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Emergence of New Fields in Ecology: The Case of Life History Studies

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ABSTRACT – We examine the emergence of the field of life-history strategies during the 1950s. (We consider a 'field' an area of scientific activity consisting of a theoretical core, a subject of research, a vocabulary and research tools). During the late 1940s and early 1950s, population ecology faced many problems, concerning its conceptual framework, its mathematical models, experimental deficiencies, etc. Research on life-history characteristics remained descriptive, lacking explanations about the causes and significance of phenomena. This was due to the deficiencies of the theoretical framework of population ecology up to the 1950s. The catalyzing factor for the emergence of the new field was the interdisciplinary impacts, and especially the impact of neodarwinism. The elaboration of a new theoretical core, invoking also methodological shifts, was the triggering factor, conditioning the emergence of the new field.

Introduction

This is a case study concerning the field of ecology dealing with the evolution of life-histories and life-history strategies of living organisms. This field is popular among ecologists.[1] However, apart from few review articles[2], its history and dynamics has not yet been studied. In this paper, we intend to describe and analyze the factors which conditioned the emergence of this field in the middle 1950s. We will also study the theoretical innovations of the new field during its first period of development (up to the mid sixties). Since we focus on the cognitive aspects of the field of life history studies, we consider it necessary to provide a brief introduction, in which we describe the method of analysis of these cognitive aspects. First of all we define the concept of 'field' as the unit of our study, and then we describe its structure and analyse the function and the relationships of its elements.

[1] M.J. Cherret, 'Key Concepts: The Results of Survey of our Members' Options'. In: M.J. Cherret (ed.), *Ecological Concepts*, Oxford: Blackwell Scientific Publications, 1989: 1-16.

[2] E.g. S.C. Stearns, 'Life-history Tactics: A Review of the Ideas', *Q. Rev. Biol.*, 51 (1976), 3-47; T. R. E. Southwood, 'Tactics, Strategies and Templets', *Oikos*, 52 (1988), 3-18; M. T. Rocha Pite, T. Avelar and M. Matos, 'The r-K Selection Model and Life-history Strategies', *Cienc. Biol. Ecol. Syst.*, 5 (1985), 269-297.

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The methodological part ends up with a general description of the kind of scientific transition associated with the case study we report. In section two we consider the status of population ecology up to the 50s, and its crisis. The aim of this section is to illuminate the origins of the new field. Furthermore, we focus on the interdisciplinary impacts and especially neodarwinism, which made the emergence of the new field possible, providing important theoretical elements. Finally, in chapter three, we analyze the development of the various components of the field of life history studies during the 50s and 60s.

The Unit of Study

In studies of the cognitive elements of science, the choice of the proper unit of study is of critical importance. There is a whole variety of terms used to define scientific units (e.g. paradigms, research programs, fields, domains, theories etc.). We consider appropriate for the present case the concept of 'field', adopted from Darden and Maull, as well as from Bechtel and Laudan et al.[3] We adopt general definitions of a scientific field, as an area of scientific activity consisting of: i) a theoretical core, ii) a subject of research, iii) a common vocabulary and iv) research tools. Some discrepancies, between our view and that of other authors, concerning the exact list of elements and the relative importance of them, are discussed below. The definition of 'field' allows us to focus separately on the different basic aspects of scientific cognitive activity, e.g. modelling, elaboration of new concepts, theorizing etc., to evaluate the relative importance of each one and to study their interplay. We define the different elements of the field as follows:

i) Theoretical core: This is a collection of general assumptions about reality (sensu Haila)[4] of any kind: hypotheses, laws, principles etc. The theoretical core identifies the kind of objects and determines the method of research.[5]

Darden and Maull,[6] as well as others, seem to underestimate the theoretical correlates determining the emergence of a field. They con-

[3] L. Darden and N. Maull, 'Interfield Theories', *Philos. Sci.*, 44 (1977), 43-64; W. Bechtel, 'The Nature of Scientific Intergration', In: W. Bechtel (ed.), *Intergrating Scientific Disciplines*, Dordrecht: Martinus Nijhoff Publishers, 1986, pp. 3-52; L. Laudan, A. Donovan, R. Laudan, P. Barker, H. Brown, J. Leplin, P. Tagard, and S. Wykstra, 'Scientific Change: Philosophical and Historical Research', *Synthese*, 69 (1986), 141-223.

[4] Y. Haila, 'Hypothetic-deductivism and the Competition Controversy in Ecology', *Ann. Zool. Fennici*, 19 (1982), 255-263.

[5] Laudan et al. (footnote 3).

[6] Darden and Maull (footnote 3).

sider particular techniques or central problems as sufficient components for scientific changes. For them, theoretical statements, concepts or laws, are not of primary importance for field emergence, or for field cognitive structure. On the contrary, in this paper we intend to show that the development of the theoretical core determines the emergence of the field and conditions its problematic, and that it also dictates the development of proper techniques by influencing experimental design. Thus, the theoretical core is the most important element of a field, though not the only one; it is necessary but not sufficient.

ii) Terms: These belong to the vocabulary which is necessary for the construction of theoretical statements and also for the development of research tools.[7] The vocabulary is specific to the particular field, although there are also terms descending from the broader theoretical background of the discipline to which the field belongs.

iii) Subject of research: This includes the set of questions scientists are trying to answer, as well as the set of problems they have to solve in order to confirm and enrich the theoretical core of the field. It corresponds to Darden and Maull's 'domain of facts related to the central problem of the field' and Laudan et al.'s 'context of inquiry'.[8] The very idea underlying the construction of the 'subject of research' is linked to the fact that the definition of a problem on empirical grounds presupposes the determination of a context of inquiry.[9] We will argue that the subject of research is defined by the theoretical core of the field, which also determines the method of research.

iv) Research tools: The items of this category are what Haila and Jarvinen call process of stepwise factualization of theoretical concepts.[10] The choice or elaboration of these tools corresponds to the theoretical core of the field and correlates it with the 'real world'. So, the research tools not only allow for the factualization of the theoretical terms, but they also testify them and make them operational. Furthermore, research tools may enrich the theoretical core of a field, and they very often lead to new theoretical developments. Research tools can be classified into three categories:

(a) Models, especially mathematical ones, are tools for defining and studying the significance of critical parameters and exploring patterns.

[7] Y. Haila, 'The Multiple Faces of Ecological Theory and Data', *Oikos*, 53 (1988), 408-411.

[8] Darden and Maull (footnote 3), p. 44; Laudan et al. (footnote 3), p. 209.

[9] Laudan et al. (footnote 3), p. 209.

[10] Y. Haila and O. Jarvinen, 'The Role of Theoretical Concepts in Understanding the Ecological Theatre: A Case Study on Island Biogeography'. In: E. Saarinen (ed.), *Conceptual Issues in Ecology*, Dordrecht: D. Reidel Publishing Company, 1982: 261-278.

In general, models are built upon certain presuppositions of 'how nature is' derived from the theoretical core of the field. In this sense, models satisfy the theoretical statements of the field providing it with an 'interpretation' of the theoretical core.[11]

(b) Operational tools, are useful elements for data manipulation and testing. Among them, various statistical techniques, life tables etc. were of great importance for the development of the field under consideration.

(c) Experimental techniques for data gathering, and experimental design models: Experimental designs are employed to organize experiments and to define the possible set of outcomes of a particular experiment within the theory under consideration.

We would like to emphasize that theoretical statements, research tools, subject of research etc., are not independent of each other. They form a dialectic unit of interacting elements. We will see later that the emergence of the new field did not only offer a new theoretical background but also triggered the development of new methodologies, encouraged the implementation of new questionnaires and so forth.

In this paper we do not deal with the displacement of a theory or with a scientific 'revolution', but rather deal with the creation of a 'field', emerging within a pre-existing general framework. The general framework along with the interdisciplinary impact on ecology constitutes a wide theoretical 'background' for the new field. It encompasses theoretical elements, concepts, research tools etc. This rather chaotic set of elements is the reference point for the new specific framework. Accordance between the new field and background thinking is essential for the acceptance and conceptual coherence of the latter. The background framework includes the ontological, philosophical and methodological 'principles' governing a scientific domain. For example, as we have already pointed out, any 'strategy of model building' is based upon certain ontological and methodological presuppositions of 'how the world is like' and 'how we should approach it' (e.g. mechanistic nature of the world, reductionistic-analytic methodologies etc.). This 'philosophical' and 'methodological' background is of great importance for the classification of a field into a certain scientific 'tradition'. More specifically, we will argue that the empirical and conceptual crisis in ecology, in association with neodarwinian and interdisciplinary impacts (from mathematics, computer sciences etc.), created the theoretical background of the evolutionary ecology. Within

[11] Haila (footnote 7); P. Taylor, 'Revising Models and Generating Theory', *Oikos*, 54 (1989), 121-126; see also P. Thompson, *The Structure of Biological Theories*, New York: SUNY Press, 1989: 29, 71.

this framework, specific observations and experimental data concerning life history evolution, along with the development of a relevant specific theoretical core concerning this subject, gave birth to the field of life history strategies. Moreover, we will argue that the development of the specific theoretical core, rendered the whole set-up coherent.

Population Ecology up to the Fifties

In the early 1950s, population ecology had been in existence for more than fifty years and considerable progress had already been made. Many theoretical elements, regarding population characteristics, had been accumulated from a wide variety of disciplines, such as morphology, reproduction biology, human demography, as well as physics and mathematics. The theoretical frame of population ecology included hypotheses explaining population growth and involved inter- and intra-specific relationships (e.g. competition, predation, parasitism) and environmental variables (e.g. carrying capacity). A large research area tackling relevant subjects was established.[12] A set of mathematical tools describing changes in population size was available. The introduction of the logistic equation into population dynamics, by Pearl in 1920, entailed from the very beginning the concepts of determinism, equilibrium and homogeneity which, referring to the ontological status of population ecology, had a central role in the whole theoretical construction.[13] In the same vein were the efforts by the theoreticians Voltera and Lotka as well as those by the biologists Thompson and Nicholson. Nicholson in particular guided the development of the field of population ecology during 1930s and 1940s. Indeed, Nicholson's paper (in collaboration with the physicist V. Bailey) was of decisive importance for the further development of population ecology.[14] In this paper, Nicholson and Bailey formulated a deterministic model for a parasite-host system. The structure of this model focused on the average individual and it was explored for factors regulating parasites and host density. According to Krebs, '...Nicholson's (regulation) theory was predominantly a biotic one...'[15]. For Nicholson,

[12] For an extensive account of these subjects see: Sharon Kingsland, *Modeling Nature*, Chicago: University of Chicago Press, 1985; R.P. McIntosch, *The Background of Ecology*, Cambridge: Cambridge University Press, 1985, and idem., 'The Background and Some Current Problems of Theoretical Ecology', *Synthese*, 43 (1980), 195-255.

[13] S.A. Levin, 'Pattern, Scale and Variability: An Ecological Perspective'. In: A. Hastings (ed.), *Community Ecology*, Berlin: Springer-Verlag, 1988: 1-12.

[14] A.J. Nicholson and V.A. Bailey, 'The Balance of Animal Populations', *Part. I. Proc. zool. Soc. Lond.*, 1935, 551-598.

[15] C.J. Krebs, *Ecology*, 2nd edition, New York: Harper and Row Publishers, 1978: 288.

population density determined food and space availability to individual organisms as well as the intensity of parasitism. Hence, density-dependent feedback mechanisms were of primordial importance for population dynamics.[16]

Descriptions of population growth were practised in two steps: (i) description of population structure and abstraction of essential parameters, mainly based on life table techniques, and (ii) description of processes by elaborating mathematical models defining relationships between life-history characteristics and demographic parameters.[17] Leslie, was the first to study in detail the life-history characteristics of animals. He stressed that the understanding of field populations requires better knowledge of the life tables. He was especially interested in the study of the breeding cycle and was the first to construct a life table for rodent populations in one laboratory.[18] Leslie also introduced matrix models in population dynamics (see also Lewis 1942).[19] The structure of matrix models involved both demographic vectors corresponding to animal age structure and transition matrices containing the demographic parameters. Leslie also did a tedious work on estimation of model parameters. The estimation of the intrinsic rate of increase (the parameter *r*) was central to his approach. Without the aid of a computer, the whole enterprise was laborious. Leslie adopted iterative techniques and utilized either the Lotka equation for the precise estimation of the parameter *r* or, as an alternative, he estimated the first latent root of the transition matrix.[20]

The development of mathematical models and statistical tools characterized ecology from 1920 to the early 1950s. According to Morowitz, the main concern of mathematical ecologists was to transform verbal statements, regarding population structure under certain conditions, into equations or models.[21] Thus, theoreticians were able to establish logical relationships among the elements of the models and to organize explanations. Occasionally, this step was followed by the experimental and observational testing of these equations. Lotka-Voltera's and logistic equations were central to this fabrication. All

[16] For an extensive treatment of this matter see G.C. Varley, G.R. Gradwell and M.P. Hassell, *Insect Population Ecology*, Oxford: Blackwell Scientific Publications, 1973.

[17] H.J. Morowitz, 'The Historical Background'. In: T.H. Waterman and H.J. Morowitz (eds.), *Theoretical and Mathematical Biology*, New York: Blaisdell Publishing Company, 1965: 24-35.

[18] P.H. Leslie and R.M. Ranson, 'The Mortality, Fertility, and Rates of Natural Increase of the Vole (*Microtus agrestis*) as Observed in the Laboratory', *J. Anim. Ecol.*, 9 (1940), 27-52; Kingsland, *Modelling Nature* (footnote 12), p. 133; S.C. Stearns (footnote 2), pp. 8-9.

[19] E.G. Lewis, 'On the Generation and Growth of a Population', *Sankya*, 6 (1942), 93-96.

[20] P.H. Leslie, 'On the Use of Matrices in Certain Population Mathematics', *Biometrica*, 33 (1945), 183-212.

[21] Morowitz, (footnote 17), pp. 28-30.

these models were the tools used by ecologists in their effort to study their main subject which was the regulation of population size.[22] The whole period from 1920 to 1940 was fruitful for the theoretical development of ecology and is very often referred to as the 'Golden Age of Theoretical Ecology'.[23] Nevertheless, in spite of euphoria among theoreticians, the progress of theoretical ecology until the early 1950s was a mathematical progress rather than a theoretical one,[24] in the sense that although analytic tools were developed, no coherent conceptual structures were elaborated. After the 1940s, ecology entered a period of major controversies and unsolved problems.

A significant debate on the role of density-dependence, density-independence and to a minor extent the importance of genetic factors in controlling population size, was taking place. The dispute among the representatives of the 'climatic school' and the 'biotic school'[25] began in 1933 with a paper by Nicholson.[26] The dispute persisted 20 years later and Andrewartha and Birch in their textbook summarized, from the 'climatic' point of view, the strong criticism of the deterministic ideas about density-dependence regulation of Nicholson and the other proponents of the 'biotic' school.[27] Andrewartha and Birch stressed once again the importance of abiotic factors for population regulation. Relevant in this regard are the controversies concerning fur commerce. Andrewartha and Birch dedicated a whole chapter of their textbook to exploring original data for field populations in answer to the question of whether these data represent real cycles or simple recurrent phenomena resulted from climatic variations.[28] They tend to adopt the latter explanation. Nevertheless, their answer left the question unsolved, since field data were not sufficiently precise as to provide a definite answer for the issue.[29] Furthermore, data gathered under stable laboratory conditions did not fit the explanations provided by Andrewartha and Birch. Indeed, Pratt showed that the population size of *Daphnia magna* cultured at 25°C displayed rather regular oscillations with time.[30] These (and many other) types of

[22] J.P. Collins, 'Evolutionary Ecology and the Use of Natural Selection in Ecological Theory', *J. Hist. Biol.*, 19 (1986), 257-288.

[23] F.M. Scudo and J.R. Ziegler, *The Golden Age of Theoretical Ecology*, 1923-1940, Berlin: Springer-Verlag, 1978.

[24] McIntosh, 'The Background and some Current Problems' (footnote 12).

[25] The terms are adopted from Krebs (footnote 15), pp. 285 and 288 respectively.

[26] A.J. Nicholson, 'The Balance of Animal Populations', *J. Anim. Ecol.*, 2 (1933), 132-178.

[27] H.G. Andrewartha and L.C. Birch, *The Distribution and Abundance of Animals*, Chicago: University of Chicago Press, 1954.

[28] Andrewartha and Birch (footnote 27), cpt. 13.4.

[29] Krebs (footnote 15), p. 155.

[30] D.M. Pratt, 'Analysis of Population Development in *Daphnia* at Different Temperatures', *Biol. Bull.*, 85 (1943), 116-140.

data apparently did not fit the hypotheses leading to the formulation of the logistic equation, and demanded for a concrete answer. In 1948 Hutchinson questioned the idea of instantaneous density regulation.[31] He modified the logistic equation introducing time-delayed responses of demographic parameters to population density changes. In the case of *Daphnia magna* for example, it seems that density increase immediately affects fecundity, while the response of mortality to size-changes is a later event.[32]

A major problem concerned the elucidation of the conceptual framework since

> ...the understanding of density-dependent and density-independent regulation was inconsistent, as was the whole notion of regulation. The very idea of the population itself was unclear... [and as a consequence]... much of the controversy centered on the definition of basic concepts.[33]

Andrewartha and Birch's textbook is full of questions concerning the meaning, the ontological status and the empirical content of concepts like those of carrying capacity,[34] intrinsic rate of increase,[35] etc. We would like to pinpoint here that criticism on conceptual matters plays an important role in the process of scientific crisis, as demonstrated in the work of philosophers like Laudan,[36] who suggested that theories are appreciated due to their ability to solve both empirical and conceptual problems. Conceptual problems concern contradictions within the theory or within the methodology of a field or even between them and other scientific, methodological and metaphysical beliefs. An example characteristic of and relevant to life-history studies example is provided by ornithology, especially by the research on clutch size. Ornithological research flourished from the beginning of the century and two of its main characteristics were: (i) the emphasis on life history traits such as parity, clutch size, age at maturity etc., and (ii) the organization of field experiments that provided an appropriate data sample for hypothesis testing. The hypotheses describing and explaining observed patterns, built upon concepts lying within the classic theoretical structure were dis-

[31] G.E. Hutchinson, 'Circular Causal Systems in Ecology', *Ann. N. Y. Acad. Sci.*, 50 (1948), 221-246.

[32] Models for time-delaying responses describe oscillating dynamics and were intensively explored later in the 1970s (for a relevant account see: R. May, *Stability and Complexity in Model Ecosystems*, 2nd edition, Princeton: Princeton University Press, 1975, pp. 95-98; and J. Maynard-Smith, *Models in Ecology*, Cambridge: Cambridge University Press, 1974: 36-42). Using this hypothesis and exploring equations ecologists managed to describe oscillating dynamics and even chaotic behaviours.

[33] Kingsland, *Modelling Nature* (footnote 12), p. 173.

[34] Andrewartha and Birch (footnote 27), pp. 481, 540-545.

[35] Ibid., p. 54.

[36] Laudan et al., 'Scientific Change' (footnote 3); see also L. Laudan, *Progress and its Problems*, Berkley: University of California Press, 1977.

counted by experiments. It was obvious that, for ornithology, the existing framework could not offer viable theoretical explanations, and a different point of view was needed. This was elaborated by Cody, who formulated a theory of clutch size in terms of strategic thinking.[37] The case of ornithology indicates the weakness of 'classic' demography to provide explanations, due to the lack of suitable concepts (e.g. strategy, allocation etc.). Furthermore, this illustrates also the inability of the previous theoretical structure to accommodate new hypotheses.

Another important criticism referred to the hypotheses underlying model building, especially the concepts of homogeneity and stability over time, and the deterministic nature of the predictions of models. Numerous discussions dealt with the suitability of models to fit phenomena dominated by stochasticity as well as with the perception of the environment as an homogeneous and stable factor, which does not affect phenomena.[38] Andrewartha and Birch questioned the hypotheses leading to the formulation of the logistic equation and characterized them 'non realistic.'[39] They characterized 'double non realistic'[40] the hypotheses leading to the Lotka-Voltera model for two competing populations.

A criticism of the lack of methods for the estimation of equation parameters developed among entomologists. During the period under consideration, applied ecologists could not establish a correspondence between model parameters and ecological reality, and models failed in the factualization of the theoretical presuppositions.[41] For example, the solution of the Lotka-Voltera equations for two competing populations is not formally obtainable. Hence these equations remained a theoretical structure standing for 'a guidepost to what the world would be like if it were simple'.[42] The logistic equation and Nicholson's model were criticized on the grounds that they were suitable only for special laboratory studies, non-appropriate to fit field data.[43] It is noteworthy that the elaboration of theoretical models forego the

[37] M.L. Cody, 'A General Theory of Clutch Size', *Evolution*, 20 (1966), 174-184; for a more extensive review of that case see Stearns (footnote 2).

[38] McIntosh, *The Background of Ecology* (footnote 12), pp. 171-177, 278; Kingsland (footnote 12), especially chapter 6; P. Palladino, 'Defining Ecological Theories, Mathematical Models, and Applied Biology in the 1960s and 1970s', *J. Hist. Biol.*, 24 (1991), 223-243.

[39] Andrewartha and Birch (footnote 27), cpt. 9.23, and cpt. 10.1.

[40] Ibid.

[41] Kingsland (footnote 12), p. 139.

[42] Krebs (footnote 15), p. 193.

[43] S.C. Stearns, 'The Evolution of Life-history Traits: A Critique of the Theory and a Review of the Data', *Ann. Rev. Ecol. Syst.*, 8 (1977), 145-171; P.J. Richerson and R. Boyd, 'Simple Models of Complex Phenomena: The Case of Cultural Evolution', In: J. Dupre (ed.), *The Latest on the Best. Essays on Evolution and Optimality*, Cambridge: MIT Press, 1987: 25-52.

elaboration of methods for gathering and exploiting census data.[44] As Smith pointed out, the logistic equation had never been supported by an experiment made in an appropriate environment.[45] In 1954 Andrewartha and Birch ascertained that '...Life-tables were first used by students of human populations. It is only in recent years that ecologists have begun to realise their importance'.[46] It follows that ecology was supplied with weak research tools. There are many examples in the history of science of failed research programmes due to their inability to develop suitable operational tools.[47] This is associated with the inability of a given theory to define the properties of the experimental work. During the early 1950s together with the complaints of field workers as to the applicability of models, there was a lack of sufficient data in support of hypotheses. For example, Leslie's main problem was the lack of sound data for the exploration of models. Thus, he resorted to the study of artificial populations.[48] This general problem was echoed in E. Wilson's words in 1934: 'What we require at the present time is more measurement and less theory, or, if you like it better more experimental analysis of phenomena, and less integration.'[49] Smith also argued that '... in spite of the many curves recorded, the many fits made, the work will have to be largely discounted as evidence in support of any particular theories. A repetition of all of it, with more appropriate and more carefully detailed designs, will have to be initiated...' and also '...almost all the evidence used in support of various interpretations is, at best, inconclusive...'[50] To this end, we have to point out that the fitting of models to data was inherently difficult due to inappropriate presuppositions underlying the deep structure of models. For example, Lotka-Voltera's equations were isomorphic to those used by physicists to describe overdamped oscillations.[51] However, the purely random behaviour of physical phenomena does not comply with the ecologist's insights for the behaviour of organisms, considered by no means random. On the contrary, this behaviour is considered targeted in relation to the principle of the 'struggle for

44 E.g. in 1927, logistic equation in ecology was in existence for about 7 years. In this year Elton complained for the quality of original data. See Ch. Elton, *Animal Ecology*, 1927, 8th edition, London: Methuen & Co., 1971: 173, 175.

45 F.H. Smith,.'Experimental Methods in Population Dynamics: A Critique', *Ecology*, 33 (1952), 441-450: 449.

46 Andrewartha and Birch (footnote 27), pp. 39, 54.

47 The failure of the International Biological Program (IBP), is probably a classic example on that case: see R. Levins, 'Ecological Engineering: Theory and Technology', *Q. Rev. Biol.*, 43 (1968), 301-305.

48 Leslie (footnote 20).

49 Referred in Kingsland (footnote 12), p. 130.

50 F.H. Smith, 'Experimental Methods' (footnote 45), pp. 448-449.

51 See J. Maynard-Smith (footnote 32), especially cpt. 2.

existence'. Hence the system of physicists is not isomorphic to the ecological system. Accordingly, ecologists were never entirely convinced of the utility of models, so that the metaphor was not fruitful.

The conclusion from the above discussion is that, due to the lack of a suitable vocabulary and empirical reference, as well as to confusing concepts and weak research tools, the theoretical core remained fragmentary and incoherent. More specifically, concerning the studies on life-history characteristics, there were many scientists, like Leslie, especially interested in the study of life-cycle schedules, as an important parameter for population fluctuations. Again, their work was merely descriptive, lacking explanations about the cause and the significance of phenomena. The study of life-history characteristics was a by-product of the effort of population ecologists to answer their central problem, i.e. the regulation of population growth, whereas no independent research field, concerning life-history studies, had been established. The key-factor to trigger the creation of a coherent new theoretical framework was, following the new synthesis, the incorporation of animal population ecology within evolutionary ideals.

Ecology was greatly affected by other scientific disciplines, especially: i) Evolutionary theory and genetics, mainly through the interdisciplinary network of the 'neodarwinian synthesis' and ii) mathematics, and computer sciences.

During the late 1940s neodarwinism was well established in the areas of evolution and genetics and optimality models became central to evolutionary thinking.[52] Its impact was also obvious in the area of ecology. Population ecologists believed that in the theoretical framework of neodarwinism they could find the concepts, tools and explanations they were seeking.[53] As Caswell pointed out, the connection between demography and evolution follows from the recognition that life-history traits are part of the phenotype, and hence as much (or as little) subject to adaptive explanation as are morphology, physiology and behaviour.[54] This means that if it would be possible to explain life cycle in terms of adaptive utility, then an explanation for the observed patterns in nature could be reached. These ideas resulted in the creation of evolutionary ecology.[55] The concern of ecologists with evolu-

[52] J. Beatty, 'Optimal Design Models and the Strategy of Model Building in Evolutionary Biology', *Philosophy of Science*, 47 (1980), 532-561.

[53] In some cases ecologists began to believe that '...the only general theory which now seems possible is that of natural selection' and 'evolution would seem to be the only real theory of ecology today' [In: G.H. Orians, 'Natural Selection and Ecological Theory', *Am. Natur.*, 96 (1962), 257-263: 262].

[54] H. Caswell, 'Life-history Strategies'. In: M. Cherret (ed.), *Ecological Concepts* (footnote 1), pp. 285-307.

[55] J.P. Collins (footnote 22), pp. 283-287.

tionary strategies was an aspect of their interest in adaptation and the mechanisms of natural selection which followed the modern synthesis. As Caswell says, the analysis of life-history strategies follows naturally from the recognition that demographic patterns are subject to adaptive interpretation.[56]

As regards the role of mathematics, Morowitz said that 'there are few areas of biology where mathematical studies have had as much impact as they had in ecology.'[57] Population ecologists hoped that with the exploration of mathematical models, they would manage to unravel the causes of population fluctuations that they did not manage to do with descriptive methods alone. Moreover, mathematics offered population ecologists the opportunity to test their basic hypotheses, (competition and the struggle for existence), as well as to model ecological thinking by using the methods of physics.[58] Concerning computer sciences, we must keep in mind that analytic solutions of the basic equations used in population ecology are not readily obtainable. Computer techniques helped ecologists (especially later, in the 1960s) to manipulate their data and to make predictions by obtaining graphic solutions. Thus, they managed to overcome the 'deadlock' of the end of the 1940s.[59]

The Emergence of the Field of Life-History Strategies

L.M. Cole in a stimulating publication introduced 'strategic thinking' to ecology.[60] According to Kingsland, Cole's article helped eco-logists to think in strategic terms, i.e. to consider the life history of an organism as a strategy designed to maximize fitness.[61] Cole himself, declared: ...'The modern conception of population growth regards the potential rate of increase as a more or less fixed characteristic governed by life history features;'[62] and again 'the total life history pattern

[56] Kingsland, *Modelling* (footnote 12), pp. 173-175; H. Caswell (footnote 54), p. 303.

[57] Morowitz (footnote 17), p. 29.

[58] In Kingsland, 'Mathematical Figments, Biological Facts: Population Ecology in the Thirties', *J. Hist. Biol.*, 19 (1986), 236-256.

[59] The optimism caused by the rapid development of computer science is obvious in, for e.g., Slobodkin, who believes that '...the ecological research will eventually permit the production of a relatively simple program for a very large computer' and 'all suggest the possibility of constructing a general ecological theory which will permit an automatic computer to simulate, in a general sense, the kinds of landscapes we know', (L.B. Slobodkin, 'Preliminary Ideas for a Predictive Theory of Ecology', *Am. Natur.*, 95 (1961), 145-153:147,152.

[60] L.M. Cole, 'The Population Consequences of Life History Phenomena', *Q. Rev. Biol.*, 29 (1954), 103-137.

[61] Kingsland, *Modelling Nature* (footnote 12), p. 174.

[62] Cole (footnote 60), p. 107.

of a species has meaning in terms of its ability to survive, and ecologists should attempt to interpret this meaning.'[63] Although evolutionary ideas concerning life-cycle characteristics were also included in papers by Lack and Medawar,[64] it was Cole's paper that triggered the formulation of a family of hypotheses and the rapid development of the new field. On the first pages of his article, Cole summarized the basic trends, as well as the problems of population ecology, emphasizing the matter of mathematical oversimplification, the forceful criticisms against analytical theories, the non-justification of theories by biological data, and the restriction of research on purely demographic aspects, especially on human populations. Cole blamed population ecologists because '...the analysis of the ways in which differences between the life histories of species may result in different characteristics of their populations has remained relatively unexplored.'[65] According to Cole, regardless of the many examples of life history phenomena that had been regarded as adaptive, there had been relatively few attempts to evaluate quantitatively the importance of specific features of life histories in ecological literature.[66] Cole declared his purpose to consider some parts of this 'neglected branch of ecology',[67] because he believed that...

> ...the entire problem of potential growth and its relationship to the resources of the environment is clearly one of the fundamental problems of ecology, but one which has never been adequately summarized in a way to reconcile the mathematical approaches, such as those of Lotka (1925), Volterra (1927), Kuczynski (1932, 1935), Kostitzin (1939), and Rhodes (1940), and the purely biological approaches which have concentrated on life history features such as longevity, fecundity, fertility and sex ratios. In the present paper we will consider the mathematical form of potential population growth and certain subsidiary phenomena and the way these are related to particular life history phenomena. It is hoped that this will bring to attention some of the possible adaptive values of observed life history phenomena and will lead ecologists to a greater consideration of population problems which are essentially ecological. Life history features do in fact control potential population growth, but the quantitative relationships have still been insufficiently elucidated...[68]

The reason why Cole's article catalysed the emergence of the new field was not simply the fact that he stressed the importance of life history

[63] Ibid., p. 104.
[64] D. Lack, *The Natural Regulation of Animal Numbers*, Oxford: Clarendon Press, 1954; P.B. Medawar, *An Unsolved Problem of Biology*, London: H.K. Lewis, 1952.
[65] Cole (footnote 60).
[66] Ibid., pp. 103-105.
[67] Ibid.
[68] Ibid., p. 106.

studies to answer one of the major questions raised among ecologists. As we tried to show earlier, this idea was rather common within the framework of evolutionary ecology. Cole's major contribution was rather that he illustrated the basic lines of thoughts. These thoughts comprising the cornerstone idea of 'strategic thinking' should guide relevant research (nevertheless, notice that Cole himself did not use the term 'strategy').[69]

The basic line of strategic thinking, axiomatically illustrated by Cole, is as follows:

> – the reproductive potentials of existing species are related to their requirements for survival...
> – any life-history feature affecting reproductive potential rate is subject to natural selection...
> – such features observed in existing species should be considered adaptations, just as purely morphological or behavioural patterns are commonly so considered...[70]

The other cornerstone of the new theoretical framework is the impact of neodarwinism on ecology. It concerns the concept of allocation and the related idea of energy trade-offs. The concept of natural-selection-dependent allocation was developed by Fisher and Dobzhansky. Fisher first formulated what later became known as the 'principle of allocation', i.e. an hypothesis formulating the possibility of an approach of life history phenomena based on energy allocation.[71] Dobzhansky linked the 'principle of allocation' to demographic parameters and the impact of the environment on them. He suggested that natural selection acts in a radically different way in the tropics and in the temperate zones. Dobzhansky's hypothesis was the first attempt to interpret demography as a result of different modes of natural selection.[72]

[69] The term strategy seems to appear in the ecological literature after the mid 1960s, probably as a 'contribution' of economics and of the 'theory of games' (R.H. MacArthur and J. Connell, *The Biology of Population*, New York: John Wiley and Sons, Inc., 1966; R. Levins, *Evolution in Changing Environments*, Princeton: Princeton University Press, 1968; R.H. MacArthur and E.O. Wilson, *The Theory of Island Biogeography*, N.J.: Princeton University Press, 1967). It is interesting that the first explicit definition of the term was given in 1968, by Levins, who defined 'strategy' as '...the sum of characteristics which consist adaptations to environmental patterns in space and time' (R. Levins, ibid., p. 10), and then again as late as 1976, in Stearns (footnote 2).

[70] Cole (footnote 60), p. 104.

[71] R.A. Fisher, *The Genetic Theory of Natural Selection* (1930), New York: Dover, 1958. Fisher's ideas about energy allocation and the connection between natural selection and life-history attributes are expressed in the following very well-known and much quoted remark: '...it would be instructive to know not only by what physiological mechanisms a just apportionment is made between the nutriments devoted to the gonads and the rest of the parental organism, but also by what circumstances in the life history and the environment would render profitable the diversion of a greater or a lesser share of the available resources toward reproduction', ibid., p. 47; see also M.T. Rocha Pite, T. Avelar and M. Matos (footnote 2).

[72] T.H. Dobzhansky, 'Evolution in the Tropics', *Am. Sci.*, 38 (1950), 209-221.

The schematic reconstruction of the theoretical core of the new field would help to realise what kind of new elements it offered to ecology and the way it affected ecological thinking:

1) The amount of resources available to an organism (time and energy) is limited.

2) Natural selection dictates optimal allocation of time and energy among processes.

3) Optimal allocation is associated with the effective solution of the specific problems, an organism has to overcome, in a specific environment.

4) In different environments, the environmentally induced allocation of energy results in the development of different life-cycles as well as in different organismic characteristics.

5) Life-cycle characteristics shape-up an integrated set of coevolved traits that can be referred to as strategies.

The new approach flourished and the new ideas spread rapidly in ecological literature, especially after the 1960s. For example, Orians stated that '...it is difficult to think about populations without considering the selective advantage of various life history features'[73] and L.C. Birch acknowledged that Cole pointed out that '...the pattern of life history of the species ...which will be more effective (for increasing *r*), depends on selection...'.[74] For Harper 'the great value of this type of theoretical approach (i.e. life history studies) lies in the extent to which it focuses attention on quantitative aspects of the life history and behaviour of species which are of acknowledged importance but have remained part of natural history rather than of science.'[75] Cody went further and considered his work an application of the 'principle of allocation', in an attempt to formulate a general theory of clutch size. He declared...

> It is possible to think of organisms as having a certain limited amount of time or energy available for expenditure, and of natural selection as that force which operates in the allocation of this time or energy in a way which maximizes the contribution of a genotype to following generations.[76]

MacArthur and Connell enlarged this view by considering that the answer of population biologists to the problem of adaptation concerns a strategy. According to them, this makes up the weighty difference between population biology and other branches of biology.[77]

[73] G.H. Orians, 'Natural Selection and Ecological Theory' (footnote 53), 261.
[74] L.C. Birch, 'The Genetic Factor in Population Ecology', *Am. Natur*, 94 (1960), 5-23.
[75] J.L. Harper, 'A Darwinian Approach to Plant Ecology', *Ecology*, 55 (1967), 247-270: 258.
[76] Cody (footnote 37), p. 174.
[77] MacArthur and Connell (footnote 69), pp. ix-x.

The emergence of the new field was related to changes in the specialist's worldview. As we showed previously, up to the 1950s, the insight of population ecologists, particularly demographers, was pervaded by the so-called reductionistic-analytic approach. Populations were presumed homogeneous and demographic parameters stood for arithmetic means. Moreover, environmental oscillations were ignored and density was the only parameter regulating population size. The new worldview preserving its reductionistic character was radically modified during the 1950s. The quotations from Cole's article indicate that life-history theorists focus on reproduction as the essential activity of an organism. This is the common methodological characteristic of populations-based reductionistic ecology and 'contribution to future generations' dominates the theoretical set-up. However, contribution to future generation can be gained from balancing among processes (body size increase versus fecundity, iteroparity versus semelparity, etc.). Theorists viewed life-history traits as being energetically interconnected and the concern with interactions was fundamental to evolutionary ecology in general, and to life history studies in particular. Consequently, organisms should be studied as adapted complex systems.[78] The concepts of allocation and strategy are apparently the most important innovations introduced in ecological terminology. Life history studies introducing allocation thinking underline the importance of energy trade-offs among processes. Thus, next to the reductionistic methodology, the new field showed also holistic insights. An analogous reconciliation of holistic thinking with a reductionistic methodology, giving birth to 'systems ecology' in early the 1960s was identified by Palladino.[79] Strategic terminology emphasized interaction between organism and environment and interpreted life-history characteristics as adaptations to environmental conditions.[80] Moreover, populations conform to neodarwinian ideals in that life-histories and life-history characteristics are changeable entities: the same species displays different life-histories in different environments, while life history features of an organism may change with time.

[78] Very important in this respect is the comment by Burnett, that '...as little relation has been found between population density and the intrinsic rate of increase of each species, the analysis of population control has centered on the many interactions that produce mortality during the life history of the insect.', T. Burnett, 'Interactions in Insect Populations', *Am. Natur.*, 94 (1960), 201-211. For similar reasoning see also C.A. Istock, 'The Evolution of Complex Life Cycle Phenomena: an Ecological Perspective', *Evolution*, 21 (1967), 592-605; G.I. Murphy, 'Patterns in Life-history and Environment', *Am. Natur.*, 102 (1968), 390-404; H.M. Wilbur, D.W. Tinkle and J.P. Collins, 'Environmental Certainty, Trophic Level and Resource Availability in Life History Evolution', *Am. Natur.*, 108 (1974), 805-817.

[79] Palladino, 'Defining Ecological Theories' (footnote 38).

[80] '...natural selection is identical with the interactions between organisms or populations and their secular environments...', C.A. Istock (footnote 78).

Although, influenced by ecosystemic studies, the new approach was distantly developed from ecosystemic ideals. Ecosystem is an hierarchical entity, the function of which is dominated by the first order subsystem (the producing of green plants). On the contrary, population systems do not conform to hierarchical structures: The function of organisms involves efficiency ('adaptiveness') provided for by optimal allocation of resources among traits. It is noteworthy that this property does not derive from the properties of'the system components and the concept of optimal allocation remains an ideal basis for the organizing principle of the system. It follows from the above discussion that the emergence of the field of life-history strategies, compromising holistic with reductionistic world views, contributed to an important enrichment of population ecology, although it did not create a new 'paradigm'.

The theoretical core of the new field had a profound effect also on the topic of research. The aim of researchers centered on the following issues:

i) The traits of the life cycle which are important for adaptation. Research focused on subjects like parity,[81] clutch size,[82] reproductive value and age at first reproduction,[83] reproduction rates,[84] size of offsprings,[85] evolution of sex ratios,[86] etc.

ii) The selective forces (biotic or abiotic) that are decisive for the development of a life history in a specific environment.[87] The main selective forces, usually considered by life history theorists during the late 1950s and 1960s were density-dependent competition,[88] stability of the habitat,[89] predation,[90] and food supply.[91]

[81] J.L. Harper (footnote 75); L. Cole (footnote 60); W.W. Murdoch, 'Population Stability and Life History Phenomena', *Am. Natur.*, 100 (1966), 5-11.

[82] L. Cole (footnote 60); M.L. Cody (footnote 37); L.C. Birch, 'The Genetic Factor in Population Ecology' (footnote 74).

[83] G.C. Williams, 'Natural Selection, the Cost of Reproduction, and a Refinement of Lack's Principle', *Am. Natur.*, 100 (1966), 687-690; W.D. Hamilton, 'The Moulding of Senescence by Natural Selection', *J. Theoret. Biol.*, 12 (1966), 12-45; R.C. Lewontin, 'Selection for Colonizing Ability', in: H.G. Baker & G.L. Stebbins (eds.), *The Genetics of Colonizing Species*, New York: Academic Press (1965), pp. 75-108.

[84] D. Amadon, 'The Evolution of Low Reproductive Rates in Birds', *Evolution*, 18 (1964), 105-110.

[85] Harper (footnote 75).

[86] Orians (footnote 53), Fisher (footnote 71).

[87] As Charlesworth puts it: '...the fundamental problem with which ecologists are concerned is that of how natural selection shapes patterns of survivorship and reproduction as functions of age. This breaks down into a set of related questions, such as why be iteroparous rather than semelparous? why is senescence an apparently universal phenomenon in mutlicellular organisms? how should resources be allocated between reproduction, growth and survival?', (see B. Charlesworth, 'The Evolutionary Genetics of Life Histories', In: B. Shorrocks (ed.), *Evolutionary Ecology*, Oxford: Blackwell Scientific Publications, 1984: 117-133).

[88] R.H. MacArthur, 'On the Relative Abundance of Species', *Am. Natur.*, 94 (1960), 25-34, and 'Population Effects of Natural Selection', *Am. Natur.*, 95 (1961), 195-199; D.W. Tinkle, 'Population Structure and Effective Size of a Lizard Population', *Evolution*, 19 (1965), 569-573.

[89] P.H. Klopfer and R.H. MacArthur, 'Niche Size and Faunal Diversity', *Am. Natur.*, 94 (1960), 293-300; Harper (footnote 75).

[90] Cody (footnote 37).

[91] Murdoch (footnote 81).

iii) The potential combinations of life history traits, or in other words, the potential life history strategies.[92] Scientists studied combinations of the various life history characteristics like reproduction, dispersal ability and predator avoidance,[93] breeding and survival,[94] parity, age at first reproduction and survival,[95] maintenance and productivity,[96] as well as the evolution of complex life histories.[97] Most of these studies were limited to providing estimations of the impact, that the combinations of life history characteristics had on the intrinsic rate of increase (i.e. on fitness).

iv) The establishment of relationships between selective forces and life histories in specific environments, mainly through the development of models like the 'r-k selection' model, the 'bet-hedging' model and so forth. These research aspects were developed later on, during the 1960s onwards.

The reorientation of the work was also crystallized, although to a minor extent, at the methodological level. L.M. Cole first delimited the research tools of the new field. The analysis was based upon Lotka's characteristic equation:

$\int_0^{\infty} 1_x m_x e^{-rx} d_x = 1$, where 1_x survivorship and m_x fecundity of the life stage x, $\oint$ and its variants.

This equation '...provides the methods for interpreting the relationships between life history features and their population consequences.'[98] It describes the interrelationships among the fundamental demographic parameters (fecundity, survivorship, time), as well as between them and fitness, expressed as intrinsic rate of increase (r). It also enforces the idea of optimal allocation since the availability of resources is limited (the value of the product is always equal to unity). The wide use of this particular equation is a good example of how an isolated tool, which within the old framework was occasionally used to estimate the exact value of parameter r, changed status within the new coherent context that articulated the theoretical fabric of the new

[92] MacArthur expresses it by declaring that the aim of population ecologists is to discover the strategy with which an organism survives in the world. (R.H. MacArthur, 'Ecological Consequences of Natural Selection', In: T.H. Waterman and H.J. Morovitz, *Theoretical and Mathematical Biology* (footnote 17), 1965, pp. 388-397).

[93] Birch, 1960 (footnote 74).

[94] Murdoch (footnote 81); P.W. Frank, 'Prediction of Population Growth Form in *Daphnia* Pulex Cultures':, *Am. Natur.*, 94 (1960), 357-372.

[95] Cole (footnote 60).

[96] J. Connell & E. Orias, 'The Ecological Regulation of Species Diversity', *Am. Natur.*, 98 (1964), 399-414

[97] Istock (footnote 78).

[98] L. Cole (footnote 60), p. 108.

field.[99] There were also other population models used in life history studies, like the 'classic' logistic equation, and Lewontin's model for estimation of the parameter *r* etc., but Lotka's characteristic equation dominated the field, followed by the familiar life-table and related functions.

Despite the important progress made in the early 1950s, as well as in the early 1960s, questions were soon raised concerning the one-way environment-organism relationship. As we intend to show in a forthcoming paper, the reasons limiting progress were related to the weakness of methodological tools, especially mathematical models. Life-history theorists were unable to produce adequate models with which to describe reality, that included the influence of environmental factors. Instead, their models consisted of only life-table parameters, such as fecundity and longevity. Hence, the whole enterprise was reduced, almost exclusively to the study of reproductive strategies, while environmental effects were usually dealt with as white noise.[100]

Concluding Remarks

In this paper we have evaluated the contributions from the field of life history studies to population ecology and especially to the enrichment of the theoretical core with new statements and concepts, the creation of a new subject of research, and the elaboration of new methodologies. From this case-study, we draw the following conclusions:

i) The emergence of the field of life-history studies is an example of the decisive influence that 'neodarwinian synthesis' exerted on biology and especially on ecology.

ii) Among other catalysing factors of field emergence, the interdisciplinary impacts are fundamental. This supports the views of Bechtel who considered as an important reason for '...crossing disciplinary bounds..., the acquiring of guidance in developing a theoretical explanation.'[101]

[99] It is interesting to mention here that Cole wondered how '...the exceedingly important ecological questions of what potential advantages might be realized if a species were to alter its life history features have remained largely unexplored', despite the fact that ecologists had such a powerful tool on their hands. He ascribed the fact to the mathematical difficulties of the model, but as we showed it was rather the lack of theoretical progress which created that paradox (L. Cole, footnote 60, p. 108).

[100] P.J. Den Boer, 'Spreading of Risk and Stabilization of Animal Numbers', *Acta Biotheoretica*, 18 (1968), 165-194.

[101] Bechtel, 'The Nature of Scientific Intergration' (footnote 3), p. 30; For similar approaches see also R.E. Anderson, 'Cognitive Explanations and Cognitive Ethology', and W.A. Mason, 'Behavior Implies Cognition', in Bechtel's *Intergrating*, pp. 323-336 and 297-308, respectively.

iii) The creation of a new rather coherent theoretical core triggered scientific transition and conditioned the emergence of the new field. The elaboration of the new theoretical framework, also invoked methodological shifts.[102]

iv) The use of the concept of 'field' is considered useful with respect to the study of the emergence of new disciplines within ecology, especially in the case where strong interdisciplinary influences occurred.[103] Nevertheless, in this paper the original definition of the concept is slightly modified in order to highlight the role of theory in the emergence and the establishment of the field of life history studies. Besides, following Darden and Maull[104], we can suggest that there is '...no reason to prejudge the still open question as to where there is one analysis applicable to all theories or instances of unification and progress'.

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102 For a similar conclusion concerning the case of island biogeography, see Haila and Jarvinen (footnote 10); See also P. Haccou and W. van der Steen, 'Towards a Practical Methodology of Optimal Foraging Theory' (forthcoming).

103 For an extensive discussion on this subject see Bechtel (footnote 3).

104 Darden and Maull (footnote 3).