Roots of Current Concepts in the Studies of Social Behavior in Animals

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Introduction

I will have to start with a mild reservation about the title of the paper. The term ‘ethology’ is used here in a broadest sense, as, for example, by Tinbergen in one of his latest papers (Tinbergen 1976). He considers it possible to refer the word ‘ethologist’ to any biologist who is occupied with studies of behaviour. The ‘ethology in a narrow sense’ should be distinguished from this broad meaning, as it is the discipline founded by K. Lorenz, N. Tinbergen and their followers. This trend, called ‘classic ethology’ today, marks only one historical period and only one of several approaches in the evolution of views of the discipline that I tentatively, and for the sake of brevity, will call further ‘zoosociology’.

My main task is to show the intricacy and contrariety of the process of our knowledge of evolution. It is hardly possible to track in this process as a fluent progressive advance that is due only to the gradual accumulation of facts. Any respectable scientific community, any school of ideas—and sometimes a ‘lone-wolf’ scientist who had his own word to say—presented their own concepts. Those concepts were aimed at the solution of different tasks. Different approaches and tasks demanded specific research methods to be applied. The same facts were pretty often interpreted differently, and sometimes, even as being contradictory to each other. At times, contemporary scientists did not have a slightest idea about the existence of each other. In other cases, different scientific schools entered confrontation and acute ideological competition that resulted in scientific discussion for many years. Finally, there were cases of peaceful co-existence of schools—despite the obvious inconsistency in their basic foundations.

It is hardly surprising that in this heterogeneous interwining of views and trends, the scientific tradition among the generations of scientists was not as strong as it

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could seem at the first glance. Some problems that were adequately formulated and nearly close to a logical solution over a hundred years ago, lost their shape later and emerged as something absolutely new after many decades. At times, novel concepts were constructed almost as a blueprint, while an absence of their links with previous ideas was justified by an assertion that all that had been done before was nothing more than an anachronism of the pre-scientific mode of thinking.

With all difference in approaches and methods that will be considered below, an adherence to two different—and to some extent alternatively oriented patterns of thought—may be revealed retrospectively.

For one of them the leading principle is to study the whole through reducing it to certain elements that are considered explicitly specific and constant in their properties. It is conventional to regard this position as "elementarism". The whole thus seems to be as something secondary to the elements that form it, so that the property of the whole is determined mainly by specific features of these elements.

The alternative viewpoint states that the properties of parts can be grasped only through the knowledge of the whole. The whole is given in the first place and can be divided into part by many different ways. Just the splitting method is most important in determining the properties of the parts obtained. This attitude is often called "holism" (from Greek «holos»—wholeness). It can be also called "organisms", indicating the similarity between any complex whole entity to an organism that can be split in parts only surgically. One of the manifestations of this cognitive approach is an attempt to consider communities of social insects as 'superorganisms'. In my view, holism and organisms are, in fact, different names of what is accepted today as the systemic thinking.

There is a common belief that elementarism has many in common with the mechanistic worldview and by no means is compatible with the dialectic approach. Or, in other words, progress of our knowledge about the world can be viewed as a gradual transition from the elementaristic ideas to holistic ones. In reality, the situation seems to be more complex (Fig. 1).

The commitment of a scientist to a given cognitive attitude is determined in general by the specificity of the object under study and goals of research. These two aspects are more or less interconnected, but can be present in different proportions in the one or another doctrine. Until there is a reasonable parity between the generality of the approach, on the one hand, and its modes of the objects' analytic dissection, on the other, both organismism and elementarism are indisputable retained their cognitive value.

For the beginning, I tried to represent a history of the scientific ideas on animal social behaviour in their development in form of the rather simplified scheme shown in Fig. 1.

Here, eight scientists are under consideration whose scientific activities cover a period a little more than a hundred years. Their views and general works seem to me the most important, in such an extent that they may be regarded as the certain landmarks in shaping of our up-to-date notions.

Not surprising that since the main object of their research were community and population, i.e. complex objects of systemic nature, the majority of those scientists

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	Holism **Organismism** **Systemic thinking**		**Elementarism** **Atomism** **Mechanistic worldview**
	A. Espinas, 1877 1.Place of the biosociality in the general system of knowledge 2. Individual in relation to society		
	W.C. Allee, 1931-1938 3. Limits of the biosociality	Classical ethology	**K. Lorenz, 1931-1935** 4. Mechanisms of communication
		Classical ethology	**N. Tinbergen, 1951** 5. Adaptive evolution of communication
Socioethology	**V.C. Wynne-Edwards, 1962** 6. Social behaviour as a mechanism of the population homeostasis	Sociobiology	**W.D. Hamilton, 1964** 7. The theory of genetical evolution of social behaviour. Origin of eusociality (altruism)
Socioethology	**J.H. Crook, 1970** 9.Concept of socio-demographicsystem	Sociobiology	**E.O. Wilson, 1975** 8. "New synthesis"

Fig. 1 Simplified scheme of the history of development of scientific ideas in studies of the interpopulation organization

were adhering to the holistic position. However, along with them there were two quite reputable schools, namely, classical ethology and sociobiology. that, in my view, appeared to be devoted to rather elementaristic approaches. Below, I shall explain in detail what I mean.

Figure 1 illustrated a plan of the further review as well. There, ordinal numbers correspond to those topics I shall discuss one by one. Although either of them was touched by all authors mentioned, although in more or less extent, some of them made a greater contribution than others to the development of certain ideas. For a start, two issues should be clarified. First, what is the subject of zoosociology and where is its place among other disciplines. Second, I shall examine how the ideas about social groupings, the main object of our science are seen in light of different views on what are an individual and biological individuality as such.

Alfred Espinas and First Steps of Zoosociology

The first serious review of the theme was offered by the French philosopher Alfred V. Espinas. His work was first published in 1877, about 150 years ago. The full title of the book is "Social Life of Animals. An essay in comparative psychology with addition of brief history of sociology". I must say that though this book is always cited by all authors who write about the history of ethology, these references are usually not informative.

Espinas formulated a task—to combine the data accumulated to his time of historical sociology and comparative biology in the frames of unified knowledge and acquired unified principles. Being the author of a number of historical-philosophic works—such as, for example, "The history of economic doctrines", Espinas was deeply interested at the same time in the problem that is titled today with an intriguing name of the "problem of interrelation of biological and social".

Espinas was quite right when argued that during the whole history of human knowledge development, starting with ancient times, at least from the 4th century BCE, the greatest minds of the mankind searched for an analogy between the human society and communities of animals. "While naturalists in their unconscious aspiration for generalization—Espinas wrote—compared animal communities with human ones, politicians, governed by the same impulse, compared likened human societies to the societies of animals". Regretfully, continued the author, none of them tried to elaborate the general principles for such comparisons and thus made the matter still more intricate.

But does it mean that the attempt itself to compare is vain? Not in the least. "There is no science of particulars!"—exclaimed Espinas. "The two groups of facts under examination that show an obvious analogy and are defined with the same word can become clear to us only when they are brought together to the single law that stems from their mutual properties".

Espinas suggests that this law should be found by revealing what in the modern language are the main organizational principles governing such complex natural structures, as the communities of individuals. In Espinas's opinion, zoosociology should be not an introduction to the general sociology but Chap. "Roots of Current Concepts in the Studies2 of Social Behavior in Animals" in it.

But would not then zoosociology duplicate the works by biologists? Espinas answers this question in the following way: "Among many specific features that characterize organic pieces of matter nutrition and reproduction are the most important. Sociology studies neither of them; it investigates only the most general character of organized social structures—say, the grouping patterns favoring implementation of one or another of the above functions, which gives it a specific role even in studies of those phenomena where it meets another life science—biology".

So, the subject of zoosociology is the specific character of interrelations among the elements within a certain organized structure; the ties that appear in situation when formation of the groups takes place to promote their further existence and biological functioning.

The next question Espinas had to solve was what may be regarded as those elementary 'bricks' that being extracted from the wholeness do not lose its own essence and thus remains an independent actor. In the human sociology for a long time the answer was simple: an individual. But this point of view was not accepted unanimously. For example, according to Aristotle, the elementary unit in human

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society is not an individual but a couple, because the individual is incomplete and inexplicable from himself. Hegel also believed that the family is more independent than the individual (Hegel 1821, 1940). This position was favorable to Espinas as well ideas and he persistently keeps upon it throughout the text of the book.

Espinas pointed out that when dealing with plants and many lower animals the question often arises—what one means when used a term "an individual". At that time, in the second half of the nineteenth century, this period of tumultuous development of biology, it appeared that there is, in fact, a firm ground for such an uncertainty about the matter. Namely, numerous creatures were found, in respect of which it was not clear if their bodies would be divided into parts being "independent", to more or less extent, from each other.

In the 1940s–50s botanists M. Schleiden and T. Schwann discovered that all living organisms consist of cells. They offered the idea that the very life of a plant is combined beings of its cells. Then it became possible to consider the cell itself as an elementary organism. Soon prominent German scientist R. Virchow developed on this basis the so-called 'theory of cell state'. "Any creature—he wrote—is a sum of living units, so that each of them has everything necessary for life" (Virchow 1863). This concept, atomistic in its essence, asserted strong influence over the development of Espinas's ideas, as we will see it below.

In his time, zoologists knew well some amazing creatures about which one could not say for certain whether they are individuals in a strict meaning of the word or peculiar colonies of many creatures organically connected with each other. Such are, for example, so called siphonophores, belonging to marine coelenterates. Like a tree, with its roots, branches and leaves, the body of a *Siphonophora* is composed of several "individuals-organs". One of them only capture food, others execute the reproduction function, still others protect the whole creature against predators, still others provide its motion in the water column. In 1866 the outstanding German biologist E. Haeckel designated such compound organisms as cormi, singular—cormus[1] (Haeckel 1866). Later their components "individua organs" were called zooids.

As a result of these and many other discoveries in biology the issue of the essence of concepts of "collectivity" and "individuality" grew more and more cloudy. At the end of the XIX century F. Engels in his "Dialectics of Nature" wrote that the notion of an individual has become absolutely allusive. Cormus, colony, tapeworm on the one hand and the cell and metamere, on the other, can be identified as individual in a certain sense (Engels 1883).

In his book that was almost an "age-mate" of "Dialectics of Nature", Espinas explained the situation to readers: "We take our own type of individuality as a norm and deny the quality to any other creature that is too distant from such a type. As soon as a certain creature loses definite shape and an ability to move independently, we refuse to regard it as an "individual" (Espinas 1898).

[1]From Ancient Greek κορμός (kormós, "trunk of a tree with the boughs cut off").

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Meanwhile, Espinas wrote, individuality may be expressed in different extent. According to Virchow's views, a cell should be regarded as an elementary individual because it is actually an indivisible biological atom. Hence, individuality of a multicellular creature is a kind of collective individuality. In favour of such inference speaks the fact that in the multicellular organisms there are always cells that remain relatively autonomous and are able to move actively inside tissues. Such are, for example, wandering ameboid cells in sponges, spermatozoids, etc.

A special attention of Espinas such cormi attracted in which along with individual-zooids such structures are present that serve the cormus as a whole. These can accomplish, for example, the excretory function (the common cloaca in the colony of sea squirts (Ascidiacea) or ensure the fulfillment of locomotion—like in the case of the so-called creeping sole in mobile colonies of some moss animalcules (Bryozoa).

When discussing such phenomena taking of octocorals as an example, Espinas wrote: "Along with individual life of polyps as such an another life is in progress being independent of individuality of each member of the colony and belonging to the hydranth as a whole. The latter can be regarded in this case as an individual. It is obvious that a certain individual loses its rights relative to those of the community by surrendering a part of its activity to it" (Espinas 1898).

Functionally, heterogeneous colonies of coelenterates, moss animalcules, tunicates, etc. are a bright illustration of submission of a part to the whole, an individual to the community. The same principle Espinas saw in the family's communes of termites, bees and ants that consist of morphologically autonomous individuals but inseparable from each other socially and functionally. The author even tries to look farther ahead and to include into the same line collectives of higher vertebrates. But here, because of almost complete absence of reliable information his speculations assume a flavour with of scholastic characteristic of the natural philosophy. Yet the main idea is clear and Espinas illustrated by analogy with the human society: "Not individuals create the society but society creates individuals because they exist only in the society and for interests of it" (Espinas 1898).

Ernst Haeckel in his work "General morphology of organisms" (1866) distinguished six classes of organic individuality. Individuals of class I are cells, of class II —organs, etc. An individual as we used to think understand is a creature of the class V, and the aforementioned cormus belongs in this classification to the class VI.

The problems raised by Espinas in the framework of the biosociality origin remain of a great importance still today. As the outstanding Russian zoologist V.N. Beklemishev stated, "the notion of organic individuality is undoubtedly one of the basic concepts of biology" (1964). This topic laid down the foundations of the so-called "colonial theory" of the multicellular organisms origin from the monocellular ones. It was initiated with works by E. Haeckel, I.I. Mechnikov[2] and other eminent scientists. The concept of collective individuality turned out to be highly multidimensional and extraordinarily complex.

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[2]See Metchnikoff 1892 (Fr) and Mechnikov 1950 (Rus) (eds).

Formation in evolution of superindividual structures of the cormi type promotes an increasing specialization of its constituents—zooids. This process that leads, according to Beklemishev, to the more and more reinforcement of the cormi individuality. Espinas interpreted the matter as "a transition from bondless homogeneity to specified and consolidated heterogeneity" (Espinas 1898).

This principle undoubtedly also operates in the processes of formation in evolution of highly integrated social communities of multicellular animals, both invertebrates and vertebrates. Let us see now what has been done during the development of zoosociology in this sphere of the research.

Warder Allee and the Problem of Putative Limits of Biosociality

Just after sixty years since the publication of the Espinas's work in 1938, another book appeared under the same title: "The social life of animals". It was written by Professor Warder Allee from the University of Chicago (Allee 1938). In this important publication he summarized both the results of his own studies accomplished during 26 years of his scientific career and the main data obtained in zoosociology since the time of Espinas.

A few words should be said about the author. His first influential work "Animal aggregations: a study of general sociology" was published in 1931. In 1949, he published the book "Principles of animal ecology", which has been widely cited in subsequent years. His last book, "Ecological animal geography", written in co-authorship with K. Schmidt comes out in 1951. Thus, Allee made a remarkable contribution in general zoology and ecology.

A brief outline of the general trends in disciplines relevant to our topic at the time of publication the book "The Social life of animals" (1938) is necessary to understand main ideas presented in it. For the same sake it will be helpful to get acquainted with the literature sources cited in the book. Their distribution in time (Fig. 2) can to serve as an indication of the growth of interest to zoosociology at roughly the turn of the first and second decades of the 20th century.

It can be seen that Allee was familiar well with the studies in human sociology. Like Espinas he advocated the idea of the general sociology establishing. To a great extent, it was due to his efforts that demography, which was brought to life in the studies of human populations, was introduced into ecology and sociology of animals.

Figure 2 also shows a list of names of scientists who made a considerable contribution into the development of the topic of our interest by the moment of Allee's book publication. These are, among others, four Russian scientists: P.A Kropotkin, B.P. Uvarov, G.F. Gauze and Th. Dobrzhansky. The first of them was stressing persistently the importance of cooperative relations in communities of animals (Kropotkin 1902). Gauze contributed much to the development of principles of biological competition (Gause 1934). Dobrzhansky together with S. Wright

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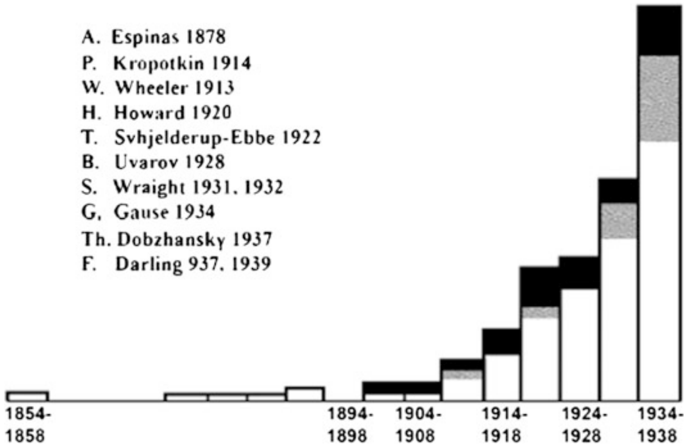

Fig. 2 Distribution by year of literature references, cited in the book of Allee (1938). Papers by Allee are shown in hatching; studies on sociology and demography of man are shown in *black*

is one of the founders of population and mathematical genetics (Dobzhansky and Wright 1942). B.P. Uvarov discovered the phenomenon of the solitary and swarming phases in locusts (Uvarov 1937).

W.Wheeler was an outstanding specialist in social insects (Wheeler 1928). H.E. Howard was one of the founders of the idea of territoriality (Howard 1920). F. Darling put forward the ideas of social stimulation of reproduction in crowded assemblies of animals (Darling 1938).

And what are actual main peculiarities and results of the activities of Allee's school in the 1930s, in comparison to those that we saw in Espinas's theory? I have already mentioned that the work of the latter, due to the very essence of science of his time, had something in common with a natural philosophical mode of thinking. For Allee just the contrary, the main research method became experiment—which is, in general, characteristic of American behavioural science from the very start. In his discourses Espinas uses ordinary language at large. In Allee's works we see quite a broad diverse special scientific terminology. He uses such concepts as population, population size and density, hierarchy, rank order, territory, mass effect, social hormone, social facilitation, etc. The experimental approach and the start of creating a special scientific language mark a transition of zoosociology from a speculative mental constructs to the truly scientific stage of development.

In his approach, Allee, following Kropotkin, stresses the importance of cooperative relations, as opposed ideas about bloodstained struggle for existence dominating at that time. And another very important postulate is the idea about the influence of the population density on biological success of individual (Allee 1931; Allee and Bowen 1932).

Although a view that overpopulation negatively influenced upon growth in postnatal ontogenesis, reproduction and some other characteristics was not new, almost nothing was said about the negative role of abnormally low density or

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underpopulation. In a number of elegant experiments with different species of animals—from protozoa to mammals Allee demonstrated this second effect. It leads to the well-known "Allee's principle". The Allee's principle gives the idea of optimal density—not too low and not too high.

Speaking about Allee's views, I would like to pay special attention to how he defined the subject of our science and, consequently, to his reasoning about limits of its competence. I mean his opinion about meaning the notions "social behaviour" and "social species". We will have to examine Allee's argumentation in more detail here.

After Espinas, Allee believes that as, speaking strictly, there are no solitary animals in the full sense of the word biosociality to a certain extent is common to all species of animals and in a sense—even to plants. So the question is: is it possible inside this continuum to draw the natural line between subsocial species and those that are accepted as truly social (intuitively). The latter primarily includes social insects. But before that I would like to stress that the answer is negative—this line can be only absolutely provisional, based solely on the agreement among scientists.

Argumenting, Allee examined three possible criteria of sociality. The first one is presence of the so called social instinct; the second is an adherence to family life style; the third is division of duties between members of the animal community.

In respect of some of scientists' adherence to the idea of social instinct Allee wrote that, fortunately, not many researchers share it. For Allee- experimenter this criterion could not seem practically useful since the very notion "instinct" appears extremely vague.

As for the second criterion—a practice of a family life-style, Allee contended that there is no any fixed point or sector where ephemeral sexual encounters would suddenly change into stable family. Examples that confirm this conclusion can easily be found in any well-studied taxon.

Thus, the third criterion remains—biological division of labour. Here, Allee stressed, the division of duties arises still at the earlier stage of evolution when the phenomena of gender and sexual reproduction appear. In modern terms, a male and female in the majority of species are bearers of the principally different social roles. At the same time, Allee came to conclusion that females are often much more social (or sociable) as compared to males much earlier than a number of other researchers of later times.

Therefore, it is not obvious for Allee where the sex-related division of duties ends and social division of functions starts. Traditionally, the relations in communities of social insects have been the standard of the latter. But even there, Allee wrote, the caste division is closely dependent on the sex of individuals. For example, sociable females in ants and bees are divided into reproductive and functionally asexual, or workers. The third caste consists of haploid males—drones that execute mainly the sexual, not social function.

The phenomena partly similar to caste polymorphism, or polyethism of social insects can be found in other animals whose sex determination depends on instantaneous intrapopulation social background.

Allee illustrates such cases with several examples. I would like to discuss one of them, taking place in the mollusk *Crepidula furnicata*. The phenomenon of

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protandry is its characteristic feature: each individual is asexual at early stages of ontogenesis, then it becomes a functional male and having reached a certain age turns into a female. Males of small size try to find those like them and remain in close contact groups consisting of individuals that include several species of both genders as well as those in the phase of transition from a male to a female. Several males can copulate with the same female simultaneously.

It is important that males that took part in copulations turn into females faster than those that failed to find a sexual partner. It was shown both experimentally and on the basis of field data. As a result, in *Crepidula* the sex ratio is different in different populations.

Allee gives many other examples of the influence of social environment and population density on sexual differentiation of some individuals. I shall present an example unknown to Allee. In many fishes sex change in ontogenesis occurs in opposite way than in *Crepidula*: a young individual is at first a female; then it turns into a male (protogyny).

It takes place, in particular, in the coral fish *Anthias squamipinnis* that live in heterosexual groups of various numbers. Sometimes it is a polygynic unit with one male and several females, sometimes groups consisting of several hundreds of individuals with the male to female ratio approximately 1:9. If a male is taken away experimentally from a polygynic group, one of females turns into a male in less than a week. In the case of withdrawal of several males from a large group, the number of females equal to the number of withdrawn males turns into males in the same short period.

An obvious analogy can be easily seen the phenomenon of regulation of family composition in social insects. According to Allee, a family of thermites *Zootermopsis* recently established by a pair of individuals has only one soldier in the first year. If it is withdrawn from the nest, its absence is compensated by the appearance of several (up to six) other soldiers. However, the compensation effect will not be as strong as that when a big family includes many hundreds of individuals. Allee believes that in the latter case a peculiar effect of "dilution" takes place and, correspondingly, hypofunction of a certain agent, or, as he calls it, a social hormone that is capable of suppressing the development of excessive number of soldiers.

No matter how highly specialized is the mechanism of the caste composition regulation, it shows, according to Allee, a certain analogy with much simpler "group effects". Among them one is a follows: an increase of resistance to harmful substances diluted in water inhabited by in large groups of fishes, being absent in the cases of small groups and single individual.

The search for such broad analogies is by no means a goal in itself. It appears to be an important methodological approach. It allows one to realize logically the possible ways of the complex regulatory mechanisms' evolutionary development from the moment when they are in a vestigial state yet and, strictly speaking, are still not complete formed. In this sense, Allee's quite perspective guideline is, in my opinion, the repetition and development of the ideas of Espinas who recommended to study not only advanced forms of social life but its earliest forms as well.

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Allee illustrates effectiveness of this approach with the example of establishing a developed social system in thermites on the base of simple gatherings of individuals in places of plentiful food supplies, like what we can see in the common German cockroach *Blattella germanica*). The hypothetical intermediate stage is represented, according to Allee, by some subsocial species of cockroaches that feed on fiber like thermites Both these cockroaches and thermites process of digestion as well as ability to survive are possible only because of the presence in their intestines of the symbiotic flagellated protozoans recycling fiber. Newly born insects do not have protozoans and can only get them through contacts with a skin of adult individuals being shed by them in the course of their moult (in *Cryptocercus*) or from another imago in thermites. However, adult individuals of *Cryptocercus* do not moult, and that is why an isolated pair of a male and a female is not capable to start a new deme.

In thermites imago loses protozoans in the course of each moult, so that the presence of other individuals is a vital necessity for all. Therefore, a male and a female with protozoans in their intestines are capable of establishing a new colony that facilitates keeping self-developing sociality in thermites, which is not the case in *Cryptocercus*.

Contribution of Classical Ethology to Research of Social Behaviour

Just in 1931–1938, that are the dates of the two first influential Warder Allee's books publication in the USA, another school in the behavioral research arose on the other side of the Atlantic. I mean the discipline known as classical ethology. Its origin can be dated tentatively by 1931, when 28-year old Konrad Lorenz published his first large paper "Beiträge zur Ethologie sozialer Corviden" in the German "Journal für Ornithologie"[3]. In 1935 and 1937a, b, c, two other basic papers of his were published: "Der Kumpan in der Umwelt des Vogels" and "Über die Bildung des Instinktbegriffes". In 1938, Konrad Lorenz and Nikolaas Tinbergen offered another paper on the role of innate components in the organization of integral behavioural patterns. Despite the fact that Allee and Lorenz developed their theories practically simultaneously, the essence of their approaches turned out to be quite different.

As we could see, Allee did not touch upon the distinction between the innate and acquired behaviour. For him it was a secondary matter, and he tried to avoid this aspect when possible, as he could not study it experimentally. For K. Lorenz and N. Tinbergen the a priori division between innate and acquired components of behaviour and establishment of relations between them was the basis of all further speculations.

[3]Currently Journal of Ornithology-Springer.

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These points are the heart of the whole fundamental differences in views of the American and European schools. For Allee the word "instinct" smelled of scholastics, was a kind of 'refuge of ignorance', while Lorenz and Tinbergen created an immense concept designated by them the "modern theory of instinct" (see, for instance, Tinbergen 1951).

Allee stresses the lability of the individual behaviour, its partial unpredictability, due to the variability of the social environment or social climate experienced by individuals. Ethologists of the European school, on the contrary, emphasize the stereotype aspects of social conduct, its conservative species- specific qualities.

Allee and his colleagues are interested primarily in consequences of the interaction of individuals joined into groups. Lorenz, Tinbergen and their school concentrate their attention on subtle mechanisms of these interactions rather than on their influence upon the subsequent life of the society. Allee is interested in the group structure at various parameters of the population number and density. Lorenz and Tinbergen are busy with how acting the given individual in the presence of other conspecifics performing different social roles. The centre of attention for the American school is various group and mass effects in local population, while European researchers analyze the dynamics behaviour of an individual mainly in pair interactions.

I shall not discuss the principles and methods of the ethologic concept in more detail, as it is covered much more than any other concepts in the literature (see e.g. Panov 1975, 2012). I would only like to accentuate some methodological aspects.

What is an elementarisic essence of classical ethology? I dare say, it become apparent in the intention to regard social behaviour as a chain of discrete events, so that each of them is rather constant and stable in its manifestations. Such constancy is reflected by a rigid classification of several "principal patterns" of interactions—for instance, a territorial conflict, treating a subordinate by a dominant, pair formation, copulation, etc. The stereotype feature of interactions within either such class of events is reflected from the start by Lorenz' scheme of several "companion" types: for example, companions-parents, companions-offspring, companions-spouses, social companion.

According to ethologists of the classical school, an interaction of each type is performed as a determinate exchange of stereotype signals between two individuals belonging to a category of a given type of companions.

These signals are called "fixed action patterns". Just standard types of interactions and standard communicative stimuli that are strictly determined genetically in this approach those further indivisible elements to which is reducing all, or almost all, social life in animal collectives.

We do not find anything like this in Allee's theory which is concentrated on the dynamism of a whole entity. It seems much more dialectic than the approach of classical ethologists that obviously have a propensity for mechanism.

It is important however, that being not adequate enough for the analysis of social processes in all their diversity, this approach, namely because of its typological features, has played and continues to play a very important role in the behavioural taxonomy and in modern systematics as a whole. This approach also contributed much

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to the understanding of organizational principles of individual behaviour functioning. The studies of organization of individual behaviour remain of a lasting value.

The general principles revealed here are inevitably modified with the progress of our knowledge, but further studies in the framework of fundamental theme “individual and society” cannot be conducted without them. Unfortunately, today it is too often overlooked.

But the ethological approach oriented at the individual and its interactions with the environment, including conspecifics, appeared to be quite insufficient for the comprehensive understanding of the biosociality phenomena. Then time demanded that in the centre of researchers’ attention should be the population as an organized system of the superindividual level.

Vero Wynne-Edwards and the Idea of the Intrapopulation Homeostasis

This new approach was shown in a most consistent way (arguably too consistent) in the book by Vero Wynne-Edwards “Animal Dispersion in Relation to Social Behaviour”. When it was published in 1962, its author, University Professor in the Scottish town of Aberdeen, was 56 years old. This work became one of the most cited publications in the literature on animal behaviour for the subsequent twenty years. It was a thick volume of about 650 pages. The list of references includes over 840 items (Fig. 3a).

We are interested in the analysis of the cited references in two ways. First, we see that the author widely uses literature in zoology of the past that shows his wide knowledge of biology and, possibly, a shortage of more modern special research in the topic of his interest. For example, papers published in 1911–1940 make about 34 % in the reference list. For comparison, of the reference list to the paper by Adam Watson and R. Moss (Watson and Moss 1970) on a close topic published eight years after the publication of the book of Wynne-Edwards citations of 1911–1940 comprise less than 2 % (Fig. 3b).

Second, the analysis of the literature used by Wynne-Edwards makes it possible to understand to what extent earlier authors influenced his ideas. It can be seen that Wynne-Edwards extensively cites the papers of ecologists Charles S. Elton, Huib N. Kluijver, David L. Lack, Alexander J. Nicholson[4]. He was also acquainted with the theory of Hans Selye who forwarded the concept of stress, or of the general adaptation syndrome (Selye 1956), and papers by John J. Christian and Dennis H. Chitty[5]) who tried to establish in the 1950s the idea of the influence of the social stress on the density and genetic contents of population.

[4]See, for examples, Elton (1958), Kluyver and Tinbergen (1953), Lack (1947), Nicholson (1933) (eds).

[5]See, for examples, Christian (1950), Chitti (1960).

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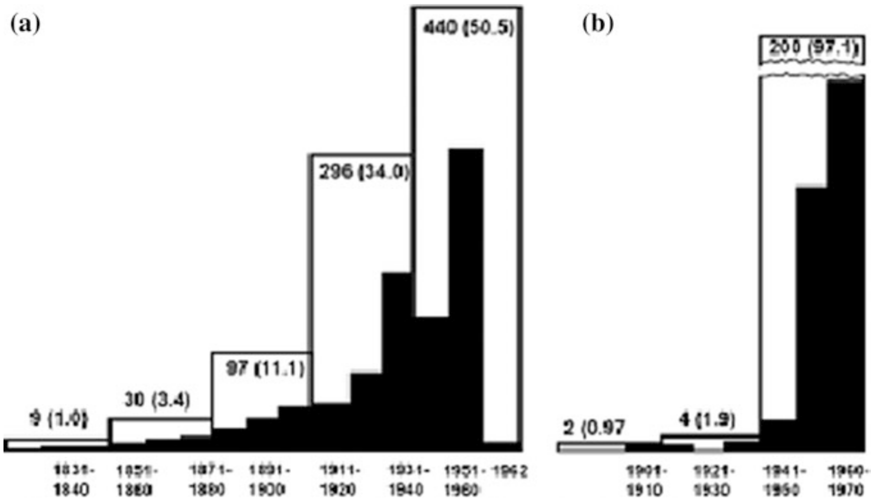

Fig. 3 Distribution by 10-year periods (*hatched*) and by 30- and 20-year periods (*contour lines*) of literature references cited (**a**) in the book by V. Wynne-Edwards (Wynne-Edwards 1962) and (**b**) in the paper by A. Watson and Moss (1970). Figures—the number of sources, in brackets—percentage

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The main idea of Wynne-Edwards is that all forms and types of social behaviour accomplish, in essence, the same major, and, may be, a single function, namely, to maintain a population in state of homeostasis, or, in other words, at a certain optimal level of its numbers and density. There are some mechanisms, according to the author, at the expense of which a population as an organized system protects its environment against overexploitation.

Wynne-Edwards believes that one of such mechanisms is the phenomenon of territoriality. Individuals that manage to conquer and keep then a territory become owners of abundant resources that they cannot can not to use completely. Other individuals turned out to be deprived of enjoyment of their own territory and so are forced to remain in the status of outsiders. They suffer from high mortality owing to hunger, predation, etc. This unequal access to resources serves the basis for the so called social selection.

It is important also that the transition of a part of individuals to the category of outsiders does not necessarily occurs forcibly. According to Wynne-Edwards, an individual has an ability to evaluate the population density. If density is high the individual itself refuses from attempts to conquer a territory and subsequent participation in reproduction.

This capacity to evaluate adequately the level of the population density is called “epideictic behaviour” which in translation from Greek means something like “presentation and analysis of a sample” (these concepts are taken from statistics).

Having postulated such a capacity, Wynne-Edwards tries to understand what may be possible mechanisms of its emergence in evolution. It is difficult to do if to believe in the paradigm according to which the evolution is advanced only by unequal success of individuals. In the given case individuals-outsiders doom themselves to failure and even death.

Thus, Wynne-Edwards comes to conclusion that the biological success of a group, namely, the guarantee of its future survival, is exactly the advantage granted by social behavior. In the frames of his conception an unit of evolution is not an individual but a group. Instead of individual selection, group selection is offered to explain the evolution of social behaviour.

I shall not discuss controversial points and some drawbacks of the Wynne-Edwards' model. Here it is important to stress that in my scheme it appears as a concept of obviously organismic character based on holistic approach to the understanding of society. Processes taking place in groups of individuals are regarded as the most important, while the features of the individual behaviour is deduced from characteristics of the group structure. It should be also noted that accent in the Wynne-Edwards' work shifted, in general, from the attempts to analyze group structures to questions of their hypothetic evolutionary origin.

Sociobiology by William Hamilton and Edward Wilson

By contrast the organismic theory of Wynne-Edwards and almost simultaneously, only two years later, in 1964, another doctrine was set forward that, in the frames of my scheme, can be appreciated as utmost elementaristic. It is the so-called "genetic theory of evolution of social behaviour" developed by the English naturalist William Hamilton. Like Wynne-Edwards Hamilton is concentrated not on analysis of what are animal communities now, but rather on ways and mechanisms of their formation in evolution. This topic became the main and most principal for him. But in unlike Wynne-Edwards, Hamilton believes that there is no need to postulate group selection as everything can be explained via individual success of an individual. While Wynne-Edwards thought that specificity of the species behaviour provides the success of the group as a whole, according to Hamilton, everything occurs quite in the contrary way: success of an individual is provided mainly with its existence as a member of a group.

As opposed to other neo-Darwinian theories, the success of an individual is evaluated here not just by the number of offspring left but with the quantity of those who will become in one way or another the bearers of the genes the same as present in this individual. It can increase the fraction of its own genes bearers either in the "egoistic" way by reproducing in maximum possible rate, or indirectly, promoting the survival of its close and distant relatives. Hamilton called the second strategy as "altruistic" behaviour. Thus, according to him, it is possible to draw a sharp dividing line between non-social and social species.

From this point of view, the appearance of what he called the "true sociality" takes place at the moment when "absolute altruists" emerge in a population, i.e. such individuals that do not reproduce themselves at all but instead take care of their relatives. Thus they preserve their own "altruism genes" for the subsequent

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generations. This is the essence of the concepts “inclusive fitness” of the individual, and “kin selection” offered by Hamilton (for details see Panov 1983).

The whole theory is built on the axiomatic principle, on the basis of theorems of mathematical genetics developed earlier on the grounds and for the analysis of another sphere of biological reality. This circumstance makes unnecessary for the given theoretical construct almost everything that was made earlier in the field of zoological research of the social behavior. For instance, a most interesting problem of organic individuality disappears automatically. The border between social and “non-social” species is drawn quite unequivocally. From the classical ethology only the idea of the innate determination of behaviour was taken, while one of the most interesting and promising topics, namely, causality of the behaviour dynamics in time (in particular, in ontogenesis) and its alterations influenced by changes in social environment was practically left unattended.

Nearly all ties with the richest earlier achievements in biology were cut off. The integral phenomenon of biosociality with all complexity of its intrinsic links disappears; it breaks down into certain behavioural “traits” each of which is controlled by its own genetic determinant. It appears that the whole approach is apparently simplified, abiological and has a little explanatory potential. In fact, on its base many hypotheses were set forth and, as a result of it, very large empiric material was accumulated during the subsequent years. But, as a rule, obtained data turn out to be fatal for the hypotheses themselves, being in obvious contradiction with its prediction. It is no surprise, taking into account the formalistic, scholastic and far-fetched character of the majority of sociobiological speculations.

In 1975 the book “Sociobiology: The new synthesis” by Edward Wilson was published. It is a review collection of about 700 pages. If the reference list in Allee’s paper contained 129 sources, Wynne-Edwards’s 879, in Wilson’s monography there were 2500.

Let us see what the book by Wilson is in its essence, what are its connections with preceding stages of zoosociology development. And is it possible to consider it as an organic synthesis of the previous knowledge, as the author asseverate? At the very beginning of Chap. Roots of Current Concepts in the Studies2 of Social Behavior in Animals, under a rather surprising title “The morality of the gene”, we read: “The main theoretical problem of sociobiology is to understand how altruism that lowers adaptation of an individual could develop in evolution”. Here the author expresses his main credo: like a chicken hatching from an egg is no more than a means to reproduce another egg, the organism is essentially not more than an instrument for preserving and transition of genes. It is obvious that Hamilton’s ideas are the main source for ideology of Wilson.

In the Chapter dealing with animal communication Wilson punctually retells the basic points of the ethology theory of instinct, and sometimes—in its most archaic form. The third component of the Wilson’s sociobiology is the modern population ecology in development of which Wilson himself made an important contribution, in particular, with the book “The theory of Island biogeography” written in co-authorship with R. H. MacArthur (MacArthur and Wilson 1967). In many parts

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of his “Sociobiology” Wilson regularly cited his previous book on social insects that he knows excellently.

Therefore, there is no denying that the author of the “Sociobiology: The new synthesis” is an erudite in many facets of the biology. But is his book actually a synthesis of the preceding knowledge? One can get an impression that Wilson’s work is, in essence, rather eclectic than synthetic. The true synthesis presupposes combining different views and concepts in such a form when their inner contradictions are not hidden but shown as clearly as possible. It is what really stimulates science to advance.

As for the Wilson’s book, all preceding concepts, both apparently atomistic and holistic ones, peacefully co-exist in it. Perhaps, only in respect of the ideas of Wynne-Edwards, Wilson is predisposed negatively and spares them almost no place in the book. It is interesting that Wilson calls himself a holist that seems far from the real state of things. A lot of his constructions have obvious typological character and thus undoubtedly tend to elementarism of the classical ethology and the genetic atomism of Hamilton.

Programme of Studies of Socio-demographic Systems in Socioethology

Sociobiology is today a quite influential discipline, although in recent years a noticeable wane of its prestige can be traced. And it is not the only approach in the zoosociology today. There is another concept of a holistic character that ideologically opposes sociobiology. I mean the so-called socioethology whose subject and tasks were outlined in the early 1970s by the zoologist J. Crook from Oxford.

Both the object of the study—a local population, and its subject (social behaviour) in socioethology differs at the first sight little from as they are seen in the sociobiology of Hamilton and Wilson. However, the principle approaches and the general accents in treating of the evolutionary questions are different here in many aspects. First of all, Crook’s attitude seems to be much more realistic. For him speculations about the evolution of social behaviour is not the first task but the second one, executable only after the clear understanding of the essence of systems under consideration is achieved. These systems appeared as an immense complex structures reciprocal with very complex interweaving of the demographic parameters and social behaviour are designated by Crook as the socio-demographic systems. For Crook the appear not as a certain stable entity but as a society the understanding of society as a process, where the development of individual behaviour proceeds under the influence of both interweaving and socialization, which demands very close attention (Crook 1970).

In fact, the matter is one of the most complex and not properly understood problems of biology: how the genotype, which is no more a program of the individual development, is realized, under the influence of outward information coming from outside, into the phenotype of the competent actor. In general, Crook actively

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keeps aloof from a primitive understanding of heredity as a simple mechanical transition of the so-called 'traits', including behavioural ones.

Hence, a conclusion naturally follows that speaks that the role of genetic factors in determination of social behaviour and, thereafter, in a maintenance of intergroup structure is heavily exaggerated by sociobiologists. The cause of it, Crook, affirmed, is rooted, among others, in the wrong (and characteristic especially of layman audience) notion that structural characteristics of society are equated to the "fixed action patterns" of the classical ethology (Crook 1970). Such misconceptions, Crook believes, are formed under the influence of some publications addressed to the general public. He means such books, for example, as the Lorenz's "On aggression" (1963), D. Morris "The Naked ape" (1967), R. Ardrey "The Territorial imperative" (1966). The book by R. Dawkins "The Selfish gene" (1976) may be added to them. These publications spreading ideas like that on inborn aggression in humans, Crook calls "pseudobiology".

In recent years, this pseudobiology of the human behaviour is flourishing in adapted for the elite books by Wilson and his colleagues.

Crook, who specialized in studies on the divergence of socio-demographic systems in primates, concluded that in their evolution the main role was played by phenotypic adaptations that put in motion with individual learning and intergroup traditions. These factors became of the key value at the early stages of anthropogenesis. The genetic factors in that the forthright form, as Hamilton, presents it, plays, in Crook's opinion, a rather subordinate role.

It does not mean at all, however, that we should ignore genetic aspects of social evolution. But here it is necessary to develop experimental genetics of behaviour—instead of wordy juggling with genetic terms, like "mutations" of certain abstract 'genes of egoism' and altruism. Let us see as the matter looks from the point of view of specialists dealing with the scientific language. "Terminology within the biological sciences gets its import not just from semantic meaning, but also from the way it functions within the rhetorics of the various disciplinary practices. The 'sociobiology' of human behaviour inherits three distinct rhetorics from the genetic disciplines. Sociobiologists use population genetic, biometrical genetic, and molecular genetic rhetorics, without acknowledging the conceptual and experimental constraints that are assumed by geneticists. The eclectic blending of these three rhetorics obscures important differences of context and meaning. Sociobiologists use foundational terms in genetics, such as 'gene', 'fitness', 'evolution", 'heritability' 'trait' and 'polygenic inheritance', in starkly different ways from geneticists, while basing their analysis of human behaviour on the implied authority of genetics. As a free-floating 'gene talk' moves across different disciplinary contexts, and before different audiences, it takes the form of an over-simplified and misleading arch-determinism. The result is widespread application of vague, incomplete, and distorted biological theory. If most sociobiologists, do not deliberately promote biological determinism, still less a political agenda, there is ample evidence that they misconstrue the implications of the genetic language that they borrow" (Howe and Lyne 1992).

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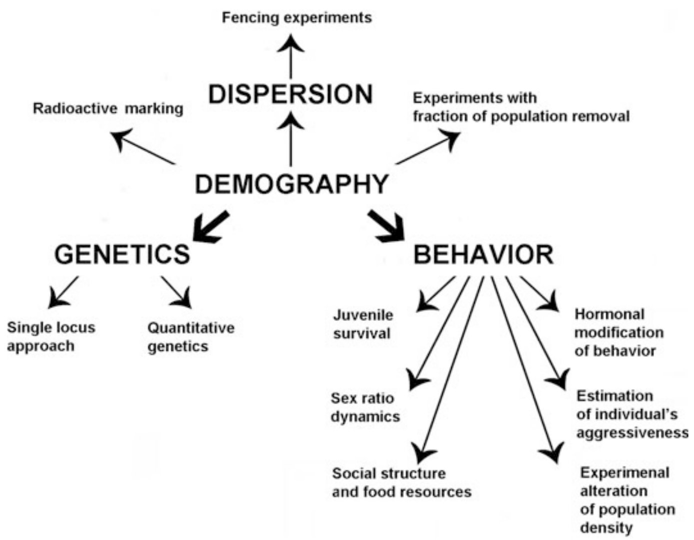

Fig. 4 Strategy and methods of research of the socio-demographic system (from Krebs 1979). Explanations are in the text

I would not discuss in more detail the system of views of socioethology. It will be illustrated points of its main tasks, approaches and methods with a scheme from the paper (1979) by the Canadian researcher Charles Krebs on long-term studies of socio-demographic systems of vole *Microtus townsendii* (Fig. 4).

It can be seen from this scheme that socioethology has rich hidden prospects that give hope for the really deep understanding the essence of intrapopulation processes on the basis of comprehensive application of ethological, ecological and genetic methods of research.

Conclusion

It is not easy to avoid certain schematism and declarativity in a brief review of a hundred-year history of scientific research, discoveries and disappointments. I only have a mild hope that I managed, maybe partially, to show the important place that zoosociology occupies in the general system of biological knowledge. The cornerstones of this discipline are rooted in the period of tremendous upgrowth in biology in the middle of the 19th century. Is not it surprising that the topics related to the studies of social behaviour of animals, which seems to have appeared quite recently, nearly before our eyes, have actually such a long and complex history? It should be stressed that studies of social behaviour and group structures are by no means a by-path of biology. This topic is directly connected with such fundamental issues of biology as formation of multicellularity in phylogenesis, formation of the

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phenotype in ontogenesis and autoregulation of most complex systems of the supraorganismal level.

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