Ultimate explanations concern the adaptive rationale for organism design

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Abstract   My understanding is that proximate explanations concern adaptive mechanism and that ultimate explanations concern adaptive rationale. Viewed in this light, the two kinds of explanation are quite distinct, but they interact in a complementary way to give a full understanding of biological adaptations. In contrast, Laland et al. (2013)—following a literal reading of Mayr (Science 134:1501–1506, 1961)—have characterized ultimate explanations as concerning any and all mechanisms that have operated over the course of an organism's evolutionary history. This has unfortunate consequences, such as allowing random drift to form the basis for ultimate explanations, and allowing proximate and ultimate explanations to bleed into each other until their distinction is meaningless. Here, I suggest Laland et al's explanatory framework of "reciprocal causation" is not conducive to successful biological science, and that they have misunderstood key elements of the theory of Darwinian adaptation.

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It's more than just a question of time.
It's more a question of reason and rhyme.

The Bluetones, Solomon Bites The Worm.

Proximate versus ultimate explanations

There are two basic kinds of explanation that a biologist can give for an organismal adaptation. Proximate explanations concern the mechanism by which the adaptation

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operates, including environmental triggers, ontogeny and the physics and chemistry underlying the final trait. That is, they provide an account of how genetic information is translated into a phenotype that manifests design. Ultimate explanations concern the adaptive rationale of this design. That is, they provide an account of how the phenotype is translated into the organism's fitness. Proximate explanations have been described as the domain of the functional biologist, and ultimate explanations, the domain of the evolutionary biologist. However, healthy biological science seeks an interplay between the two, leading to a fuller understanding of biological adaptations.

Here, I am explicitly framing both proximate and ultimate explanations in the context of understanding organismal design. However, biologists are generally squeamish about invoking the D-word, and so the distinction between proximate and ultimate explanations has often been framed ways that avoid the language of goal, purpose and intentionality. Specifically, proximate explanations are often recast in terms of how an adaptation typically operates, rather than how it is supposed to operate. For example, ventricular fibrillation doesn't provide a proximate explanation for how the heart works, despite being something that hearts sometimes do. Happily, the high precision of organism design makes this only a very subtle distinction, which does not interfere with biological practice.

And ultimate explanations are often recast in terms of the historical process of natural selection, which is another way of talking about how the adaptation acts to maximize fitness. Biologists may legitimately translate between backwards-looking, dynamical accounts of the past action of natural selection, on the one hand, and forward-looking, purposeful accounts of the organism maximizing her fitness, on the other hand, as has been formally shown by Grafen (2002). This is because there is a mathematical equivalence between the dynamics of Mendelian gene frequencies under the action of natural selection, on the one hand, and an optimization program in which the organism is conceived as a fitness maximizing agent, on the other hand. But this doesn't mean that all historical dynamics can be recast in terms of future goal. Non-Darwinian factors—such as random drift—certainly mediate the evolution of organismal traits, but their dynamics are not isomorphic with any notion of organism design, and hence they cannot form the basis for ultimate explanations.

Mayr (1961)

The above account of the proximate/ultimate distinction is different from that given by Mayr (1961). One difference is that Mayr gave a firmly historical interpretation of ultimate explanations, advocating the backwards-looking, dynamical view rather than the forwards-looking, purposeful view of adaptation. As discussed above, this is an entirely legitimate—if somewhat narrow—approach, apparently motivated by the desire to achieve a respectable, causal account of biological explanation, with cause always preceding effect in time. The one instance in Mayr's article that explicitly links the words "ultimate", "final cause" and "goal" is very cautious, and done by way of an unattributed quotation, as if guarding against accusations of naïve, teleological thinking.

A second difference is that Mayr framed ultimate explanations as "evolutionary", whereas I have specifically highlighted the central importance of natural selection. This is, at first sight, a substantive difference, as Mayr's approach would appear to allow non-Darwinian factors, such as random drift, to form the basis of ultimate explanations. However, I believe that Mayr was simply being sloppy, with his writing or his thinking or both. With regard to sloppy writing, note his spurious use of the term "DNA code" throughout his paper, which he clearly intended to refer to the genetic source (e.g. GATTAC…) and not the genetic code itself (e.g. GAT $\rightarrow$ Asp, TAC $\rightarrow$ Tyr, …). With regards to sloppy thinking, recall that he was writing at a time when many biologists were not being clear about the distinction between natural selection and evolution, and labouring under the assumption that evolution is necessarily progressive. Moran's (1963) bombshell soon highlighted the dangers of such naïvety.

My reading of Mayr's article suggests that he intended "evolutionary" to be synonymous with "Darwinian", and "ultimate" explanations to concern the selective value of an adaptation for its bearer. Ariew (2003) provides a detailed analysis of Mayr's thinking, in this respect, noting that it is "difficult to imagine anyone accepting, say, genetic drift as a species of 'ultimate explanation'". That is, the essential quality of ultimate explanations seems to be that they relate specifically to the design-generating action of natural selection, and not simply to any mechanical process that has operated in the evolutionary past.

Laland et al. (2013)

I therefore believe Laland et al. (2013) are incorrect to interpret ultimate explanations as concerning any and all factors in a species' evolutionary history. Specifically, I take issue with their claim that, although "Mayr presented ultimate explanations as invoking natural selection, … other evolutionary processes, such as drift, may also be important". And, consequently, I disagree with Laland et al's conclusion that—because ontogeny and behaviour may mediate evolution, and *vice versa*, in an infinite regress of reciprocal causation—proximate and ultimate explanations bleed into each other such that the distinction between them ceases to have any utility. Indeed, I view this tangled mess of causation as a kind of proof—a *reductio ad absurdum*—that they have got their fundamental concepts wrong.

To illustrate, consider Laland et al's example of the peacock's colourful tail. A proximate explanation for one of the tail's adaptive properties is that the physical spacing of barbules on the tail feathers leads to a particular scattering of light waves, which gives rise to the tail's iridescent coloration. An ultimate explanation for this property is that, because peahens are more inclined to mate with handsome males, the peacock sports a colourful tail in order to improve his fitness. These are clearly distinct kinds of explanation; the proximate explanation addressing the mechanism by which the peacock makes his tail attractive, the ultimate explanation addressing why he makes his tail attractive. Of course, biologists can—and do—enquire as to why peahens prefer colorful tails, and part of that explanation lies in the proximate neurological details of the peahen's brain. In that sense, neurology does feature in

the evolutionary history of the peacock's tail. But this is of no concern to the peacock. The ultimate, final, adaptive rationale for his showy tail is that it maximizes his fitness.
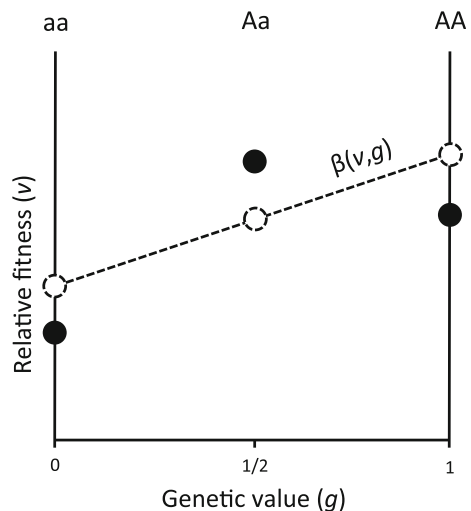
Additivity and adaptation

Moving beyond the proximate/ultimate distinction in the study of adaptation, Laland et al. also question the validity of adaptationism itself. Specifically, they claim that Fisher's (1930) genetical theory of natural selection fails to consider non-additive genetic effects, and that the logic of adaptationism is built upon the assumption that the effects of genes are weak and additive. I disagree with both of these points.

First, Laland et al. point out that Fisher "made additive genetic variation central to his view of natural selection", and suggest that this is in conflict with empirical evidence of "widespread epistatic interactions, across a broad range of taxa". However, this is a serious misunderstanding of Fisher's contribution to evolutionary theory. Fisher did not assume that the gene action is always strictly additive. Rather, he showed that natural selection responds only to the additive genetic variance, with non-additive genetic effects acting as irrelevant noise.

This result is readily shown using Price's (1970) equation, which defines natural selection as the population change in the average genetic (i.e. heritable) value of any trait of interest that owes to the covariance between genetic trait value (g) and relative fitness (v) across all the individuals in the population: $\Delta_S E(g) = \text{cov}(v,g)$. Assuming nonzero genetic variance then, without any loss of generality, this change can be rewritten as $\Delta_S E(g) = \beta(v,g)\text{var}(g)$, where the coefficient $\beta(v,g) = \text{cov}(v,g)/\text{var}(g)$ happens to be equal to slope of the straight line fitted through the population (g,v) data by means of least-squares regression (Price 1970; Fig. 1). That is, the

Fig. 1 The isomorphism between dynamics and statistics. Natural selection changes gene frequencies according to the slope of the straight line (*dashed*) fitted through genotype-fitness data (*black discs*) by means of least-squares regression. Although the straight-line fit does not capture all of the genotypic variance in fitness, this is the only part of the variance that natural selection cares about. See Gardner et al. (2011) for more discussion

action of natural selection is given by the product of the straight-line relationship between genes and fitness and the additive genetic variance in the population.

This appearance of the mathematics of least-squares linear regression terms in the genetical theory of natural selection has long fuelled a misunderstanding that, somehow, Fisher was assuming strictly additive gene action in his evolutionary model. This is incorrect. Fisher's model allows for arbitrarily complicated relationships between genes and phenotypes and fitness. Rather, it is natural selection who has 'chosen' to fit straight lines to population data by means of least-squares regression, and to change gene frequencies according to the results of her regression analysis. That is, Fisher didn't suggest that non-additive genetic effects don't exist; he discovered that natural selection simply doesn't care about them.

Second, Laland et al. claim that the logic of adaptationism is founded upon the assumptions that gene effects are weak and additive. However, this is not true of what I have called "weak adaptationism"; that is, the view that organisms are designed—perhaps imperfectly—by natural selection for the purpose of maximizing their fitness (Gardner 2009). Formal justification for weak adaptationism lies in the isomorphism between the dynamics of natural selection and an optimization program that captures the idea of the organism as striving to maximize her fitness, and this requires no assumption of weakness or additivity of gene action (Grafen 2002). The further commitment to the idea that organisms actually achieve optimality is what I have called "strong adaptationism" (Gardner 2009). This is clearly an untenable view, in its literal sense. But the application of strong adaptationism as a pragmatic research tool for enabling the generation of readily-testable predictions about real-world populations has enjoyed enormous empirical success. To the extent that practising biologists employ strong adaptationism, its justification lies in its clear empirical utility, and not in assumptions of weakness or additivity of gene action.

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