THE FEATHERED ONE IN THE FLOCK OF MODELS: *GALLUS GALLUS* AS A MODEL ORGANISM FOR DEVELOPMENTAL BIOLOGY

MIGUEL LÓPEZ-PALETA
EDNA SUÁREZ-DÍAZ

ABSTRACT. This paper aims to provide a critical picture of the role of domestic fowl (*Gallus gallus*) as a "model organism" in developmental biology. As such, it seeks to be a contribution in the field of historical epistemology, broadly defined. We take into account the characterization of model organisms by Ankeny and Leonelli (2011) and, secondarily, the one developed by Rheinberger (2010), in order to discuss the ways in which chicken fulfils, or not, the epistemic and material features of current model organisms. In a similar manner, we bring up some new arguments to those that chicken researchers have provide when facing the fact that *Gallus gallus* is not an organism frequently used in certain genetic research contexts. Finally, we consider some interesting topics in the philosophical reflection on model organisms that could be illuminated by the case of the domestic fowl.

KEY WORDS. Model organisms, *Gallus gallus*, chicken, developmental biology, modeling, representation, vertebrate biology, philosophy of biology, scientific practice.

1. CHICKEN AND DEVELOPMENTAL BIOLOGY

Domestic fowl (*Gallus gallus*) is one of the most common domestic birds in the world, with a population estimated in more than nineteen billion individuals by the year 2010 (FAO, 2012). Although its importance in agriculture and food production is well known, chicken is also a relevant species in biological and life sciences research. Domestic fowl is commonly used as a model in developmental biology, where biologists employ it for enquiries about the vertebrate and tetrapoda embryonic development.

Moreover, *Gallus gallus* has been involved in important breakthroughs in biological disciplines such as immunology, virology, oncology, and genetics (International Chicken Genome Coordinating Committee, 2004).

Grupo de Estudios Sociales de la Ciencia. Facultad de Ciencias, Universidad Nacional Autónoma de México.
miguelpaleta@comunidad.unam.mx / ednasuarez@ciencias.unam.mx

Within embryology and developmental biology, some biologists claim that the history of this domestic bird dates back to the European Antiquity, when Aristotle made observations about the embryo formation inside a chicken egg (Stern, 2004; Tickle, 2004; Wolpert, 2004). Even if it is clear that research interests, focus, styles and research practices have changed since then, chick embryos were part of the enquiries and investigations carried out by many different thinkers since the Renaissance to the nineteenth century. Fabrizi de Acquapendente, Marcello Malpighi, and William Harvey are just but a few names linked to the employment of hen eggs to observe, describe and discuss the formation of the embryo and its organs and systems (Needham, 1934).

In a more recent context, all along the twentieth century, another series of breakthroughs took place in developmental biology due to the work in *Gallus gallus*. Some of these include the production of chicken cell cultures where different tissues could be grown; the experiments conducted by Conrad H. Waddington in the 1930s which showed that the endoderm was capable of controlling the beginning of the three germ-layers development; the patterning of vertebrate limb and the identification of areas which control the formation of the limb axis; the "developmental plasticity" introduced to account for the fact that separate cells of the same embryo can give rise to different individuals; the study of cell movements due to vital dyes [1]; the fate of the cells which formed the neural crest, described in a series of experiments with chick-quail chimeras made by Nicole Le Douarin, and the first set of genes that control the left-right asymmetry in the embryo (Stern, 2004; Stern, 2005; Wolpert, 2004).

Although *Gallus gallus* is a long-running character in embryology and developmental biology, and it has been involved in the establishment of several long-standing concepts (such as "plasticity" or "epigenesis"), as well as in historically relevant disputes about the embryo formation (such as epigenetism vs. preformationism) (Needham, 1934; Mendehlsson, 2005), its role does not seem to be fully considered. In fact, a few biologists who make chicken research claim that nowadays chicken's role in fields such as molecular biology is not well appreciated (and even one of them complains about "anti-chick racism") (Stern, 2005).

At the present time, it seems that *Gallus gallus* has become less conspicuous among the group of organisms employed in biological research. Probably the notoriety of chicken in developmental biology has diminished in the last twenty years due to the introduction of new model organisms such as the zebrafish (*Danio renio*) or the nematode *C. elegans*, which have achieved great importance. A quick query in *PubMed* shows that during the year 2012, zebrafish appeared in 787 papers published, while in 1993 they amounted to only 21. The translucent nematode *C. elegans* followed a similar growing path, with 49 papers in 1993 and 250 in

2012. Meanwhile, although the numbers of research articles in which *Gallus gallus* appeared in 2012 (343) is larger than in 1993 (212), that was not such an impressive growth as the other two model organisms.

The reasons why domestic fowl has become less conspicuous, and the related complaints of the scientists involved in research around this bird, can be brought out by focusing on current descriptions of the wider group of "model organisms." In this article, we will first make an account of those *Gallus gallus*' advantageous traits that biologists tout when they perform experiments with this bird. Secondly, we will see how these properties are important to situate the domestic fowl in the model organisms group, i.e., that set of species which share common epistemic and material features (Ankeny and Leonelli, 2011). Finally, we will suggest that a reflection on how chicken is used in developmental biology can contribute to the broad model organisms discussion.

2. WHY USE *GALLUS GALLUS*?

Usually, biologists talk about *Gallus gallus* as an adequate organism to perform certain kinds of experiments related to various aspects of embryological vertebrate biology. For instance, in a National Human Genome Research Institute report, Twyman (2002) claims that the chicken is "a good experimental model" of vertebrate embryonic development; while in a review article, Dave Burt (2007) states that domestic fowl is "an ideal system" for the study of that phenomenon. Even if it is possible to question in which sense this is so and what being "a good experimental model" really mean in developmental biology, scientists argue that there are several reasons for employing *Gallus gallus* in their work.

In this respect, some biologists claim that chicken has technical advantages that enable scientists to acquire them easily. Due to farming activities, chicks seem to be available all over the year and all around the world, and also are relatively inexpensive (Antin, Fallon and Schoenwolf, 2004). Additionally, artificial incubation allows eggs to be set in closed environments such as laboratories, where incubators are convenient tools for following the process of embryonic development over several days.

The reasons for using domestic fowl are based in this kind of advantages. In this regard, we will focus on two general claims that developmental biologists make:

(1) Chick embryos are easy to manipulate in vivo (which in this case, usually means *in ovo*) (Tickle 2004). This claim refers to the fact that chick embryos develop within an eggshell, which the researchers are able of break without interfering dramatically with development, so that they are capable of intervening (e.g., conduct microsurgeries, or insert proteins embedded in a polymer bead or DNA fragments in a vector). Afterwards, they can

put back the egg into an incubator and monitor the results of the interventions at different time lapses.

(2) Chicken has a relatively close "evolutionary position" with respect to other groups of vertebrates. As mentioned in some papers appeared a few months after the publication of the chick genome in 2004, *Gallus gallus* is an amniote vertebrate just like mammals, from which Aves were split in a relatively recent time [2]. Following this idea, chicken genetic regulation and developmental processes are supposed to be similar to other members of the Vertebrata (Stern, 2004; Tickle, 2004).

We will call the first point a "practical claim", since it refers to the manipulability appeal of the chicken embryos and the characteristics that make them relatively easy to handle in a laboratory. Although this manipulability includes those chick's individual traits mentioned above, it certainly may include some general practical traits of the wider group of "model organisms." As asserted by the editors of *The Scientist* special issue on this sort of organisms, "researchers selected this weird and wonderful assortment from tens of millions of possibilities because they have common attributes as well as unique characteristics [3]" (Bahls, Weitzman and Gallagher, 2003). Those "common attributes" are associated to genetic features such as small physical and genomic sizes, short life cycles, high fertility rates, short generation times, and high mutation rates or high susceptibility to techniques of genetic modification (Ankeny and Leonelli, 2011). Debatably, chicken fulfils this picture (see below). Biologists conducting research on *Gallus gallus* sometimes argue that, in fact, chicken has a relatively small-size genome (one third the size of mammalian genomes), it is somehow susceptible to a couple of techniques of genetic modification (McPherson, et al., 2002), and it is also capable of producing a large number of offspring.

The second point refers to an "evolutionary claim." The assertion that Aves and Mammals are evolutionary "near" purportedly means that genetic breakthroughs such as the chicken genome sequencing would be useful in several fields, including comparative genomics, evolutionary biology, and systematics (Burt, 2007; Stern, 2005). The chicken—is said—"provide an intermediate perspective between those provided by mouse and fugu" (pufferfish) (both vertebrate organisms used in biological research) (McPherson, et al., 2002) and it is expected that the knowledge derived from research on *Gallus gallus* (e.g., some genetic mechanisms in the embryonic development) will be applicable to those other members of the Amniota group, including humans (Tickle, 2004). These comparative aims of the researchers working on chicken are also closely related to the focus on the genetic features of model organisms, and to a research context where genetic experimentation is relevant. In this sense, comparativeness between organisms is almost directly referring to similar genetic traits (compositionally and maybe functionally) from different species.

It is also important to point out that these practical and evolutionary claims are actually intertwined in scientific practice. A model organism is seen as a relatively simplified form of those others that aims to represent, as is seen in those practical features of the model organism, such as the size of its genome (Ankeny and Leonelli, 2011). Similarly, Lewis Wolpert claims that chicken is a practical organism to make interventions in the so-called "normal development" and observe results, as opposed to mice or other mammals which develop in an inaccessible womb and whose embryonic structures (cells, organs, systems) are not so easily analyzable (e.g., the epiblast, which in mice is curled up, while in chicken is flat) (Wolpert, 2004). Of course, this doesn't mean at all that those "other organisms" become unimportant for the researchers interested in chicken, it means that *Gallus gallus* is an important model as far as it can be used to understand the development of a more extensive group of vertebrates. A further fact that links its practical and evolutionary advantages is the fact that, ultimately, biological research seeks for medical application in humans: the fact that Aves belongs to the Tetrapoda group, like mammals, accounts for its possible role in understanding relevant mechanisms with future applications.

Even so, opposing those claims of usefulness and convenience is the fact that chicken does not seem to be well-suited to some practices in experimental genetics. For example, transgenic lines of chicks are more difficult to obtain than in mammals due to some traits of the domestic fowl's reproductive system: chick development during the first 24 hours after fertilization takes place inside the oviduct of the hen, and while the zygote's first cleavage occurs, the egg-shell is just been formed in the uterus. This means that the very initial divisions of the egg are not easily observable by the most common used techniques of microscopy and thus chick embryos are not very useful to study the early phases of embryonic development. It also means that the embryo is inaccessible for inserting transgenes at those stages of development. Thus, an alternative method to produce transgenic chickens has been to insert them in the germ cells (located near a specific embryonic structure known as the germinal crescent) once the egg has been laid. Still, though the method of opening up windows in the egg is convenient in order to observe the results of some kind of interventions, it decreases the hatching rate, making it difficult to obtain an adequate population of G0 transgenic birds (Mozdziak and Petitte. 2004). Again, some improvements have been made for enhancing the hatching rates, including egg-shell transplants from other embryos, less invasive interventions and setting up more sterilized environments. Nevertheless, *Gallus gallus* is also problematic because a significant population of adult individuals is difficult to keep in proper facilities within a laboratory, and because it takes a relatively long time (17-20 weeks) to grow chicks to its reproductive age (Chapman, et al., 2005).

At least in the case of development biology research, some practical advantages of the chicken are only *local and temporary*, in the sense that they are only useful in determinate lines of research and within specific periods of time. Thereby, the manipulability of an embryo enabled by the "egg-shell window" method is effective for conducting experiments at certain stages of development (those after the egg is laid), but it becomes problematic for studying primary stages of development or even for genetic manipulation techniques and research approaches, such as the production of transgenic birds.

3. *GALLUS GALLUS* AS A MODEL ORGANISM

In virtue of the aforementioned, it is worthwhile to question how useful can *Gallus gallus* be to biological sciences research, where genetic modification and transgenic organisms' production constitute key practices in contemporary experimentation. Additionally, as far as genetic features have a significant role in comparability among species, it is reasonable to ask if domestic fowl is indeed an adequate model for other species. In this sense, first, it is important to establish which are the features of model organisms according to recent literature in the field of philosophy of biology. In the influential work of Hans-Jörg Rheinberger,

> (a) model organism is a living thing from the plant, animal or bacterial kingdom that has been tailored to experimental purposes; manipulating it can generate insights into the constitution, functioning, development, or evolution of an entire class of organisms. The operative criteria for selection of a model organism are the ease with which it can be maintained and handled, the quantity and quality of the knowledge already accumulated about it, and the relative accessibility of the phenomenon under investigation [4] (Rheinberger 2010 p. xiii).

To illustrate this, Rheinberger has worked on the role of xenia in *Pisum sativum* and *Zea mays* in the hybridization experiments of Carl Correns (that took him to the "re-discovery of Mendels laws), the role of the protozoa *Eudorina* in Max Hartmanns experiments in regulation, the use of *Ephestia* in Alfred Kuhn's physiological genetics and of tobacco mosaic virus in research at the Kaiser Wilhelm Institutes for Biochemistry and Biology in the 1930s and 1940s (Rheinberger, 2010).

Rheinberger's definition of model organisms and his productive use in several case studies have a series of advantages. Mostly, the openness of his characterization makes it useful to portray different fields of research in the life sciences and different periods of experimental research since the nineteenth century constitution of modern biology. From a more formal philosophical approach, however, other more restrictive definitions have been developed (we will come back to Rheinberger's analysis).

Thus, for the philosophers of biology Rachel Ankeny and Sabina Leonelli (2011), "model organisms" are not equivalent to the wider group of "experimental organisms" (to which Rheinbergers definition seems to make reference). Briefly, experimental organisms are all those species that are used in biology research due to their suitability for conducting certain kinds of experiments. Although model organisms are part of this wider group of species, they have distinctive material and epistemic features. With respect to these epistemic features, model organisms have a broad "*representational scope*" and a particular "*representational target*."

3.1 REPRESENTATIONAL SCOPE AND REPRESENTATIONAL TARGET

The representational scope of an organism refers to how widely the results of research in this particular organism can be extended onto a broader group of species. The projection of these results can vary from a single species to a wider taxon of organisms such as a class or a kingdom, and the extension of the representational scope assumed by scientists is related to the criteria for the selection of a species in the first instance, together with the question to be investigated (Ankeny and Leonelli, 2011).

The representational scope of model organisms is broader than that of experimental organisms, such as pigeons, frogs, or turtles, according to this definition. And, as opposed to several cases where the results of experiments in an organism are expected to be extended only to its own species or a few other ones, "model organisms are always taken to represent a larger group of organisms beyond themselves" (Ankeny and Leonelli, 2011). This is why model organisms are considered "models" of other species, because "they serve as the basis for articulating processes that it is thought will be found to be common across all (or most) other types of organisms, and particularly those processes whose molecular bases can be articulated" (Ankeny and Leonelli 2011).

On the other hand, Ankeny and Leonelli (2011) claim that "representational target" refers to the phenomena to be explored through the use of a particular organism. From that standpoint, *phenomena* refers to the different labels used by researchers to define concepts, entities, and processes related to their own research interests. Although these authors reckon that there is a long discussion on the status of phenomena in philosophy of science, by using the term "representational target" they refer to the fact that there are specific situations which researchers are keen to study when they use a particular organism. In this sense, "the representational target describes the conceptual reasons why researchers are studying a given organism" (Ankeny and Leonelli, 2011). Therefore, model organisms have a specific representational target, namely they serve "as models for whole, intact organisms," which means that they are models of a range of processes and systems occurring in living organisms (Ankeny and Leonelli, 2011). This also means that they are not used as models for specific research questions (such as the action potential studied in the giant squid axon), but that they are used as models of whole organisms.

3.2 *GALLUS GALLUS'* MATERIAL FEATURES AND INFRASTRUCTURE

Moreover, model organisms have distinctive material features that require the establishment of infrastructures enabling communication and exchange of materials among the scientists interested in a particular organism, as well as social structures built to enhance collaboration. This kind of social links and infrastructure are not observable in other experimental organisms (Ankeny and Leonelli, 2011).

3.2.1 STANDARDIZATION

In this regard, the standardization of an organism is a distinctive feature of its use as a model organism, closely related to the dominant genetic approach in which these organisms are used. Model organisms usually are reproduced in standard strains that serve as a basis for research and genetic comparative approaches. This feature distinguishes model organisms from other organisms used in laboratories (Ankeny and Leonelli, 2011). In this sense, in the particular case of chickens, it is worth to notice that laboratories are environments where precision and reliability of results are in high demand; scientists then try to standardize practices and materials in order to communicate and reproduce the results of a research project. It is expected, also, that standardizing methods will prevent biases or unexpected variables from coming into play.

Anyhow, it is worthwhile to say that currently extended standardization methods by no means imply that the introduction of an organism into biological sciences research is determined completely by clear and distinct parameters. In other words, it would be misleading to take this kind of standardization as a criterion to account for a general history on the introduction of organisms in a laboratory, because many of them have a long history in biology before they were promoted as "model organisms" and long before they were standardized in the current way. Although the zebrafish case is an example of how this genetic approach has gained importance (Ankeny and Leonelli, 2011; Hopwood, 2011), the pathways of the entry of different organisms into the laboratory environments are usually less directed.

For instance, *Drosophila melanogaster*, renowned by its genetic advantages, was first projected as an organism to study "experimental evolution" and its introduction to classical genetics in Thomas Morgan's laboratory at Columbia University was much messy than usually portrayed (Kohler, 1993). Moreover, despite the fact that it is currently used for developmental biology, *Xenopus laevis* took its first steps in endocrinology and pregnancy tests research (Burdon and Hopwood, 2000). In this sense, it is useful to distinguish the current claims about *practicality* and *evolutionary closeness* from the reasons that made scientists utilize an organism for investigations in the first place, and the contingent histories associated to these pioneer uses. This does not mean that organisms are passive agents within a laboratory, since the history of species utilized in the laboratory is a dynamic one, and both the material features of a particular species and the interests and aims of the community associated play an important role (Leonelli, 2007). Also, the choice of an organism by researchers is based on different criteria which have changed in the course of time and on the various approaches scientists employ, choices that always create new opportunities and sets limits (Hopwood, 2011).

Having said that, let's get back to the current genetically-based approaches. Chicken flocks don't seem to be an exception to the standardization aims of scientists. It is a common feature of developmental studies that fertilized eggs are acquired in farms specialized in raising "specific pathogens-free" (SPF) organisms. This kind of bird is bred in controlled, closed environments, where only authorized staff is permitted entrance. The SPF farms are committed to external regular evaluations that allows them (or not) to claim that its flocks are free from the most common avian diseases, including Newcastle disease, avian flu, and avian leucosis. Those evaluations are also conducted with internationally standardized methods.

This shows a contrasting characteristic of the use of chicken compared to other laboratory organisms. As an example, *Arabidopsis thaliana* (the model plant) has a long history of centralized research goals and plans that eventually set up the establishment of stock centres where plant biologists all around the world acquire specimens (Leonelli, 2007). Although there are some strains of mutants in some institutions in the United States, chicken biologists apparently don't have an equivalent world-wide acknowledged stock centre. Additionally, SPF chickens are not exclusively used for biomedical or biological sciences research, but they have a great importance in the manufacture of vaccines.

The origin of the use of SPF chickens seems to be closely related to commercial interests. In a brief recount on the commercial production of this type of birds, R. E. Luginbuhl, former president of one of the most important SPF producer companies (SPAFAS Inc., nowadays part of Charles

River Laboratories), states that although chicken embryos were used to vaccines production since the first years of the twentieth century, apparently there was no knowledge about the fact that embryos could carry viruses and pathogens from their parents until some decades later. Even if some groups of research in avian diseases and some vaccines producing companies developed SPF flocks of chickens by the 1940s, it was until 1960 that the commercial production of SPF chickens and eggs for research begun. This meant that the companies interested in raising SPF had to create an adequate knowledge of viral transmission and the necessary infrastructure to isolate flocks, produce eggs and chicks, and transport their products (Luginbuhl, 2000).

There is a lot more to say about this topic, and what it is important to notice is that at some point in the history of chicks flocks biologists from other fields of work began to utilize this kind of birds in research not closely related to avian diseases, and that (contrasting with the cases of *Arabidopsis* or *Drosophila*) these standardized flocks do not come from a community effort within biological research groups, but from commercial and agricultural interests.

Within the companies that produce them, the SPF chickens don't seem to be selected using genetic approaches, but the most usual practices of farming. These include selecting healthy individuals from flocks already present in a population, and selective crossing and breeding. The health of the individuals is analyzed using immunological probes as ELISA or immunoprecipitation in agar gel. Although it cannot be taken as a general case, the director of the avian division of a Mexican company oriented to develop SPF chickens and other materials of agricultural importance stated that genetic tools are just starting to be used in the selection of SPF flocks [5].

In this sense, *Gallus gallus* does not fulfiel one crucial material feature of model organisms as defined by Ankeny and Leonelli (2011): the standard strain. This seems to be related to the fact that, as we said in the last section, biologists have been struggling to develop some genetic tools for chicken research and, maybe, that genetic inheritance studies does not seem to be the most common approach in the use of chicks in the history of biology. Despite the existence of some tools that enable scientists to genetically modify chickens and work with them, and the fact that developmental biologists focus on genetic analysis or different traits, it is not clear that researchers are concerned about the development of a standard strain. Apparently some existing strains with specific mutations and the use of SPF chicken suffice the necessities of chicken researchers.

3.2.2. CHICKEN INFRASTRUCTURE

In addition to the standard strain and the world-wide stock centres, nowadays model organisms require the establishment of cyber-infrastructure, such as community databases for improving the communication between researchers interested in the same organism. These databases are developed within specific social structures that bring together researchers interested in a particular model organism (see Leonelli, 2007 for the *Arabidopsis* case, and De Chadarevian, 2004 for *C. elegans*). The formation of collaborative communities of researchers and their "community resources" such as stock centres and databases are recognized institutionally and play a significant role in the genome sequencing projects of all model organisms (Ankeny and Leonelli, 2011).

Despite its disadvantages in genetics contexts, *Gallus gallus* remains an extensively used organism in developmental biology. In fact, the proposal to sequence the domestic fowl as part of the Human Genome Project was submitted in February of 2002 by John McPherson from the Washington University Genome Sequencing Centre (currently in the Ontario Institute for Cancer Research); Jerry Dodgson, from Michigan State University, and Robb Krumlauf and Olivier Pourquié, both from the Stowers Institute for Medical Research (the latter currently ascribed to the Institute de Génétique et de Biologie Moleculaire et Cellulaire in Strasbourg) (McPherson, et al., 2002) [6].

In their proposal for such sequencing, the authors emphasized an important resource: "the community." They claim that the size of the population of researchers working on chicken is best exemplified by the amount of papers that appeared in a *PubMed* search included in the white paper. However, they recognized that the *chicken community* was split in two main fields: those researches "interested in chicken as a model biological system and those interested in agricultural productivity." The authors claimed that genomics could play the role of a bridge between these two fields; for example, complex traits of chickens' biology which are agriculturally relevant are by now important for molecular biologists, and it is thought that the "foundations" of these traits are identifiable at a molecular level (McPherson, et al., 2002).

This claim about how genomics serves as a bridge between these two groups of chicken researchers continued to be an issue for some time (cf. Burt, 2005). Also, it is similar to other model organisms' cases, such as *Arabidopsis thaliana*, where the growing attention to genetically oriented research and the campaign for its use as a model, made mouse-ear cress an adequate organism to conduct plant research since the basic hereditary mechanisms were expected to be the same in all plants (including those valuable for their agricultural importance) (Leonelli, 2007). In this sense, for many model organisms (including *Gallus gallus*), genetically oriented research has been seen as a provider and synthesizer of relevant information and explanations for different research fields.

Thus, there is a scientific community more or less defined for whom the study of chicken is central. The names of David Burt, Claudio Stern, Olivier Pourquié, Jerry Dogson, and Mary Delaney often appear in reviews papers promoting the advantages of using domestic fowl for some experiments. These and other researchers have also created the infrastructure related to the knowledge and communication of research on chicken. This includes databases such as ArkDB (an on-line database which comprises genomic information about several domestic animals, developed by the Roslin Institute Bioinformatics Group from The University of Edinburgh [7]) and GEISHA [8] (an on-line visual atlas of in-situ hybridization stained embryos), regular meetings (the seventh one was held in Nagoya University in Sendai, Japan), and periodic newsletters that present brief summaries of past events and a list of upcoming ones related to chicken biology and genomics. Thus, *as in the cases of any other model organism, there seem to be definite social ties among the community of Gallus gallus researchers and the establishment of infrastructure that enables communication and sharing data practices***.** Further, it is important to understand properly the relationships within the chicken community (e.g., within between agricultural and biomedical interests) and to make a deeper enquiry on the shared values of chick's researchers.

So far, we may conclude that among the group of model organisms, *Gallus gallus* is somehow weak in its genetically approach, including the fact that there is not a standard strain of chicks. Nevertheless, there is a community that has developed the infrastructure and tools for communicating their investigations.

3.2.3. THE EPISTEMIC FEATURES OF *GALLUS GALLUS*. IS DOMESTIC FOWL A MODEL?

Now, what about the epistemic features of model organisms? By discussing these features we pretend to give an account on whether chicken can be regarded as a "model organism" or not.

Taking the Ankeny and Leonelli (2011) approach, we can see how this domestic bird has indeed a wide representational scope. This means that, on the one hand, the extension of applicability of the results of research conducted in *Gallus gallus* spreads to many other vertebrate species and, consequently, the domestic fowl purportedly *represents* a wider group of organisms beyond itself (e.g., every species of amniotes). In other words, domestic fowl is not only studied for itself, but, in developmental biology and other fields, chicken is taken as a model of all birds or even of a broader group of vertebrates. For instance, when chick limb development is studied, there are continuous references on how this representos all "vertebrate limb development", and then *Gallus gallus* is purportedly a model of tetrapoda. In this sense, *domestic fowl has a broad representational scope similar to other model organisms* [9].

In biological sciences, chicks are also models of whole organisms. The development infrastructure around domestic fowl shows that scientists are not trying to understand a particular process in the chicken (peak formation, feather evolution, etc.), they are interested in a range of relations, processes, and systems occurring in many organisms that can be studied through its genetic properties which, in turn, can be stored in on-line public community databases. In virtue of this interest, researchers use *chicken as a model for whole organisms***.** Thus, we consider that the epistemic features of model organisms are fulfilled by *Gallus gallus***.**

Anyhow, the fact that chicken researchers are still struggling to develop some genetic aspects of this bird could be problematic in this respect. It then is important to point out that:

— *Model organisms representational scope does not imply that, in practice, every researcher interested in a particular organism pretends that a single species should be used to investigate every single biological property***.** For instance, it is not the case that the *Arabidopsis thaliana* community pretends that this plant should be used as a model for programmed death cell in animals. And scientists interested in the embryonic development of animal eyes would not try to answer their questions by means of studying a non-eyed organism such as *C. elegans*.

— On the other hand, *the standardization processes of model organisms differ and depend upon the interests and aims of researchers***.** Building a standard strain is related to certain relevant comparative goals in biomedical contexts, but this does not mean that this kind of standardization is the paradigmatic example for the successful use of a species as a model organism.

As far as *Gallus gallus* is an organism that is used to answer specific, but nonetheless general questions about vertebrate development, its standardization process is thought to be adequate for using this bird as an organism for conducting relevant experimentation which, in turn, can the aim to be extended to a wider group of species. Moreover, giving that "model organisms can be viewed along a continuum, with some fitting the idealized set of criteria... more precisely than others" (Ankeny and Leonelli, 2011). Considering that chicken fulfils the epistemic features related to other model organisms and it is surrounded by community efforts to develop infrastructure and media of sharing data, we argue that *chicken is indeed a model organism*, yet one where some traits related to the genetically-focused perspective are not uniformly distributed among the complete range of species of that group.

This is an important point, as model organisms are not an absolute category, but a gradual one. It is also important to emphasize that the species included in this group have different particular traits, appeals and diverse histories of insertion into this relatively recent assortment of organisms. Thus, species such as *Gallus gallus* can be weaker in a particular aspect (some genetic features) and nevertheless fulfill the epistemic features of model organisms. Indeed, according to a more flexible (but nevertheless useful) definition of models organisms, such as the one advanced by Rheinberger (2010), chicken can be definitely a model organism for developmental biology and life sciences research.

In some sense, a deeper standardization process may not be necessary for using chicken as model for embryonic development or immunology. At some point, a less standardize model can also be a less canalized organism, which means a less divergent bird from those species it intends to model (cf. Bolker, 1995; Ankeny and Leonelli, 2011). Nevertheless, it does not mean that all standardization is omitted in *Gallus gallus*, which is clear in the case of SPF chickens and in the genetic standard deployed in the genome sequence introduced in 2004.

When scientists use model organisms, the kind of experiments in which these species are thought to be used influences how an organism is standardized. As Burian states: "the nature of the variation from organism to organism must be understood and counteracted where it interferes with the experimental protocol [and] both protocols and organisms must be adjusted to one another in the service of the aim of the experiment" (Burian, 1993). Although this claim refers to the experimental organisms in general, this kind of situations are also evident in the history of model organisms (cf. Kohler, 1993) and influences the way in which *Gallus gallus* is currently employed.

Finally, it is also worthwhile to point out that through the history of the domestic fowl uses in biological enquiries—as with many other organisms—there have been different approaches depending on the changing perspectives of researchers. For instance, in 1835 the chick embryo was touted by physiologist Gabriel Gustav Valentin as a more adequate specimen for human embryological studies than those rare and abnormal human embryos then used in research. Several years later, within an evolutionary perspective, Ernst Haeckel rejected it as a species phylogenetically misleading, and even if it survived later as a useful animal embryo for teaching and a significant experimental organism, nowadays researchers still argue for its position as an important animal for developmental biology studies (Hopwood, 2011).

WHAT IS THE CONTRIBUTION OF *GALLUS GALLUS* TO THE DISCUSSION ON MODEL ORGANISMS?

Discussing the status of *Gallus gallus* as a model organism is relevant in contemporary philosophy of biology for various reasons. The first one that comes to mind concerns an evaluation of the costs and benefits of a constraining—but more formal—definition of model organisms, situated in contemporary genetic practices (*sensu* Ankeny and Leonelli), versus a more flexible and historically situated account (*sensu* Rheinberger). While Ankeny and Leonelli have provided a robust philosophical account, it might be the case that it is extremely attached to genetic and genomic practice, discounting historical reflection on the different uses of model organisms. This is a subject that needs further reflection.

Moreover, as we have shown, chicken has a long history in biological enquiries, a fact often exploited by scientists interested in promoting its use as a model. This fact often provides the picture of chicken as a "venerable" model (Hopwood, 2011), and it also means that there are more research resources available for its study, compared with other bird species (McPherson, et al., 2002). This sense of "historical appeal" by *Gallus gallus* may play an important role when discussion the practical implications of choosing chicken over other bird species.

At the same time, chicken is undoubtedly an organism of agricultural interest. This makes *Gallus gallus* a model which is—in a still unexplored way—between the laboratory "scientific" contexts and the agro-technologic industry. We think that this is a relevant trait of domestic fowl that needs to also be explored in future investigations focusing in the standardization process of SPF chickens. Further, instead of seeing this "double life of the chicken" as a disadvantage, we claim it can further open the scope of life sciences research, in a context where applications are actively seek as part of the biotechnological revolution.

Both the chicken's long-running presence in biological studies, and its spatial location between labs and farms, could provide new information about the model organisms group, which is portrayed as a very distinctive group within biological research, and could be an important focus of discussion about the sometimes divided fields of agriculture and biomedical research. In the context of biotechnological applications, opened up by the rise of genomics research, this is not a minor matter for philosophers of science. The use of chicken as model organisms could open new, historically situated, debates on the distinction between "pure" and "applied" research, a subject often discussed in contexts of science policy as well as in philosophy of science and technology (Martinez and Suarez, 2008).

After the 1970s, research agendas went into a profound transformation within molecular biology. This movement can be seen as a "molecularization" of developmental biology, or as an involvement of molecular biology with questions of development and cell differentiation (De Chadarevian, 1998, is an excellent case. See also Suárez and García, forthcoming). This transformation had to do with the sense that everything had been solved already in respect to bacterial and virus molecular genetics (Stent, 1968 is a classical reference to this mood). Equally important was the need to look for medical applications in genetic engineering, becoming a priority beginning the 1970s (De Chadarevian, 2002, chapter 11). In this context, research on "higher organisms" has been actively promoted in the last four decades. The use of chicken in contemporary research and its inclusion in the Human Genome Project speaks of this trend.

The reflection on chicken as a model organism of tetrapod development takes the philosophical analysis of biology to the problems, fields and interests of recent and contemporary research in biological sciences. We are convinced that if philosophy of biology is to contribute to philosophy and science alike, it needs to be fully and deeply intertwined with research practices. We hope this essay contributes to debates in *historical epistemology*, an umbrella term for historically and practically-situated philosophical analysis.

ACKNOWLEDGMENTS

This essay is the result of Miguel Lopez Paleta's master's dissertation at the Posgrado en Filosofía de la Ciencia, UNAM (Universidad Nacional Autónoma de México). He was awarded a CONACYT grant during his studies, and had support from UNAM-PAEP and CONACYT for a three months research stay between March and May 2012 at the ESRC Centre for Genomics in Society (Egenis) at the University of Exeter, to work with Sabina Leonelli. We thank Leonelli's generosity and full support for this project. We also thank Vivette García Deister and Víctor Anaya for their insightful comments. This research was supported by CONACYT research project on Standardization and Internationalization of Science after World War II (152879). Research Project PAPIIT-UNAM IN 303111, and by a research stay of Edna Suarez Diaz at Rühr University at Bochum (Germany) and the Max Planck Institute for the History of Science, Berlin. For that, Suarez Diaz had the support of the Mercator Research Group (Spaces of Anthropological Knowledge) and of UNAM-PASPA.

NOTES

1 "Vital dyes" refers to stain techniques which can be applied into living cells without killing them. When intervening embryos, these dyes are useful to identify and follow groups of cells which are in motion and acquire a fate throughout embryonic development.
2 As it is stated in a review article, fossil record divergence time between mammals and birds is 310 million years (Hedges 2002) during the Carboniferous Period.
3 However, it's important to notice that there are several different histories of the introduction of an organism to a laboratory. And there is not a single straightforward way to do it, since those histories are frequently contingent and "not as rational as is sometimes portrayed" (Kohler 1993).
4 In fact, this is the definition, followed by Rheinbergers examples, given by Timothy Lenoir in his Preface to *An Epistemology of the Concrete. Twentieth Century Histories of Life*. Nevertheless, it formally sticks to Rheinbergers case studies in that book.
5 Information obtained in an interview of Miguel López Paleta with Alfonso Valenzuela from ALPES, SA de CV (February 13, 2012).
6 McPherson's currently research focuses on cancer. On the other hand, Dodgson is interested in genomics of birds. Finally, Krumlauf and Pourquié interests of research are focused in molecular developmental biology.
7 http://www.thearkdb.org/arkdb/
8 http://geisha.arizona.edu/geisha/
9 Nevertheless, it is worth to question how shared is this vision in the field of agricultural studies, where due to its farming importance we dare to suggest that it is important to study chicken by itself. A deeper discussion about how extendible are the results of *Gallus gallus* research to other agricultural species, the extension of the term "poultry", and how the researchers interested in "poultry science" work would be an important related issue in the future.

BIBLIOGRAPHY

Ankeny, Rachel A., y Sabina Leonelli (2011), "What's so special about model organisms?" *Studies in History and Philosophy of Science* 42, 2: 313-323.

Antin, Parker B., John F. Fallon, y Gary C. Schoenwolf (2004), "The chick embryo rules (still)!" *Developmental Dynamics* 229, 3: 413.

Bahls, Christine, Jonathan Weitzman, y Richard Gallagher (2003), "Biology's models," *The Scientist* 17, Supl. 1: S5.

Bolker, Jessica A. (1995), "Model systems in developmental biology," *BioEssays* 17, 5: 451–455.

Burdon, John B., y Nick Hopwood (2000), "The introduction of *Xenopus laevis* into developmental biology: of empire, pregnancy testing and ribosomal genes," *International Journal of Developmental Biology* 44, 1: 43-50.

Burian, Richard M. (1993), "How the choice of experimental organism matters: epistemological reflections on an aspect of biological practice," *Journal of the History of Biology* 26, 2: 351-367.

Burt, David W. (2005), "Chicken genome: current status and future opportunities," *Genome Research* 15, 12: 1692-1698.

Burt, David W. (2007), "Emergence of the chicken as a model organism: implications for agriculture and biology," *Poultry Science* 86: 7460–1471.

Chapman, Susan C., Aaron Lawson, , William C. MacArthur, Russell J. Wiese, Robert H. Loechel, Maria Burgos-Trinidad, John K. Wakefield, Ram Ramabhadran, Teri Jo Mauch, y Gary C. Schoenwolf (2005), "Ubiquitous GFP expression in transgenic chickens using a lentiviral vector," *Development* 132, 5: 935-940.

De Chadarevian, Soraya (1998), "Of worms and programmes: *Caenorhabditis elegans* and the study of development," *Studies in the History and Philosophy of Biological and Biomedical Sciences* 29, 1: 81-105.

De Chadarevian, Soraya (2002), *Designs for Life. Molecular Biology after World War II.* Cambridge: Cambridge University Press.

De Chadarevian, Soraya (2004), "Mapping the worms genome: tools, networks, patronage," in *From Molecular Genetics to Genomics: The Mapping Cultures of Twentieth Century Genetics*, Jean Paul Gaudilliere, and Hans Jörg Rheinberger (eds.). New York: Routledge, pp. 95-110.

FAO. Production - Live Animals (23 Feb, 2012), http://faostat.fao.org/site/573/DesktopDefault.aspx?PageID=573#ancor (last access: March 13th, 2012),

Hedges, S. Blair (2002), "The origin and evolution of model organism," *Nature Reviews Genetics* 3, 11: 838-849.

Hopwood, Nick (2011), "Approaches and species in the history of vertebrate embryology", in *Vertebrate Embryogenesis (Methods in Molecular Biology*), Francisco J. Pelegri. New Jersey: Human Press, pp. 1-20.

International Chicken Genome Coordinating Committee. Trans-NIH Gallus Initiative (20049, http://www.nih.gov/science/models/gallus/index.html (last access: March 14th, 2012),

Kohler, Robert E. (1993), "*Drosophila*: a life in laboratory," *Journal of the History of Biology* 26, 2: 281-310.

Leonelli, Sabina (2007), "Growing weed, producing knowledge. an epistemic history of *Arabidopsis thaliana*," *History and Philosophy of the Life Sciences* 29, 2: 193-224.

Luginbuhl, R. E. (2000), "The commercial production of specific-pathogen-free eggs and chickens: the evolution of an industry," *Avian Diseases* 44, 3.

Martínez, Sergio and Edna Suárez Díaz (2008), *Ciencia y tecnología en sociedad. El cambio tecnológico con miras a una sociedad democrática*. Mexico: Limusa/UNAM.

McPherson, John D., Jerry Dodgson, Robb Krumlauf, y Olivier Pourquié (2002), "Proposal to Sequence the Genome of Chicken,"

Mendelsohn, J. Andrew (2003), "Lives of the cell," *Journal of the History of Biology* 36, 1: 1-37.

Mozdziak, Paul E., y James N. Petitte (2004), "Status of transgenic chicken models for developmental biology," *Developmental Dynamics* 229, 3: 414–421.

Needham, Joseph (1934), *A History of Embryology*. Cambridge: Cambridge University Press.

Rheinberger, Hans-Jörg (2010), *An Epistemology of the Concrete. Twnetieth Century Histories of Life*. Durham: Duke University Press.

Stern, Claudio D. (2004), "The chick embryo—past, present and future as a model system in developmental biology," *Mechanisms of Development* 121, 9: 1011-1013.

Stern, Claudio D. (2005), "The chick: a great model system becomes even greater," *Developmental Cell* 8, 1: 9-17.

Suárez Díaz, Edna and Vivette García Deister (forthcoming) "'*That 70s Show*': regulation, evolution and development beyond molecular genetics".

Tickle, Cheryll (2004), "The contribution of chicken embryology to the understanding of vertebrate limb development," *Mechanisms of Development* 121, 9: 1019-1029.

Twyman, Richard (2012), "Model organisms: Frogs and chickens," Wellcome Trust-The Human Genome. 08 28, 2002. http://genome.wellcome.ac.uk/doc_WTD020805.html (último acceso: 13 de marzo de 2012),

Wolpert, Lewis (2004), "Much more from the chicken's egg than breakfast—a wonderful model system," *Mechanisms of Development* 121: 1015-1077.