

ASCAP

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"[W]ee must yeelde humbly to our superiour, perswade gently with our inferiour and agree quietly with our equall. And by that meanes there shall nver bee any falling out." Stefano Guazzo, 1581¹

Newsletter Aims

- A free exchange of letters, notes, articles, essays or ideas in brief format.
- Elaboration of others' ideas.
- Keeping up with productions, events, and other news.
- Proposals for new initiatives, joint research endeavors, etc.

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President: John K Pearce
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 Past Presidents: Michael A Chance, John S Price, Paul Gilbert
 Editor: R Gardner, Graves Bldg, D-28, University of Texas Medical Branch, Galveston TX 77555-0428, Tel: (409) 772-7029
 Fax: (409) 772-6771
 E-Mail: ASCAP@beach.utmb.edu
 Previous volumes are available. For details, contact Managing Editor: Erica Ainsbury, at above address.

ASCAP Society Mission Statement

The society represents a group of people who view forms of psychopathology in the context of evolutionary biology and who wish to mobilize the resources of various disciplines and individuals potentially involved so as to enhance the further investigation and study of the conceptual and research questions involved. This scientific society is concerned with the basic plans of behavior that have evolved over millions of years and that have resulted in psychopathologically related states. We are interested in the integration of various methods of study ranging from cellular processes to individuals in groups. The ASCAP Newsletter is a function of the ASCAP society.

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Concerning paleobiology, sociophysiology, interpersonal and group relations, and psychopathology

ADDRESSED TO & FROM ...

PRACTICAL ETHOLOGY FOR ASSESSING DEPRESSION TREATMENT

I was very interested in reading about your "Harbinger (i)": Clinical work at Austin State Hospital (ASH) concerning the practical ethology of Gordon Paul.

In Denmark, Fredericksberg Hospital, we are studying the nonverbal behavior of depressed as well as schizophrenic patients compared to that of normal controls. Our observational methods are systematic and quantitative, and data are processed statistically.

Our aim is to construct a behavioral observation and assessment system, which can be used by doctors and staff to get more systematic and objective observational information. Such behavioral observations no doubt will contribute to more precise diagnostics and treatment assessments, i.e. the nonverbal behavior is a very valid expression of the patients' mental states.

Just to mention a few examples which are very much in favour of the validity of ethological observations:

(1) A depressed woman was assessed as completely recovered after 11 weeks of hospital stay - both by clinicians and Hamilton-rating. However, the ethological observations in the ward showed a dramatic relapse of diversity and activity from week 8 to week 11. The patient was discharged - but

tried to commit suicide immediately after returning home.

(2) A schizophrenic man showed behaviors that to some extent suggested depression (e.g. look down at social contact; slow, but fairly normal social speech, and others). After a couple of years the clinicians changed the diagnosis from "schizophrenic" to "schizo-affective", a change which was more in accordance with the ethological observation and assessment.

(3) In some cases patients' self-assessments have turned out to be more closely related to ethological parameters like diversity and activity than to Hamilton-rating. Even if the Hamilton-rating shows a gradual improvement the patients don't feel the disappearance of depression until they are in close social interaction with staff and other patients. This stage corresponds to the ethological rise of various social activities such as affiliation and assertion.

(4) Comparisons between recovered depressed patients and normal controls have demonstrated that the two groups are very similar at discharge regarding nonverbal communication. The only significant difference is that the recovered depressed patients talk less.

In short: these -- and other examples - demonstrate that ethological observations have a number of advantages: they are more systematic and objective; nonverbal assessments are rather precise; nonverbal observations

can differentiate diagnoses; patients in the ward cannot really dissimulate, because the nonverbal behavior is very revealing; new, basic information can be obtained about patients' behavior patterns which cannot be discovered by "common", general observations, e.g. markers of depression, transition, improvement and recovery.

Based on the results of the systematic, quantitative investigations it is possible to establish an assessment system for *practical, clinical use*.

It is also possible to construct a very exact measurement system based on significant markers of depression and recovery. Such a system would be of great value in *testing psycho-pharmacological medicine*. Many kinds of psychopharmaca only reduce symptoms, whereas they don't develop social interaction/communication. It is considered a crucial point for being recovered that patients/persons master social interaction to a great and stable extent.

As mentioned above, recovered depressed patients are very similar to normal controls according to social communication.

Social behavior markers can also be used to assess the interaction capacity of schizophrenic patients: being sufficiently social is equal to being recovered, normal, and fit. Experience shows that

ARTICLE: **A socio-mental bimodality: How the human hedonic society is maintained.** **Part (iii) of (iii)**

How the human hedonic society is maintained

Play is the distinguishing feature of the young of all mammals and much is made of the undoubted fact that when it takes the form of rough and tumble play between siblings it serves the purpose of practice of the means by which social rank is established between adults. Even in the classes of mammals other than primates, individuals in the wild play with physical objects like leaves, pieces of stick, and foxes have been seen to bat tennis balls left on a lawn! Piaget established parallels between assimilation of information and play and White, re-examining Piaget's findings, discovered that competence was achieved by contented children in play. This is especially evident in the young of two tribes; the Mbuti, hunter-gatherers of the tropical rain forest of N.E. Zaire, studied by C.M. Turnbull, the !Kung hunter-gatherers of the Kalahari Desert in Africa studied by P. Draper¹ and the hunter-gatherers, the Fore of New Guinea, by E.R. Sorenson.²

Like the Mbuti child, young infants of the Fore "remained in almost continual bodily contact with their mother, her housemates or her gardening associates", and which led throughout childhood to unrestricted exploratory activity.

Once the child can crawl the youngster will explore the floor and the dwelling just as thoroughly as he explored his mother's body. If he comes to minor harm in his explorations of space, she quickly comforts him before turning him loose to try again. Up to this point he has learnt a subtle combination of dependence and independence.

Beyond the relationship with mother there are relationships with other children. These are well described, Patricia Draper of the !Kung.¹ !Kung children, like children anywhere, will argue, tease, cry, lose their tempers, and strike out at each other. There are frustrations in this society for even the youngest age groups. The !Kung have a special way

of handling anger and physical assaults by one child against another. When two small children quarrel and begin to fight, adults don't punish them or lecture them; they separate them and physically carry each child off in an opposite direction. The adult tries to soothe and distract the child and to get him interested in other things. The strategy is to interrupt misbehaviour before it gets out of hand; for older children, adults use the same interventionist technique.

This way of disciplining children has important consequences for aggressiveness in childhood and later in adulthood. Since parents do not use physical punishment, and since aggressive postures are avoided by adults and devalued by the society at large, children have relatively little opportunity to observe or imitate overtly aggressive behaviour. This situation, of course, is made possible by the fact that children and adults occupy the same close living space and by the fact that on any typical day there will be many adults in camp who are keeping an informal watch on the children.

As James Steels has put it, "combinatorial competence is expressed in two forms, namely technology (the hierarchical assembly of elements into a compositive tool) and mental modelling (the cognitive manipulation of abstract representations of sensory phenomena to generate blueprints for novel actions)." What are the factors influencing these capabilities?

The phylogenetic increase in exploratory variability

Christopher Parker gave a rope to semiferal caged members of several primate species and recorded the way they behaved towards it.³⁴ His conclusions were that the great apes were more diverse than other species in their manipulative behaviour in at least six ways: (1) They used more different body parts to contact the object. (2) They performed more

different actions while in contact. (3) They formed a greater number of unique combinations of body part and action. (4) Their degree of behavioural predictability was far less, as indexed by the information-theory measure of uncertainty (H), which integrated the number of different combinations of body part and action categories with their relative frequencies of occurrence. (5) The proportion of total behaviours accounted for by the thirty most frequent categories of behaviour was less for the apes. (6) The apes also performed more actions in which the object was grasped and then applied to other body parts or to other objects in the environment, that is, the apes used the object in a tool-like way; whereas the other species were much more likely to perform actions directly on the rope itself.

Another analysis of Parker's findings indicated that not only did the apes have a greater number of unique combinations of body part and action, but that they also were much more reluctant to repeat a combination once it had been performed. If the animal becomes bored with repetition, *but stays interested in the object, this would tend to produce more variation in behaviour.*

H. Mittelstaedt has showed that every time an action is undertaken, an *output copy* is sent to the sensorium so it is logical to deduce that with an increase in variability evident in the motorium between macaques and the great apes, a corresponding segregation will have taken place in the sensorium.

Brain power for exploring

Rosensweig, Bennett and Diamond, an ethologist, a biochemist and a neuroanatomist collaborated in a remarkable study, now two decades old, of the effects of introducing novel objects into cages of maturing rats each day for a month.⁶ This work has been ignored! They found that this stimulus to exploration brought about marked changes in both the anatomy and biochemistry of the neocortex of these rats indicating an enhanced activity. Significantly, they found a migration of glial cells into the neocortex. Glial cells nurture the neurones with which they become closely associated. Perhaps as a result, or cause-effect circular relationship, the rats

developed an enhanced ability to explore for longer periods of time without exhaustion, i.e. they would keep up their interest in exploring. Probably what is true for rats is true for the higher mammals especially those which, like the primates, have developed marked powers of exploration. Then more exploration is encouraged by the lifestyle the more this ability will be developed, i.e. a feedback process becomes established. Hence, those living in an hedonic social setting will exploit more fully the properties of the neocortex.

Attentional interruption

Let us now consider the conditions under which combinational competence can be exercised during or as a result of novel experiences encountered during exploration. Schneider and Schiffin (1977) distinguish between *automatic processes* of response in the long term memory store and triggered by appropriate inputs, and *controlled processing* which consists of "temporary" (my parenthesis) activation of elements of memory not yet fixed and which are easy to set up and modify or utilize in a new situation and also which require active control by attention. Clearly this process *guided by attention* to new inputs is the essential requirement of generativity.

So we can infer that operating conditions which interrupt the attention span or make overriding demands upon it will attenuate and ultimately stop generativity. This will happen in the agonic mode in which centripetal predominant attention deflects attention towards the dominant centre of the group, or, if there is indoctrination with the tenets of a culture attention within bounds will be kept.

We should note that Bamber makes the singular point that where the organism must direct its energies to self preservation as in avoiding predators and *dominant interlopers* (my emphasis), conditions necessary for play are unavailable.

We should not be surprised that the young child brought up in hedonic ways, typical of the hunter gatherers, shows a great deal of exploration and finds out what can be done with the objects, e.g.,

knives, stones, pots, woven materials and even fire, which it comes across. This is because, as Paul MacLean points out, the neocortex is "wired" to the senses, making us aware of the outside world.

Interruption of arousal control

When attention is deflected centripetally it not only interrupts control by exploration, but predominant centripetal attention prevents the fluctuation of arousal essential for the intake of information. This fluctuation has been found to be an integral part of information intake in human experiments carried out by Lacey *et al.*⁸ They report that slowing of the heart rate (accompanied by palmar conductance) accompanied and perhaps even facilitated ease of "environmental intake" in human subjects whereas cardiac acceleration accompanied or facilitated a rejection of the environment (also accompanied by increase in palmar conductance).

They also reviewed the fragmentary neurophysiological evidence for the notion that cardiac deceleration (if accompanied by lowering of arterial blood pressure) would have the effect of facilitating sensory-motor integration. This effect is mediated by visual afferent mechanisms. Increases in pressure within the *carotid sinus* that result from sympathetic-like cardiovascular changes (i.e., excitement) stimulate the baroreceptors within the carotid sinus. The resulting increase in impulses along Hering's nerve produces inhibition of cortical electrical activity and of sensorimotor activity. These two pieces of information support the deduction that relaxed social relations combined with fluctuations of arousal accompanying a daily routine, will predispose individuals to take in information while exploring the environment and to develop sensory-motor skills. Both of these would predispose to the establishment of different cultures of chimpanzees each incorporating a different set of skills, e.g., bundles of leaves, used as sponges, sticks cleared of side branches and used to extract termites, stones used as hammers to crack nuts on anvils, and the development of hunting skills to kill other species of monkeys. Such differences are found across the widely separated habitats of Africa.^{9,10}

It is now possible to see how exceptional circumstances allow the young of species hitherto regarded as of low intelligence in comparison with apes may be able to perform at a higher level.

Westgaard has reported that lion tailed macacas (*macaca silenus*) in captivity show an unexpected degree of combinatorial competence when provided with apparatus that give them the opportunity to develop skills appropriate to their mode of feeding in the wild.¹¹ But this may be a consequence of the nature of their social relations which Emory has found to be unusually relaxed in a group at the San Diego Zoo. Moreover he has observed inventiveness of a more serendipitous kind when not constrained by a *priori* experimental design, e.g., breaking off a branch from a tree and weaving it into the wire netting before perching on it and biting a hole in a rubber football to fill with water and then pour the water over another monkey.

In 1964, Neils Bolwig, who then lived in Nigeria, described how a young baboon was brought up as a pet in the family for several years. As it approached maturity (when an adult is normally more aggressive) he tested its problem-solving ability by the methods used by Wolfgang Kohler in Tenerife to study the intelligence of chimpanzees.¹² He found that she scored very high, nearly as well as the chimps. The inference is that brought up in a human family the baboon was not agonically programmed to be preoccupied with gaining social ranks and that play, rewarded with food and petting, may have engendered an habitually low and fluctuating level of arousal. If so the neocortex of the baboon possessed properties which in its normal life were suppressed.

Effects of enlargement of neocortex on exploratory behaviour and hedonic social relations

The longer an individual pays attention to an environmental object the more novel combinations are likely to arise. The enlargement of the neocortex is likely to promote this attention span for the following reasons: 1. Enhanced powers of inhibition of lower brain centres will minimize distraction. 2. The migration of glial cells into the neocortex will make it

possible for exploratory activity to last longer.

According to Chris Parker, both of these will potentiate the likelihood that the great apes will perform different acts in relation to the object and that the object itself will be used in a tool like way.³

Pari passu with such changes will go enhanced powers of mutualistic or hedonic type social relations which themselves should engender communication about mutual interests in external objects.

End Piece

This ambitious paper crosses the boundaries of several disciplines so the reader should already be prepared to extend the principle further. Only by drawing attention to similar dichotomies to the one outlined in a number of aspects of human culture can we see that all have their origin in a deep seated biological aspect of our nature.

Karl Popper writes, "if we look back into the past, its problems are the problems of our own time". This idea of freedom of thought and action has, in our age, come up against a much more severe form of social and mental control in the dictatorships of the interwar years in Europe and latterly in varied, often bizarre, forms of dictatorship which have sprung up in Africa and other parts of the developing world to replace the democratic aims on which these nations were founded. All, however, possess the ability to bind the attention of their subjects to the dictator usually by intimidation often combined with exaggerated displays - doing in modern forms what Plato advocated "in war and in the midst of peace of his leader he (the citizen) shall direct his eye and follow him faithfully" - or what agonistic primates have been doing for aeons!

Conclusion

So exploration is promoted by several factors: (1) an increase in manipulative combinatorial competence means animals combine one act on an object with another; (2) the object tends to be used as a tool; (3) the longer the time devoted to exploration, the more diverse the combinations become.

If then we make the logical assumption that neuro-anatomical and neuro-chemical changes take place in primates in the way Rosensweig *et al.* found took place following prolonged exploration by maturing rats, then the longer a young ape or a human explores, the more it will enhance its capability to explore.⁶

Early on, Kirkland argued persuasively that interest and creativity were closely related to the freedom to indulge in exploration as part of play and we have seen that this combination is a prominent feature of the activities which the young of hunter-gatherers are free to pursue. Their freedom is guaranteed because they are living and are brought up in an hedonic social group. It is argued that this is an intermediate factor between a primate and its ability to develop creativity. Before we leave this theme let us once more tackle the definition of what is going on when creativity is manifest.

Poincare is quoted by Kirkland as noting that "intuition into the solution of a problem often comes after a period of intensive work on the problem followed by relaxation when the solution appears into dramatic suddenness". When discussing the quest for the mechanism behind creativity, Perkins notes of Beethoven "that he did not just have brilliant ideas; he worked them up and worked them out, as his notebooks testify."¹³ In short there were numerous cycles of generation and selection." He continues: "One contribution purely came from his extensive exploration of motifs around which to construct a whole work - a straightforward example of a plan of problem-finding which promotes creativity specifically". What we are seeing here is an example of a recursive process by which elements retained in memory are repeatedly combined and recombined sometimes with new elements taken in from further awareness. *Clearly any overriding calls on attention such as occur in the agonistic social mode will interrupt the recursivity of attention and hence prevent creativity.*

Evidence from a variety of human studies supports the view that we have inherited from our primate ancestors a *socio-mental bimodality* representing two

mutually exclusive ways of securing social cohesion in a primate group, and that one, the hedonic, creates the conditions for the expansion of intelligence and the other, the agonic, prevents this.]

Summary

The "*agonic*" mode is a rank ordered structure of centripetal attention maintained by threat from a dominant individual who thereby exerts a persistent control over the rest of the group. The members of agonic groups remain in a state of emotional and physical tension and receive much of their information from awareness of the dominant's behaviour or, if human, from instructions.

The "*hedonic*" mode on the contrary typically comprises a network of individuals in mutual reciprocity and rewarding social interaction with a free flow of information between nodes of the social network.

The evidence, therefore, points to the emergence of creativity only in the hedonic social mode, in which the flexibility of attention and emotional state permits exploration of the environment by the individual.

This is, therefore, why some species of primate have shown in recent studies unexpected amounts of manipulative inventiveness. Since any restriction on attention and hence freedom to explore will curb creativity, the human persistence of a culture will, of itself, also restrict the opportunities for individual inventiveness.

In those species of primate which live in groups, therefore, their society is an intermediate factor determining their inventiveness.

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by R Gardner, Jr.

RESPONSE: Thanks to Michael Chance

I represent the ASCAP readership in signaling gratitude to Dr. Chance for his resurgent contribution to sociophysiology. His prose is clear, examples vivid, and evidence straightforward. Early in my learning of human ethology, Dr. Chance was known as one of the two important figures in this area. I think we all have been pleased and honored that he has not only supported our group's efforts, edited [Social Fabrics of the Mind](#), served as ASCAP's first president, but is now also continuing our education through this update.

Dr. Chance's newsletter prose is as engaging as the prose of [Scientific American's](#) special issue on "Life in the universe" (Oct 1994) by William Calvin, Carl Sagan and Stephen Jay Gould. For example, Calvin said, "We humans certainly have a passion for stringing things together: words into sentences, notes into melodies, steps into dances, narratives into games with rules of procedure. Might stringing things together be a core facility of the brain, one com-

monly useful to language, story-telling, planning, games and ethics?" I can hear Michael adding that only in the hedonic group setting does this work to its fullest.

Another article, "Sustaining life on the earth" by Robert Kates, discusses the exponential growth of the world population. He cites ASCAPian Lionel Tiger near the end, "Fifteen years ago Lionel Tiger of Rutgers University suggested that there was a "biology of hope," an evolutionary human tilt toward optimism that compensates in part for our ability to ask difficult questions such as "Can human life on the earth be sustained?"... I share his inclination ... because hope is a necessity if we as a species ... are to survive." Michael Chance, too, knows the political implications of his data. He would have us focus on mechanisms to heighten our critically needed intelligence by heightening the hedonic mode of our interactions together. We hope that [The ASCAP Newsletter](#) meets the criteria he outlines.

ARTICLE: **Selfish genes, the unit of selection and causality: Round 2. A response to Mike Waller.**

Mike Waller takes issue in the May [ASCAP Newsletter](#) with my critique of genic selectionism (in the context of my critique of Slavin's and Kriegman's "gene's eye view" reformulation of psychoanalysis.¹ Since part of his argument was inadvertently omitted in the [ASCAP](#) issue, I will briefly summarize Mike's main points.

Mike believes that the fact that genes are the main currency through which natural selection operates makes genic selection "irrefutable". This "irrefutable" argument, advanced by Hamilton and Dawkins boils down to the following. Genes are capable of making copies of themselves and surviving during a significant part of evolutionary time; individuals (phenotypes) or groups do not so endure. In Mike's estimation this "permanence" or "genes are forever" argument is *prima facie* proof of genic selectionism.

Mike says that as a "genic theorist" it is nonsense to say that genes are causal agents of the selective process. In his view the causal agent is the environment acting on natural variability. Mike thinks that Sober's distinction between selection *of* and selection *for* is useful, but that it does not constitute a major challenge to genic selectionism. However, Mike agrees with Saber's critique of Dawkins and Hamilton in their belief that selection at the level of the genome and selection at the level of the individual are equivalent. The case of the driving gene in the t allele that renders the house mouse, *Mus musculus*, sterile demonstrates clearly that the "interests of the gene and of the organism are not equivalent (the t allele is a classic example of a "selfish gene").² Finally, Mike thinks that the hypothesis of "social comparison genes" helps solve the issue of group selection and altruism. Mike uses examples from cow breeders and from Taylorism to illustrate his thesis of group selection.

I appreciate Mike's challenge. It has given me an opportunity to study the issues he raises in greater depth and clarify my own thinking on these matters. I will begin by stating what the units of selection

controversy is about. This is important because even though he describes himself as a "genic theorist", Mike abandons two key concepts of genic selectionism. The belief that selection at the level of the gene and the organism are equivalent and the belief that group selection is a fiction (he supports re-integrating group selection concepts with the "genic pale"). This makes Mike's position on the units of selection debate very confusing. Mike has every right to define for himself a *sui generis* position in this debate, but I believe his arguments are misleading. I will refute the following claims and assumptions in Mike's [ASCAP](#) article.

It is "nonsense" to say: 1. That genic selectionists believe that genes are causal agents. 2. That the argument of permanence is "irrefutable". 3. That genes are "the be-all and end-all" of evolution. 4. That group selection concepts are incompatible with neo-Darwinian theory (his assumption). 5. That the process of natural selection of (alleged) social comparison genes continues to operate at a socio-cultural level.

The units of selection controversy

The units of selection controversy was rekindled in its modern form by Hamilton's brilliant critique of group selection hypotheses.³ Hamilton argues that for every case imputed to group selection there is an alternative explanation based on individual selection that is less cumbersome and more parsimonious. Moreover, Hamilton does not stop with this critique. He argues that selection at the level of the gene and selection at the level of the individual are equivalent. This leaves the gene as the only viable unit of selection. This position was taken further by Dawkins who unambiguously states that genes are the deeper causes of evolution since organisms are merely "survival machines" that serve the purposes of the gene. More about the issue of causality later.

Mike has apparently misunderstood the critique of genic selectionism to mean that those who oppose this theory do not believe that the genes are the unit

of heredity by which differential survival and reproductive success are transmitted. Let us be clear that there is no dispute over whether genes are the unit of heredity or whether Mendel's laws are true. However, if the claim that genes are the unit of heredity is all genic selectionism amounts to, then the position is trivial. Far from trivial is Hamilton's and Dawkin's belief that genes as *units of heredity* and genes as *units of selection* are for all practical purposes the same.

Mike states that Sober, Lewontin and Gould marginalize the importance of the gene's role in the process of natural selection. It is important to note that what is being "marginalized" is not the role of genes as transmitters and recorders of the evolutionary processes, but the more extreme and deeply reductionistic claim that Darwinian selection is played out only at the level of the genes. Hypotheses that postulate selection operating at higher levels (organisms, groups, or species) are scorned or ridiculed. In short, the unit of selection controversy is about (a) which biological level(s) are the target of Darwinian selection and (b) the claim that selection at the lower levels (genes) is the only accurate representation of the selection process.

1. Genes as causal agents in natural selection

Claiming he speaks for genic theory, Mike believes it is nonsense to say that genes cause the selection process. He asserts that the positive (causal) role in the process of selection is performed "by environmental factors acting on natural variability".⁴ There are two problems with this statement. If Mike denies genes' causal link to natural selection he is in effect giving up on genic selectionism. Despite what Mike says, Dawkins does believe that genes are the "deeper" agents of evolution. Consider the following proposition.

An organism's genotype interacts with the environment to produce an organism's phenotype which results in survival and reproduction.

This is the standard neo-Darwinian model of selection. Genetic selectionists do not dispute this causal chain. In fact they embrace it with a vengeance. While it might seem that natural selection is select-

ing phenotypes, it is really only genes, they say, that matter (remember that group selection has already been ruled out as a unit of selection by Hamilton). Furthermore, Hamilton and Dawkins believe (as quoted by Mike) that "there are two ways of looking at natural selection, the gene's angle and the individual (i)f [sic] properly understood they are equivalent ..." ⁵ This leaves genes as the only domain where selective forces can operate.

Yet Mike agrees with Sober that the equivalence between genes and organisms is a fiction and constitutes, according to Mike, "the major flaw in modern genic theory of evolution".⁶ Mike agrees that not only is the "gene's eye view" and the organism's view not equivalent, but in fact there can be conflicts between selection operating at the level of genes, phenotypes or groups, as the example of the driving gene in the house mouse shows so clearly. The issue of whether selective forces operate at the level of genes, phenotypes (individual organisms) or groups depends, as Sober points out, on the structure of the population in question.⁷ The issue cannot be settled *a priori*; it is an empirical question. It seems to me an oxymoron to call oneself a "dyed in the wool genic theorist" as Mike does and then question this central tenet of genic selectionism.

There is a second problem with Mike's rejoinder. He states it is the environment acting on natural variability (not genes) that causes survival and reproductive success. But is not natural variability dependent on genetic variability? Just as area is the product of length multiplied by width, so every trait that is selected is the product of the interaction between genetic endowment with environment.⁸ How can genetic factors not be part of the causal chain that lead to survival and reproductive success? Let us take the classic example of the sickle cell trait. When the trait appears as a homozygote (SS genotype) the organism develops anemia and can die in infancy. However, when the trait appears as a heterozygote (SA genotype) the organism develops resistance to malaria. The AA genotype is neutral. In this case there is selection against the SS homozygote and selection for the SA heterozygote. None of the genotypes (SA, SS, AA) go to fixation and the result is a stable polymorphism. Clearly environmental

factors are not acting alone as causal agents. Resistance to malaria is conferred by the SA heterozygote. Vulnerability to anemia is conferred by the SS homozygote. Natural selection is a consequence of the interaction between the sickle cell genotypes and the environment. Mike's statement about the causal role of the environment only tells us half of the story.

2. The permanence argument of genic selectionism

Let us now consider the aspect of genic selectionism that Mike considers irrefutable. Mike quotes Dawkins' argument that since small genetic units have the property of permanence while organisms (phenotypes) and groups do not, genes must then be the exclusive unit of selection. Williams also disqualifies genotypes as a unit of selection because meiosis and recombination destroys genotypes "as surely as death".⁹ (You will remember that a genotype is composed of two alleles and that in meiosis the strands of the chromosome divide into two gametes that become reunited in a fertilized egg).

Despite what Williams says, genotypes and phenotypes can have permanence. Sober gives examples of permanence of gene frequencies that turn out to be casually inert, and of permanence of genotypes (the "balanced lethal" case) and phenotypes (resistance to malaria by the sickle cell heterozygote) that determine reproductive success.¹⁰

What needs to be taken into account is that the criteria for permanence must require that a specific *property* remain stable in order to be selected, *not* atomistic entities. Genes (single or otherwise), phenotypes or groups are of evolutionary significance in so far as specific properties are being selected (see below). Genes have permanence, but permanence alone does not confer evolutionary significance. We can grant that genes are the unit of *replication*, and that evolution requires there be selection *of* genes. This still leaves open the question of whether the selection *for* properties are located at lower or higher levels of biological hierarchies.

3. Are genes the be-all and end-all of evolution? The representational argument

I now will take up Mike's assertion that "genes are the be-all and end-all of natural selection". As Godfrey-Smith and Lewontin observe, one of the issues that has gotten entangled in the units of selection debate has been the argument that evolutionary processes usually modeled (mathematically) at the level of individuals or genotypes can always be redescribed as competition between alleles (as genic selection).¹¹ Based on this fact, Williams and Dawkins adopt the extreme position that any selective process that can be represented at the level of genic selection is genic selection.

The standard mathematical models used by population genetics to represent selection in diploid organisms is the Hardy-Weinberg law that states that if there are p A genes and q a genes at some locus site in a population, then the frequencies of the three genotypes AA, Aa and aa are p^2 , $2pq$ and q^2 respectively.¹²

This simplified model assumes that mating is random (not assortive) and that gamete frequencies are counted before and after fertilization. The model assigns fitness values to each of the *genotypes* by mathematically transforming genotype frequencies before selection into frequencies after selection and "normalizing" this value so that $p + q = 1$. However, as genic selectionists are quick to point out, if we know the numbers or frequencies of all possible genotypes it is a trivial (algebraic) matter to calculate the frequencies of alleles.

It is important to note that fitness values of single genes (alleles) are just weighted averages of the fitness values of the genotypes in which they appear. That is to say, the fitness values of single genes is just another mathematical way to "represent" genotype frequencies of the standard model. This way of representing selection is a convenient artifact. The model can be an adequate (causal) representation when there is selection for properties at the level of the genome such as in the case of driving genes or so-called junk DNA. The danger is that fitness values attributed to allelic frequencies can lead to the illusion that selection is acting at a lower level of the organization when in fact it is not.¹³ The assumption that selection *represented* at lower levels means that

selection is actually taking place at lower levels can seriously misrepresent the causal mechanisms doing the actual work of selection. There are many strong correlations of positive fitness values for specific genes with natural selection. But a correlation does not necessarily imply causation. Take the example of the human jaw.¹⁴ The architecture of the human jaw is such that the chin is an inevitable and fortuitous by-product. Individuals with a certain facial structure always have chins. Hence, the overall fitness of the traits (jaw and chin) are the same, yet there is selection for jaws (a causal relationship) but not for chins (a correlation).

Sober observes there is a division of labor in evolutionary theory.¹⁵ Population genetics offers a coarse grained approach. It summarizes various selective processes in the same way a vector may summarize the component forces in physics. The model has great generality regardless of what *properties* are selected. This is what is meant by the bookkeeping analogy.¹⁶ However, there is more to selection than its effects and more to physics than component forces. We want to know why and how the net selective effect took place. What properties are being selected *for* is a different matter and has to be understood separately from the mathematical models of population genetics. I should also mention here the summary of Miklos' article (February 1994 issue of ASCAP). He argues that the mathematical models of allelic frequencies are totally irrelevant if we want to understand the evolution of the 50 or so model body-plans that are left since the Cambrian explosion.¹⁷

After this detour, I can now take up Mike's analogy of the automotive industry that he uses to support the position that genes are the "be-all and end-all" of natural selection. This is Mike's analogy that was unfortunately omitted from the ASCAP article.

If I might be permitted a flight of fancy, I can put the same point a little more colorfully. Were we in the business of making automobiles, it might be fair to term the financial expression of our activities as mere bookkeeping; but if we were bankers, money would not only monitor our progress, it would also be our sole stock and trade. And is not the terrestrial

gene-bank the biggest bank of all?

Let us draw out Mike's analogy and assume that market forces are analogous to natural selection processes and market share is analogous to reproductive success. Clearly there is a *correlation* between the financial success of the company and market share. If I hold stock in the company or I am a banker, I agree with Mike that I would primarily be interested in the bottom line. However, let us ask what criteria consumers use to buy a car. Do consumers read The Wall Street Journal to get information about the financial well being of the company or the stock market prices or do consumers get their information from consumer reports or from fellow consumers? Plainly, it is the properties of the car such as quality, price, attractiveness etc., that ultimately determine consumer preference, not financial sheets or values of the stock market. (A case in point is the U.S. automotive industry. In the 1970s when the Japanese invaded the U.S. market, the U.S. companies were financially in a better position than their Japanese counterparts).

Just as the currency of the market is based on money, so the currency of evolution can be represented mathematically in the language of gene frequencies and fitness values. And just as we have correlations between the financial well being of the automotive company and the number of cars it sells, so we also have correlations between gene frequencies and fitness values on one hand (Mike's terrestrial bank-gene) and survival and reproductive success on the other. However, these correlations do not tell us what properties are being selected *for* by nature or by consumers. So to answer Mike's question, I agree that the terrestrial gene-bank is the biggest bank of all, but so what? This does not advance one iota the claims of genic selectionism.

4. Is group selection compatible with neo-Darwinian theory?

Mike takes Sober to task for failing to realize that once he established that selection at the level of the gene and selection at the level of the individual are *not* equivalent, he (Sober) does not take the next step of doing "the apparently impossible: the incorporation within the genic pale of what has hitherto been

known as group selectionism." Not so. Sober clearly sees the implications of his position, as the following quote demonstrates.

*However Dawkins (1976) thinks of the genic and the organismic points of view as equivalent, I will argue otherwise. But there is more. Some of the arguments that Williams and Dawkins present for their thesis of genic-selectionism - that the gene is the unit of selection - have a curious characteristic. They cite facts about the evolutionary process that are quite compatible with group selection and group adaptation. If genic selectionism really is incompatible with group selection, then the argument of the former should cite facts that count against the latter. As we will see, something has gone seriously wrong in these arguments.*¹⁸

As Sober demonstrates, what has gone wrong with the argument is that group selectionism is compatible with the "genic pale" if by the "genic pale" we mean the arguments that gene selectionists use to justify their claims for unit of selection *exclusivity*. Even if we accept the arguments as valid ("genes are forever", the fact that natural selection can be represented in the idiom of gene frequencies or the parsimony argument), the arguments say nothing "about whether group adaptations are common, rare, or nonexistent".¹⁹

Mike has accepted the genic selectionists' party line and assumed that group selection cannot be integrated with standard neo-Darwinian theory. Based on this mistaken assumption, Mike goes on to propose a "solution" to this problem which he believes can be resolved by two concepts: contingency and genetic fixation. Contingency takes Mike to the hypothesis of contingency behavioral genes or social comparison genes (SCG) that allow organisms endowed with these clever genes to act altruistically in one situation or selfishly in another ("crichton" genes in Mike's colorful metaphor). Genes that allow for flexible responses will sweep to fixation.²⁰

6. Social comparison genes and socio-cultural evolution

For argument's sake, let us accept SCG hypothesis as true at a biological level. Mike suggests that

social comparison genes, once they have swept to fixation (have "won" the Darwinian game), continue to operate at a human social level in order to hone in their competitive advantage and keep genetic mutants, that may have other advantages, from the competitive Darwinian game. If I understand Mike correctly, in his example from Taylorism, SCG confers a group advantage (read "group selection") by selecting individuals who perform most efficiently in companies organized under principles of scientific management.

As is well known, Taylor thought that highly mechanized and compartmentalized production lines represented the most efficient model of industrial development. Mike quotes Taylor as saying that some of the employees that were the most "intelligent, hardest working and trustworthy" in a ball-bearing factory had to be laid off simply because they did not possess the "quality of quick perception followed by quick action" that were necessary for this type of production line. In typical paternalistic fashion, Taylor justifies this action for the "ultimate good of the girls (sic) as well as the company".²¹ Further on, Mike quotes an objection to this type of ruthless managerial philosophy that was raised by a member of the House of Representatives in 1911:

Under scientific management, then, you propose that a man because he is not in the first class as a workman, there is no place in the world for him - if he is not in the first class in some particular line he must be destroyed and removed?

As Mike puts it, this type of *social* selection that rewards individuals with (ultimately selfish) social comparison genes may not be a pleasant idea, but it may still be true.

I seriously doubt it. There are two parts to my rebuttal. At a social level, Taylorism and scientific management are at best temporary manifestations of a particular stage of industrial development. But even if this mode of organization of work had withstood the test of time to allow Darwinian selection to have an effect, *socio-cultural* evolution may overwhelm whatever benefit conferred by *Darwinian* evolution.

The social level

An interesting twist to the story of scientific management is that one of the reasons the Japanese have been successful in competing in the world markets is that they never accepted Taylorism (after the defeat in WW II) and moved toward quality control (QC) concepts of management (described by Ouchi as Theory Z).²² The managerial philosophy of QC is that people are assets in efforts to improve quality and minimize waste. One of management's crucial jobs is to build cooperative teams, develop trust and encourage participation. In Japan job security is also guaranteed. To invest in people is not only humane, it is also smart. In this type of work environment it is the people who are the "most intelligent, hardest working and most trustworthy" that are valued the most. One cannot afford in the new world of technoservice to treat people as if they were things.²³ The same principles of management have come back to the U.S. and are being applied in manufacturing and service industries, accounting for success stories such as Ford's Saturn project. To paraphrase Mike, this may be a *pleasant* idea, but it may still be true!

Socio-cultural and biological evolution

Scientific management is a cultural invention. The environment of the work place is not equivalent to the environment in which natural selection operates. The rapid fluctuations of human environments do not allow enough time for natural selection to have an effect.

There is another reason to believe that even if Mike's example of Taylorism and social comparison genes were true, it may be immaterial. Human socio-cultural evolution may overwhelm biological evolution. To see why, let me give an example that I am familiar with. An interdisciplinary team collaborated on an international project that was studying fertility choices among women in third world villages before modern contraceptive techniques were readily available. In Mexico they found there was a significant difference in fertility rates in two small villages.²⁴ The poorer of the two villages, located in the high lands, had the lower fertility rate. The "richer" village (poor by first world standards), located in a fertile agricultural area (the low lands), had the higher fertility rate. What was interesting is

that psychological interviews showed the women in the high lands were happier and active. The women of the low lands were more depressed and passive.

Two differences stood out from the ethnographic material. The villagers in the high lands had never been conquered and had a long tradition as independent land holders. Both men and women could own very small plots and both men and women contributed to the mainly subsistence economy. In contrast, the farmers in the low land had all been "peones" in almost complete servitude to Spanish and creole *hacendados* (large land owners) for three centuries before the Mexican revolution. After the revolution, the land reform in the low lands gave land titles almost exclusively to men. The shift to commercial agriculture put the cash in the hands of men.

One could say that the women in the high lands with a tradition of dignity and self-reliance were more "fit" (were better adapted to their environment). Having fewer children was a reflection of the greater sense of control they had over their lives. The women in the low lands had continued to be in subservient roles reinforced by centuries of domination by the *hacendados*. They were less "fit" since they did not have an economic role in a cash economy and were forced to adapt to unfavorable circumstances. Having more children was the only viable role in their society and reflected the limited options available for their development. Historical, cultural and psychological factors had all reversed what you would expect from Darwinian evolution. The most "fit" had the lower rate of reproduction, the less "fit" had the higher rate of reproduction (I suggest this is a case of *cultural r* and *k* selection).

We must treat hypotheses that conflate the story lines from biological and human socio-cultural evolution with caution. There may be interesting analogies, parallels and points of conversion between both evolutionary processes, but their modes of transmission are radically different. Human nature is incomprehensible without a history of our biological origins, but human nature is also incomprehensible without the history of our socio-cultural origins.

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ARTICLE: Response to "Caught in the crossfire"

Thank you for sending me a copy of Thomas Joiner's paper (see last month's issue of ASCAP). I see he is working in the tradition of James Coyne, in taking an interpersonal, systems approach to depression. I had not run across his work before, and in fact only in the last year or two have I encountered James Coyne himself, and I am certainly guilty of not acknowledging the latter's ideas, such as when expressing them myself some years later. In the recent series of journal clubs I took with the Wellington psychiatric registrars (residents), we spent one session dealing with two of Coyne's papers and the students considered them a revelation. So I think you are lucky to have Thomas Joiner in your department. I wish you many years of hedonic collaboration.

I found the Joiner paper interesting, and I have only one criticism which I will get out of the way first. I think it is confusing to use the terms "positive" feedback and "negative" feedback for "positively reinforcing" and "negatively reinforcing" feedback. In terms of feedback, positive and negative already have very precise meanings, of "deviation amplifying" and "deviation reducing" respectively; so, although I do not think there is any real danger of misunderstanding, I think we should, if possible, avoid semantic confusion. If "positively reinforcing feedback" is too much of a mouthful, what about "rewarding feedback" and "catathetic feedback", as these are the meanings of those terms (to raise and lower self-esteem, respectively).

Joiner *et al.* studied mildly depressed college students and got their room-mates to rate them on a scale of "satisfactoriness as room-mates" five weeks later. They found that the depressed students were rated as less satisfactory than non-depressed students, and they try to account for it by the signals the depressed students gave to their room-mates. The authors make the point that depressives request both anathetic and catathetic feedback at the same time, the anathetic to boost their lowered self-esteem, and the catathetic to validate their low self-

esteem. Any signal which boosts them invalidates them, and any signal which validates them puts them down.

This crazy and unsatisfactory interpersonal exchange reminds me of Bateson and his double-bind (e.g., "I command you to disobey me!" Whatever you do, you disobey this two-edged command). The four criteria for a double bind are: 1) the eliciting of two incompatible responses at the same time, both of which are punished; 2) frequent repetition of the foregoing; 3) inability to "leave the field"; and 4) inability to metacommunicate (comment on the double-bind). These criteria seem to be met by the situation of Joiner's depressed students and their room-mates. So, if the room-mates felt "double-bound", it is not surprising that they found their depressed friends unrewarding to be with.

I think it might be interesting to apply our "hierarchical basic plan" system to these students.

Table 1. Some characteristics of the hypothesised basic hierarchical plans.

	Agonic mode	Hedonic mode
a) stable hierarchy dominant basic plan	punitive indignant "keep him down"	protective caring "improve him"
egalitarian basic plan	rivalrous one-upmanship	sharing friendship
subordinate basic plan	fearful coerced into obedience "placate him"	respectful voluntary obedience "honour him"
b) change in hierarchy (second order basic plans)		
up-hierarchy behavioral package	elevated mood rebellion "bring him down"	elevated mood receipt of honours "surpass him"
down-hierarchy behavioral package	depressed mood denial of former high rank	philosophical attitude devaluation of former rank

(Note: In order to take account of variation along the "horizontal dimension" we could have produced separate tables for close, middling and distant relationships, but this would not have altered the classification we have suggested.)

It is possible that the depressed students are using affiliative (closeness-eliciting) behaviour that is trying to establish a hedonic asymmetrical relationship, with the depressed student in the one-down position. The two components of their signal (eliciting rewarding and aversive feedback) relate to two different aspects of the relationship they are trying to get. The reward-eliciting signals are part of their attempt to get a hedonic relationship, of the type, "I like you, you are my friend". But the signals which elicit aversive reinforcing feedback are their attempt to establish themselves in the one-down position; they are submission signals; they are requests to be treated as a subordinate.

One can compare the depressed students with de Waal's chimpanzees seeking "conditional reconciliation". This is a kissing and hugging session which follows the fight and the loser's submission. The reconciliation is contingent on the loser establishing the fact that the other is now the dominant partner in the relationship. Once this is established, and the loser is reassured that the winner accepts his submission, they start the hedonic process of hugging. It's as if the depressed students are trying to do the two things simultaneously, to have the hugging before they have reassured themselves that the room-mate has accepted their "submission". Until they get this reassurance they are going to continue to be anxious and depressed, and feel that the relationship is in the agonistic mode.

Another reason that the room-mates may be uncomfortable is that they do not want an asymmetrical relationship. They may want to be equal, and the offers of submission are unwelcome. Not only are they being double-bound, they are being double-bound to achieve something that may be repellant to them.

Why are the depressed students seeking the one-down position in an asymmetrical relationship with a room-mate who is a peer and should be equal? One possibility is that they have difficulty in establishing and maintaining equal hedonic relationships, either as a personality trait ("authoritarian" personalities) or because they are depressed. Being depressed, they

cannot cope with either the attempt to be one-up, or the maintenance of an equal agonistic relationship (which is much the same thing, if both room-mates are competing for the one-up position. As authoritarian personalities, they are operating according to the pernicious Peter Principle that "he who is not one up is one down", possibly learned on the school playground.

Another factor affecting the room-mate relationship is the self-focus which is characteristic of depression. It is difficult to enjoy the company of someone who is self-focused. Why are depressives self-focused? We tackled this question in our debate about levels of submission. Voluntary submission is other-focused; therefore depressive submission has to be self-focused. Self-focused submission is more submissive, and therefore more effective. Other-focused submission (flattery, ingratiation, appeasement, arse-hole creeping, etc..) is a form of social climbing, and therefore not all that submissive. In a hierarchy of X, Y and Z, active submission by Z to X is a threat to Y, whereas the self-focused submission of depression is not threatening to anybody.

The two room-mates are a dyadic relationship and therefore focused submission is not going to threaten anyone. If one were to counsel these students, one could encourage the depressed one to flatter his room-mate, replacing involuntary submission with voluntary submission. To the non-depressed room-mate, one could say (apart from warning him about the anticipated flattery, which might be as unwelcome as what went before) that he should satisfy both of his room-mate's needs by saying something like, "you are a wimp, but I love you". Perhaps the dominance could be expressed physically, as in play wrestling, and the affiliation both physically and verbally. In other words, they need to have a fight, and then go to the bar and be reconciled over a drink.

Cultural factors

Family backgrounds vary very much in robustness, or "rough and tumble" qualities, both within and between cultures. Some males seeking friendship are aggressive, expecting the other to be equally

aggressive, and to indulge in a certain amount of play fighting. Males from other backgrounds do not do this, and might find it off-putting, or even misinterpret it as an attempt to establish dominance. For instance, the Maori welcoming ceremony is extremely aggressive and frightening for the guest being welcomed; it is only knowledge of the convention that enables one to stand one's ground and wait for the friendly stage of the ceremony. Were such cultural factors relevant to the miscommunication between the depressed students and their room-mates?

An after-thought. We have said that depression is one way of achieving low self-esteem, but it is only one way among many, and it can be done by philosophy and religion or it may come naturally. It is possible to be perfectly happy while believing truly that one is worthless. In our predictions about depressives, it is important to eliminate these

voluntary low self-esteem characters. Therefore we need a depression scale which does not include self-esteem items. And the reverse holds. We need a self-esteem scale which does not include any depressive items other than those directly related to ideas of self-worth. In most situations our predictions about the depressed and happy low self-esteem people would be different, and in some cases opposite. Basically, the happy low self-esteem people love themselves, and the depressed low self-esteem people hate themselves.

I hope that the approaches of the ASCAPians and the JAMERS will be cross-fertilising (I think this is a metaphor about two hermaphrodite individuals and therefore does not contain any implication of asymmetry of any kind!). Certainly, I have found this to be the case with "Caught in the crossfire". They are sufficiently like us to be compatible, but sufficiently different to be stimulating company.

ABSTRACTS & EXTRACTS...

Randall Parish A: Sex and food control in the "uncommon chimpanzee": How bonobo females overcome a phylogenetic legacy of male dominance.

Slagsvol T, Amundsen T & Dale S: Selection by sexual conflict for evenly spaced offspring in blue tits.

Lundin LG: Evolution of the vertebrate genome as reflected in paralogous chromosomal regions in man and the house mouse.

Charlesworth B, Sniegowski P & stephan W: The evolutionary dynamics of repetitive DNA in eukaryotes.

Randall Parish A: Sex and food control in the "uncommon chimpanzee": How bonobo females overcome a phylogenetic legacy of male dominance. Ethology and Sociobiology 1994;15:157-179.

Inferences for female bonding in humans have drawn on models derived from studies of nonhuman primates. In primates, strong affiliative relationships between unrelated females are rare. This is true for the social systems of apes and particularly for those of the closest living relatives of humans, the chimpanzee (*Pan troglodytes*). However, the other member of the genus *Pan*, the bonobo (*Pan paniscus*) is strikingly different in this regard as evidenced from the present comparative study that was conducted at the Wilhelma Zoo, Germany. A group of bonobos and of chimpanzees was each provided with limited access to an artificial "fishing" site (a simulated termite mound) filled with desirable

food. In chimpanzees, the adult male was dominant over all females and able to monopolize the food. In bonobos, on the other hand, the adult bonobo male was low ranking, and females controlled food access. Sex between bonobo females apparently facilitated affiliative encounters between females in the context of feeding. Until now, studies of exchanges of sex-for-food focused on heterosexual interactions. This study reveals that trading of sex for food occurs regularly between bonobo females. These exchanges appear to reduce tension and facilitate female cofeeding and cooperation. They help create stable long-term relationships among females that result in coalition formation, control of food resources, and ability to elevate their dominance status relative to males well above that of their chimpanzee counterparts. The strong affiliative relationships between unrelated female bonobos provide an alternative model from which predictions for bonding among human females can be generated.

Slagsvol T, Amundsen T & Dale S: Selection by sexual conflict for evenly spaced offspring in blue tits. Nature 1994;370:136-138.

In animals with parental care, parents rearing offspring of variable ages are typically assumed to exert less effort than those rearing even-aged offspring. This is because spaced births spread out peak loads in the combined food demands of all offspring. Creating a mixed-size sibship also helps establish a hierarchy among the young which reduces the cost of sibling rivalry and can help efficient elimination of young if food becomes short. We manipulated hatching spread within broods of the blue tit *Parus caeruleus* and studied postbreeding survival rate of the adults. We report here that, contrary to current theory, female parents suffer less when the young are even-aged than when they are of variable ages, whereas the opposite result was found for male parents. Apparently, the male contributes more in synchronous broods, thus lightening the female's total investment burden. In blue tits this sexual conflict over hatching pattern is won by the female because she alone incubates. By delaying incubation until most eggs have been laid, she reduces hatching span.

Lundin LG: Evolution of the vertebrate genome as reflected in paralogous chromosomal regions in man and the house mouse. Genomics 1993;16:1-19.

Gene constellations on several human chromosomes are interpreted as indications of large regional duplications that took place during evolution of the vertebrate genome. Four groups of paralogous chromosomal regions in man and the house mouse are suggested and are believed to be conserved remnants of the two or three rounds of tetraploidization that are likely to have occurred during evolution of the vertebrates. The phenomenon of differential silencing of genes is described. The importance of conservation of linkage of particular genes is discussed in relation to genetic regulation and cell differentiation.

Charlesworth B, Sniegowski P & Stephan W: The evolutionary dynamics of repetitive DNA in eukaryotes. Nature 1994;371:p215.

Repetitive DNA sequences form a large portion of the genomes of eukaryotes. The 'selfish DNA' hypothesis proposes that they are maintained by their ability to replicate within the genome. The behaviour of repetitive sequences can result in mutations that cause genetic diseases, and confer significant fitness losses on the organism. Features of the organization of repetitive sequences in eukaryotic genomes, and their distribution in natural populations, reflect the evolutionary forces acting on selfish DNA.

There is an extraordinary degree of variation in genome size between different eukaryotes, which bears little relation to differences in organismal complexity, ploidy level, or numbers of genes that code for proteins. For example, the newt *Triturus cristatus* has around six times as much DNA as humans, who have about 7.5 times as much as the pufferfish *Fugu rubripes*. Much of this variation is due to non-coding, tandemly repeated sequences.

Repetitive DNA sequences ... include satellite DNA (very highly repetitive, tandemly repeated sequences), minisatellite and microsatellite sequences (moderately repetitive, tandemly repeated sequences), and transposable elements (moderately

repetitive, mobile, dispersed sequences). In many cases these sequences seem to be maintained solely by their ability to replicate within the genome (the 'selfish DNA' hypothesis). Far from conferring benefits, their behaviour can sometimes result in a fitness loss to the host. Some human genetic diseases are known to be caused in this way, including mutations due to insertions of transposable elements, to chromosomal rearrangements induced by recombination between repeated sequences, or to the amplification of microsatellite sequences.

It has often been proposed that repetitive sequences are functionally important for the host organism, or are maintained because their mutagenic activities contribute to the long-term evolutionary potential of the population. But these may be consequences rather than causes of the presence of repeated sequences. Here we present the main findings of theoretical and empirical work on the evolutionary and population biology of repetitive sequences, with emphasis on how the selfish DNA hypothesis can be tested by comparing the predictions of population genetic models with the data. In addition, we will show that some general features of the organization of eukaryote genomes may be simple consequences of the evolutionary forces acting on selfish DNA.

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ALSO... *continued from page 20*

²⁰ I find it difficult to judge the merits of this hypothesis since I do not know how it could be tested. If altruism is to evolve, a two level process is required: within individuals selection favors selfishness over altruism. But when there is competition among populations altruism may be on average favored over selfishness (Sober E (pp. 95-98), 1993). How can you separate the effects of such a clever gene that chameleon-like, produces organisms that are selfish in one context and altruistic in another? If on the other hand the SCG hypothesis is meant to explain adaptive flexibility, I find the macro-evolutionary neotenic hypothesis much more compelling. According to Gould (Ontogeny and Phylogeny Cambridge: Harvard University, 1977) adaptive flexibility emerged via the regulation of the timing of development controlled by the growth hormone (an indirect effect, as opposed to direct effect of alleged contingency behavioral genes or social comparison genes).

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- ² Lewontin and Dunn (quoted by E Sober, 1984 & 1993) give an example of a driving (homozygous) gene that renders the house mouse *Mus musculus* sterile. They propose a group selection model to account for why the driving homozygotic gene did not increase with the frequency as predicted (endangering the survival of the house mouse). A driving gene or segregator distorter gene is one that captures during meiosis more than its share of Mendelian gametes (a classical example of a selfish gene). You will recall that heterozygotes normally produce half their gametes as a big "A" allele and half as little "a" allele. A gene that captured more than 50% of the gametes is a driving gene. In the case of the house mouse, at the level of the gene, selection favors the driving (selfish) gene. However, at the level of the organism there is selection against the driving gene since the homozygous gene renders the house mice sterile. Yet these competing tendencies do not fully explain the unexpectedly low frequency of the driving gene. A third force is at work. House mice live in small demes, i.e. a population of conspecifics. At a group level there is selection against all males and females that are homozygous for the driving gene. Within each deme all copies of the gene are taken out of circulation. Hence the low frequency.
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- ¹² The explanation is based on the following table: (Sober E (p. 72) 1993)

		Mother	
		P A	q a
Father	P	P2	pq
	q	pq	q2.

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