

# The Proximate/Ultimate Distinction in the Multiple Careers of Ernst Mayr<sup>1</sup>

JOHN BEATTY

*Department of Ecology, Evolution and Behavior  
University of Minnesota  
St. Paul, MN 55108, U.S.A.*

**ABSTRACT:** Ernst Mayr's distinction between "ultimate" and "proximate" causes is justly considered a major contribution to philosophy of biology. But how did Mayr come to this "philosophical" distinction, and what role did it play in his earlier "scientific" work? I address these issues by dividing Mayr's work into three careers or phases: 1) Mayr the naturalist/researcher, 2) Mayr the representative of and spokesman for evolutionary biology and systematics, and more recently 3) Mayr the historian and philosopher of biology. If we want to understand the role of the proximate/ultimate distinction in Mayr's more recent career as a philosopher and historian, then it helps to consider his *earlier* use of the distinction, in the course of his research, and in his promotion of the professions of evolutionary biology and systematics. I believe that this approach would also shed light on some other important "philosophical" positions that Mayr has defended, including the distinction between "essentialism: and "population thinking."

**KEY WORDS:** Ernst Mayr, history of evolutionary biology, theories of migration, Jacques Loeb, reductionism, funding of biology.

*In the winter of 1960–61 there was a lecture series at M.I.T. on the subject of cause and effect. I was asked to give the lecture on cause and effect in biology, and this gave me the opportunity for a systematic presentation of some ideas I had had for many years, and part of which I had already mentioned in previous publications. It will require a historian's analysis to determine how much of this lecture was new, but even some of the points made by me that were not new were articulated more forcefully than in the earlier literature, as for instance the partitioning of biology into functional biology, the biology of proximate causation, and evolutionary biology, the biology of ultimate causation. Structuring biology in this way helps to clarify much that was controversial in biology because, as I showed, no biological phenomenon is explained until both the proximate and the ultimate causes are determined. (Mayr 1982a, p. 130)*

## INTRODUCTION

There is no such thing as *the* area of Ernst Mayr's expertise. He has been Jack and master of many trades. Thus it seems quite reasonable to call upon representatives of several fields to analyze his contributions – assigning to each a different area within the overall domain of Mayr's accomplishments.

I was the designated philosopher in such an enterprise. But I strayed farther and farther from my role as I became more and more interested in the historical connection between Mayr's philosophical ideas and his scientific work. Not surprisingly, the connection proved difficult to address, not only because of the details of Mayr's life and work, but also because the very question presupposes a distinction (between philosophy and science) that is by no means straightforward.

In the meantime, two things occurred to me. First, I realized that I could avoid the issue of whether an idea is inherently philosophical or scientific by focusing instead upon the use to which the idea is put on any particular occasion. And second, I realized that I had underestimated the variety of uses to which Mayr had put his ideas. Where I initially saw simply philosophical or simply scientific uses, there was more going on.

In this paper, I will consider the role of one particular idea in several of Mayr's careers. And in the process I will try to make historical sense of his best known articulation of that idea (Mayr 1961). The idea is that there are two complementary ways of understanding why organisms come in the colours, sizes and shapes they do, and why they behave in the manners they do. That is, there are the "proximate" causes of the traits of organisms, and there are the "ultimate" causes.

The proximate causes of an organism's traits occur within the lifetime of the organism. They involve the expression of the information contained in the organism's genetic material, as mediated by the environment. The ultimate causes occur prior to the lifetime of the organism, within the evolutionary history of the organism's species. They involve the reasons why members of that species have come to have the genetic information that they do. I will discuss an example shortly.

The proximate/ultimate distinction has served at least three different roles in Mayr's work. And these three functions correspond to three different roles that Mayr has played in connection with evolutionary biology. The first role was played by Mayr the young naturalist, who grappled with the proximate/ultimate distinction in the course of his research. This career is well illustrated by the photograph of Mayr in the field in New Guinea, in 1928 [Figure 1]. The second role was played by Mayr the representative of and spokesman for systematics and evolutionary biology, who articulated and employed the proximate/ultimate distinction to promote those two professions. This is Mayr the first Secretary of the Society for the Study of Evolution, and editor of the Society's journal, and also Mayr the Harvard Professor, and Director of Harvard's Museum of Comparative Zoology. This career is well illustrated by the photograph of Mayr assuming the directorship of the MCZ in 1961 [Figure 2].



*Fig. 1.* June 1928, Mayr with his Malay assistant at Kofo, Anggi Lakes, the former Dutch New Guinea (from Mayr 1932; reproduced with permission of the American Museum of Natural History).

1961 was also the year in which Mayr published his best known account of the proximate/ultimate distinction, "Cause and Effect in Biology," which we have come to associate with his third career, as a major contributor to the philosophy of biology. We can speak more generally of Mayr's third career as a



Fig. 2. "The old order changeth, yielding place to new." Professor Romer (left) welcoming Professor Mayr (right) to his new office as Director of the Museum." (from 'Annual Report, 1960-1961', Museum of Comparative Zoology).

historian and philosopher of biology who articulated and employed the proximate/ultimate distinction as a contribution to those literatures and the training of those students. This career is well illustrated by the photograph of Mayr, the renaissance man, on the book jacket of *The Growth of Biological Thought* (Mayr, 1982a) [Figure 3].<sup>2</sup>

In this paper, I am most concerned with the proximate/ultimate distinction in the first and second careers and periods. One reason for this focus is that the earlier periods of Mayr's work are less well known, although that situation is changing, mainly due to recent analyses of Mayr's work by Joseph Cain and V. Betty Smocovitis (e.g., Cain 1993, 1994; Smocovitis 1992 and in press). My analysis of Mayr's early work is in many respects indebted to the directions pointed by Cain and Smocovitis. A second reason for the focus is my concern to make *historical* sense of Mayr's 1961 defense of the proximate/ultimate distinction. If we want to understand why Mayr had the distinction on his mind in the late 50s and early 60s, and why he elaborated the distinction in the way he did in 1961, it helps to consider the roles of the distinction in his *previous* two careers, rather than in terms of his *subsequent career*. This is not to deny that Mayr intended for the 1961 article to be primarily a contribution to philosophy of biology. Indeed, he intended for the article to reorient the physics-dominated philosophy of science of the time (I will say a little more about that later). Nonetheless, that is only a small part of the story of how Mayr *arrived* at the distinction as articulated in the 1961 paper.<sup>3</sup>

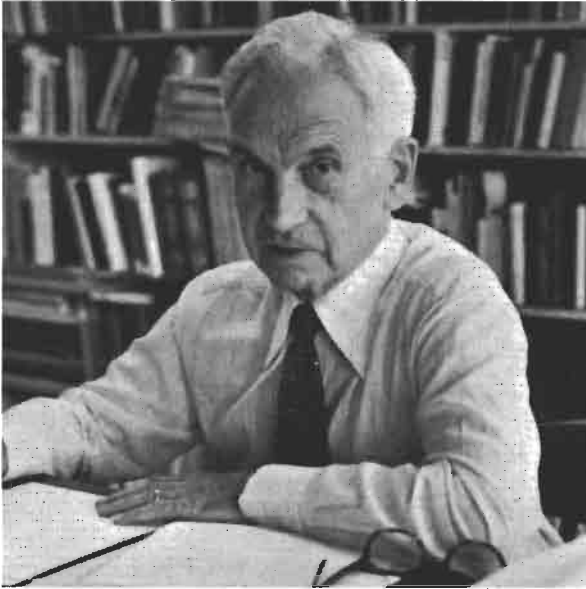


Fig. 3. "And no book has established the life sciences so firmly in the mainstream of western intellectual thought as Mayr's *The Growth of Biological Thought*" (from the book jacket; reproduced with permission of Harvard University Press).

#### THE PROXIMATE/ULTIMATE DISTINCTION IN CONNECTION WITH MAYR'S EARLY SCIENTIFIC RESEARCH

Clues to Mayr's early encounters with and interests in the proximate/ultimate distinction include the way in which he illustrated the distinction in 1961 – the example he used – and also the historical figure he chastised for having overlooked the distinction.

The example that Mayr used to illustrate the distinction in 1961 had to do with bird migration. There are, he argued, two general kinds of answers to the question, 'Why did the warbler on my summer place in New Hampshire start his southward migration on the night of the 25th of August?' (Mayr 1961, p. 1502). There are proximate-cause answers, and ultimate-cause answers. The proximate causes have to do with *how* the bird's behavior is affected by changes in its endocrine system, and *how* its endocrine system responds to shortened daylength. Mayr referred to these two kinds of proximate causes as "intrinsic" and "extrinsic physiological causes" respectively.

But this sort of account of the warbler's migration leaves open another question – namely, *why* do warblers have an endocrine system that initiates migratory behavior when days reach a certain length? Why do warblers have a neuroendocrine system that differs so much from the screech owl, which does not migrate south for the winter? Such "why" questions are best answered in terms of "ultimate," evolutionary causes. For example, in the case of the

migrating warbler, the ultimate causes have to do with the acquisition through mutation of an inheritable fall migratory tendency, and the survival and reproductive benefits of fall migrations. Mayr referred to these two subcategories of ultimate causes as “genetic” and “ecological” respectively.

It is best to quote Mayr on these distinctions:

I can list four equally legitimate causes for this migration.

- (1) *An ecological cause.* The warbler [as opposed to the screech owl], being an insect eater, must migrate, because it would starve to death if it should try to winter in New Hampshire.
- (2) *A genetic cause.* 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.
- (3) *An 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.
- (4) *An extrinsic physiological cause.* Finally, 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.

Now, if we look over the four causations of the migration of this bird once more we can readily see that there is an immediate set of causes of the migration, consisting of the physiological condition of the bird interacting with photoperiodicity and drop in temperature. We might call these the proximate causes of migration. The other two causes, the lack of food during winter and the genetic disposition of the bird, are the ultimate causes. (Mayr 1961, pp. 1502–1503; see also Mayr 1982b, pp. 67–68)

Clearly, neither proximate-cause or ultimate-cause accounts alone can provide a complete explanation of the living world, just as neither approach alone makes full sense of the warbler’s migration. But, according to Mayr, proximate and ultimate explanations are often incorrectly construed as *competing* accounts, as if one perspective necessarily rules out the other, or renders it superfluous. He cited as an example the early 20th century experimental physiologist, Jacques Loeb, who mistakenly believed that physiological accounts might substitute for evolutionary explanations. Loeb had indeed suggested on occasion that the survival and reproductive benefits of a trait have nothing to do with the trait’s prevalence in a species – that the prevalence of any trait is entirely a matter of proximate physiological factors (e.g., Loeb 1906, p. 160; I will return to this issue later). Loeb had also berated evolutionary studies, especially Darwinian evolutionary studies, on methodological grounds, for indulging in speculation about the past that could never be experimentally verified (e.g., Loeb as quoted in Kellogg 1907, pp. 393–394). Loeb’s perspective: the right answers can be found through physiological analysis; nothing can be *found* in the evolutionary past anyway.

Garland Allen has described the widespread rejection of evolutionary speculation at the turn of the century, and the adoption of experimental physiology as the model of explanation and methodology in biology. Loeb was a leader in this "revolt" (Allen 1975, 1978).

One passage from Loeb's writings struck Mayr as being so absurd that it did not require further elaboration. Mayr simply quoted Loeb: "The earlier writers explained the growth of legs in the tadpole of the frog or toad as a case of adaptation to life on land. We know [however] through Gudernatsch that the growth of legs can be produced at any time, even in the youngest tadpole, which is unable to live on land, by feeding the animal with the [extract of] thyroid gland" (Loeb 1916, p. 342, quoted in Mayr 1961, p. 1503). As if there was no evolutionary story to be told *in addition*. By taking into account the distinction between proximate and ultimate explanations, such apparently conflicting perspectives can be seen as *complementary* instead.

Taking the distinction into account, it is also easier to see what makes biology special among the sciences. Loeb had argued that biology needed the "methods of the physicist," and the "physicist's general viewpoint concerning the nature of scientific explanation" (Loeb 1918, p. 16). Mayr allowed that the study of proximate causation in biology approaches "the ideal of a purely physical or chemical experiment" (Mayr 1961, p. 1502). That leaves the evolutionary perspective most responsible for the special character and autonomy of biology.

The question arises, why would Mayr choose to criticize Loeb? Granted Loeb seems to have overlooked the distinction that Mayr was at pains to defend. But Loeb was so long gone by 1961! Why dig so far back into the past for a target? There is an interesting reason for Mayr's choice, connected to the reason why he chose to illustrate the proximate/ultimate distinction with a migration example. Consider first the reason for the migration example.

Migration and migration-related phenomena were the topics of Mayr's first two substantial scientific publications: his Ph.D. thesis published in 1926, and a theoretical review article published in 1930. Mayr did not have much use for the proximate/ultimate distinction in his thesis, which was not on an evolutionary aspect of migration. But in his first truly evolutionary contribution, the 1930 article, the proximate/ultimate distinction plays a prominent role. The differences between the two publications are worth discussing briefly.

In 1961, it was a warbler migrating south from his farm in New Hampshire that captured Mayr's attention. In the mid-20s, it was the migration of the European serin finch that interested him. At the time, he was working toward his Ph.D. at the University of Berlin's Museum of Natural History, under the ornithologist Erwin Stresemann. The dissertation topic that they settled on concerned the migration of the serin, and in particular the ongoing extension of its breeding range to the north.

In his dissertation, Mayr set out to document and explain the fact that the serin finch had, since about 1800, been migrating farther and farther north each spring from its Mediterranean winter range (Mayr 1926; see also Mayr 1982a, pp. 3-6). Mayr's major descriptive task was to establish the expanding

boundaries of the serin's range. The analysis involved differentiating the seasonal, back-and-forth, migratory phenomena from the longer-term, progressive expansion to the north. It was the progressive colonization of the north that Mayr was most concerned to explain. He set out to make "ecological" sense of the serin's expanding range, arguing that the serin occurs where there is a suitable combination of resources, climate, nesting sites, etc. The ecologically most suitable areas had been colonized first. These became centers for further colonization. This was Mayr's main perspective (Mayr 1926, pp. 619–632).

But this perspective failed him when it came to explaining why the longer northward migrations had originated in 1800 or thereabouts. Had the climate to the north changed at that time? Had resources to the north increased? Had predators or competitors to the north declined? Mayr could not identify any such changes (*ibid.*, pp. 644–647). And so briefly, and in conclusion, he suggested an evolutionary explanation, namely that the cause was a mutation affecting the ecological behavior of the serins, presumably affecting their migratory behavior and their ecological preferences and tolerances (*ibid.*, pp. 653–654).

Mayr had not set out to investigate the evolution of serin migratory behavior, and thus it is not surprising that he should have had so little to offer in this regard. Knowing what we know in retrospect about Mayr's subsequent interest in evolutionary biology, it may seem surprising that he did not elaborate. But it is important to keep in mind Mayr's training up to this point. He had not been trained as a zoologist. He was a self- and family-taught naturalist (Mayr 1982a, esp. pp. 1–3). And he had shown no early interest in evolution. In high school, he had "devoured" Ernst Haeckel's *Riddle of the Universe* (Haeckel 1899), but what interested him in that book was not so much the evolutionary speculation as the seemingly radical, anti-religious passages (Mayr, personal communication). Mayr had previously settled on a career in medicine and had completed much of his coursework before deciding to switch to zoology, largely, he recollects, in order to travel as a naturalist-collector (Mayr 1982a, pp. 2–3, 9). Stresemann, with whom he was already acquainted, helped him to pick a dissertation topic that he could complete in a short enough time – together with the prerequisite coursework – in order to qualify for a position opening up in the Museum in a year and a half!

With regard to Mayr's very brief evolutionary remarks in his thesis, it is also worth pointing out that at this time Mayr most likely shared with many others a general disenchantment with evolutionary theorizing. This was viewed by many as an overly speculative, and as a result, contentious area. Earlier in his thesis Mayr had referred to the speculative enterprise of evolutionary theorists in a rather belittling way: "I leave it to the evolutionary theorists ["decendenz theoretikern"] to draw conclusions like that!" (Mayr 1926, p. 640).

Concerns about the value of overly speculative evolutionary approaches to the distributions of animal species had been recently expressed by Richard Hesse in his *Zoogeography Based on Ecological Principles*, published in 1924.<sup>4</sup> Mayr studied this book extensively while working on his dissertation project (Mayr 1982a, p. 6).

In the first chapter of Hesse's book, he distinguished between two different approaches to animal distributions, the "historical" evolutionary approach, and the nonevolutionary "ecological" approach. Hesse acknowledged that the two perspectives were complementary, but concluded that, due to the speculative nature of the evolutionary approach, "the relative value of their conclusions is very unequal" (Hesse, Allee and Schmidt 1937, p. 7). The evolutionary approach to animal distributions, *including migrations*, had been "enthroned" in the post-Darwinian period, but that approach had actually committed many "sins... through the proposal of unwarranted and frivolous hypotheses" (*ibid.*, p. 10).

The ecological approach, he argued, is very different, because "Ecology deals with the conditions and phenomena of the present, which are subject to analysis and repeated test. Instead of being concerned with unique events, it studies processes which are largely repeated like chemical reactions or physical experiments" (*ibid.*, p. 8). Ecological hypotheses "can be verified experimentally and may be made the subject of physiological analysis" (*ibid.*, p. 9).<sup>5</sup> As he concluded the chapter, "In contrast with the situation in historical zoogeography, ecological zoogeography bears the germs of a truly causal science" (*ibid.*, p. 10).

Eugene Cittadino and Joel Hagen have described an early 20th century trend that Hesse seems to illustrate, a turn from natural history to experimental physiology as the model for ecology (Cittadino 1980 and Hagen 1986, 1991). This development in part contributed to, and in part reflected the changing ideals also being advocated by Loeb and others for biology in general.<sup>6</sup> At the time he was writing his dissertation, then, Mayr would have been very aware (at the least), and probably also influenced by, the general climate of concern about the value of evolutionary speculation.

Mayr's interest in evolutionary theory seems to have grown considerably by the time he set to work on a review of "Theories of the History of Migration." This was a paper that he had almost completed by 1928, when he set out on a two-year collecting expedition in the South Seas (see Mayr 1982a, pp. 9–11; Mayr 1932; see also Walter Bock's contribution to this volume). His friend and fellow ornithologist Wilhelm Meise completed the article in Mayr's absence and submitted it; thus it was coauthored by Mayr and Meise. It appeared in 1930, the year Mayr returned to Germany (see also Mayr 1982a, pp. 7–9).

This article is evolutionary in perspective from beginning to end. Throughout, Mayr and Meise argue that migration cannot be explained in terms of present ecological circumstances alone, but can only be "completely" explained "historically" (Mayr and Meise 1930, pp. 151, 161) or "phylogenetically" (*ibid.*, p. 162). Surely it is a speculative endeavor, they allowed, but "without hypotheses we cannot make any headway" (*ibid.*, p. 170). The whole article reflects a very different attitude toward the evolutionary perspective than Hesse had promoted, and different from Mayr's attitude toward "evolutionary theorists" in his thesis.

I will return shortly to the substance of this article. But first I would like to describe what I believe were important developments taking place in migration studies in the early 20th century. By this time, there had been proposed a

plethora of general explanations of migration (see, e.g., reviews by Eifrig 1924, A. L. Thomson 1926, Rowan 1931). Migration had been attributed to “the necessity of securing a home in which the young can be reared” (Chapman 1903, p. 59); the “desire for greater privacy in domestic affairs during nesting”; “love of home they were born in”; “failing food supply due to approach of winter” (Eifrig 1924); need for sufficient daylength for foraging; need for sufficient daylength for sufficient exposure to ultraviolet radiation to produce sufficient vitamin D; physiological changes in reproductive organs; changes in daylength resulting in physiological changes in reproductive organs; changes in temperature; changes in barometric pressure; changes in color of leaves; the ice age; and more.

Many authors defended *one* among these alternatives, as if they were necessarily competing hypotheses. But at least since the first decade of the 20th century, attempts had been made to split the issue, and the group of hypotheses, into two: the question of the “immediate determining cause,” and the “ultimate cause,” to use Shäfer’s terms from 1907 (Shäfer 1907, p. 161). For example, Shäfer argued that deprivation of food could be the ultimate cause of the fall migration south, but not the immediate cause, since fall migration so often begins when the weather is still warm and food resources still relatively abundant. Some other factor must stimulate birds to migrate in the fall, though it may be deprivation of food that explains why those that stay do not survive to reproduce their sedentary kind.

But as of the mid-twenties, it was still common to defend one general, unitary account of migration. Arguing against this approach became a major issue for A. Landsborough Thomson, who was at the time emerging as Britain’s, and one of the world’s, foremost authorities on migration.<sup>7</sup> For example, in responding to an article promoting the role of daylength as *the* cause of migration, he argued against conceiving “the cause of migration as a simple unity” (A. L. Thomson 1924, p. 641). Instead, he argued, “the question of actual causation seems to have a dual aspect,” namely, “the ultimate cause [which] must surely lie in the existence of the inborn habit and in the nature of the forces in the far past which gave it origin,” and the “immediate stimuli, periodically recurring, which evoke the habit to active expression each autumn and spring” (ibid., p. 639).

Thomson’s 1926 book, *Problems of Bird Migration*, was organized around this central theme. By 1926, Thomson had distinguished four separate categories of the causes of migration, two categories of ultimate, evolutionary causation, and two categories of immediate, physiological causation:

- (a) Factors which, without being truly causative [?], may make migration advantageous and thus give the custom a survival value; (b) Factors which may in the past have helped to originate and develop the custom in the race; (c) Factors which periodically stimulate the custom to active expression in the individual at the proper season ...; and (d) Factors which determine the manner in which migration is actually performed. (Thomson 1926, p. 264)<sup>8</sup>

The idea that there is a plurality of complementary causes of migration was a theme that Mayr and Meise explicitly endorsed as the most appropriate

framework for migration studies. They repeated Thomson's four-fold division of complementary causes. Mayr and Meise's discussion of the evolutionary aspects of migration also followed Thomson's discussion in many other respects, which they acknowledged. For example, they defended Thomson's view (which Thomson attributed to Alfred Russel Wallace) that for each species of migratory bird, there is an area within its overall range that is ecologically most suitable for the breeding season, and another area most suitable during the rest of the year. For each species, these two areas once coincided, but have since separated to a greater or lesser extent as the range of the species has increased. Migratory behavior has evolved in conjunction with the separation of the two areas (Thomson 1926, pp. 282–283).

Thomson promoted this account of the evolutionary origins of migration over earlier ice-age accounts whereby – to put the hypothesis in its most extreme form – the ice age displaced temperate climate birds from their homeland, to which they returned somehow instinctively after the ice melted in order to breed.

The ice age theory was the major foil of Mayr and Meise's paper. For example, they pointed out that the retreat of the ice had occurred very slowly. It is therefore much more reasonable to suppose that migratory routes were established *gradually*, with the opening up of new unoccupied areas suitable for breeding and with plentiful resources for the rearing of offspring (Mayr and Meise 1930, p. 157).

Mayr's earlier serin project also figured into the migration paper because it provided Mayr with a well documented and pretty well understood case of a gradual colonization of new breeding grounds leading to longer and longer migration routes (at least of the northernmost breeders), and which had (presumably!) nothing to do with retreating ice.

Mayr and Meise addressed various issues concerning the role of selection in the evolution of migration. They acknowledged that the migration drive must have some selective advantage in order to be maintained – for example, winter conditions must lead to selection against non-migrants that remain in their northern breeding grounds (Mayr and Meise 1930, p. 158). They also considered, without completely resolving, possible selective *disadvantages* of migration – for example, increased competition in tropical regions, where so many migrating birds overwinter. They suggested that a number of different species might be able to overwinter in a fairly small tropical area by utilizing different resources there (*ibid.*, p. 160). They also remarked on the difficulties of explaining, from the point of view of natural selection, those migration routes that carry birds much farther south than they really need to go in order to reach suitable overwintering habitats, and long migration routes over the ocean to relatively small island targets (*ibid.*, p. 164). They nonetheless concluded that selection must play a role in the persistence of migratory behaviors.<sup>9</sup>

At any rate, by 1928, when he wrote the bulk of the Mayr and Meise paper, Mayr's interests in and attitude towards evolutionary theorizing had changed considerably, and that change coincided with his first references to the proximate/ultimate distinction, as articulated especially by Thomson. It is not

too surprising then, that when Mayr returned to the proximate/ultimate distinction in the mid fifties and sixties, he illustrated it with examples from migration studies, since it was in this connection that he first thought hard about the distinction, and this was the occasion for his first forays into evolutionary theorizing.

There is another interesting parallel between Mayr's 1961 paper and the circumstances under which he first came to deal with the proximate/ultimate distinction. And that has to do with Mayr's criticism of Loeb in the 1961 paper. Why would Mayr have selected for criticism in 1961 a scientist so long gone from the scene as Loeb?

Interestingly, Thomson had ended his 1926 book with a discussion of Loeb's views on animal movement, and in particular Loeb's work on phototropic movements (Thomson 1926, pp. 320–321). The perceived importance of the incidence of light as an immediate or proximate factor causing migration made it all the more imperative, I would suppose, for Thomson to refer to Loeb, who had sought to explain many cases of animal movements completely in terms of photochemical reactions. As Thomson described Loeb's approach, "The explanation Loeb gives of such [movements] is purely a physico-chemical one" (*ibid.*, p. 321).

Thomson meant that Loeb seemed to have no additional need of an *ultimate* cause to explain phototropic movements. Loeb certainly recognized that phototropic movements are sometimes useful for survival and reproduction – as when a caterpillar emerges from the pupal stage at the base of a plant, and moves up the stem of the plant toward the sun, and thereby toward the leaves upon which it feeds. But Loeb sometimes suggested that the usefulness of a phototropic movement is superfluous to explaining the existence of that behavior. The frequency of phototropic movements throughout nature can be explained entirely in terms of the combined presence of phototropic substances and other anatomical and physiological conditions:

There is only one way by which such purposeful mechanisms can originate in nature: namely, by the existence in excess of the elements that must meet in order to bring them about.... The prerequisites for heliotropism [instinctive movement toward the sun] are a symmetrical body form, which seems to be present in almost all organisms ... and the presence of photosensitive substances, which is not quite so common, but certainly not infrequent.... As the two conditions mentioned above are quite common, the laws of probability make it necessary that in a certain number of cases both conditions will be fulfilled, and then we may expect heliotropic actions. If it now occurs that in an organism the turning to the light helps it to find its food, as is the case with certain caterpillars .... we have a "purposeful mechanism." (Loeb 1906, p. 161).

To which Thomson responded,

When one comes to the question of the stimuli which periodically evoke migration one may seem to be on easier ground. A superficial explanation on simple mechanistic physiological lines is possible, as has been indicated, but there remains the deeper question as to how in the history of the race the particular stimulus and the particular response have become linked together as a natural chain of cause and effect. (Thomson 1926, p. 326)

It is not clear when Mayr first read Loeb for himself, rather than just reading accounts of Loeb's views. Mayr recalls only reading Loeb carefully in the late seventies and early eighties when he was writing *The Growth of Biological Thought*. He does not recall how he chose the Loeb quotation for the 1961 article. And he does not recall when he acquired several of Loeb's books. But he does recall that Loeb had long been considered "kind of a joke" in anti-mechanist circles (Mayr, personal communication). It is clear that Mayr was early on aware of Loeb's views by "word of mouth," and through published accounts of his views by others, like Thomson.

THE PROXIMATE/ULTIMATE DISTINCTION IN CONNECTION WITH MAYR'S LATER CAPACITY AS SPOKESMAN FOR EVOLUTIONARY BIOLOGY

In his 1961 article, Mayr did not refer to his own, or Thomson's, earlier migration work, nor did he refer to his own, or Thomson's, earlier articulation of the proximate/ultimate distinction. In 1982, in *The Growth of Biological Thought*, Mayr cited as precedent for his own discussion of the proximate/ultimate distinction an article by John Baker, published in 1938.

Baker's topic, the existence of fairly distinct breeding seasons for many birds, was closely related to the issue of migration – especially spring migrations. And like migration, the phenomenon of breeding seasons had elicited a profusion of explanations. Baker sought to introduce some order to the discussion by reminding his colleagues of the important distinction between "proximate" and "ultimate" causes:

Animals have evolved the capacity to respond to certain stimuli by breeding. In cold and temperate climates it is usually clear that the season adopted allows the young to grow up in favourable climatic conditions, and one may say that in a sense these conditions are the ultimate cause of the breeding season being at that particular time. There is, of course, no reason to suppose that the particular environmental conditions favourable to the young are necessarily the one or ones which constitute the proximate cause and stimulate the parents to reproduce. Thus abundance of insect food for the young might be the ultimate, and length of day the proximate cause of a breeding season. (Baker 1938, p. 162)

To organize further the variety of proximate causes that had been hypothesized, Baker distinguished between "internal" and "external" proximate causes, the external having to do with environmental cues (changes in temperature, light, rainfall, etc.), and the internal having to do with physiological stimuli (hormonal changes, etc.).<sup>10</sup>

Although the title of the paper was "The Evolution of Breeding Seasons," Baker had very little to say about evolution *per se*. He was mainly interested in proximate causes, but more specifically proximate causes that obtain in the environments in which the species in question have evolved. A laboratory physiologist might identify factors that start and stop the reproduction of a particular species in the lab, but those factors might differ considerably from

the factors that secure survival and reproductive benefits for that species in the environment it inhabits (*ibid.*, pp. 162, 175). Overemphasis on laboratory physiology, Baker felt, had resulted in underemphasis on field observations relevant to understanding both the evolutionary history and the *actual* proximate causes of breeding seasons. His article opened with the following critique of the laboratory physiological approach, in which he compares the laboratory physiologist to a “savage!”

Few subjects call more urgently for an evolutionary and ecological outlook than that of breeding seasons. The great intrinsic interest of physiological research on means whereby reproduction may be started and stopped in the laboratory may obscure the very nature of the problem that is being investigated. This may be illustrated by a simile. If an intelligent savage were given a model steam railway engine, he might make many interesting observations on its functions. He might study its locomotion on sand and under water and discover ways in which its progression could be started and arrested. He might find the effectiveness of mud, clubs, &c., as arresting agents. Yet his studies would lack something if he did not know that the ordinary ecological behaviour of an engine is to run in air on rails, and that its progression is designed to be controlled by the throttle and brake. The design of the throttle and brake is an example in the simile of the directive agencies in evolution, whatever they may have been. (Baker 1938, p. 161)

Again, a version of the proximate/ultimate distinction that proved influential for Mayr included a critique of experimental physiology.

Whether Mayr was influenced directly by Baker in 1938, or indirectly later via David Lack is not clear. Baker’s proximate/ultimate distinction was certainly influential for Lack, who attributed the idea to Baker, and who raised the issue about a dozen times in his 1954 book, *The Natural Regulation of Animal Numbers*. For Lack, the proximate/ultimate distinction provided a way to focus on ultimate questions, while acknowledging without addressing the complementary proximate questions. Lack discussed the ultimate vs. proximate causes of various phenomena connected to the regulation of population size – clutch size, regulation of breeding season, irruption, migration, and dispersal.

Mayr and Lack were close friends as well as close colleagues with mutual interests in ornithology, evolutionary biology and ecology. Mayr read and commented on Lack’s entire manuscript before it was published (Lack 1954, see “Acknowledgements”).

Mayr read Lack’s manuscript in 1953. It was in 1954, as best I can tell, that Mayr began to take up the proximate/ultimate distinction again, employing it for somewhat different purposes than earlier. It is not surprising that Mayr should think of Baker as precedent the second time around, given the prominence of Baker’s version of the distinction in Lack’s book at the same time.

Mayr’s reading of Lack’s manuscript proved to be a significant re-encounter with the proximate/ultimate distinction, but it might not have been, were it not for the career change that Mayr was undergoing at the time. Let me briefly set the stage.

1953 was also the year that Mayr left the American Museum of Natural History and went to Harvard (Mayr 1982a, pp. 104 ff.; see also Bock’s contribution to this volume). He recalls that this was an extremely important

transition for him – from the status of museum curator to Harvard professor (ibid.; and Mayr, personal communication). He also recalls that this was an important step in his transition from ornithologist and systematist (with evolutionary interests) to evolutionary biologist – a transition most clearly marked (he maintains) by the difference between *Systematics and the Origin of Species* (1942) and *Animal Species and Evolution* (1963a), the latter of which he was engaged in writing throughout the 50s (Mayr, personal communication; see also Mayr 1982a, pp. 26–27). He further recalls that the move provided the opportunity and license to speak about biology from a different viewpoint – in short, to “philosophize,” and reflect upon the history of biology. The move also made possible, he believes, other opportunities for professional advancement, such as his election to the National Academy of Sciences, and his appointment to important professional committees, such as the Biology Council established by the National Academy of Sciences – National Research Council (I will have more to say shortly about the Biology Council).

Surely the move to Harvard reflected the fact that Mayr had already established himself as a leader in systematics and evolutionary biology, for example through *Systematics and the Origin of Species* and through his organizational efforts on behalf of the Society for the Study of Evolution and his editorship of the Society’s journal, *Evolution*. Cain and Smocovitis have made clear the extent and significance of these contributions (Cain 1993, 1994; Smocovitis 1992 and in press).

At any rate, through these contributions, and through his move to Harvard, Mayr increasingly assumed a position as representative of, and spokesman for, evolutionary biology. Mayr was certainly not evolutionary biology’s only major representative and spokesman – in the U.S., Theodosius Dobzhansky and George Simpson were also active and influential in this regard. But Mayr was certainly no less a leader and figurehead than Dobzhansky and Simpson. He also became *the* representative and spokesman for evolutionary biology at Harvard when he assumed the position of Director of the Museum of Comparative Zoology in 1961.

The use that Mayr made of the proximate/ultimate distinction in his capacity as spokesman for evolutionary biology is connected with the fact that, during the same period that his reputation as a leader in the field was growing so quickly, molecular biology was also continuing to gain in prestige. Mayr returned to the proximate/ultimate distinction in order to defend the importance of systematics and evolutionary biology at a time when molecular biology was casting an ever greater shadow over the natural historical sciences.

Imagine that some people associate 1953 not with Mayr going to Harvard, but with the discovery of DNA by James Watson and Francis Crick! This was a particularly stunning and highly touted success in what was already considered to be the most successful area of biology, and often more expansively as the “new biology.” Success spawned success, as more and more important details of the replication, transcription and translation of genetic information were discovered.

Mayr, Dobzhansky and Simpson sensed and responded to what they perceived as a “bandwagon effect,” attracting the lion’s share of attention, resources, and bright students away from more traditional areas to molecular biology.<sup>11</sup> Simpson expressed himself in the most extravagant language:

The rate of progress [in the various biological sciences] is uneven, and rapid advances take place now in one direction and now in quite another. Once a shove has been given in one direction, perhaps by a technological or conceptual breakthrough, perhaps by individual enthusiasm, perhaps by what seems pure chance, a band wagon effect ensues. Students flock to the accelerating front; money is poured into it; professional advancement, fame, and fortune follow it. That is only natural and is in one respect desirable, for the band wagon effect feeds into a circle by which the rate of discovery in some one field is indeed increased.

Fortunately, more than one aspect of biology may accelerate at the same time, and with the great increase in numbers of biologists not all crowding onto the same band wagon. The gaudiest band wagon just now is manned by reductionists, travels on biochemical and biophysical roads, and carries a banner with a strange device: DNA. There are, however, a good number of other, perhaps less gaudy band wagons, going down other, perhaps less rapid roads, under banners perhaps less vehemently saluted. At any rate, we salute them all, and yet may fear that these band wagons diminish travel on still other roads, which are falling into neglect but which are also essential to reach the destination toward which all are, or should be travelling. (Simpson 1964, pp. 113–114)

In an editorial in *Science*, Mayr expressed his concern somewhat less extravagantly, but much more straightforwardly:

Bright young students quite naturally look for the greenest pastures. Recruitment thus becomes a serious problem. This is aggravated by the attitude of the Young Turks in the new areas. They tend to regard the more classical branches of their science with unconcealed contempt. At worst, this intolerance leads them to attempt to cut off funds from the more classical fields. The situation is further aggravated by the attitude of some foundations and science administrators. They are justified in fostering exploitation of breakthroughs, but it seems unwise for them to pour most of their funds into the glamor fields. The follow-up of breakthroughs rarely requires large foundation support. (Mayr 1963b, p. 1)

In his autobiographical “Recollections on my Scientific Development,” Mayr recalled this period of his life, and this role, as follows: “This was near the beginning of the upsurge of molecular biology and it required constant vigilance to prevent that all financial resources and new positions would be given to this new field” (Mayr 1982a, p. 120; see also pp. 131–132).

Mayr and Simpson did not merely *complain* about disparities in status and funding. Mayr, Dobzhansky and Simpson had, by this time, actually tried to compete with the molecular biologists for foundation support, and had lost. During the early fifties, the three of them met several times with William Loomis and Warren Weaver of the Rockefeller Foundation, the foundation that had, especially at the hands of Weaver, used its powers of patronage to try to reform biology through the application of techniques from physics and chemistry. Mayr, Dobzhansky and Simpson tried but failed to get Loomis, Weaver and the Rockefeller to pledge greater support to systematics and evolutionary biology – or more specifically, to what the three of them were calling “the new

systematics” (see Loomis’s diary entries Nov. 13, 1950, and Jan. 23, 1951; also inter-office correspondence from Loomis, Jan. 19, 1951 and Jan. 23, 1951; also Mayr to Weaver Jan. 24, 1951; these records are all located in Record Group 2–1951, Series 200, Box 157, Folder 3454, at the Rockefeller Archive Center).

That is the context for appreciating Mayr’s re-encounter with the proximate/ultimate distinction. In 1954, in the midst of his concerns and efforts with regard to the decreasing status of evolutionary biology relative to molecular biology, and at the time when his reputation as a leader in evolutionary biology was growing, he accepted the position at Harvard that, he felt, authorized him to speak on behalf of evolutionary biology. It was at this time that he read Lack’s manuscript, in which the proximate/ultimate distinction was so prominently featured.

Shortly thereafter, Mayr was invited to serve on the Biology Council, a deliberative body of the Division of Biology and Agriculture of the National Academy of Sciences – National Research Council. The purpose of this group, which met approximately monthly, was no less than to map out the “conceptual structure” of biology, to spell out its “intellectual order.” The leaders of the Council, Paul Weiss and Ralph Gerard, envisioned that the discussion would have wide-ranging, concrete consequences, including the institutionalization of biology. As Gerard asked, “What are the logical ways in which the great area of biology ought to divide itself in the future? Are the academic departments that have come down from the past now outdated, and should there be a new kind of organizational structure in universities” (Gerard 1958, p. 104)? In connection with their discussion of the conceptual structure and institutionalization of biology, the Council members were also encouraged to consider issues of future funding, and the “recruitment of more superior students” (*ibid.*, p. 103).

Mayr seized the opportunity to secure the place of evolutionary biology in the biology of the future, a place that he feared was being threatened by the success of molecular biology. He used the proximate/ultimate distinction over and over again in correspondence and in conferences to make the point that there is more to biology than the study of proximate causes. As he pleaded with Weiss early on:

As you a true biologist knows, this is only part of biology. There is an equally large part which might be called even more typically biological which deals with historical phenomena and population phenomena.

Some branches of biology are traditionally neglected.... You have pointed out in some of the your writing the lure of the bandwagon. Biology has certainly suffered badly from this phenomenon.... Now I am afraid there is not much one can do about this bandwagon phenomenon except to be keenly aware of it and try not to tear down any branch of biology merely because it is either in temporary eclipse or *has just now no outstanding representative*. (Mayr to Weiss, Jan. 18, 1954, provided by Mayr: my emphasis).

The passage I emphasized is quite revealing with respect to the position Mayr felt himself to be preparing for.

One of the activities of the Council was a two-day conference, held in October, 1955, at which many of the issues before the council were discussed formally and recorded in the conference transcript (Gerard 1958). Despite the presence of a number of eminent and vocal biologists on the Council, representing most every area of biology, Mayr was a dominant presence at this conference, articulating and illustrating the proximate/ultimate distinction and coaxing the other council members into endorsing it as an important way of conceptualizing the structure of the biological sciences. For example:

MAYR: There is another viewpoint or scheme of classification which is very useful and was mentioned yesterday, but has not yet been incorporated into our system. I am referring to the classification of causes in biology into proximate and ultimate factors and to the confusion resulting from failing to make this distinction. In almost any natural history phenomenon, like bird migration, you have different ultimate or proximate factors – proximate factors being something purely physiological that makes a given individual under circumstances go, while the ultimate factor is natural selection creating a genetic system which then responds to these proximate factors. Should we discuss this and does it belong to this system?

...

MAYR: That has been one cause of confusion in the past. The physiologist, quite obviously, tends to see first the proximate factors, while, let's say, the evolutionist thinks and talks about ultimate factors. Statements then come out that look like they were opposing each other, while actually there is no conflict whatsoever. (Gerard 1958, p. 161)

It is not surprising that Mayr would come back to the proximate/ultimate distinction for a defence of evolutionary biology in a period that he believed was marked by a one-sidedly reductionistic conception of biology, because this was the way he had seen the distinction employed by Thomson and Baker. Mayr continued to find it a helpful tool throughout the 50s and 60s, during which time, as he and Dobzhansky and Simpson perceived matters, the status of evolutionary biology relative to molecular biology continued to slide.

Mayr witnessed this locally as well as nationally. Consider two related examples: in 1958, a special committee was convened by President Pusey to review the future of biology at Harvard. The committee included some non-Harvard members, notably Warren Weaver. As Weaver described the issues before the committee: 1) Should Harvard continue to maintain its “prized breadth of training” in biology?, and 2) (a related question) should the natural history institutions at Harvard, including the Museum of Comparative Zoology and the Gray Herbarium, be absorbed into the Department of Biology (W. W. Diary, Apr. 17, 1958, Rockefeller Archive Center)? Presumably, a decision to absorb the Museum and the Herbarium would be consistent with a decision to refocus and narrow the training of biologists at Harvard.

One year later, in 1959, Weaver was invited back by Pusey, this time to serve on a committee overseeing two appointments in biology – specifically, in botany. There was no question that the top two candidates were accomplished, but there was a problem with their credentials, namely the focus of their

training in physics and chemistry rather than biology. As Weaver described the problem,

the botany group at Harvard is worried about the future, and disturbed indeed that most of the recent appointments, including the two now under consideration, are in modern experimental fields. There is a great deal of discussion of this dilemma, with the different witnesses brought before the committee taking positions which could be accurately forecast in advance. Of the two appointments now under consideration one is in plant physiology, or more strictly in the biochemical aspects of plant growth and development.... The person being sought for this position, interestingly enough, had essentially no training in biology, but all of his graduate training in chemistry. The other appointment is that of a biophysicist who, in fact, had all of his graduate training in physics rather than in biology. He has, however, subsequently trained himself in genetics and he could now be described as a molecular geneticist. (W. W. Diary, Feb. 4, 1959, Rockefeller Archive Center)

And as Weaver summarized the discussions that resulted,

However badly the old guard feels about the matter, it is quite clear what is happening to biology at Harvard and what will continue to happen. They will not be able to move forward in the new fields and maintain all of their old *strength* and *breadth* in the classical fields. (ibid.)

The future direction of biology at Harvard, the organization of the biological sciences, and the allocation of funds among the various biological programs, were the subject of considerable inhouse politicking. Mayr, the new Director of the Museum, employed the medium of the annual reports to the President, and his own publicity reports, to remind the administration and his fellow faculty members that molecular biology was only *part* of biology. The 1967–68 annual report employed the proximate-ultimate distinction to defend the research carried out in the Museum, and the courses offered by its faculty:

No other branch of science ranges between such extremes as biology. Biologists who attempt to unravel the secrets of the structure of organic molecules or cell physiologists who study the physical chemistry of intracellular membranes seem to be dealing with an entirely different world than that of the students of evolution or behavior. The reason these worlds are so different is that every organism in itself seems to comprise two worlds.

On the one hand is the body, with its chemistry and physiology.... From the moment that the fertilized egg cell begins to develop, until death, an almost unlimited number of functional tasks must be performed, from the molecular level up to the level of the behavior of the organism as a whole. It is the task of functional biology to study this aspect of organisms. On the other hand is the individual's heritage, contained in the genetic program of the DNA of every nucleus. This genetic program is the result of evolution; it is the result of natural selection through countless past generations. The evolutionary biologist, the research worker in the MCZ, studies the forces that lead to evolutionary changes. He deals with all the phenomena related to the evolutionary success of various organisms as determined by their genetic endowment.

...

The differences between the two kinds of biology are reflected not only in research but also in instruction. There is great need for instruction in evolutionary, behavioral, and systematic

biology, and such instruction must be handled by qualified experts in these fields. This is why the scientific staff of the Museum is making an increasingly large contribution to both undergraduate and graduate instruction, as set forth in recent annual reports. (Mayr 1969a, pp. 6–7)

Given the special contribution to research and teaching made by the Museum faculty, it was imperative that the Museum not be fully merged with the Department of Biology (one of the issues under consideration during the 50s by the Pusey committees, and still under consideration in the 60s). The Museum should instead be fairly autonomous, with, for example, final say over appointments (see also Mayr 1969b).

#### CONCLUDING REMARKS

Ernst Mayr's defense of the distinction between "proximate" and "ultimate" causes is generally considered to be a classic contribution to the philosophy of biology. His best known discussion of the subject, "Cause and Effect in Biology," is required reading for all who wish to enter that field. Lack of familiarity with Mayr's position would be inexcusable; any more than minor disagreement with his insistence on the proximate/ultimate distinction would be heretical.

Among philosophers of biology, that is. Philosophers of science who specialize in the physical sciences, and who do not show much appreciation for the distinction, might be excused as simply provincial. And therein lies part of the importance of the distinction for philosophers of biology. The fact that the distinction is believed to be crucial for understanding biology, if not physics, suggests that philosophers should be wary of extrapolating from the character of physics to the character of science in general.<sup>12</sup>

Mayr indeed intended to reorient the physics-dominated philosophy of science of the time. It was not a difficult transition from the role of spokesman for evolutionary biology to philosopher of biology. Just as, for Mayr, there is no unitary form of explanation in biology, there can be no unitary philosophy of science. Just as the need for ultimate (in addition to proximate) explanations protects biology from being reduced to molecular biology and finally to chemistry and physics, and as the need for ultimate explanations thus ensures the autonomy of biology, so too it ensures the autonomy of philosophy of biology. It is hard to exaggerate the significance of Mayr's defense of the proximate/ultimate distinction in establishing philosophy of biology as a legitimate *special* area of inquiry.

Mayr himself categorizes the 1961 paper as a contribution to the philosophy of biology, and enjoys the impact it eventually had in the philosophy of biology community (although he laments that the distinction took so long to catch on among philosophers of biology! – Mayr 1982a, pp. 129–131, 148). Describing the presentation of a later paper, which dealt with the proximate/ultimate distinction, Mayr recalls,

I repeated my thesis and in a deliberately provocative manner I pointed out all sorts of phenomena that are different in biology from physics. I also emphasized that one cannot talk about a philosophy of science when one only deals with the phenomena of physics. Rather amusingly the speaker who followed me in the session on December 27, 1965 was a physicist lecturing on philosophy of science. He was sufficiently rattled by my sharp attack on the physicists that throughout his lecture he corrected himself whenever he said philosophy of science, to philosophy of physics. (Mayr 1982a, p. 148; the reference is to Mayr 1969c)

But this just makes it all the easier to think of Mayr's articulation of the proximate/ultimate distinction first and foremost as a contribution to philosophy of biology, and to overlook its earlier roles in Mayr's scientific research and in his promotion of evolutionary biology. Again, if we want to understand why Mayr had the proximate/ultimate distinction on his mind in the late 50s and early 60s, and why he elaborated the distinction in the way he did in 1961, then it helps to consider the roles of the distinction in his *previous* two careers, rather than in terms of his *subsequent career* as a philosopher/historian of biology.

I believe that a similar story could be told about several other ideas that we attribute to Mayr and construe as significant contributions to the philosophical literature, like the distinction between essentialism and population thinking, which was initially important to Mayr in his scientific research, and then in his role as representative and spokesman for evolutionary biology (e.g., in the Biology Council meetings discussed above), and finally as a means of legitimizing philosophy of biology as a special area of inquiry.

#### NOTES

<sup>1</sup> I would like to thank Mark Adams, Joe Cain, Jane Maienschein, and Marc Swetlitz for their help. Thanks also to John Greene for organizing this tribute to Ernst Mayr. And thanks to Ernst Mayr for providing the occasion, through his many contributions in so many roles.

<sup>2</sup> To be sure, the careers and periods described above overlap somewhat. But the fact that Mayr has sometimes worn two, or even three, hats at one time should not distract us from noticing that he has, after all, worn more than one hat. It is also quite possible that the three careers I have described do not exhaust the different roles that Mayr has played.

<sup>3</sup> I should further clarify what this paper is about, and what it is not about. It is about the role(s) of the proximate/ultimate distinction in the historical development of Ernst Mayr's thought. It is *not* about the role of Ernst Mayr in the historical development of the proximate/ultimate distinction. The latter story would concern the respects in which the proximate/ultimate distinction as articulated by Mayr is similar to or different from a number of much early distinctions that are *sufficiently similar* that the idea of comparing and contrasting them to Mayr's distinction is not outlandish. These earlier distinctions would include the distinction between material and efficient causes vs. final causes as drawn by Aristotle, the distinction between primary and secondary causes as drawn by mechanical philosophers like Descartes, Newton and Boyle, the distinction between mechanical and teleological explanations as drawn by Kant; etc. Mayr himself has gone to great lengths, beginning with the 1961 article to distance himself from these earlier thinkers, which suggests that there are indeed similarities to be overcome. Moreover, precisely because Mayr addresses the similarities and differences, it is reasonable to consider his place in a tradition that includes the other distinctions.

That very long story interests me very much, but not here. John Greene addressed these issues in an interesting essay that caught Mayr's attention (Greene 1986, Mayr 1986). One of the things about

the longer story that interests me most is that, beginning in the 18th century, these distinctions were used more and more to differentiate the study of the living world, where mechanical *and* teleological reasoning were deemed appropriate and necessary, from the physical sciences, where teleological reasoning was considered increasingly inappropriate. This part of the story, and Mayr's place in it, is sketched in Beatty 1990a.

Because I am not concerned here with the general history of the proximate/ultimate distinction, I will also not be referring to several important or otherwise interesting 20th century elaborations of the distinction that were not particularly influential for Mayr. These include the distinction as drawn by Huxley (1916, p. 161) and Tinbergen (1951, pp. 151–152, and especially 1963).

<sup>4</sup> Hesse's book was translated, but also partly revised, by Allee and Schmidt (Hesse, Allee and Schmidt 1937). The portions of the book that I rely upon here were not revised. In what follows, I quote from Allee and Schmidt's translations of these unrevised sections.

<sup>5</sup> Hesse was also a physiologist. He worked in particular on vision and the structure of the eye.

<sup>6</sup> Hesse, however, was by no means as extreme in his criticisms of evolutionary theorizing as Loeb. Indeed, Hesse was the author of a general textbook on evolutionary biology, *Evolutionary Theory* (Abstammungslehre) *and Darwinism*, which went through at least six editions, the first published in 1901, the sixth in 1922. Hesse also insists that a complete account of animal distributions requires an evolutionary/historical, in addition to a physiological/ecological perspective, though again, the speculative nature of the former enterprise reduced the value of its contribution.

<sup>7</sup> Thomson was son of the evolutionist and popularizer of science, J. Arthur Thomson, who was also very interested in ornithology, and who also wrote a major text on the subject (J. A. Thomson 1923). The connection between A. L. Thomson's views on the need for ultimate as well as proximate-cause explanations in biology, and the antireductionist views of his father, is probably worth exploring (see e.g., J. A. Thomson 1920).

<sup>8</sup> Like Thomson, Mayr (1961) invoked two main categories of causation, and four subcategories, though the four subcategories that Mayr settled upon in 1961 clearly differ from Thomson's. However, Mayr originally adopted Thomson's classification, as I proceed to point out in the text above.

<sup>9</sup> Though selection could not be responsible for the origin of migratory behaviors, since selection only destroys, it never creates (a conception of selection that Mayr would later vigorously argue against!; Mayr and Meise 1930, p. 158).

<sup>10</sup> Recall that Mayr (1961) also employed the intrinsic/extrinsic distinction in his discussion of proximate causes.

<sup>11</sup> I have discussed their reaction elsewhere (Beatty 1990a). In what follows, I will summarize those points and add a few more.

<sup>12</sup> See, for example, the issues as posed by Rosenberg (1981, Chapter 1 et passim).

## REFERENCES

- Allen, Garland: 1975, *Life Science in the Twentieth Century*, Wiley, New York.
- Allen, Garland: 1978, *Thomas Hunt Morgan: The Man and His Science*, Princeton University Press, Princeton.
- Baker, John R.: 1938, 'The Evolution of Breeding Seasons', in G. R. de Beer (ed.), *Evolution: Essays on Aspects of Evolutionary Biology*, Oxford University Press, Oxford.
- Beatty, John: 1990a, 'Teleology and the Relationship of Biology to the Physical Sciences in the Nineteenth and Twentieth Centuries', in F. Durham and R. Purrington (eds.), *Newton's Legacy: The Origins and Influence of Newtonian Science*, Columbia University Press, New York.
- Beatty, John: 1990b, 'Evolutionary Anti-Reductionism: Historical Reflections', *Biology and Philosophy* 5, 199–210.
- Cain, Joseph: 1993, 'Common Problems and Cooperative Solutions: Organizational Activity in Evolutionary Studies, 1936–1947', *Isis* 84, 1–25.
- Cain, Joseph: 1994, 'Ernst Mayr as Community Architect: Launching the Society for the Study of Evolution and the Journal *Evolution*', *Biology and Philosophy*, this issue.

- Chapman, Frank M.: 1903, *Bird-Life: A Guide to the Study of Our Common Birds*, Appleton, New York.
- Cittadino, Eugene: 1980, 'Ecology and the Professionalization of Botany in America, 1890–1905', *Studies in the History of Biology* **4**, 171–198.
- Eifrig, G.: 1924, 'Is Photoperiodism a Factor in the Migration of Birds?', *Auk* **41**, 439–444.
- Gerard, R. W., ed.: 1958, *Concepts of Biology*. National Academy of Sciences – National Research Council, Washington, D. C.
- Greene, John C.: 1986, 'The History of Ideas Revisited', *Revue de Synthèse* **4**, 201–228.
- Haeckel, Ernst: 1899, *The Riddle of the Universe*, translated in 1900 by Joseph McCabe, Harper, New York.
- Hagen, Joel B.: 1986, 'Ecologists and Taxonomists: Divergent Traditions in Twentieth-Century Plant Geography', *Journal of the History of Biology* **19**, 197–214.
- Hagen, Joel B.: 1991, 'Organism and Environment: Frederick Clements's Vision of a Unified Physiological Ecology', in Ronald Rainger *et al.* (eds.), *The American Development of Biology*, Rutgers University Press, New Brunswick.
- Hesse, Richard: 1922, *Abstammungslehre und Darwinismus* (6th ed.), Teubner, Leipzig.
- Hesse, Richard: 1924, *Teirgeographie auf ökologischer Grundlage*, Fisher, Jena.
- Hesse, Richard, W. C. Allee and Karl P. Schmidt: 1937, *Ecological Animal Geography*, Wiley, New York.
- Huxley, Julian: 1916, 'Bird-Watching and Biological Science: Some Observations on the Study of Courtship in Birds', *Auk* **331**, 142–161, 256–270.
- Kellogg, Vernon: 1907, *Darwinism To-Day*, Holt, New York.
- Lack, David: 1954, *The Natural Regulation of Animal Numbers*, Oxford University Press, Oxford.
- Loeb, Jacques: 1906, *The Dynamics of Living Matter*, Columbia University Press, New York.
- Loeb, Jacques: 1916, *The Organism as a Whole, from a Physico-Chemical Standpoint*, Putnam, New York.
- Loeb, Jacques: 1918, *Forced Movements, Tropisms, and Animal Conduct*, Lippincott, Philadelphia.
- Mayr, Ernst: 1926, 'Die Ausbreitung des Girlitz (*Serinus canaria serinus* L.): Ein Beitrag zur Tiergeographie', *Journal für Ornithologie* **74**, 569–671.
- Mayr, Ernst and Wilhelm Meise: 1930, 'Theoretisches zur Geschichte des Vogelzuges', *Der Vogelzug* **1**, 149–172.
- Mayr, Ernst: 1932, 'A Tenderfoot Explorer in New Guinea', *Natural History* **32** (1), 83–97.
- Mayr, Ernst: 1942, *Genetics and the Origin of Species*, Columbia University Press, New York.
- Mayr, Ernst: 1961, 'Cause and Effect in Biology', *Science* **134**, 1501–1506.
- Mayr, Ernst: 1963a, *Animal Species and Evolution*, Harvard University Press, Cambridge.
- Mayr, Ernst: 1963b, 'The New versus the Classical in Biology', *Science* **141**, 763.
- Mayr, Ernst: 1969a, 'Annual Report, 1967–1968', Museum of Comparative Zoology, Harvard University, Cambridge.
- Mayr, Ernst: 1969b, 'The Museum of Comparative Zoology and its Role in the Harvard Community', Museum of Comparative Zoology, Harvard University, Cambridge.
- Mayr, Ernst: 1969c, 'Discussion: Footnotes on the Philosophy of Biology', *Philosophy of Science* **36**, 197–202.
- Mayr, Ernst: 1982a, 'Recollections on My Scientific Development', manuscript provided by Mayr.
- Mayr, Ernst: 1982b, *The Growth of Biological Thought*, Harvard University Press, Cambridge.
- Mayr, Ernst: 1986, 'The Death of Darwin?' *Revue de Synthèse* **4**, 229–236.
- Rosenberg, Alexander: 1985, *The Structure of Biological Science*, Cambridge University Press, Cambridge.
- Rowan, William: 1931, *The Riddle of Migration*, Williams and Wilkins, Baltimore.
- Shäfer, E. A.: 1907, 'On the Incidence of Daylight as a Determining Factor in Bird-Migration', *Nature* **77**, 159–163.
- Simpson, George Gaylord: 1964, *This View of Life*, Harcourt Brace, New York.
- Smocovitis, V. Betty: 1992, 'Unifying Biology: The Evolutionary Synthesis and Evolutionary Biology', *Journal of the History of Biology* **25**, 1–65.

- Smocovitis, V. Betty: 1994, 'Organizing Evolution: Founding the Society for the Study of Evolution,' *Journal of the History of Biology* **27**, 241–309.
- Thomson, A. Landsborough: 1924, 'Photoperiodism in Bird Migration', *Auk* **41**, 639–641.
- Thomson, A. Landsborough: 1926, *Problems of Bird-Migration*, Witherby, London.
- Thomson, J. Arthur: 1920, *The System of Animate Nature*, Holt, New York.
- Thomson, J. Arthur: 1923, *The Biology of Birds*, Sidgwick and Jackson, London.
- Tinbergen, Nikolaas: 1951, *The Study of Instinct*, Oxford University Press, Oxford.
- Tinbergen, Nikolaas: 1963, 'On the Aims and Methods of Ethology', *Zeitschrift für Tierpsychologie* **20**, 410–433.