



Ernst Mayr's 'ultimate/proximate' distinction reconsidered and reconstructed

ANDRÉ ARIEW

Department of Philosophy, University of Rhode Island, Kingston, RI 02881, USA (e-mail: ariew@uri.edu)

Received 6 August 2001; accepted in revised form 22 May 2002

Key words: Cause, Development, Drift, Explanation, Fitness, Mayr, Probability, Teleology, Ultimate vs. Proximate

Abstract. It's been 41 years since the publication of Ernst Mayr's "Cause and Effect in Biology" wherein Mayr most clearly develops his version of the influential distinction between ultimate and proximate causes in biology. In critically assessing Mayr's essay I uncover false statements and red-herrings about biological explanation. Nevertheless, I argue to uphold an analogue of the ultimate/proximate distinction as it refers to two different kinds of explanations, one dynamical the other statistical.

Introduction

It's been 41 years since the publication of Ernst Mayr's "Cause and Effect in Biology" wherein he develops his version of the ultimate/proximate distinction hailed by some as "justly considered a major contribution to the philosophy of biology" (Beatty (1994), 333). Yet despite its widespread recognition, the distinction is not universally taken to heart among biologists and philosophers. In 1994 Mayr complained that in the four or five papers and one book on development that he had read in the last two years ultimate and proximate causes "were hopelessly mixed up." Mayr writes: "I hope that the day will come when people realize that the decoding of a genetic program [*qua* proximate cause] is something very different from the making and changing of genetic programs that is done in evolution [*qua* ultimate causes]" (p. 357). I think an appropriate question to ask is 'Why don't people get it?'

We could answer this question several ways, historically, sociologically, psychologically, etc. I wish to answer the question analytically, critically examining what Mayr's distinction entails for a theory of biological explanation. Part of the reason people don't get it is what distinguishes "ultimate" from "proximate" is unclear, even in Mayr's own mind. According to John Beatty, Mayr's distinction played at least three different roles throughout his career. Part of the confusion has to do with Mayr's outdated interest in applying an informational metaphor to development and evolution. The metaphor obfuscates rather than clarifies. Further, some features of the concepts 'ultimate' and 'proximate' that Mayr takes to be essential turn out to be wrongheaded. For example, Mayr treats "evolution" as a synonym for "natural

selection” despite the fact that natural selection is just one of many explanations for evolutionary changes. Migration, mutation, drift are a few others.

Once the numerous red herrings and false assertions have been cleared from the tracks it is my thesis that we will find a useful distinction between two fundamentally different and indispensable types of explanation, token causal explanations of developmental events and population-level explanations of evolutionary events.² I am reasonably sure that Mayr would not endorse the distinction I introduce, yet the fundamentals are found within Mayr (1961) paper. I proceed by taking each side of the distinction in turn.

Proximate cause

A common interpretation of Mayr’s conception of “proximate” is that it refers only to causes in an organism’s development. At least one critic charges that Mayr’s ultimate/proximate distinction is superfluous because “we have a perfectly good pair of terms for parsing causes in this way, which long antedates the proximate/ultimate distinction: ‘ontogenetic’ and ‘phylogenetic’” (Francis (1990), 405). However, as Mayr notes in reply to his critic, “proximate” refers, in addition, to causes of physiological processes such as “reflex” and “excretion of urea in the kidney” (Mayr (1993), p. 93). How are both physiological and developmental processes subsumed under “proximate causes”?

According to Mayr, biology can be divided into two sorts of disciplines, functional morphology and evolutionary biology. Functional morphologists are concerned with the causal capacities of “structural elements, from molecules up to organs and whole individuals” (p. 1502). They answer questions like “How does something operate?” through an analysis of how structural elements causally contribute to larger capacities of the organism. For example, to study how warblers migrate, one cites either the operation of the warbler’s physiology or the external conditions that trigger it. Mayr calls the former cause of warbler migration the “intrinsic physiological cause”: “The warbler flew south because its migration is tied in with photoperiodicity. It responds to the decrease in day length and is ready to migrate as soon as the number of hours of daylight have dropped below a certain level” (p. 1503). Mayr calls the “triggering” cause of warbler migration the “extrinsic physiological cause”: “the warbler migrated on the 25th of August because a cold air mass, with northerly winds, passed over our area on that day. The sudden drop in temperature and the associated weather conditions affected the bird, already in a general physiological readiness for migration, so that it actually took off on that particular day” (p. 1503). Mayr’s two examples from the physiology of

²The analysis of Mayr’s proximate/ultimate distinction affords me an opportunity to clarify my contribution to two recent co-authored papers on the distinction between fitness ascriptions at the token causal level and population level fitness ascriptions employed in evolutionary explanations (Matthen and Ariew 2002; Walsh et al. forthcoming 2002).

warbler migration are meant to illustrate proximate causes, the subject of functional morphology.

Despite the critic's charge that Mayr's concept of proximate cause refers only to ontogeny, surprisingly Mayr's discussion of functional morphology does not refer to developmental processes at all. Neither of Mayr's two examples of the proximate causes of warbler migration refer to warbler *development*. Rather, the proximate causes that Mayr cites pertain only to the warbler's fully formed adult capacities. So, where does ontogeny fit in the discussion of proximate causes?

The answer is that Mayr takes the study of developmental processes to be within the domain of molecular biology and subsequently within the domain of functional morphology. He thinks that functional morphology is well-equipped to answer the developmental questions: "The functional anatomist who studies an articulation shares this method [of functional analysis] with the molecular biologists who studies the function of a DNA molecule in the transfer of genetic information" (p. 1502).

There are two claims here. First, Mayr takes development to be within the domain of molecular biology insofar as developmental biologists "decode the genetic program". In response I will argue that Mayr's informational metaphor that dominates his discussion of proximate causation and teleology is a red herring. Mayr's second claim is that the analytic method of functional morphology is well-suited for the study of development. Here, I will argue in Mayr's favor on methodological grounds. Out of my critique of Mayr's two claims I will lay out the foundations of a reconstruction of what is uncontroversial about Mayr's ultimate and proximate distinction. However, I will urge us to replace Mayr's concept of "ultimate cause" with the concept of "evolutionary explanation".

Mayr *defines* proximate causes in terms of "decoding the genetic program". Further Mayr thinks the information metaphor is essential to providing a mechanistic explanation for the goal-directedness of proximate causes. Mayr writes, "The purposive action of an individual, insofar as it is based on the properties of its *genetic code*, therefore is no more nor less purposive than the actions of a computer that has been programmed to respond appropriately to various inputs. It is, if I may say so, a purely mechanistic purposiveness" (p. 1504, my italics). Instead of ascribing "teleology" to the seemingly purposive activity of individuals, Mayr recommends that we ascribe the term "teleonomy" to distinguish between real-world purposiveness and mechanistic purposiveness.

Mayr's definition of proximate cause in terms of a genetic program is superfluous. Proximate causes can be identified without reference to an information metaphor. It is more appropriate to define proximate causes in terms of the causal capacities of structural elements. Perhaps Mayr realizes the superfluousness of the "language of information theory" when, following a discussion of causal capacities, he characterizes it as "*still another* characterization of both proximate and ultimate causes" (p. 1502, my italics).

Further, Mayr's grounding of a mechanistic teleology to a "genetic code" within the DNA molecule provides too narrow a view of development to be useful for explaining ontology. Developmental endstates are mechanistically explained by reference to the complex interactions between genes, extra-cellular mechanisms and

environmental conditions, not merely the action of DNA molecules (Lewontin 2000). In short, there is more to development than the study of the DNA molecule. Fortunately, Mayr's conception of proximate causes is perfectly consistent with a broader view of development whereby proximate causes range over the various cellular and environmental conditions that constitute development as well as the actions of the DNA molecules. However, once we acknowledge that development can be understood as a *causal process* involving more than DNA molecules, the concept of a "genetic program" becomes superfluous.

In sum, Mayr's discussion of genetic information is completely inappropriate to the issue of what makes developmental biology a study of "proximate causes". Developmental biology much more than the study of the DNA molecule. Yet, there is no harm in replacing Mayr's narrow conception of development as the decoding of a genetic program with a broader conception of development as the study of the causal interactions between genes, extra-cellular mechanisms, and their environmental conditions. We can subsume the broader conception of developmental explanation under the label "proximate cause" explanation.

Recall that Mayr's second claim is that the analytic method of functional morphology is well-suited for the study of development. Methodologically, Mayr is on solid ground. Developmental biologists study the complex interactions of genes and environments by analyzing the capacities of structural elements or complexes of elements over organism's lifetime (Amundson 2001). For example, a developmental biologist will introduce either a gene mutation or an alteration in the environmental condition (e.g. a shock) and determine what effect it has on the developmental outcome. That's how I take Mayr to subsume development under functional morphology. By performing functional analyses on certain structural elements (or certain stages of development of structural elements) you answer two sorts of questions, "How does the element work?" and "How does the element contribute to the development of the larger capacity in question?"

However, it does not follow from the methodological claim that one should subsume developmental biology under functional morphology. There is a difference between the study of functional morphology and the study of development. Functional morphologists answer questions like "how does something operate?", e.g. "how do hearts contribute to circulation?", while developmental biologists ask questions like "how does something come to be?", e.g. "how do hearts come to develop out of embryonic cells?". These questions get distinct answers because the causal processes to which they refer are distinct; physiological causation is distinct from developmental causation.³

So, what remains of our discussion of Mayr's conception of proximate causes? So far I've endorsed a category of individual-level *causal explanations* that answer questions about an organism over its lifetime. I emphasize "causal explanations"

³I thank Kim Sterelny for this point. Kim suggests further that Tinbergen's 4-way distinction between explanatory projects in biology may be apt here especially considering the relation between proximate causation developmental biology. I think the project of mapping Tinbergen's 4-way distinction and the conception of individual level causal explanations deserves its own separate essay.

because I shall argue that there is an important distinction between the biological study of individual level causal events and the study of statistical level events pertaining to evolutionary change. I shall also argue that the individual level causal vs. statistical level evolutionary distinction should replace Mayr's proximate/ultimate distinction.

To reach my conclusion about proximate causes I had to negotiate the following issues: 1) Mayr's narrow view of development as the study of the DNA molecule; 2) his neglecting to illustrate proximate causes with an example from development; 3) his obscuring the discussion of proximate cause with an information metaphor that is superfluous to the central definition. Now let's turn to a discussion of "ultimate" explanations.

Ultimate cause

According to Mayr, evolutionary biologists, distinct from functional morphologists, are interested in answering basic "Why?" questions about the structure of populations as opposed to the morphology of individuals. He interprets the "Why?" as a "how come?" concerning how traits have become prevalent in populations. The evolutionary biologist is "impressed by the enormous diversity of the organic world. He wants to know the reasons for this diversity as well as the pathway by which it has been achieved" (p. 1502). Mayr illustrates the sort of evolutionary questions with his warbler example: "The warbler has acquired a genetic constitution in the course of the evolutionary history of its species which induces it to respond appropriately to the proper stimuli from the environment. On the other hand, the screech owl, nesting right next to it, lacks this constitution and does not respond to these stimuli. As a result, it is sedentary" (p. 1502). With this much I agree: evolutionary biologists seek to answer questions about how certain traits have become prevalent in populations.

I disagree with much else that Mayr thinks about evolutionary biology and the "ultimate" side of the ultimate/proximate distinction. Mayr takes the following to be essential features of what "ultimate" refers to: 1) Natural selection is the sole explanation for nature's diversity, hence "ultimate" refers to natural selection explanations only. 2) Ultimate *qua* evolutionary explanations are essentially historical. 3) Since ultimate *qua* evolutionary explanations are essentially historical, they are not purposive. 4) "Ultimate" like "proximate" refers to individual level causal processes. I disagree with all of that. In what follows I will explain why I disagree with each point. Then, I offer my own account motivated by two ideas. First, perhaps uncontroversially, the term "evolutionary explanations" should substitute "ultimate explanations" (partly because there are other evolutionary explanations besides natural selection explanations and it would be difficult to imagine anyone accepting, say, genetic drift as species of "ultimate" explanations)⁴. Second, what

⁴I thank an anonymous reviewer for this point.

distinguishes evolutionary explanations from “proximate” or individual-level causal explanations is that the former type of explanation is a statistical population-level explanation.

Evolution and evolution by natural selection

Mayr takes evolutionary biology to be the exclusive study of adaptations *qua* products of natural selection. He writes, “[ultimate causes] are causes that have a history and that have been incorporated into the system through many thousands of generations of *natural selection*” (p. 1503, my italics). However, natural selection is only one explanation of nature’s “diversity”. Indeed, natural selection is one explanation of how populations evolve. There are others: migration, mutation, genetic recombination, and drift. If all of these other sorts of explanations answer the appropriate evolutionary questions, then they too should be included as part of the conception that undergirds “ultimate” explanations.

Historical evolutionary explanations

Mayr identifies only the *historical* questions that evolutionary biologists seek answers for. He writes, “it is obvious that the evolutionist has in mind the *historical* ‘how come?’ when he asks ‘why?’ . . . [T]hese are causes that have a *history* and that have been incorporated into the system through many thousands of generations of natural selection” (p. 1502–3, my italics). Yet again, Mayr is overly restrictive about the domain of evolutionary biology. He provides no reason to think that evolutionary biologists should not ask non-historical questions about, e.g. traits that are *currently* undergoing evolution. For example, one might ask whether a trait is being maintained by natural selection. Or, of a trait that is currently spreading through the population, whether its spread is the result of natural selection or drift or some other evolutionary means (e.g. see Alcock and Sherman (1994), p. 60).

Mayr’s reluctance to include questions about current or future populations is perhaps explained by his view that evolutionary biologists “cannot make reliable predictions, except through such trivial and meaningless circular statements as, for instance: ‘the fitter individuals will on the average leave more offspring’” (p. 1504).⁵ On this Mayr is surely mistaken. Evolutionary biologists can and do offer predictions about the likelihood of a trait’s spread based on empirical evidence of the population’s size or the current reproductive success of individuals possessing a particular trait-variant. To assess a trait’s current contribution to trait fitness one either assesses a trait’s physical propensities or compares the number of deaths or births that possessors of particular variants undergo (Sober (2000), p. 68). Both ways allow us to make empirical predictions about how traits might be maintained in future populations.

⁵Mayr cites an unpublished manuscript from M. Scriven as the source of his view on prediction.

Teleology

On the issue of teleology, Mayr writes, “the development or behavior of an individual is purposive, natural selection is *definitely not*” (p. 1504). Mayr thinks that natural selection exhibits none of the apparent purposiveness that individual development and behavior expresses. Hence natural selection is not teleological (or teleonomic). Recall that for Mayr it is legitimate to speak of apparently purposeful activity *only when* you can ascribe the information metaphor—“a program”—to the activity. The genetic program explains the apparent future-directedness or end-directedness of development and physiology. In contrast since natural selection is an historical process natural selection doesn’t appear to be end-directed (p. 1503).

However, some contemporary writers on the teleological nature of evolutionary theory take a different view. Contrary to Mayr there is a perfectly legitimate answer to the teleological question “what is x *for*?”, e.g. “what are bird wings for?”. The answer to the “what for?” question, in turn, provides an answer to an evolutionary “Why?” question (Enç 1979).⁶ To repeat, those evolutionary “Why?” questions can pertain either to the prevalence of a trait, as in “Why do birds have wings?”, or questions of a trait’s maintenance, as in “Why will future birds continue to have wings?” The answer to the former is etiological, issuing in an historical evolutionary explanation. “Wings are for flying” is shorthand for the claim that in the past, birds that possessed wings that were capable of flying enjoyed reproductive success over their conspecifics. The answer to the latter refers to the current reproductive capacities of birds with wings in the present selective regime. Sometimes the answer to the former is not an answer to the latter. For example, at some point of evolutionary time it might have been the case that the answer to the etiological question, “Why do penguins have wings?” was “for flying”, but the maintenance question, “Why will penguins continue to have wings?” was “for swimming”. In other words, depending on whether the evolutionary question concerns the etiology of the trait or the future maintenance of the trait, the answer to the “What for?” question could change (see Walsh and Ariew (1996), Bigelow and Pargetter (1988)).

Mayr does not accept any of this. He explicitly denies that evolutionary biologists provide answers to the “finalistic ‘What for?’” questions. Instead, Mayr thinks “it is *obvious* that the evolutionist has in mind the historical ‘how come?’ when he asks ‘why?’” (p. 1502). However, we are armed with two responses. First, recall that Mayr is mistaken about evolutionary explanations being essentially historical. Rather, heritable differential reproductive success is an ongoing process. Second, even historical questions can be teleological as they provide answers to questions about the prevalence of certain traits by citing what the item in question is *for*.

So far, I’ve given reason to believe *at least* that ultimate and proximate refer to two different *explanations* that answer different sorts of questions. Proximate explanations answer causal questions of individuals and the ultimate explanations answer questions about the prevalence and maintenance of traits in a population. I

⁶See Matthen (1997) for a different view of the legitimacy of teleological explanations.

have also argued, with Mayr, that *proximate* explanations are causal as they issue in functional analyses of a system's causal capacities (including developmental analyses) whereby the function of a trait is its causal capacities.

At this point, perhaps we have a minimum view about a distinction between proximate (causal) and evolutionary interpretations of the concept of "function". The proximate conception of "function" pertains to what an item does or how it works. We might ask this question without asking why the item exists in the present population. Function ascriptions in evolutionary explanations are different. They answer questions—e.g., "why prevalent?" or "why will be maintained?"—that pertain to what the item is for in the way I described above (see also Sober (2000), p. 87). I like the distinction as it pertains to natural selection explanations, but I reject limiting evolutionary explanations to only natural selection explanations.

Statistical vs. individual level explanations

Finally, I reject Mayr's interpretation of "ultimate" to refer to evolutionary *causes*. Considering the extant literature this is probably the least controversial of Mayr's claims. For example, it is commonplace to think about the results of natural selection as products of a sum of causal "forces", of which natural selection is one of them (see Sober (1984)). Mayr uses the language of "forces" throughout his essay, but even if he does not mean to invoke the concept of a Newtonian force, it is clear that Mayr thinks (as do many other theorists) that evolution is a "dynamical" process meaning that it ranges over individual level causal properties (see Matthen and Ariew (2002), Walsh et al. (forthcoming 2002)).

However, I think it is misguided to think that *evolutionary* explanations are dynamical. My position is a bit delicate. I am not denying that causal processes occur over the lifetime of an individual, and that citing them explain the organism's differential reproductive success over others. What I am denying is that citing those causal processes for each individual constitutes an *evolutionary explanation*. Evolutionary explanations range over statistical attributes of a population, not dynamical properties of individuals.⁷ My position saves a proximate/evolutionary distinction from arguments that seek to reduce one for the other (as I will outline below). I will demonstrate why evolutionary and proximate (more precisely, individual-level causal) explanations are distinct, irreducible, and both indispensable. Both answer different questions in ways that cannot be answered by referring to the other.

By referring to both ultimate (evolutionary) and proximate explanations as "causal", Mayr is open to the charge that ultimate causes are dispensable in light of a description of the proximate causes that contribute to each individual's reproductive success or failure. After all, as Lickliter and Berry (1990) put it, "phylogeny is best characterized as an historical description of progressive variants in on-

⁷The conclusion I draw here, that evolutionary explanations are statistical, is the same one presented in both (Matthen and Ariew 2002; Walsh et al. forthcoming 2002). However, the argument I present here is distinct. It originates in Ariew (1998).

togenesis” (p. 357). Accordingly, ultimate causes *reduce* to a series of individual proximate explanations. Reference to the proximate causal details provides a richer causal explanation than explanations that refer to evolutionary events as an ensemble. Let us call this the “dispensability argument” or “DA”. If DA is right that evolutionary arguments amount to an aggregate of proximate causes ranging over individual life histories, then Mayr’s contention that ultimate explanation are a *distinct* type of explanation from proximate causal ones is false.

Yet, it does not follow from DA that explanations from proximate cause sufficiently explain *evolutionary events*. On my view evolutionary explanations are *statistical explanations of population-level phenomena* to be distinguished from “proximate” or individual level causal explanations. The result is that evolutionary explanations are indispensable even if one knows the complete causal story about how each individual in a population lived and died. In other words, evolutionary explanations are not reducible to individual-level causal explanations. My argument, in short, is as follows. Proximate causes of individual life histories vary between individuals in a population. No two individuals live and die in exactly the same way or necessarily give birth to the same number of individuals. So, after tracing out proximate causes for every individual in a population, there is something left over to explain, namely what some of these disparate life histories have *in common* that set them apart from their conspecifics. Evolutionary explanations identify these commonalities in terms of statistical properties of an evolving *population*. Hence, evolutionary explanations differ *in kind* from proximate explanations. Evolutionary explanations are statistical, they range over the ensemble of individuals, taken as a class. Proximate explanations are individual level causal explanations ranging over individual life histories.

Sober (2000), Rosenberg (1978) offer a DA-like argument on the concept of fitness. The starting assumption is that fitness ascriptions are placeholders for deeper causal accounts of individual life histories. Once told the enumerated life histories of organisms and their kin completely explain evolutionary events without reference to fitness. To illustrate with an example from Sober, suppose we notice that a chromosomal inversion changes frequency in a population of *Drosophila* over the course of a year. Upon investigation we determine that the changes in frequency are due to differential fitness of heritable features. One type has a greater fitness than its conspecifics and the difference in fitness provides the evolutionary explanation for the spread of the new genotype. Now, suppose we inquire about the *physical basis* of the difference in fitness and as a result it is determined that the chromosomal inversion causally contributes to the development of a thicker thorax which helps insulate against an increasingly colder climate. As Sober puts it, “once this physical characterization is obtained, we no longer need to use the word ‘fitness’ to explain why the traits changed frequency. The fitness concept provided our initial explanation, but the physical details provide a deeper one” (Sober (2000), p. 75). Notice, the “deeper” causal story amounts to the proximate causes that influence the development of the thicker thorax that in turn contributes to the relatively successful reproductive capacities of the flies.

I (like Sober) do not think that the story necessarily demonstrates the dispensabili-

ty of explanations that involve the concept of fitness. On my view (as distinguished from Sober (2000)), the trick is to be clear on what is the concept of fitness that evolutionary explanations invoke. There are at least two concepts of fitness under consideration.

Individual fitness is the propensity of an *individual* to survive and reproduce in its environment given the traits it possesses. The fitness propensity is the causal property of an individual just as solubility is a causal property of a lump of sugar to dissolve in water. Since proximate explanations range over the causal properties of individuals the discovery of an individual's fitness is an appropriate subject of proximate explanations and hence susceptible to a DA reductionistic argument. We reach judgments about an individual's fitness by examining its physical make-up and the environmental conditions it encounters over its lifetime. Notice since individual fitness refers to *individuals*, and individuals differ (even if slightly) in the traits they possess and how they interact with their environmental conditions, it follows that no two individuals have identical individual fitnesses. Even twins might have different propensities to survive and reproduce given the vagaries of their environments. A detailed microcausal story about each individual and its kin—including the details of ontogeny—would provide us with a deep causal account of how individuals and their kin lived or died. In light of the details, individual fitness is dispensable.

While individual fitness is an important concept, it is not the same as the concept of fitness used in natural selection explanations. Natural selection utilizes the concept of *trait fitness* which issue in a different sort of explanation (Walsh et al. forthcoming 2002). Trait fitness is the average (individual) fitness of individuals possessing a particular trait. As an *average*, trait fitness does not reflect a property that any individual necessarily possesses (e.g. no human couple has 2.3 children). Do not confuse the probability of trait fitness with the probability associated with individual fitness. Trait fitness is the average survivability of a group of individuals possessing a type of trait. Individual fitness is the chance associated with an individual's survivability and reproductive success given all the traits it possesses (like an insurance life table). As an average, trait fitness is a property of *populations* and not of individuals. It is these population level properties rather than the individual level properties which are of interest to evolution. After all, populations, not individuals, evolve; individuals, not populations develop.

To explain the population-level phenomenon of evolution, explanations from the perspective of DA would enumerate the life histories of each individual, one by one. Yet, every individual's causal life history is different. Every individual differs morphologically. No two individuals interact with environmental conditions in exactly the same way. So, the causal life histories vary between individuals. What is missing in this dynamical explanation are what *some* individuals have *in common* that sets them apart from the others, namely that possession of certain features provide their bearers, on average, a greater chance to survive and reproduce offspring with similar features to their own. In natural selection explanations the features in common are expressed as the *average* or probability of reproductive success associated with "trait fitness".

The point of natural selection explanations of evolutionary population changes is

to explain those changes by citing varying features of the population. Those features are what some ensembles of individuals have in common that vary from other ensembles, namely varying trait fitnesses.

Consequently, natural selection provides an explanation of *what several evolutionary events have in common*. In other words, it allows us to subsume distinct evolutionary events under one explanation (Sober 2000). Despite the disparate features and environmental conditions that impinge upon, on the one hand, individual macaws of the Amazon, and on the other, Saguaro cacti of the Sonoran Desert, the evolutionary changes of both populations can be explained under one general phenomenon. What is distinctive and indispensable about evolutionary explanations from natural selection is that the ensemble features they cite, i.e. trait fitnesses, pick out these important general patterns that unify evolutionary events under one description. Explanations from proximate cause miss these general patterns. Macaw biology is so different from Saguaro biology and the environmental conditions of the Amazon starkly differs from that of the Sonoran Desert, that a causal account of the individual life histories of one population will have just about nothing in common with the causal account of the other. This is not to say that one type of explanation is *more important* than the other, but that they are two entirely *distinct* and irreducible forms of explanation.

Notice, by viewing evolutionary events as ensemble level properties we can see why “drift” explanations are indispensable too. Natural selection is not the only explanation for evolution. Small populations that feature non-fitness enhancing mutations are particularly susceptible to evolutionary changes by random drift. Just as it is not uncommon for a sequence of fair coin tosses to exhibit high proportion of heads over tails within a few number of flips, random drift might change trait frequencies in favor of a neutral (or even debilitating) mutations. Proximate causal accounts that explain the evolution of such a population by enumeration would dispense with the concept of drift just as it would dispense with the concept of individual fitness. From a proximate cause individual life history point of view, accidents and probable deaths are indistinguishable; both are part of the dynamical description of an individual life history. Yet, on my view, drift and selection are distinct evolutionary explanations. They represent different statistical-level events. Trait fitness *qua* population average is analogous to the expected proportion of heads to tails in a series of coin tosses when the coins share a certain feature in common, e.g. the coins are “fair”. Trait fitness is the *expected* survivability and reproductive rate of success of individuals sharing a common feature. Drift is the deviation of the *actual* outcome from the expected. In the coin analogy, drift occurs when the trial of coin flips results in a proportion of heads to tails that deviates from what we would have expected from a trial of fair coin tosses. Like drift, the deviation from expected coin tosses is likely to increase when the number of trials is small (for a detailed description of the difference between drift and selection from the statistical point of view see Walsh et al. (forthcoming 2002)).

Since drift is an alternative explanation to natural selection for the diversity of life (however applicable it is) drift explanations are a species of evolutionary explanations.

Recall that Darwin’s key insight was to provide a theory that explains the

diversity of life. That is the essential feature of evolutionary explanations to which Mayr and I agree. However, Mayr's concept of 'ultimate' cannot boast of this feature, for 'ultimate' refers to a dynamical process or force rather than an explanation of general patterns within an ensemble of processes. Hence Mayr's "ultimate" and not my conception of "evolutionary explanation" is susceptible to (at least) the reductionistic argument from DA.

Conclusion

In sum, contrary to Mayr, I take "evolutionary" and "proximate" as distinguishing distinct *kinds* of explanations. Proximate explanations are dynamical as they cite the causal properties during an individual's lifetime including development and physiological processes. Reference to proximate causes answer various questions including, "How does something get built?" and "How does something operate?". Evolutionary explanations (which substitute Mayr's "ultimate cause") are not dynamical. Rather they are statistical explanations that refer to ensemble-level events that track trends in populations rather than the vagaries of individual-level causal events. By averaging out individual-level differences, evolutionary explanations pick-out patterns in common to all evolutionary events. That is how natural selection, for example, successfully unifies disparate evolutionary phenomenon under one explanatory description. Evolutionary explanations answer questions pertaining to the diversity of life, including "Why is something prevalent?" and "Why will something continue to persist?"

Acknowledgements

Thanks to Paul Bloomfield, Chris Stephens, Tim Lewens, and Denis Walsh for discussions leading up to this paper. Thanks to Elliott Sober, Mohan Matthen, Kim Sterelny, and an anonymous reviewer for comments on various drafts. I wish to thank an audience at Ishkabbible 2001 in Quinnipiac, CT for bearing through a presentation of this essay who suffered the misfortune of two overhead blow-outs.

References

- Alcock J. and Sherman P. 1994. The Utility of the Proximate-Ultimate Dichotomy in Ethology. *Ethology* 96: 58–62.
- Amundson R. 2001. Adaptation and Development: On the Lack of Common Ground. In: Orzack S.H. and Sober E. (eds), *Adaptation and Optimality*. Cambridge U. Press, pp. 303–334.
- Ariew A. 1998. The Probabilistic Character of Evolutionary Explanations. *Biology and Philosophy* 13: 245–253.
- Beatty J. 1994. The Proximate/Ultimate Distinction in the Multiple Careers of Ernst Mayr. *Biology and Philosophy* 9: 333–356.
- Bigelow and Pargetter 1988. Functions. *Journal of Philosophy*.

- Enç B. 1979. Function Attributions and Functional Explanation. *Philosophy of Science* 46: 343–365.
- Francis 1990. Causes, Proximate and Ultimate. *Biology and Philosophy* 5: 401–415.
- Lewontin R.C. 2000. *The Triple Helix: Gene, Organism, and Environment*. Harvard U. Press.
- Lickliter R. and Berry T.D. 1990. *Developmental Review* 10: 348–364.
- Matthen M. 1997. Teleology and the Product Analogy. *Australasian Journal of Philosophy*.
- Matthen M. and Ariew A. 2002. Two ways of Thinking about Fitness and Natural Selection. *Journal of Philosophy* 49: 55–83.
- Mayr E. 1993. Proximate and Ultimate Causation. *Biology and Philosophy* 8: 95–98.
- Mayr E. 1994. Response to John Beatty. *Biology and Philosophy* 9: 359–371.
- Mayr E. 1961. Cause and Effect in Biology. *Science* 131: 1501–1506.
- Nagel E. 1977. Teleology Revisted. *Journal of Philosophy* 74: 261–301.
- Rosenberg A. 1978. The Supervenience of Biological Concepts. *Philosophy of Science* 45: 368–386.
- Sober E. 1984. *The Nature of Selection: Evolutionary Theory in Philosophical Focus*. MIT Press.
- Sober E. 2000. *Philosophy of Biology*. 2nd edn. Westview Press.
- Walsh D. and Ariew A. 1996. A Taxonomy of Functions. *Canadian Journal of Philosophy* 26 Reprinted (1999) in D. Buller (ed.) *Function, Selection, and Design*, State University of New York Press, 257–280: 493–514.
- Walsh D., Lewens T. and Ariew A forthcoming 2002. *Trials of Life*. *Philosophy of Science*.

