Mathematical biology and the existence of biological laws¹

in D. Dieks, W. Gonzales, S. Hartmann, T. Uebel, M. Weber (eds), *Probabilities, Laws and Structure*, Springer, 2011, pp.109-121, DOI 10.1007/978-94-007-3030-4_8

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1. Introduction

An influential position in the philosophy of biology claims that there are no biological laws, since any apparently biological generalization is either too accidental, fact-like or contingent to be named a law, or is simply reducible to *physical* laws that regulate electrical and chemical interactions taking place between merely physical systems.²

In the following I will stress a neglected aspect of the debate that emerges directly from the growing importance of *mathematical*

Thanks to the editor D. Dennis for some helpful comments and suggestions.

See for one John Beatty, "The Evolutionary Contingency Thesis", in Gereon Wolters and John Lennox (Eds.), Concepts, Theories and Rationality in the Biological Sciences, Pittsburgh University Press, 1995, pp. 45-81.

models of biological phenomena. My main aim is to defend, as well as reinforce, the view that there are indeed laws also in biology, and that their difference in stability, contingency or resilience with respect to physical laws is one of *degrees*, and not of *kind*.³

In order to reach this goal, in the next sections I will advance the following two arguments in favor of the existence of biological laws, both of which are meant to stress the similarity between physical and biological laws.

1) In physics we find an important distinction between laws of *succession* (holding between timelike-related or temporally successive events/facts) and laws of *coexistence* (holding between spacelike-related, coexisting events).⁴ Examples of laws of coexistence are the Boyle-Charles law, relating pressure P and volume of gases V to their temperature T (PV=kT), Ohm's law, relating resistance R to voltage V and intensity of current A (V/A=R), or the relation between the length and the period of a pendulum – $T=2\pi(L/g)^{1/2}$. While all of these laws relate events or properties that

For a previous defense of this thesis, see Sandra Mitchell, *Unsimple truths: Science, Complexity, and Policy*, Chicago: University of Chicago Press, 2009. I hope to add new arguments so as to strengthen her view. For the idea of degrees of lawhood, see Marc Lange, "Laws, Counterfactuals and Degrees of Lawhood", in: *Philosophy of Science*, 1999, pp. 243-267.

See Carl Hempel and Paul Oppenheim, "Studies in the Logic of Explanation", in: *Philosophy of Science*, Vol. 15, No. 2. 1948, pp. 135-175, who contrast causal laws (of succession) with laws of coexistence. The difference between causal laws and laws of coexistence had been originally proposed by John S. Mill.

are in some sense simultaneously existing, laws of succession instead describe the unfolding of physics systems in time.

Against the possibility of biological laws, it is typically argued that biological laws of evolution law are either non-existent or just too complicated to be formulated. For the sake of the argument, let us suppose that this thesis is true. It then follows that if we could prove that (i) in biology, unlike physics, there are also no laws of coexistence, or that (ii) such laws, if existent, are really all physical, we would have concluded against the existence of biological laws tout court. In section 2, I will counter (i) and (ii) by discussing some examples of genuine biological laws of coexistence that I will refer to as *structural biological laws*.

2) Those who claim that there are no biological laws typically argue that lawlike-looking regularities in biology are either merely *mathematical* (and therefore a priori) *or purely physical*. In the former case, they are devoid of empirical content, in the latter they are empirical but not biological. The former claim has been put forward in particular by Brandom and Sober, and recently defended also by Okasha, by discussing examples like Price's equation, formulas in population genetics like Fisher's, or the simple Hardy-

By biological laws of succession I don't mean laws of law, but simply laws regulating the evolution of biological phenomena in time.

⁶ I don't think it is true, by the way, but I want to concede to the enemy of biological laws all the ground she needs.

Weinberg's law in genetics (2006). Even though Sober (1997) does not think that this is an argument against the existence of laws in biology, tild clearly could be used in this way. What I will do in section 3 is to counter this claim by citing some mathematical models that seem to be applicable to various biological entities, from cells to flocks of birds, and that are certainly *neither* tautologies nor interpretable just with entities or data models referring to the ontology of current physics.

Before discussing these two arguments in some more detail, however, it is important to clarify two methodological points raised by the issue I have been presenting so far. i) The first point is: when should we regard a regularity/law as biological or physical? In order to answer this first question, let me simply stipulate that a regularity/law can be regarded as biological (or physical) if it is formulated in the language of *current* biology (or physics). As long as a law contains notions or concepts that are regarded as belonging

By referring to Price's equation, Okasha writes: "though the equation is little more than a mathematical tautology...", Samir Okasha, *Evolution and the levels of selection*, Oxford: Oxford University Press, 2006, p. 3. Sober explains the Heady Weighers's law with the properties of soin tessing. And then he

the Hardy-Weinberg's law with the properties of coin tossing. And then he adds "if we use the term mathematical tautology sufficiently loosely, then many of the generalizations in biology are tautologies" in Elliott Sober, *Philosophy of Biology*, Oxford: Oxford University Press, 1993, p. 72.

In Elliott Sober, "Two outbreaks of lawlessness in Recent Philosophy of Biology", in: *Philosophy of Science*, 64, 1997, S459, we read: "Fisher's theorem of natural selection says that the rate of increase in fitness in a population at a time equals the additive genetic variance in fitness at that time. When appropriately spelled out, it turns out to be a mathematical truth". And yet, he argues, a law need not be empirical but could also hold a priori.

to current biology, we should consider it as biological, even if the notion in question were reducible to physics. 9

I will therefore completely ignore appeals to wholly vague and undefined *future and complete* physics or biology. After all, "in the long run", as Keynes would say, "we will all be dead", and what matters to us is to try to solve our problems relatively to our current state of knowledge.

ii) The second point is the criterion of demarcation to be used to draw a distinction between genuine laws and merely accidental generalizations. Here I will appeal to counterfactuals, intentionally ignoring the difficulties raised by this criterion. After all, such difficulties apply to physics as well as to biology, and it is not clear at all why the defenders of the existence of biological laws should solve them. Simply put, the main idea to be presupposed in the following is that while empirical generalizations do not hold counterfactuals, laws do. To repeat an oft-quoted example by Reichenbach, a generalization like "all gold cubes are smaller than one cubic kilometer", if true, is true accidentally, since the counterfactual "if x were a gold cube, it would be smaller than one

Here I assume that reducibility does not entail elimination; and the case of thermodynamics is a clear exemplification of this claim: the reducibility of thermal physics to statistical mechanics does not entail that the properties that are typical of the former together with its laws disappear or are eliminated.

One of these is the smell of circularity raised by the criterion: one analyzes the notion of lawhood with counterfactuals but in order to know whether a counterfactual is true, one must already know which laws hold.

cubic kilometer" does not hold, since no law prevents gold cubes from being larger that one cubic kilometer. On the contrary, given the laws of radioactive decay, "if x were a uranium cube, it would be smaller than one cubic kilometer" is true.

2. Laws of coexistence in biology

The reader will recall that in the previous section I posed the following two questions: (1) do we have laws of coexistence in biology? If so, (2) are they reducible to physical laws? I will now try to answer them in turn.

(1) An important but often neglected source of biological laws might concern exactly laws of the "form", or of the structuring of biological space, in the tradition that spans from Goethe to Cuvier, and from D'Arcy Thomson to Thom and Gould and Lewontin. In this tradition, the permanence of forms or structures from one generation to another "is interpreted in relation to the pure game of three-dimensional space within which the constructive parameters of the organism are established." In this sense the distinction, originating from physics, ¹² between laws of coexistence and laws of

¹¹ Barbara Continenza, and Elena Gagliasso, *Giochi aperti in biologia*, Franco Angeli, Milano, p. 67.

The principle of locality might induce one to think that physical laws of succession are more important than physical laws of coexistence, so that the latter somehow reduce to, or supervene on, the former. However, quantum

succession would correspond in biology to the distinction between diachronic "laws of evolution" and "structural laws", the former related to *time*, and the latter constraining the structure of the *spatial* relationships between coexisting biological phenomena and entities.

From this perspective, the recent use of powerful computers has made us discover *structural* biological laws:

"Cardiovascular systems, respiratory systems, plant vascular systems, and insect tracheal tubes all exhibit the same continuously *branching structure* that increases or decreases in scale as a quarter power of body size.¹³ (my emphasis)

This wide-scope biological regularity seems sufficient to allow us to respond positively to question 1): there are indeed biological laws of coexistence and they play a very important and generalized role. The following question is whether they are reducible to physical laws.

2) The law of the quarter power mentioned in the quotation above

non-separability and entanglement, even in the absence of action at a distance as in Bohm's interpretation, has rehabilitated the importance of laws of coexistence at a fundamental level.

J. Brown, G. West, B. Enquist, *Nature*, CCLXXXIV, 1999, pp. 1607-1609. The work cited is taken from the website http://www.santafe.edu/sfi/publications/Bulletins/bulletinsummer97/feature.html. A later study published in Nature excluded plants from this generalization.

is related to Kleiber's law, which connects the metabolic rate *R*, (*i.e.* the quantity of energy consumed in one second), to the dimensions of the animal, according to a precise ratio of proportionality, expressed by the cube of the fourth root of the organism's *body mass M*

$$R = (M)^{3/4}$$

For example, an animal c weighing one hundred times another animal $m - M_c = 100 \, M_m$ – would have a metabolic rate that is only more ore less *thirty* times greater. ¹⁴ This law is quite universal, as it holds from mitochondria, unicellular organisms to the largest animals (see figure 1), so that it definitely holds counterfactuals: if a were an animal, it would be related to its metabolism by the above relation.

It could be argued that in virtue of the criterion above, 1) it counts as a *physical* law, because it only contains *physical* parameters ("the quantity of energy consumed in a second", "mass"). On the other hand, "metabolism" is typically applied in biological contexts, and "organism's mass" is after all a *physical* property of a *biological* entity. Laws of this kind are sort of mixed between physics and biology, and it should be no surprise that in many cases it is indeed difficult to conclude that a given nomic statement belongs to physics or biology. Consider "bridge" disciplines *bio*physics or *bio*chemistry

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Brown and Enquist, work cited. Note that $M_c = (100)^{3/4}$ equals approximately 31 M_m .

or molecular biology: any law in these fields cannot but "overlap" between the two disciplines. The existence of such an overlap, however, is good news for the defenders of biological laws, unless their enemies give them ground and retreat to the more limited claim that it is in purely biological domains that laws don't exist. Since this claim will be discussed in what follows, I can move on with my argument.

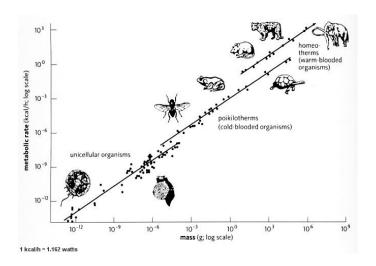


Fig.1 (taken from http://universe-review.ca/R10-35-metabolic.htm)

Interestingly, various hypotheses to explain this universal principle have been put forth since 1932. Lately, Kleiber's law has been derived, or explained, by a more profound law of coexistence, namely that the same ramified model - which refurnishes a vegetable or animal organism's vital fluids (lymph or blood) - fills the living organism's space like a fractal. 15 In a word, this type of ramified structure, which is essential to transport material to and from the cells, would be capable of explaining the existence of the otherwise mysterious proportionality between dimensions and the metabolic rate.

The omnipresence of forms branching out like a "tree," and repeating themselves in different scales like fractals, can be explained by the fact that these structures optimize the transport of energy in all living species; as West, one of the authors of this theory expresses, "when it comes to energy transport systems, everything is a tree."16

While the key concepts entering Kleiber's law are somewhat

Other geometrical considerations, involving the fixed percentage of the volume of the body that is occupied by the vessels, explain the presence of the cube in the formula above. The fractal law contributes only the the quarter power component. For more explanatory details, see http://universereview.ca/R10-35-metabolic.htm.

¹⁶ Ibid.

mixed, the quotation above mentions "cardiovascular systems, respiratory systems, plant vascular systems, and insect tracheal tubes, all exhibiting the same continuously branching structure". We have seen that since all these notions are biological, the criterion for identifying a law as biological allows us to conclude that the fact that "all these structures have a tree-like shape" is a biological law. It could be noticed that it is implausible that a physical or "mixed", biophysicallaw like Kleiber's can be explained by a purely biological, structural law, exemplified by biological entities carrying life-sustaining fluids or, more in general, by entities that optimize energy transport. This could create evidence in favor of the view that also the fractal law is really a physical law. However, there is no violation of the causal closure of the physical world in this case, since it is the shape of the fractal that carries the explanatory role, and shape in a sense is an abstract, geometrical notion, and in another sense, when we consider it exemplified, is a spatial, topological property of biological entities. As such, the fractal law is a biological law.

The question of the relationship between such structural biological laws and evolutionary principles (or laws of succession, in my vocabulary) naturally poses itself at this point. I cannot enter this complex debate here, if not to note that there is a sense in which biological evolution is constrained by laws of coexistence of the

kind we discussed above. On the other hand, however, against recent attempts at downplaying the role of natural selection, ¹⁷ it should be admitted that selection would obviously choose the organisms whose "forms" render more efficient the transport of those bodily fluids that are necessary for sustaining the life of the whole organism. In a word, if we could identify biological laws of succession with the family of models generated by the Principle of Natural Selection, ¹⁸ biological laws of coexistence and biological laws of succession could and should coexist peacefully, at least if we want to succeed in explaining the fact of evolution.

In this respect, the tradition of the study of laws of the forms, if helped by the development of new mathematical models of the relevant phenomena, could help us to look at the sterile debate between selectionists and defenders of laws of the form in a whole new way. This claim will be illustrated in the next section, which will also provide evidence for the fact, too neglected by philosophers, that the development of a future "mathematics of living beings" will contribute much to both biology and

¹⁷ J. Fodor, M. Piattelli Palmarini, What Darwin got wrong, New York, Farrar, Straus and Giroux, 2010.

For the view that the Principle of Natural Selection is really an abstract scheme to form more concrete models (like *F=ma*), see Mauro Dorato, *The Software of the Universe*. Aldershot: Ashgate, 2005. For the view that the Principle of Natural Selection is to be understood within the semantic view of theories, see Marcel Weber, "Life in a physical world", in F. Stadler, D. Dieks, W. Gonzales, S. Hartmann, T. Uebel & M. Weber (Eds), *The Present Situation in the Philosophy of Science*. Dordrecht: Springer, 2010, pp.155-168.

mathematics.

3. Some examples of mathematical models in biology

The currently burgeoning field of mathematical biology can be regarded as providing crucial reasons to believe in the existence of biological laws. The argument for this claim is based on the following four premises, which presuppose a distinction between scientific laws (a defining feature of the model we use to represent the world) and what they purport to describe, namely lawmakers that I refer to as *natural* laws.

- 1. Scientific laws in physics are mainly dressed in *mathematical language*, a fact that is not an accidental feature, but rather an *indispensable* component of physics;
- 2. Mathematically formulated scientific laws in physics are part of the definition of the mathematical models of those natural phenomena (natural laws) that we intend to represent *via* the model itself;
- 3. The amazing effectiveness of mathematical models in *predicting* and *explaining* physical phenomena¹⁹ can only be

 19 The claim that mathematics can be used also to $\emph{explain}$ physical phenomena is

accounted for if there are natural laws in the physical world, laws that the models mentioned in 2. refer to or partially represent;

4. The three premises above apply also to biology, and guarantee the existence of biological laws rather than accidental generalizations if they do so in physics.

I take it that premise 1. is uncontroversial: since the modern times, it would be hard to do any physics without the abstract models of natural phenomena provided by mathematics. Premise 2. can also be granted: take for instance ma = -kx, which is Hooke's law; clearly, this statement also defines the main features of the corresponding abstract model, in the sense that anything that satisfies that law can be represented by the model of the harmonic oscillator. Premise 3. is based on the claim that the existence of mathematical models that enable us to predict and explain physical phenomena *suffices* for the existence of physical laws. This premise is of course as controversial as is any realist claim based on inferences to the best explanation. Here I don't need to defend this premise explicitly, and actually I can take it for granted. Note that 3. is sometimes accepted for the existence of physical regularities,

defended in M. Dorato and L. Felline, "Structural explanation and scientific structuralism", in A. Bokulich and P. Bokulich (eds.), *Scientific Structuralism*, Boston Studies in Philosophy of Science, Springer, 2011, pp.161-176.

Giere, Ronald (1988), Explaining Science, Chicago, University of Chicago Press.

²¹ For a defence of this argument, see S. Psillos, *How Science tracks Truth*. London: Routledge.

and that here I could be content only with the conditional claim that *if* the inference works for physical laws *then*, in virtue of the analogy between physical and biological models of phenomena on which 4. is based, it also works for biological laws. A case study taken from a recent study of the collective behavior of starlings will, I hope, suffice to argue in favor of the analogy stated in 4.

4.1 Flocks of starlings and their scale invariant and topologically-dependent interactions

Under the attack of a predator or even independently of it, flocks of starlings (*sturnus vulgaris*) can assume highly symmetrical and rapidly changing geometrical forms. These birds can synchronize their flight in such a way that one is led to think of the flock as a single, *super-individual organism*, whose parts always remain together in a strikingly coordinated fashion.

In the years 2006-8, the Italian group of statistical physicists and biologists led by Giorgio Parisi has taken thousands of pictures of these birds (which some years ago had invaded parts of Rome with imaginable consequences...) in order to provide a precise empirical basis to study their collective behavior in three dimensions.²² The

²² M. Ballerini, N. Cabibbo, R. Candelier, et al (2008). "An empirical study of large, naturally occurring starling flocks: a benchmark in collective animal behaviour", <u>Animal Behaviour</u>, Volume 76, Issue 1, pp. 201-215.

guiding idea of the research program was that this empirical study, if suitably modeled, could be generalized to school of fishes, herd of mammals, flight of insects, etc. The scope and universality across the animal kingdom of these dynamical laws, if they could be found, would have been quite impressive.

The collective, cooperative behavior of the starlings is particularly important from an evolutionary point of view. Stragglers have a significantly larger probability of being attacked, while if the group remains together, each individual bird ends up being much safer.

The main question raised by this amazing collective behavior is, of course, how individual birds can remain in the group even when the latter, under attack by a predator changes significantly its form and density.²³ The biological qualitative laws that had been advanced so far presumed that the interaction among individuals decreased with the *metric* distance between any two birds, as in Newton's law of gravitation. However, this hypothesis would not explain the fact that even after density changes that are typical of starlings flight, the group continues to exist as such.

On the basis of models based on spin glasses and computerized

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M. Ballerini, N. Cabibbo, R. Candelier, A. Cavagna, E. Cisbani, I. Giardina, V. Lecomte, A. Orlandi, G. Parisi, A. Procaccini, M. Viale, and V. Zdravkovic (2008) 'Interaction ruling animal collective behavior depends on topological rather than metric distance: Evidence from a field study', *Proc. Nation. Acad. Science*, USA, 105, pp. 1232-1237.

vision, Parisi's group has advanced the new hypothesis that the birds' interaction depends not on *metric* distance (how many meters they are apart from each other) but on their *topological* distance, which is measured by *the number of birds separating each bird from the others with which it interacts*. This implies, for instance, that two birds separated by ten meters and two birds that are one meter apart "attract" each other with the same "strength", independently of distance, since the number of intermediate birds in the two cases is the same.²⁴ This topological dependency — which I regard as a biological law, possibly interspecific and not just holding for sturnus vulgaris — allows cohesion to the flock even when the density changes. This hypothesis was tested with some simulations:

"Thanks to novel stereometric and computer vision techniques, we measured 3D individual birds positions in compact flocks of up to 2600 starlings... whenever the inter-individual distance became larger than the metric range, interaction would vanish, cohesion would be lost, and stragglers would 'evaporate' from the aggregation. A topological interaction, on the opposite, is very robust, since its strength is the same at different densities".(ibid.)

So the first species-specific law that we can express in this

²⁴ Ibid.

context, a law that can be expressed in a qualitative and quantitative way, is that the interaction between starlings does not depend on metric distance but on topological distance. According to our above specified criterion, this regularity is certainly purely biological. Does it hold counterfactuals, so that, in virtue of the other criterion mentioned above, it counts as a law? Relatedly, can we generalize this law to other highly social species?

In order to answer these question, it is appropriate to mention the fact that the mapping of the flight of the individual birds has shown an interesting *anisotropy*, which could be linked to the nervous system of the birds; this anisotropy means that it is more probable to find the neighboring birds on the side rather than in the direction of flight, and this holds up to six-seven individuals, since there is no interaction with the 10th nearest individual. Charlotte Hemelrijk, a theoretical biologist at Groningen, had found the same sort of anisotropy in school of fishes.²⁵

The resilience of the flock against losing individual birds is a metaphor for the resilience of the following regularity: starlings keep track of topological distance by keeping track of 6/7 individuals against possible disturbing factors due to the presence of predators. I would add that the regularity in question is capable of holding counterfactual conditionals: "if a were a starling within a

²⁵ Toni Feder, "Statistical physics is for the bird", *Physics today*, 60, 28, p. 29.

flock, it would adjust to changes of densities by keeping track of its 6/7 neighbors". Amazingly enough, the direct interaction with such a limited number of individuals is sufficient to spread correlation among a group that can be formed by thousands of birds!

In order to formulate another species-specific law that can generalize to other species, let me define the *correlation length* as the spatial length or spread of the behavioral correlation existing in a group, and the *interaction range* as the number of animals with which each animal is directly interacting: the former concept can be global, the latter is always local. An effective way to illustrate the difference between these two notions is using the example made by the authors of the research on the scale-free correlation of starlings flocks, 26 namely the "telephone game" played by n people. Suppose that each person in a group of n whispers a message to her neighbor and so on, and that there is no corruption of the message (no noise):

"The direct interaction range in this case is equal to one, while the correlation length, i.e. the number of individuals the phrase can travel before being corrupted, can be significantly larger than one, depending on how clearly the information is transmitted at each

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A. Cavagna, Alessio Cimarelli, Irene Giardina, Giorgio Parisi, Raffaele Santagati, Fabio Stefanini, and Massimiliano Viale, "Scale free correlation in starlings flocks, Proce National Academy of Science, 107 (26), Jun 29, 2010, pp. 11865–11870, available also on line at www.pnas.org/cgi/doi/10.1073/pnas.1005766107, p.1.

step.",27

In the hypothesis of no noise, the whole group of n person is correlated (so that the correlation length in this example is n); of course, in more realistic examples, the information is always transmitted with some noise. We could note in passing that the possibility of sending the same (email) message to n people at once (interaction range = n) makes the correlation length grow exponentially in a very rapid time.

Cavagna et al. note furthermore that there are various ways to achieve order or correlation among social animals like starlings. One would be via a coordination of all birds' behavior with that of a *single* leader or of a few leaders; such a top-down method, however, would not be very efficient for the survival of birds. For example, if the leader did not notice the presence of a predator or of any other danger, the rigid rule of following the leader would not be of very much help, even if *all* birds, unlikely, had cognitive access to the remote position of the leader (flock can be made by numerous individuals). Furthermore, in this way any fluctuation in the behavior of one bird would not be correlated to the behavior of another, unless the bird in question is the leader.²⁸

A much more efficient way to get really cooperative and adaptive

²⁷ Ibid., p.2.

²⁸ Andrea Cavagna, et al. "Scale-free...", quoted.

behavior is to avoid a centralized global order, but create a global correlation between all animals, a correlation that can be originally caused just by any one individual, the one, say, who notes the presence of a predator. If the change in direction of flight of this individual can rapidly influence all the flock via a few direct interactions between the single animals that is transferred to whole group, then the survival chances of each single animal will be enhanced, because no bird will be isolated. No part of the group can be separated from the rest, and the flock behaves like a critical system, capable of responding in a maximal way to a perturbation occurring to a single individual. With the words of our authors:

"For example, in bacteria the correlation length was found to be much smaller than the size of the swarm. In this case parts of the group that are separated by a distance larger than the correlation length are by definition independent from each other and therefore react independently to environmental perturbations. Hence, the finite scale of the correlation necessarily limits the collective response of the group. However, in some cases the correlation length may be as large as the entire group, no matter the group's size. When this happens we are in presence of scale-free correlations". ²⁹

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²⁹ Andrea Cavagna et. al., work cited, p. 1

The degree of global ordering in a flock is measured by the socalled polarization Φ ,

$$\Phi = \frac{1}{N} \sum \frac{\overline{v_i}}{|v_i|}$$

where v_i is the velocity of bird i and N is the total number of birds within the flock (ibid.). Note that the fact that the polarization Φ is very close to 1 (birds fly parallel to each other) may be also considered to be an empirical, quantitative law, since also this statement holds counterfactuals.³⁰ Polarization is in fact a measure of the correlation of the animal's behavior, in the sense that when the correlation is, as in the case of starlings, close to 1, it is interpretable as the fact that the velocities of the birds are parallel, while when it is 0 "it means uncorrelated behavior, that is, non-parallel velocities.

5. Conclusion

The idea that in biology there are no laws (or event quantitative laws) seems to be simply due to a lack of imagination on our part, and to the fact that mathematical biology has not penetrated enough

³⁰ "Polarization is... a standard measure of global order in the study of collective animal behavior", since when the value is close to 1 it corresponds to parallel velocities, while when it is 0 is mean uncorrelated velocities", "Scale free, quoted, ibid.

the community of philosophers of biology. So I conclude by quoting from an excellent, recent introduction to mathematical biology, which here I want to advertise, thereby signalling two interesting areas of research in mathematical biology, namely, population biology and ecology on the one hand, and philogenetics and graph theory on the other.³¹

Population biology and echology The problems in population genetics and echology are similar to those illustrated in the case of the collective behavior of starlings, since they relate interaction between single members and collective, global properties. Imagine that a tree in an equally spaced orchard has a disease that, in analogy to the case of starlings, can be transmitted only to the nearest neighbors with a probability p. The problem is to calculate the probability that the correlation becomes scale-free, so that every tree in the forest becomes infected. Let E(p) be the expected probability in question:

"Intuitively, if p is small, E(p) should be small, and if p is large, E(p) should be close to 100%. In fact, one can prove that E(p) changes very rapidly from being small to being large as p passes through a small transition region around a particular critical probability p_c .

Michael Reed, "Mathematical Biology", in Timothy Gowers, June Barrow-Green and Imre Leader (eds.), The Princeton Companion to Mathematics, Princeton University Press, pp. 837-848.

One would expect p to decrease as the distance, d, between trees increases; farmers should choose d in such a way that p is less than the critical probability, in order to make E(p) small. We see here a typical issue in ecological problems: how does behavior on the large scale (tree epidemic or not) depend on behavior at the small scale (the distance between trees)."³²

In this example scale-free correlations (epidemics among trees) depend on the existence of critical probabilities; it should be obvious how in this case, as in the previous one, the possibility of gathering empirical data allow us to make precise predictions about, say, the existence of scale-free correlations among individuals in a group (flocks, schools, trees in a forest, etc.).

Philogenetics and graph theory

A connected graph with no cycles is called a tree. The tree has a vertex ρ , or root, and its vertices that have only one attached edge are called leaves. The problem consists in determining the trees that are consistent with our empirical and theoretical information about evolution (ibid.). Such phylogenetics rooted trees are used to select a particular empirical characteristic, say the number of teeth, and then

Reed, quoted, p. 845.

define a function f from the leaves X, the set of current species, to the set of nonnegative integers. For a given leaf x (a species in X), one then let f(x) be the number of teeth of members of x.

"It is characters such as these that are measured by biologists. In order to say something about evolutionary history, one would like to extend the definition of f from X to the larger set V of all the vertices in a phylogenetic tree. To do this, one specifies some rules for how characters can change as species evolve. A character is called convex if ... between any two species x and y with character value c there should be a path back in evolutionary history from x and forward again to y such that all the species in between have the same value c....A collection of characters is called compatible if there exists a phylogenetic tree on which they are all convex. Determining when this is the case and finding an algorithm for constructing such a tree (or a minimal such tree) is called the perfect phylogeny problem." (ibid, Reed, p. 846).

The reader will excuse these long quotations. They have the purpose to allow me to conclude that it is by paying more attention to questions like these that a more thorough understanding of the relation physics and biology (and their nomic features) can be gained, a relation that is going to be deeper and deeper the more

mathematics is becoming the common language of both. It seems fair to say that biology is becoming more and more, despite what is usually believed, a Galilean science, based as physics is "on sensible experiences and necessary demonstrations". ³³

See S. Drake, *Essay on Galileo and the History and Philosophy of Science*, vol. III, selected and introduced by N. Swerdlow and T.Levere, University of Toronto Press, p. 84.