter one another on a breeding rookery, they vocalize toward each other and usually one retreats, but in some cases a fight decides who is displaced.

We do not have the requisite historical information to explain the evolution of the elephant seal's unusually low-pitched vocalization, but recent studies from frogs suggest a feasible hypothesis. There is experimental evidence that male frogs, *Acris crepitans*, use the level of bass frequencies in a rival's call to asses fighting ability, and that they lower their voice facultatively when trying to intimidate a rival (Wagner 1992). Primitive male elephant seals also may have used the lowest frequencies in the threat call of a rival as an indication of body size (which is positively correlated with success in an actual fight, Le Boeuf 1974; Haley et al. 1994). If males with deeper threat calls were able to win more contests by intimidation, rather than by fighting, then their fitness would increase. Such selection favors the accumulation of genes producing low-frequency threat vocalizations. This counter-selects receptor systems that provide an increased threshold required for intimidation, which, in turn, selects deeper threat vocalizations. To the extent that the gene loci controlling bass-bias in threat vocalizations and those controlling its reception/processing are different, then escalation via ICE could ensue.

The elephant seal scenario is clearly conjecture, and is mentioned only to illustrate the way one might expect ICE to participate in agonistic displays. This same logic can be applied to virtually any signal/reception system that mediates contest between individuals, e.g., appeasement displays. Ryan (1990) provides a fuller analysis of coevolution between signals and receivers.

Combat

West-Eberhard (1983) found that traits used in intraspecific combat are useful in distinguishing closely related species and are therefore evolving rapidly. Combat includes both offensive and defensive phenotypic traits. To the extent that the offense and defense phenotypes are coded by different gene loci, ICE can develop between them.

A naive view would be that the evolution of combat can be described as simple escalation between fighting organs (e.g., antlers or horns), where a bigger organ makes a better fighter. But fighting is far more complex and includes both offense and defense components, especially at the behavioral level. To illustrate this, consider the familiar case of martial arts in humans. Modern students are trained in an amazing variety of offensive and defensive moves. Early on, this large repertoire was absent and must have developed sequentially – as each new offensive move was developed a new defensive move was sought to counter its effect. In a cultural sense, offense and defense in the martial arts coevolved over time. Loci that control genetically programmed offense and defense structures, and especially behaviors, can also antagonistically coevolve in an open-ended fashion, with each new offensive adaptation selecting for a defensive counter-adaptation.

Plants

So far all of our examples have been restricted to animals. There are three clear circumstances for ICE to operate in plants: pollen versus pollen, pollen versus eggs (and associated floral structures) and root versus root.

Pollen tube competition is the analog of sperm competition in animals. Different genotypes of pollen tubes grow at different rates and this produces scramble competition between them (Stephenson et al. 1992; Delph and Havens 1997). Recent evidence indicates that interference competition also can take place between pollen tubes (e.g., Marshall et al 1996). Assuming that this is determined by substances excreted by one pollen tube that retards the growth rate of other tubes, these substances would be analogous to seminal fluid proteins that affect sperm competition (except that in the case of pollen tubes, the proteins would not be coded by the paternal diploid genotype).

Consider next pollen versus egg (and associated female-function floral structures). We found no direct evidence that pollen tubes secrete pheromones, analogous to seminal fluid proteins, that benefit the seeds sired by a particular pollen donor, but it is not clear that researchers have specifically looked for this phenomenon. The process of double fertilization in plants, in which a nutritive endosperm is produced, may provide an opportunity for pollen tube genes to influence the level of maternal investment in a specific offspring (Haig and Westoby 1989).

Concerning the conflict that arises due to polyspermy, there is evidence (Marshall and Folsom 1992) that multiple pollen tubes may reach the same micropyle (the opening to the egg sac of flowering plants, through which the pollen tube must pass). Two tissues seem to prevent polyspermy in plants. First, in many plants pollen tubes must grow through an elongate style before reaching the ovary. This may act much like the "torturous reproductive tracts" of many animals (Eberhard 1996) and limit access of pollen tubes to the ovary. Marshall and Folsom (1992) review studies that indicate that pollen tube growth rate sometimes depends on the match between male and female genotypes, which would provide the requisite genetic basis for ICE to operate. Second, in many species the pollen tube must pass through a second tissue, the nucellus, that separates the egg sac from the micropyle. This tissue clearly acts to prevent more than one pollen tube from reaching the egg sac but the molecular mechanism is still unclear (van Went 1992). The nucellus may function much like the protein matrix of the abalone egg in preventing polyspermy or other maladies associated with multiple sperm penetration of the egg.

Most opportunities for ICE in animals involve social interactions between individuals. In plants the major forms of interference competition involve shading of one stem by another and root-root competition between neighboring individuals. Caldwell (1987) reviews the evidence that roots, rather than stems, are typically the major structures determining the competitive ability between different genotypes of plants. The processes (probably chemical in nature) that mediate root competition are almost totally unknown, and because taxonomists rarely measure roots, it is unclear if root phenotypes evolve more rapidly than the rest of the plant phenotype. If ICE is operating, then it is predicted that factors mediating root competition, especially interference competition, will be found to evolve rapidly.

Speculation on the human brain

Too little is known about the genetic basis of intelligence to construct an accurate trajectory for its evolution via natural selection. Nonetheless there is reason to suspect that ICE may play a role.

The rapid evolution of human intelligence, as indicated by the rapid increase in brain size (reviewed in Futuyma 1986), is correlated with the extensive use of language. Language permits individuals to share information and its use includes both signal and receptor functions. Since other signal-receptor systems seem susceptible to super-stimulation (Ryan 1990), language may provide an exceptional opportunity for sensory exploitation and ICE.

Conflict arises in information exchange in a way that is analogous to genetic exchange via internal fertilization. Just as seminal fluid proteins accompany sperm, so too may persuasion accompany information. Because individuals need to receive information from conspecifics they simultaneously make themselves vulnerable to persuasion that may cause them to deviate from their optimum behavior.

In this context, offense is the construction and sending of signals that persuade others to do what is best for the signal-coding genes, and defense is reception and processing of information sent from others in a way that is best for the reception coding genes. The observation that different parts of the brain contribute to speech construction (frontal lobe) and language comprehension (temporal lobe) supports the idea that the genes that mediate offense and defense are different, at least in part, and that the opportunity for ICE is manifest (Kalat 1992).

Information signaled to a receiver can be over-influential by super-stimulating instinct/emotional components of the signal reception process, and genes that contribute to this can be favored by natural selection. Genes coding for the receiver system can respond by changing the signal-processing algorithm so that it is not over-stimulated and/or by using logic rather than instinct/emotion to evaluate the information signal. As language skills increase, so to does the opportunity for ICE. The phenomena we refer to as intelligence may be a byproduct of intergenomic conflict between genes mediating offense and defense in the context of language.

ICE as an evolutionary catalyst

Although only a minority of loci are hypothesized to be directly involved in the ICE process, perpetual coevolution at these loci may cause other, interacting loci also to evolve at an accelerated rate. Consider the case of the genes that code for the proteins that make up the integument of sperm. These proteins are likely to be targets of (a) seminal fluid proteins that mediate sperm competition, and (b) female reproductive tract proteins that reduce excess sperm access to her eggs. Intergenomic conflict is expected to cause the loci coding for these integument proteins to evolve rapidly. But changes in the integument proteins will likely have an impact upon the function of other proteins that interact with the integument during both the developmental and mature stages of the sperm. As a result, strong selection, via intergenomic conflict, to change the integument proteins will select for concomitant changes in other, interacting proteins. In this way the rapid evolution of loci directly involved in ICE will spread to a larger segment of the genome.

Speciation

In the context of the biological species concept (Mayr 1963), speciation requires genetic divergence among populations for traits that cause pre- and postzygotic reproductive isolation. ICE is a process likely to drive such genetic divergence owing to its perpetual nature and due to the types of characters involved in intergenomic conflict.

Consider a pair of populations that are newly separated by a geographic barrier. Independent evolution in the two populations will cause them to diverge genetically and phenotypically. Once this divergence is sufficient to make the two gene pools reproductively incompatible, allopatric speciation has occurred. Clearly there can be no direct selection for the evolution of reproductive isolation in the allopatric populations. So the critical question is, what process drives that specific genetic divergence that is responsible for the evolution of reproductive isolation?

Because of its perpetual nature, ICE it will continually drive genetic and phenotypic divergence for the kinds of traits enumerated in the previous sections; reproductive anatomy, physiology, and behavior. These are the traits that typically produce pre- and postzygotic isolation. As a consequence ICE may be a major engine of speciation (Rice 1996). A fuller discussion of ICE and speciation can be found in Rice (1997).

The Y chromosome

The major dichotomy in chromosome types is between autosomes and sex chromosomes. Among the X and Y sex chromosomes, the Y is most divergent in structure from the autosomes. The Y chromosome evolves by first evolving suppressed recombination with the X, and then this is followed by decay in Y-linked genetic function. The breakdown in recombination between the X and Y is thought to be driven by a genetical chain reaction associated with the accumulation of sexually antagonistic alleles (Fisher 1931; Bull 1983; Rice 1987a, 1992). The decay of the Y is thought to be driven by Muller's ratchet and background selection/background trapping (Charlesworth 1978, 1991; Rice 1994, 1996) as well as by genetic hitchhiking (Rice 1987b).

ICE can play a major role in the decay of the Y chromosome via genetic hitchhiking of mildly deleterious mutations. In the primitive state, a nonrecombining

Y (or its nonrecombining differential segment) carries hundreds to thousands of genes, all of which became newly male-limited when the Y stopped recombining with the X. These Y-linked genes are freed from any counter-selection in females. Recent experiments (Rice 1992, 1996) demonstrate that such a nascent Y will be a hot spot for the accumulation of male-benefit alleles. Experiments also indicate that the male-benefit alleles that accumulate on the Y may commonly reduce female fitness (Rice 1996, manuscript). The accumulation of male-benefit alleles on the Y that reduce the fitness of females will initiate ICE by selecting for female-benefit counteradaptations at X and autosomal loci. As female-benefit counteradaptations accrue, this selects for new Y-linked male-benefit alleles – and perpetual ICE of Y-linked male-benefit versus X/autosomal-linked female-benefit loci can ensue.

Each time a new Y-linked allele is recruited it can drag along one or more mildly deleterious mutations (Rice 1987b, manuscript). Perpetual ICE between the Y and the rest of the genome can thereby continually erode the genetic quality of the Y via genetic hitchhiking of mildly deleterious mutations. The decay of the Y is due to genetic hitchhiking, but it is the ICE process that acts in a catalytic way to continually drive the male versus female antagonistic coevolution.

Social behavior

Although a minority of loci in the genome as a whole are expected to be involved in the ICE process, this pattern is expected to be reversed for the subset of loci controlling social behavior. Unless social interactions occur between individuals with identical genotypes or between truly monogamous mates, then there is the opportunity for many forms of evolutionary conflict and hence many opportunities for ICE to operate. Many, perhaps most, forms of social behavior involve signal-receptor systems and/or offense-defense systems, and when conflict occurs the loci that control these processes can antagonistically coevolve.

The obvious prediction is that, on average, social behavior should evolve faster than non-social behavior and that social behavior should diverge among related species far more rapidly than most other aspects of the phenotype that are not involved in ICE, e.g., metabolic rate, cardiovascular system. Mayr (1976, p. 681), in surveying many forms of both vertebrates and invertebrates in the context of taxonomically informative characters, remarks that "Behavior characteristics have proven particularly useful in distinguishing morphologically very similar species, the so called sibling species." He also notes that "hostile and courtship movements" are among the rapidly evolving behavioral traits. West-Eberhard (1983, 1984) surveys broadly across taxa and concludes that traits which mediate social interactions are generally evolving faster than other traits.

Coadapted versus counteradapted gene complexes

Just as species within the same community coevolve in a mutualistic or antagonistic fashion, so too do gene loci within the genome of a single sexually recombining species. It has long been appreciated that coadapted gene complexes (in the general sense and not limited to tightly linked genes) commonly evolve and play an important role in adaptive evolution. Organisms are generally viewed as "triumphs of adaptation" when the integrated sets of adaptations in, for instance, swimming marine mammals, flying bats, or running cheetahs, are described. Our purpose in writing this paper is to emphasize that the converse, counteradapted gene complexes also commonly evolve, due to ICE, and play a critical role in evolution. The extent of conteradaptation among loci depends on the degree of inter-individual social interaction: the more social the species the greater the role of ICE in producing counteradapted gene complexes.

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