



## The Units of Selection Revisited: The Modules of Selection

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**Abstract.** Richard Lewontin's (1970) early work on the "units" of selection initiated the conceptual and theoretical investigations that have led to the hierarchical perspective on selection that has reached near consensus status today. This paper explores other aspects of his work, work on what he termed "continuity" and "quasi-independence", that connect to contemporary explorations of modularity in development and evolution. I characterize such modules and argue that they are the true units of selection in that they are what evolution by natural selection individuates, selects among, and transforms.

**Key words:** levels of selection, modularity, units of selection

### Introduction

Richard Lewontin's seminal paper of 1970, "The Units of Selection", initiated a conceptual/theoretical shift in evolutionary biology of great significance. In that paper Lewontin argued that Darwin's theory of evolution by natural selection could be stated in an abstract and general way that made no reference to any particular level of biological organization. Although Darwin and most of his successors thought of selection acting at the level of individual organisms, the logical skeleton of the theory was by no means tied to the organismic level.<sup>1</sup> Any entities that had heritable variation in fitness would evolve by natural selection.<sup>2</sup> Theoretically these entities could range from short nucleotide sequences to species and even ecological communities. Empirically, both suborganismic and superorganismic entities have been identified that have the requisite properties to be "units" of selection (Brandon 1990, chapter 3). Thus even though there is still some conceptual/theoretical work to be done in determining just what counts as a unit of selection, and even more methodological and empirical work to be done in deciding how

to track multi-level selection in nature and in finding good systems to study, it seems to me that serious biologists and philosophers of biology have no choice but to take a hierarchical approach to selection. This is (a part of) Lewontin's legacy.

In their recent review of philosophical work on units of selection, Elliott Sober and David Sloan Wilson state that objects "at level  $X$  were units of selection in the evolution of trait  $T$  iff [if and only if] one of the factors that influenced  $T$ 's evolution was that  $T$  conferred a benefit on objects at level  $X$ " (1994: p. 536). Although how exactly this is to be cashed out is still controversial, I think this formulation is basically correct.<sup>3</sup> From it we can see that group adaptations (i.e., adaptations that result from group selection) are to be distinguished from organismic adaptations and those from genic adaptations and so on. For example, altruism is a possible group level adaptation, but it could not evolve by individual organismic selection alone. The traits that result from "differential fertility" of transposable elements are genic adaptations and are often contrary to the organism's interest. The hierarchical approach to selection makes all this fairly clear.

But there is another issue of considerable importance in evolutionary biology that might reasonably be called a "units of selection" problem. It is presently discussed under the heading "modularity". That will be the primary focus of this paper, but first I want to show how it flows out of two earlier strands of Lewontin's work.

## 1. The genome as the unit of selection

The last chapter of Lewontin (1974) is entitled "The genome as the unit of selection". One might see this chapter as a more thorough development of an earlier idea of Ernst Mayr's which he termed "the genetic theory of relativity". Mayr argued that the fitness of a gene depends not only on its ecological context, but also on its genetic context, thus, "no gene has a fixed selective value, the same gene may confer high fitness on one genetic background and be virtually lethal on another" (1963: pp. 295–296; also see Mayr 1954).

Lewontin's chapter focuses on two facts typical of genetic systems and their interaction. The first fact is that different genetic units (genes, or in Lewontin's primary example, a chromosome inversion) interact in their effect on organism phenotype, in particular on organismic fitness. This is called *epistasis*. For example, suppose we have two genetic loci, **A** and **B**, each with two alleles,  $A$  and  $a$  and  $B$  and  $b$  respectively. Suppose we look only at the **A** locus and that we start numerous experimental populations at 50:50 frequencies of the **A** alleles. Our results are that some populations go to fixation of  $A$ , other to fixation of  $a$ , while still others go to some intermediate frequencies

of the two alleles. This might be due to genuine indeterminism of the system; but it might also be a deterministic outcome that would be perfectly understandable once the **B** locus was factored in. For instance, *AA* might be the fittest genotype in the presence of *BB*, *aa* fittest in the presence of *bb*, while *Aa* is fittest in the presence of *Bb*. In that case experimental populations all starting at 50% *A* will have quite different evolutionary trajectories depending on allele frequencies at the **B** locus. Lewontin mentions a number of empirical examples that exemplify this point.<sup>4</sup>

The lesson Lewontin draws from this sort of example is that once one has a synthetic understanding of the two locus interactions, one can abstract from that an account of the single loci and build up from that an understanding of the genome as a whole.

The second fact is that genes on the same chromosome do not assort independently in gamete formation. This is called *linkage*, or *linkage disequilibrium*.<sup>5</sup> The relevance of this fact is that when different loci are in linkage disequilibrium, knowledge of allele frequencies at those loci will not enable one to predict gamete frequencies, and so will not enable one to predict genotypic frequencies in the next generation. This becomes particularly problematic when, as in the example above, there are epistatic interactions among the loci. (But it is problematic enough if there is any dominance at any locus.) Again Lewontin concludes that one cannot get a predictive and explanatory model of evolution based solely on allele fitnesses and frequencies at single loci.

These facts argue persuasively against the sort of genic selectionism proposed by Williams (1966) and later by Dawkins (1976).<sup>6</sup> (Another phenomenon unfavorable to the genic selectionist case is *pleiotropy* – the effect of a single gene on multiple phenotypic traits. This is not discussed in Lewontin’s chapter, but will be relevant to our later examination of modularity.) But they do not argue for what is suggested by the title of Lewontin’s chapter, namely that the genome as a whole is the unit of selection. Indeed, nowhere in that chapter does Lewontin argue for that strong conclusion. In a section on the effects of linkage Lewontin suggests that the *characteristic length*, which is the length of chromosome centered on any arbitrarily chosen point within which genes are linked and outside of which genes are in linkage equilibrium, is the “unit of evolution” (1974: p. 312). The important point to note is that this is a quantitative concept and so it becomes a quantitative question as to how large are the hunks of the genome that are acting as units. A similar point could be made with respect to epistasis – not all genes are equally connected with every other gene in terms of their phenotypic effect. The strength of connectivity between any two genes is an empirical question, and if “units” are to be picked out by epistatic interaction the size of these

“units” relative to the genome as a whole remains an open question. But the facts Lewontin cites in no way support, nor does he take them to support, the conclusion that the genome as a whole is the “unit” of selection.

William Wimsatt’s (1980, 1981) early work on units of selection was much influenced by the chapter of Lewontin (1974) that we have just discussed. He used Lewontin’s example of epistasis to not only thoroughly refute genic selectionism, but to also diagnose the reductionist biases that make that position so attractive to some. He then adds to Lewontin’s (1970) influential analysis of units of selection. Recall that Lewontin argued that any entity that had heritable variation in fitness would be a unit of selection. Wimsatt showed that this condition was necessary but not sufficient. It was not sufficient because an entity that was *composed* of units of selection might satisfy Lewontin’s condition, but not itself be a unit of selection. To expand on an example from G.C. Williams (1966: pp. 16 ff.), if there is organismic selection for increased speed within a population of deer, and if there is among-group variation in mean speed, and if new groups are formed in a way that makes for group heritability of mean speed, then Lewontin’s conditions will be satisfied at the level of groups, but we might still want to say that this is just organismic selection, not group selection. We must distinguish between a “herd of fleet deer” and a “fleet herd of deer”. Wimsatt adds a further condition, which he considers sufficient, in the following definition:

*A unit of selection* is any entity for which there is heritable *context-independent* variance in fitness among entities at that level which does not appear as heritable context-independent variance in fitness (and, thus, for which the variance in fitness is *context-dependent*) at any lower level of organization. (1981: p. 144)

In our deer case, if individual deer fitness varies in a way that is not dependent on group context, i.e., if all that matters is how fast the deer is, and its group matters not, then the groups of deer do not qualify as units of selection. If, on the other hand, group membership does matter with respect to individual deer fitness, then the groups do qualify as units of selection.<sup>7</sup>

When I first wrote on the “units” of selection problem (Brandon 1982), Wimsatt’s analysis was the state of the art. The main issues driving the units of selection controversy were: (1) the question of superorganismic units of selection; and (2) the Williams-Dawkins position of genic selectionism. As stated earlier, I think that Lewontin (1974, Chap. 6) had already decisively refuted the later position, but Wimsatt (1980, 1981) and Sober and Lewontin (1982) added further nails to the coffin.<sup>8</sup> While Wimsatt’s position on higher levels of selection, e.g., group selection, was, perhaps, in need of further refinement, it seemed basically right-headed to me. But it seemed fundamentally wrong-headed when it came to question of what makes *organismic*

selection truly organismic. Wimsatt does advert to the genetic phenomena of epistasis and linkage in arguing against genic selectionism, but according to his definition above, if all genetic loci were in linkage equilibrium and if there was no epistatic interactions among loci, then genes would be the units of selection in ordinary cases of organismic selection, e.g., Kettlewell's famous melanic moths. That I thought, and still think, completely missed the fundamental ecological facts that make organismic selection organismic. Furthermore, as pointed out above, epistatic connections and gene linkages are matters of degree, and at best point to some larger genetic unit in cases like Kettlewell's moths, not to the genome as a whole, and certainly not to the organism. Thus I thought a new beginning was needed.

What I argued (in Brandon 1982) was that there were two distinguishable questions that had previously been conflated in the units of selection controversy. Simultaneously, but unknown to me at the time, David Hull (1981) and Richard Dawkins (1982) were coming to the same conclusion.<sup>9</sup> In Hull's terminology, we must distinguish the question **of what entities are interacting directly with their environment in a way that leads to differential reproduction (*interactors*)**, from the question **of what entities are reproducing their structure directly and accurately (*replicators*)**. I, correctly or not,<sup>10</sup> linked Wimsatt's analysis with the later question and so coined the term *levels of selection for the former*. What makes organismic selection organismic, as opposed to genic or group, is that it is **the organismic phenotype that directly interacts with environment and so is directly exposed to selection**. That is, selection in such cases **cannot "see" the genes**, it "sees" the organismic phenotype. I analyzed this in terms of screening-off. In cases of organismic selection the organismic phenotype screens-off genotype from reproductive success (see footnote #3 above). This screening-off is totally unaffected by the amounts of epistasis and/or linkage. For reasons that will be laid out in section 3 below, I now think that the terminology **of levels of selection, as opposed to units of selection**, is particularly appropriate to this question of the level of biological organization at which the ecological process of selection occurs.

## 2. Continuity and quasi-independence

The last paragraph of Lewontin's (1978) thought-provoking article on adaptation is worth quoting in its entirety:

It [the phenomena of adaptation] can only be workable if both the selection between character states and reproductive fitness have two characteristics: continuity and quasi-independence. Continuity means that small

changes in a characteristic must result in only small changes in ecological relations: a very slight change in fin shape cannot cause a dramatic change in sexual recognition or make the organism suddenly attractive to new predators. Quasi-independence means that there is a great variety of alternative paths by which a given characteristic may change, so that some of them will allow selection to act on the characteristic without altering other characteristics of the organism in a countervailing fashion; pleiotropic and allometric relations must be changeable. Continuity and quasi-independence are the most fundamental characteristics of the evolutionary process. Without them organisms as we know them could not exist because adaptive evolution would have been impossible. (1978: p. 230)

Given that adaptive evolution occurs, and that continuity and quasi-independence are necessary conditions for it to occur, we can validly infer that continuity and quasi-independence exist. But that valid argument no more explains continuity and quasi-independence than do the facts that the Sun is necessary for human life on Earth and human life does exist on Earth explain the existence of the Sun.<sup>11</sup>

Some recent attempts to explore how quasi-independence evolves will be mentioned in the next section. Here I want to point out that quasi-independence, together with ecological interactions, pick out what are the real traits from an evolutionary point of view. The problem of what constitutes a trait from an evolutionary point of view is one Lewontin has raised in a number of places (see e.g., 1978, 1983b). On the one hand the organism-environment relationship defines what counts as functional trait. This, as Lewontin's *constructionist* view of evolution by natural selection implies,<sup>12</sup> needs to be thought of as a coevolutionary circuit. **The organism's choices, physiology, activity, etc. constructs its own selective environment,** while that constructed environment carves up the organism into functional traits. On the other hand, the genetic quasi-independence of the trait, part of what we will shortly describe as the **modularity of the trait, determines what counts as a trait from the point of view of its evolvability.** Thus from the point of view of evolution by natural selection, what counts as a trait is a product of (a) ecological function – which is itself both cause and effect of organism-environment coevolution; and (b) genetic architecture – which, as we will see in the next section, is both cause and effect of evolutionary change.

To illustrate the first point – that what counts as a trait is determined in part by the organism-environment relationship – consider the following example from Lewontin (1983b). A lizard lives in a moderate climate in which food is abundant but must be caught. The lizard must expend energy carrying its weight about and the food that it can avail itself of depends on its own size. The spatial distribution of that food in part determines the lizard's hunting

site preferences. Thus lizard size and site preferences together form a trait – “predation effectiveness”. But now suppose the climate becomes hotter so that the lizard faces the physiological problem of overheating. Size, more specifically the surface-volume ratio, and color affect heating, and so are linked together as the trait “heat tolerance”. Importantly, genes affecting size and color will now have epistatic interactions in their effect on heat tolerance whether or not their biochemical products ever meet in development. Selection on this trait will depend, in part, on the lizard’s activity. But that means that the lizard’s site preferences, a part of the trait “predation effectiveness” is now part of the trait “heat tolerance”. Thus genes affecting site preferences will now have pleiotropic effects on both “predation effectiveness” and heat tolerance”. Further changes to the lizard’s external environment, e.g., the introduction of a new predator, and the lizard’s responses to such changes may further complicate this picture.

Without carrying this example further we can see that there is no way, even in principle, to carve up an organism into its functional traits apart from its selective environment. And since the organism’s activities, choices, physiology, etc. construct its environment, which in turn leads to further evolution of those traits, we can see that from the point of view organism-environment coevolution, **organisms construct their “traits”**.

Discussion of the second point – that what counts as a trait is determined in part by genetic architecture – will await the next section. I will end this section by briefly commenting on continuity. Continuity is the idea that small changes in character space will result in small changes in fitness. This is often described as the degree of ruggedness of the fitness landscape (Kauffman 1989). A rugged fitness landscape means that small changes in character space may result in large changes in fitness, and conversely for a smooth fitness landscape. It might be thought that the topology of the fitness landscape is a brute fact of physical law with which organisms have to live (or die). That is, to some extent, true. For example, the effect of the surface-volume ratio on heating would be such a brute fact. But organisms may avoid inconvenient facts. A lizard may bury itself in the heat of the day, or, over a longer time-span, organisms may evolve physiological mechanisms of cooling. Thus over evolutionary time organisms are not stuck with a particular fitness landscape – it too can evolve in ways that make adaptive evolution more likely.

### 3. Structure the genotype-phenotype map: modules in development and evolution

According to Webster's (New International Dictionary, 2nd ed.) a unit is "a distinct part or member analyzable in an aggregate or whole". Units of selection, in this (primary) sense of 'unit', are the parts of evolutionary transformation – i.e., the parts that change over evolutionary time in a way that is more or less independent of other parts of the whole. For the moment, let us think about standard cases of organismic selection. What are the units, in this sense, of organismic selection? A good example would be the mammalian forelimb. Whales, bats and human beings all have functionally and anatomically derived forelimbs. The arm of a human, the front flipper of a whale and the wing of a bat are recognized as *homologues*, structures derived from a forelimb used for walking in their common ancestor. Thus they are *variants* of the same thing. (In contrast to, e.g., the wing of a bat and the wing of an insect.) Clearly, the mammalian forelimb has been able to evolve more or less independently of other parts, e.g., eyes or the circulatory system. This is what makes the forelimb a good example of a unit or module of selection. In terms of the last section, the mammalian forelimb varies in ways that are quasi-independent of other mammalian parts.

The existence of such modules is, as Lewontin pointed out, a prerequisite for adaptive evolution. The same point has been recognized in the field of genetic algorithms. If one is to use random variation and natural selection (where the criteria of selection are imposed by the designer) to improve the performance of computer programs, these programs must be decomposable into quasi-independent parts (Holland 1992; Wagner and Altenberg 1996). Just what are these units or modules?

I have already suggested (following Wagner 1995, 1996) that from the point of view of phenotypic evolution, modules are the units of evolutionary transformation. They are things like the mammalian forelimb that evolve more or less independently of other characters (you do not have to completely change mammalian body plan to get a flying mammal). I want to break this concept down into its two fundamental components. The first has to do with ecological function, the second with genetic architecture, or with the genotype-phenotype map.

Something is going to count as a unit or module of selection only if it, as a whole, serves a primary ecological function. Phenotypic selection acts on trait variants that serve a particular function more or less well. If, for example, the function is Batesian mimicry, as in the Viceroy butterfly's mimicry of Monarchs, it is the wing pattern as a whole, not some subpart of it, nor some larger aggregate such as wing pattern plus leg length, that counts as a



module of phenotypic selection. In other cases of Lepidopteran evolution, for instance where large eye spots that ward off certain predators have evolved, it is not the wing as a whole, but rather that particular part of it, that is a unit of phenotypic selection.<sup>13</sup> In the case mentioned earlier of the mammalian forelimb, it is presumably the forelimb as a whole that has been selected for different functions in the lineages leading to bat, whale and humans. If, as many have speculated, there was in our ancestors strong selection for the ability to manipulate objects with our hands, then the hand, not the whole forelimb, is a module relative to that selection. The point is that phenotypic selection picks out some parts, parts that function more or less independently of other parts, as the modules of selection.

But this is just half of the story. For this phenotypic selection to be evolutionarily effective the functional parts must be able to evolve more or less independently of other parts. **This requires genetic modules.** In his book on the evolution of complexity, John Bonner (1988) argues that the evolution of adaptive complexity requires modular “gene nets”. For Bonner a gene net is “a grouping of a network of gene actions and their products into discrete units during the course of development” (p. 174).

This [grouping of gene effects] not only was helpful and probably necessary for the success of the process of development, but it also means that genetic change can occur in one of these gene nets without influencing the others, thereby much increasing its chance of being viable. The grouping leads to a limiting of pleiotropy and provides a way in which complex developing organisms can change in evolution. (1988: p. 175)<sup>14</sup>

Bonner’s point should, of course, remind one of Lewontin’s argument for the necessity of quasi-independence.

Günter Wagner and Lee Altenberg (1996, see also Altenberg 1995 and Wagner 1996) have put this point in terms of the structure of the genotype-phenotype map. Figure 1 (reprinted from Wagner and Altenberg 1996: p. 971) shows the mapping of two “gene nets” {G1, G2, G3} and {G4, G5, G6} onto two character complexes C1 = {A, B, C, D} and C2 = {E, F, G}. The two gene nets, or gene modules, are such because most of the genetic interactions occur within the nets with relatively few between them. This means that selection acting on different variants of C1, which are differentially adaptive for function F1, can occur and have evolutionary consequences without much disturbing the rest of the genotype-phenotype map.

Again, it is one thing to argue that this sort of genetic architecture is a necessity for evolutionary adaptation, it is quite another thing to explain how such architecture evolves. It is beyond the scope of this paper to explore this topic in any detail, suffice it to say that some current work on this problem appears promising. In particular lineage selection offers one possible explana-

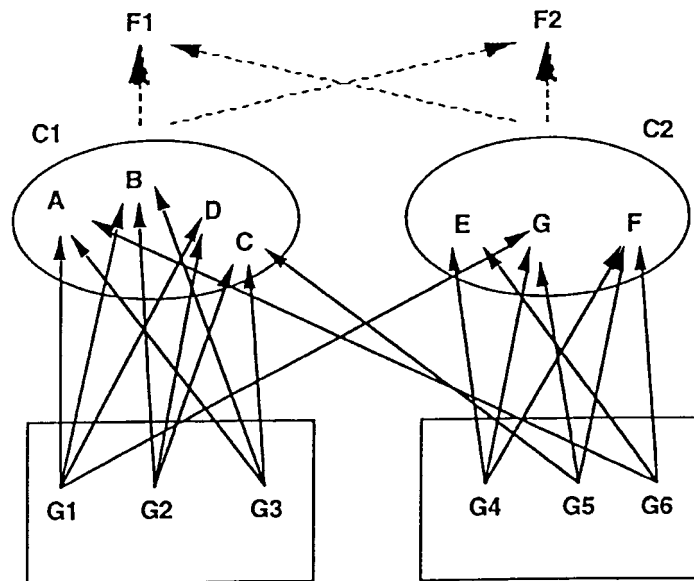


Figure 1. Example of a modular representation of the character complexes  $C1 = \{A, B, C, D\}$  and  $C2 = \{E, F, G\}$  which serve two functions  $F1$  and  $F2$ . Each character complex has a primary function,  $F1$  for  $C1$  and  $F2$  for  $C2$ . Only weak influences exist of  $C1$  on  $F2$  and vice versa. The genetic representation is modular because the pleiotropic effects of the genes  $M1 = \{G1, G2, G3\}$  have primarily pleiotropic effects on the characters in  $C1$  and  $M2 = \{G4, G5, G6\}$  on the characters in complex  $C2$ . There are more pleiotropic effects on the characters within each complex than between them. [Reprinted from Wagner and Altenberg 1996: p. 971.]

tion here. Only those lineages that have the sort of genotype-phenotype map that allows for adaptive evolution will survive and thus those are the ones we see today (Dawkins 1989). The problem with this hypothesis, as Altenberg (1995) points out, is that it provides no mechanism for the generation of this sort of map within lineages in the first place. Altenberg's theory of constructional selection, which is a form of gene level selection, provides such a mechanism. He argues that when new genes are introduced there is (viability) selection for genes with low levels of pleiotropy, because such genes have a better chance of becoming useful and necessary for the organism. Wagner (1996) argues that a combination of directional and stabilizing selection will select for genetic modularity.

The "units" or "natural kinds" of a process are picked out by that process (Quine 1969; Wagner 1996). The units of the process of evolution by natural selection are the units individuated by that process. That process is itself composed of two subprocesses that are useful to separate. To use the language of quantitative genetics, one is the process of phenotypic selection. This is, as I have emphasized in many places (see e.g., Brandon 1990, or 1997),

an ecological process. The second subprocess is the genetical response to selection. Corresponding to these two subprocesses I have separated out two components of modules of selection: (1) ecological function – the module as a whole must serve a primary function; and (2) genetic modularity – the genes affecting the character complex serving the ecological function must have a high degree of internal integration and a low degree of external connectivity, i.e., pleiotropic connections must largely be within-module. These two components correspond quite closely to the suggestions Lewontin has made concerning what counts as a trait from an evolutionary point of view (discussed in section 2 above).

As I pointed out in section 1 above, much of the early work on the units of selection problem was flawed by the failure to separate out two distinct questions – in Hull’s (1981) terms, questions concerning replicators vs. questions concerning interactors.<sup>15</sup> Much ink and paper was wasted over the question of whether the “units of selection” were really genes or organisms (or groups, etc.). One can imagine a similarly sterile question concerning what I have characterized as modules of selection. Are they the underlying gene nets, or are they the character complexes? I think they are both and more. Figure 1 is particularly perspicuous here. A module of selection is a set of genes, their products and interactions (their developmental pathways), the resulting character complex and that complex’s functional effect. This is what evolution by natural selection picks out, selects among, and transforms. These modules are the units of evolution by natural selection.<sup>16</sup>

#### 4. A terminological coda

“If I was king and ruled the world” That is a line from a song by one of my favorite local bands.<sup>17</sup> If I were king and ruled the world I would decree that the question concerning the level or levels of the biological hierarchy at which selection occurs would hereby be labeled the “levels of selection question”. Lewontin’s famous paper of 1970 largely initiated the revolutionary and highly fruitful conceptual and theoretical investigations that leave us today with the hierarchical view of selection that all sensible biologists must embrace. There are many known levels of selection, and other potential levels. Unfortunately, that paper was entitled “The units of selection”. I think that appellation better fits the question discussed in the last section – the question concerning the modular units picked out by the process of evolution by natural selection. And thus I would decree that label be used in that manner. We have also seen how Lewontin’s insightful comments on quasi-independence and continuity, and his thoughtful queries on what should

count as a trait from an evolutionary point of view, lead rather directly to the contemporary inquiries into **modularity**.

Of course, I have no power to make any such decrees. And ultimately, although our terminological choices do matter and should not be taken lightly, what matters more is that the two questions mentioned above, however named, be taken seriously. The legacy of Lewontin (1970) assures that the first question – the one I prefer to call the levels of selection question – will continue to be taken seriously. In this paper I hope to have provided persuasive reasons for taking the second question seriously.

## Notes

<sup>1</sup> Darwin did entertain some exceptions to this, e.g., he clearly thought group selection was responsible for the evolution of altruism in man. See Darwin 1871: pp. 159–167.

<sup>2</sup> This is not quite correct. It is at least theoretically possible for an “inheritance bias” to exactly counterbalance selection so that the three conditions are satisfied in an equilibrium situation.

<sup>3</sup> My own preferred approach is in terms of “screening-off”. See, e.g., Brandon 1990, 1997 and Brandon et al. 1994

<sup>4</sup> His main example comes from a study of two chromosome inversions in the grasshopper *Moraba scurra*. See Lewontin 1974: pp. 274–281.

<sup>5</sup> Linkage equilibrium is defined as follows: Let  $P_a$  be the gametic frequency of  $a$ ,  $P_b$  the gametic frequency of  $b$ , and  $P_{ab}$  the frequency of gametes containing  $a$  and  $b$ , where  $a$  and  $b$  are alleles at the **A** and **B** loci as in the example above. When  $P_{ab} = P_a P_b$ , then  $a$  and  $b$  are in linkage equilibrium.

<sup>6</sup> Briefly, genic selectionism is the idea that all of evolution can be understood in terms of selection acting at the level of genes.

<sup>7</sup> Lloyd 1988 offers considerable refinements to Wimsatt’s analysis.

<sup>8</sup> Some corpses are particularly stubborn. My own take on genic selectionism is most fully laid out in Brandon (1990, chaps. 4 & 5). Basically I argue that genic selectionism cannot offer an explanatory theory of adaptation because: (1) it fails to distinguish different levels of adaptation; and (2) since it studiously avoids the ecological process of selection it cannot possibly explain what makes an adaptation adaptive.

<sup>9</sup> Brandon and Burian 1984 contains the relevant articles, and a discussion of the relations among them, pp. 87–89.

<sup>10</sup> See Lloyd 1988: p. 81 for a contrary view.

<sup>11</sup> I am aware that there is a crazy philosophical view – dubbed the “Anthropic Principle” – that holds otherwise. But it is crazy.

<sup>12</sup> See Lewontin 1983a and 1983b. Also see Brandon and Antonovics 1996 and Brandon forthcoming for further discussions of Lewontin’s constructionism.

<sup>13</sup> Butterfly wing patterns are perhaps the best studied examples of traits that are modular in sense relevant here. See e.g., Nijhout 1991, 1994.

<sup>14</sup> Quoted in Wagner and Altenberg 1996. See that work and Wagner 1995 for further discussion.

<sup>15</sup> Let me forestall one possible confusion. One of the main points of this paper is to distinguish the question of what I prefer to call “levels of selection”, but what most, following

Lewontin 1970, call “units of selection” from the question discussed in this section – that having to do with the “modules” or “units” of selection. Both are important. This distinction should not be confused with the interactor/replicator distinction made in the early eighties, a distinction that was crucial in clarifying what the original “units” of selection question was all about. As it concerned the possibility of sub- and super-organismic “units” of selection it was about interactors. This has led to fruitful theoretical and empirical investigations. The “replicator” question, in contrast, has yet to yield much of interest. Indeed the concept of replicator has probably outlived its usefulness. A possible replacement on the horizon is Jim Griesemer’s as yet unpublished work on what he calls “reproducers”. This concept is likely to be quite important for evolutionary studies, in particular, for studies of major evolutionary transitions. See Szathmáry and Maynard Smith 1997.

<sup>16</sup> Space precludes considering the modules of selection from a hierarchical perspective. If the mammalian forelimb is a module of organismic selection, what might be a module of group selection, or of genic selection? My aim has been to clarify the basic concept of module of selection, once that is done these other questions can be addressed.

<sup>17</sup> The Backsliders, *Throwin’ Rocks at the Moon*, 1997 Mammoth Records.

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