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Animal culture: But of which kind?

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ABSTRACT

Is animal culture a real entity or is it rather just in the eye of the beholder? The concept of culture began to be increasingly used in the context of animal behaviour research around the 1960s. Despite its success, it is not clear that it represents what philosophers have traditionally thought to be a natural kind. In this article I will show, however, how conceiving of animal culture in this fashion has played a role in the "culture wars", and what lessons we can draw from this. First, an analysis of the epistemological landscape of author keywords related to the concept of animal cultures is presented, thus vindicating the centrality of the concept in describing a broad range of findings. A minimal definition that encompasses the multiple strands of research incorporating the notion of culture is proposed. I then systematically enumerate the ways in which culture thus conceived cannot be considered a natural kind in the study of animal behaviour. This is accomplished by reviewing the efforts and possibilities of anchoring the elusive idea in specific mechanisms, homologies, selection pressures, homeostatic property clusters, or alternatively, its reduction or elimination. Finally, a plausible interpretation of the scientific status of the animal culture concept is suggested that is compatible with both its well established use in animal behaviour research and its inferential limitations. Culture plays the role of a well-established epistemic kind, a node that connects different areas of research on common themes.

1. Introduction

Towards the late 20th century, the concept of culture was rejected or unendorsed by more than a few of anthropology's chief practitioners (Brumann, 1999). Yet around the same time it found fertile ground in the discipline of animal behaviour, hinting to some form of strong naturalization. Indeed, as various strands of anthropology negated the theoretical power of "culture" as an explanatory device, the term's use continued to spread, eventually permeating animal ecology textbooks (Manning & Dawkins, 1998). During this period, many philosophers and social commentators also continued using the concept of "culture" or the adjective "cultural" in a theoretically loaded way (Pinker, 2003), often presupposing this predicate's high inferential power, that is, an ability to refer to a property whose very attribution warrants the inference of other properties to which it is related. Tacitly assuming such inferential powers, one thing or behaviour being termed 'culture' or 'cultural' usually meant that a diverse bundle of properties could be attached to it (Bueno, 1997).

But does "culture" constitute what philosophers term a natural kind? In Section 4, I will unpack the relevance of this matter more thoroughly. For the time being, it is worth noting that whether culture possesses an inherent essence revealed by science, or at least real projectable properties from which reliable inferences toward other interesting and non-trivial properties or predictions can be made is not an insignificant question. It has been raised many times before, first in the context of old classical debates concerning the similarities and differences between the natural sciences and the humanities (Harris, 1968; Sperber, 1996). The question, however, has never been raised specifically in an effort to examine the status of "*animal* culture" as a natural kind. This is not an ineffective approach to the problem of determining the value and scope of the concept of culture. Triumph in revealing the contours of the kind "animal culture" may provide a basis for its naturalization more generally. Conversely, lack of success in establishing a scientific natural kind may also be judged, in the extreme, as an indicator of the unreasonableness of trying to make culture part of the natural furniture of the world, to be conceived on equal footing with other more prototypical natural kinds such as electrons, chemical elements, cells, or galaxies. Somewhere between the two poles of complete vindication and complete dismissal, we might at least gain a better understanding of the role this concept plays in the actual configuration of a field of study in animal behaviour.

At the risk of revealing what comes next, my goal in this article is to promote that improved understanding. I will argue how animal culture, understood as a common phenomenon appearing in different species,

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currently fails to show "the sort of stability a property cluster needs to possess to serve the epistemic functions we are used to natural kinds serving", to use the words of a prominent account of natural kinds in the biological sciences (Slater, 2015). At the same time, the realist presumption of animal culture — that is, the quest for the naturalness of culture in non-human animals — has clearly guided a research landscape which has truly produced a panoply of valuable discoveries in the study of animal behaviour. Such a concept deserves a dignified status. For that, I will borrow the notion of 'epistemic kind', which has been fruitfully used, for instance, by historians of heredity in the life sciences (Müller-Wille, & Rheinberger 2012). I will not deal with the specific naturalness of 'culture' in particular species such as the naturalness of culture in orangutans or the naturalness of culture in New Zealand keas. Nonetheless, I believe that what I will be saying about animal culture in general is not irrelevant to more specific local claims about culture, including human culture.

Here is a brief outline of what follows. In Section 2, I will show that animal culture is not just a notion conceived while contemplating in the rocking chair, but an actual concept connecting a range of findings in animal behaviour research. In Section 3, I provide a simple definition which covers the usage of "culture" in decades of work by a myriad of scientific teams studying animal behaviour. This definition is a sort of common denominator. And it is aimed to be descriptive – philosophers are often used to normative definitions stating how other people should use terms. It also provides us with a bundle of properties (cultural properties) whose "sociability" or "clumpiness" can be questioned in the framework of the philosophical ideas surrounding natural kinds. In fact, I will begin Section 4 by outlining why the question of the natural kind status of culture is particularly relevant in this area and pointing at ways in which influential figures in the discipline of animal behaviour tacitly used classical natural kind notions of culture. Section 4 offers a synoptic view into various ways in which animal culture could be a natural kind. This section is not supposed to exhaust all possible ways in which this could be the case, nor entirely settle the issue once and for all, that being to a large extent an empirical question. However, it will offer arguments, which I hope are relatively persuasive, as to why it might be misleading to conceive of animal culture as a natural kind. I will build the case. Let others be the jury.

2. A conceptual landscape in animal behaviour research

First, let us see the way scientists use the concept of culture in the context of animal behaviour research. One possible way of tackling this question is by exploring how the term is linked to other terms and by measuring their co-occurrences in a corpus of relevant data. To answer this question, I assembled a collection of approximately four hundred scientific articles closely connected to the idea of animal culture and available for easy metadata extraction through the database Scopus, one of the largest databases of peer-reviewed scientific literature which allows easy navigation through its search menus. The decision to limit the search to the article format was made in order to extract easily analyzable information in the abstract and keywords of those references. The first step of the search, which was conducted in April 2020, was to run a query on articles containing "culture" or "tradition" in the title, abstract or keywords of journals in animal behaviour, ethology, and comparative psychology. On a second step, the collection was enlarged by adding the results of a query on more specialized international journals on primatology and ornithology as well as in high impact general scientific journals such as *Nature, Science, PNAS, and Proceedings of the Royal Society B*. On a third step, "false positives" articles were deleted manually if the work only linked to the study of human behaviour or human evolution to the exclusion of interspecific comparisons. Other false positives not related to the study of animal culture (for instance, articles dealing with 'aquaculture' in fish) were also deleted. Next, the choice of bibliographic sources was compared with an already existing extensive scholarly bibliography on animal culture by two prominent researchers in the domain (Lachlan & Whiten, 2020). The comparison was favorable, highlighting that similar journals had been covered. In addition, it led to the inclusion of approximately 50 references which had not been previously included. The different data sets were combined into a.csv file which can be found in the electronic supplementary materials.

This assemblage of a broad sample of scientific works in this domain allows us to make certain quantitative and qualitative statements.[1] One first way of getting a glimpse of this information is to verify what specific conceptual stems stand out statistically from the rest in the section of the articles describing the relevance of the published work in this area. Fig. 1 shows the most frequently used lexical stems in the abstracts of these articles, once stop-words ("and", "of", "after", "can") and other frequent non-specific words ("study", "shows") have been discarded. A series of epistemological foci are manifest: the centrality of learning ("learn-"), the social aspects of behavioural ecology ("social-", "behaviour-", "group", "popul-"), as well as the stability and variability of acquired behaviour ("tradit-", "song", "differ-") are among the interests that researchers allude to most often in one of the most visible parts of their publications. If these statistics inform us of the most recurrent terms in the abstract of these works, we might also ask not how frequent but how connected are the key concepts.

A network analysis of the connection of concepts can be performed on the keywords that the authors of these works submitted to publish their articles. Thus, we can see which 'regions' the concept of culture links to in this literature. Of the approximately 400 references in the database, 272 had author-keywords. After merging keywords to avoid different spellings of the same words, this yielded a total of 737 keywords which could be seen as nodes in a semantic network (Alfano & Higgins, 2019). To create the graph, a term-document matrix using text mining was built with the author-keywords as the main field of interest. This was transformed into a term-term adjacency matrix, where the rows and columns represent terms, and every entry is the number of co-occurrences of two terms (Zhao, 2012) Next, a graph was built using the R package 'igraph', where key concepts are the nodes, and edges represent co-occurrence of those concepts in the keywords section. To visualize the graph, I used Gephi, an open-source network analysis and visualization software package.

A central section of the resulting conceptual landscape is depicted in Fig. 2 and the whole network can be visualized and consulted at the following github repository (https://anonymized-author.github.io/network/). The layout is the result of applying the Fruchterman-Reingold algorithm which incorporates both an attractive force bringing closer connected vertices to each other, and a repulsive force that repels all vertices. Size of edges indicate how frequently those two keywords appear together in a published article. Size of nodes indicate how many connections (other keywords) point to the concept in question. The different colors represent different communities or modularity groups to which the nodes can belong (only the largest groups are colored). Modularity was calculated in Gephi using weighted edges and a resolution of 1.0. Membership to a modularity group simply means here that members tend to co-occur together more often than those that do not belong to the group according to a pre-specified threshold.

Curious about the other concepts into which these keywords branch out? You can navigate the full network and distinguish its different regions or communities. A conceptual landscape emerges. Although it would be easy, by hopping from node to node, to reach almost any other neighborhood of the network – more than 95% of the nodes belong to one single giant connected component – some of the main regions seem to

[1] The bibliographical data base has its own limitations. For instance, some of the most influential works in this domain may be in the form of monographs or edited volumes which might have not been captured. Other publications might not have an author-keywords field, etc. This bibliographical data base and the ensuing analysis is thus conceived to be broadly representative but certainly not exhaustive of the intellectual production in this domain.

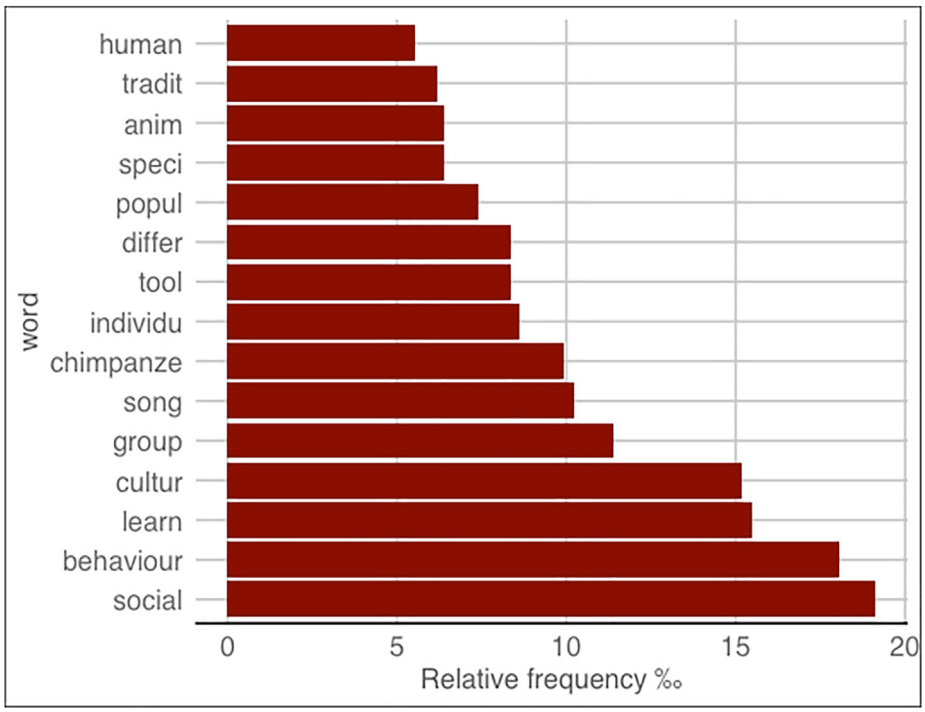

Fig. 1. Barplot containing the most employed word stems contained in the abstracts of the assembled scientific papers related to "animal culture".

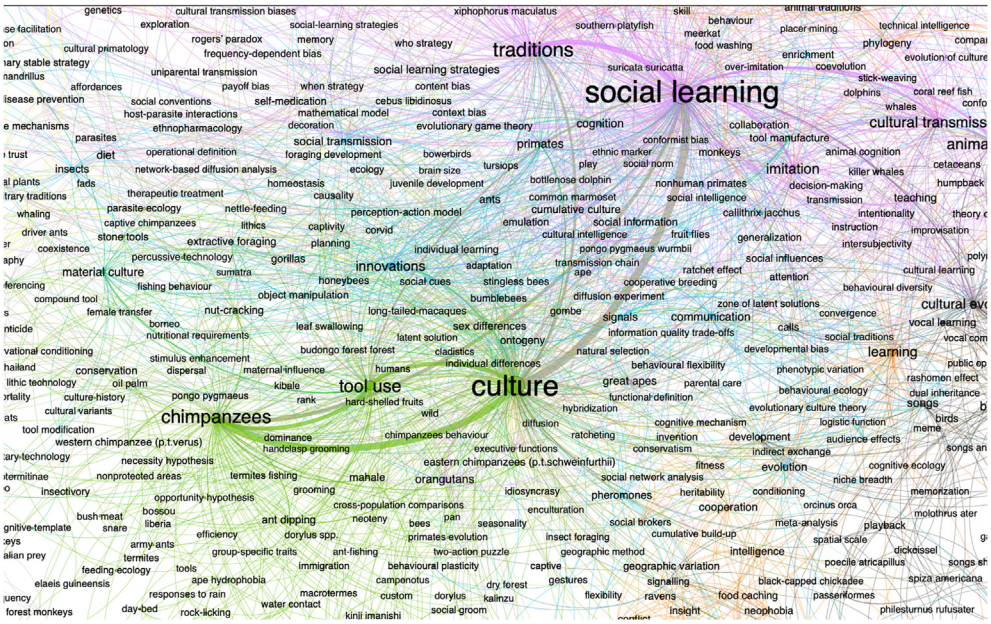

Fig. 2. Extract of the conceptual network of animal culture. A central portion of the author-keywords co-occurrence network of a sample of published articles touching the topic of animal culture is shown. Links represent co-occurrence of concepts in the same article. Thickness of links represent frequency of co-occurrence. Node size represents degree or how interconnected the concept is. Different colors represent partially different epistemological regions or communities as calculated by a modularity algorithm. In this fragment, some of the main nodes from the two largest and most central epistemic communities are shown, one module involving chimpanzee behaviour and tool use (green) and the other one delving into the study of traditions and transmission biases in a wide range of taxa (purple). Layout: Fruchterman-Reingold. See text for explanations. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

constitute partially distinct epistemological areas. This happens at least in the sense that some of the most connected keywords do not always link (or only weakly) to other regions. Among these, one might point to various areas that crystallize around different objects of study. To name just a few: a general region related to primate behaviour, tool-use, and differences in foraging technology (pale green, modularity group 3); another region more connected to learning mechanisms and avian and cetacean vocal communications (dark grey, group 6); or another linked to social learning biases and traditions and encompassing the study of a diverse range of taxa (light purple, group 5). (The online network visualization provides additional information about the different modularity groups).

Fig. 3 depicts the fifteen main keywords connecting the findings of this sample of works. The selected concepts are the ones scoring highest in weighted degree, a measure of how many links from other keywords – weighted by the importance of the linking node in the graph – they receive. In the figure, edges between concepts represent the co-occurrence of two keywords together within the same article. The thickest links represent pairs of concepts that co-occur more often than others. This figure is helpful in representing the "branching" concepts, so to speak, in animal behaviour to which the concept of culture is most often connected.

By looking at patterns of prevalence and co-occurrence, we have just seen that animal culture is in fact a widely used term in the discipline of

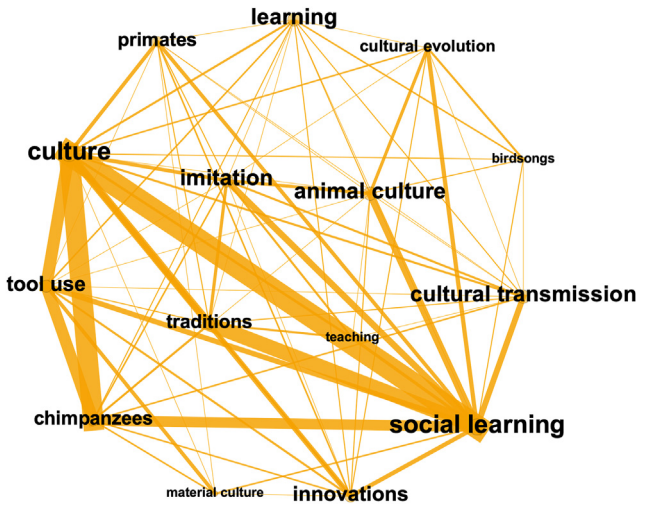

Fig. 3. Fifteen most central author-keywords in articles related to culture in the study of animal behaviour as measured by weighted degree. Thickness of links is proportional to frequency of co-occurrence of these author-keywords. Layout: Fruchterman-Reingold with some manual adjustment.

animal behaviour. Moreover, the concept appears as a key term that connects a wide range of areas, linking for instance mate choice in fruit flies with the study of the general dynamics of social conformity in primates, or connecting speciation in birds with the study of cognitive mechanisms in humans. In what follows, we will define this connector and following philosophical theories of biological kinds we will survey how natural as a form of classifying things it is in the biological realm.

3. A minimal definition of animal culture

Which concept of culture unites all of the aforementioned work in the study of the evolution of behaviour? Success in solving this question should be determined by the adequacy of the definition for generally describing the scientists' activity in this area of expertise. If I was to advance a definition of culture that does not address what researchers do and how they use the language of culture to describe their findings, I would have either failed miserably or have attempted something entirely different. Some animal researchers (e.g., Galef, 1992) and philosophers (e.g., Ramsey, 2017) have attempted something different and have offered a normative concept of culture, proposing how other scientists should use the term. My aim here is instead only descriptive. In order to pursue this goal, I will mostly follow a definition of the concept of "animal traditions" proposed by Susan Perry and Dorothy Fragaszy (2003) and adapt it to a general characterization of animal culture, which can be defined as follows:

A phenotypic character, an artifact, or any byproduct of an individual's behaviour can be said to be 'cultural" to the extent that it fulfills, to varying degrees, the following cultural properties:

(a) being the result of a specific mechanism of social learning.
(b) being distributed in a population.
(c) having a certain stability or permanence in time.

A corollary to this definition is that each of these different dimensions of what constitutes a cultural entity admits of degrees.

This definition unifies the conceptual landscape displayed in Fig. 2. Why? Because there is no intrinsic originality in it. Indeed, the anthropologists Alfred Kroeber and Clyde Kluckhohn famously brought together and inventoried more than 150 definitions of culture in the 1950s. The list has surely expanded considerably since that time. Philosopher Kwame Anthony Appiah (2005) once echoed a famous dictum, only half-jokingly suggesting that "when you hear the word "culture", you reach for your dictionary". The above-given tripartite characterization breaks cultural traits down into three different properties. This tripartite description roots itself as much in a neo-Darwinian concept of animal tradition (see e.g., Baldwin, 1902; Elton, 1930), as in the early efforts of pioneers of American anthropology – most notably Franz Boas' disciples – in characterizing an alternative, non-genetic, social form of heredity (e.g. Sapir, 1921 "… culture that is.. the socially inherited assemblage of practices and beliefs.."; Kluckhohn, 1942 "Culture consists in all transmitted social learning", quoted in Kroeber & Kluckhohn, 1952; see also Kroenfeldner 2008). Besides, this characterization is consubstantial with other efforts at providing canonical definitions in this domain. For instance, when in 1999 a team of primatologists presented their systematic synthesis of behavioural variation in chimpanzees, their working definition stated that "a cultural behaviour is one that is transmitted repeatedly through social or observational learning to become a population-level characteristic" (Whiten et al., 1999).

Wearing the philosopher's hat, one could call the above-given properties "cultural properties" and claim that they jointly minimally define the existence conditions for animal culture. In this fashion, they are jointly necessary for a trait to be cultural. As these cultural properties can be seen as dimensions in a hyperspace that might be instantiated by well-known cases of specific animal cultures, the minimal concept here presented can be seen as one based on prototypes. These prototypes are common instances of what actual practicing scientists consider cultural behaviour in this field. This means that occurrences or cases can be ranged as they come closer to or move further away from well-known prototypes of the concept of culture, in an almost gradualist fashion. Both variation and sharedness or similarity at the level of the population are part of this minimal concept, thus qualifying as a populational concept in spirit (Godfrey-Smith, 2009), although some of its instantiations can be too far removed from the populational idealization and instead fall within the idiosyncratic. This could be the case, if for instance, the population of agents sharing the cultural characteristic is close to $N = 1$, as is perhaps the case of certain minimally cultural traits, such as in human trained quasi-linguistic apes. To see this, consider how one could rank various well-known examples of animal culture as they can be placed in different coordinates along these axes. Some local cultural traits of the small group of bonobos at the Great Ape Trust in Iowa, whose most famous representative is Kanzi, would probably score very low on the second dimension, given the extent to which it distributed in the population, the trait in question being (in certain cases) the privilege of just one or a few individuals. At the same time, it would score very high in terms of how much of that trait results from the influence of social learning, since acquiring the use of lexigrams in these ape "language" studies is highly conditional on their social learning environment. The famous sweet-potato washing of Japanese Macaques on Koshima island could be placed on these dimensions as relatively less dependent on social learning but more distributed in the population and temporally stable, as the tradition has been documented throughout several decades. Alternatively, socially learned fads such as the famous milk-bottle opening by birds of the tit family that was all the rage in the mid 20th Century in certain European countries was perhaps relatively highly distributed in the local population of birds but only very slightly dependent on social learning and not necessarily persistent across generations.

3.1. *Alternative proposals and some objections*

The minimal concept of culture described above is intended to capture the largest set of studies in animal behaviour which, using the term 'culture', can be encompassed by a coherent definition. At the risk of being redundant, the aim here is not to provide a brand-new definition, but rather to take stock of what unites all of the interesting animal behaviour research conducted to date that addresses the notion of culture. This concept might certainly appear to be too minimal. After all,

how do we make sense of "being the result of a specific mechanism of social learning" or "having a certain stability"? In the first case, it denotes and encourages the efforts to test whether the behaviour in question is actually influenced to a greater or lesser extent by other conspecifics, the null hypothesis so to speak, being that the individual in question who shows the supposedly cultural behaviour would have in fact developed that trait all by itself without any kind of social input. Sometimes behaviour previously thought to be cultural in certain species, has been shown to be the result of individual learning after being investigated under controlled conditions (e.g., Tebbich et al., 2001; for a non-binary conception of social learning, see below). In the second case, the question of cultural stability is less obvious and more interesting than it might appear (Charbonneau, 2020), one frequent, almost commonsensical, intuition being that culture is, or tends to be, not ephemerous but stable and persistent over time. Against this, this dimension would allow a continuum of cases: at the zero point of stability, one would have something like transient forms of animal communication, without subsequent lasting effects on the individuals at the receiving end. At the other extreme, one could perhaps cite the existence of archaeological sites that show the continuous use of certain stone tools in different primates for centuries or even millennia (Haslam et al., 2017).

It is important to acknowledge that there are alternative proposals in the literature which point to a more restricted use of the concept of culture in the study of animal behaviour. It would be impossible to do justice to even the main ones in the space of this article, but at least a few are worthy of brief mention. Philosopher Grant Ramsey has argued at various places (2013, 2017) that animal culture should be understood exclusively as the information transmitted between individuals or groups through behaviour that brings about lasting change in behavioural traits. This is an interesting theoretical proposal, and – to the extent that the idea of information is proposed at the exclusion of behaviour or artifacts – also a clear revisionist move in relation to how the term is actually used by many practicing scientists.

The definition of animal culture which has been presented equates it broadly with animal tradition, the difference between the two being, if anything, a matter of degree in relation to its persistence or stability over time. Equally, it must be acknowledged that if many authors in this field treat the two terms as being synonymous, there is also a strand of thought that approaches the two notions distinctly, animal culture requiring something more than 'mere' tradition, this extra thing usually being something special which brings it closer to human culture in some way. Below, I will mention how psychologist and animal learning specialist Bennett Galef tried to pinpoint the essential properties of the natural kind of culture by highlighting the role of imitation and teaching. Another approach is illustrated by Susan Perry's proposal (Perry, 2009) where she focuses on characteristics including group identity and conformity to underline the specialness of culture as opposed to mere traditions. All these attempts at shifting the meaning of what is cultural have merit, and we will not discuss them here in detail. But it should be understood that they are of a revisionist nature, that is, they propose to change the way the term culture is used by most practitioners in the various disciplines covering this field of study. In fact, were they to be followed strictly, many of the things that we qualify as cultural, even in humans, would cease to be referred to in that way.

In another case of the distinction between animal traditions and animal cultures, primatologists Whiten and Van Schaik (2007) suggested, while putting forward an interesting hypothesis linking Machiavellian intelligence in primates and the complexity of cultural repertoires in different species, that animal culture could be defined as "the possession of *multiple traditions, spanning different domains of behaviour*, such as foraging techniques and social customs". This distinction is one which merits exploration in the context of searching for the projectable properties of a natural kind. It helps to answer the question of whether increased capacities for processing the social complexity of group living, and increased encephalization are both causally linked with the existence of multiple and complex traditions in different taxa across diverse branches in the tree of life. As we will survey below, empirical success here could mean that the contours of the kind are redefined in what otherwise could be seen, again, as a revisionist terminological proposal.

I have highlighted how the minimal concept of culture opens a gradualist understanding of certain traits, artifacts or behaviours which can be seen as more or less cultural. This can be disputed, since the dimensions opened up by the three cultural properties might not be on a continuous scale, but also it is unclear how being dependent on a mechanism of social learning is something which can be seen as a gradual phenomenon. After duly acknowledging that the populational or distributional nature of the concept is the basis of an idealization, one could still defend that there is room for a gradualist understanding of what is otherwise a qualitative phenomenon, namely the specificity of the mechanisms of social learning. In fact, in studying *how cultural* are certain animal behaviours, the study of the partition of variance between different sources, genetic (Langergraber et al., 2011), microecological, or socially learned, has been embraced not only from a theoretical perspective (Laland & Janik, 2006) but also in field studies (Möbius et al., 2008) and laboratory experiments (Feher et al., 2017). Studying the extent to which certain behaviours are cultural in relation to the degree of social learning involved also amounts to a recognition that certain end states in the development of the behaviour of the animal species in question are more probable both with and without social input. No doubt, certain complexities in the study of the zone of latent solutions (Tennie et al., 2020) in a given species, and its relationship with the processes of social learning will not come close to being captured by a single quantitative dimension.

This minimal concept of culture can also seem unsatisfying to some in terms of other aspects, not least being its relative triviality (see more on this in the next section). However, I believe some of the objections might be based on an insufficient understanding of its merits. A reader of a previous version of this article complained, for instance, that this minimal concept of culture allows for promiscuous inferences regarding traits not always thought to be "cultural" traits. For instance, the reader claimed, if courtship behaviours are socially learned in some species of animal, then successful mating will be the result of a specific mechanism of social learning. And if the mating produces offspring, they (and their genetic constitution) will be the result of a specific mechanism of social learning. It follows that genetic differences, and their associated phenotypic trait differences, are cultural in this case. Whereas my critic saw it as a weakness of the concept of culture which I endorse here, I do not. Again, it is a matter of degree. These types of promiscuous inferences, though initially counterintuitive, help to explain a number of crucial phenomena of gene-culture coevolution (See Sperber (2007) on our commonsensical notion of culture not capturing gene-culture evolution appropriately). Also, please note that the "intuitive plausibility test" that the critic was proposing would be only relevant if I was implying that the genetic differences in offspring are strongly cultural or prototypically cultural, which I am not. The study of cultural influences in mate choice decision making in non-human animals, is, incidentally, an active research program recorded in the network presented in section 2.

I have provided and defended a minimal definition of animal culture which encompasses the largest set of works in the animal behaviour literature using this concept to describe a range of findings. There are other alternative proposals of what animal culture really is, to which I cannot do justice here, but which often attempt to redefine the notion by departing from its current use. In what follows, we will see that the question about the naturalness of the classificatory approach that includes culture as part of the animal kingdom is of genuine relevance.

4. An elusive natural kind

As we have shown above, the concept of culture has been prevalent in the study of animal behaviour for some decades now. However, the question arises as to whether animal culture is a natural kind. But why is this an interesting question at all? Why does it matter?

The question should arise particularly when considering the culture concept I presented in section 3. The above given definition attempts to represent what most researchers in animal behaviour refer to when they use the notion of culture, thus tracing the outline of a very minimal concept. In fact, the requirements for the behaviour of a social animal to qualify as cultural are very low indeed. Under this concept of animal culture, animal culture becomes a relatively trivial phenomenon by itself. With such a low threshold for qualifying as a cultural behaviour, the interesting question becomes not so much whether a certain animal behaviour is cultural, but rather: how is it cultural? In other words, what are the mechanisms contributing to the propagation of behaviour? What are the diffusion patterns followed in its propagation? What is the ecological function of these mechanisms?

Given the broad range of species to which the concept can be applied, any apprehension one might have concerning the prospects of understanding culture in terms of a natural kind might be justified. A typical argument for what it means to be a natural kind states that a grouping of entities within the framework of a well corroborated scientific theory is a natural kind if the category formed by those entities is underpinned by a series of deep and intrinsic characteristics that allow a series of coherent causal generalizations to be based on the existence of that category. An early defendant of the idea of real or natural kinds, John Stuart Mill (1843) gave the example of Linnaeus' classificatory system based on the number of pistils and stamens in their flowers. Such groupings, Mill remarked, do not share enough other characteristics or properties to be considered a natural classification of plants.

In philosophy it is often claimed that an inventory of natural kinds aspires to capture the "furniture of the world" (Russell, 1920) or at least the main elements that emanate from the scientific view of reality. Typically, the most basic categories of the physical sciences— such as electrons or chemical components — are considered to be prototypical bona fide natural kinds. More recently, however, an increasing number of voices in philosophical theory have recognized the need to expand this view to include a larger set of natural kinds (Khalidi, 2013). On this more liberal view, it is not only the hard sciences that can provide us with the most basic elements of reality, but largely corroborated elements of "soft" sciences such as psychology or economics are also candidate natural kinds.

From this new perspective of natural kinds, it is no longer the case that scientific categories are either natural or spurious (Hacking, 2007). Rather, certain scientific kinds can be seen as positioned somewhere between two extremes, one purely explanatory of the structure of reality and the other linked to more particular interests of a pragmatic kind (Craver, 2009). Kinds can be seen as more or less natural. Our concern, therefore, should not be so much to list or make an inventory of the deep constituents of reality, but rather to establish some rigorous regulative ideals as to what kind of categories should be part of science. The aim, to be sure, is both regulative and descriptive, since by examining the way scientific communities structure their conceptual landscapes, questions about the naturalness of kinds may also inform us about which practices are useful for the pursuit of scientific knowledge.

To further understand the relevance of the question, it may first be useful to quickly mention two different ways in which culture was seriously (and unsuccessfully) thought by influential animal behaviour researchers to be based on a natural kind. The way the concept of animal culture is currently used in animal behaviour research is largely independent on the exact social learning mechanisms at the root of cultural propagation. In fact, the great diversity of mechanisms of social learning has been and continues to be a subject of intense study (see Whiten et al., 2004; and also, Hoppitt & Laland, 2013, Chapter 4). Up until the 1990s, however, imitation was considered by some researchers to be a key diagnostic sign of the presence of culture in a species.

In 1992, in a much-cited article provocatively titled "The question of animal culture", Bennett Galef (who later became president of the Animal behaviour Society for a number of years) noted that in the absence of proof of the existence of real imitation or teaching, certain behaviours observed in birds or chimpanzees could not be said to be cultural. Primatologist Michael Tomasello took the logic behind this idea a bit further by conceiving of a general model of cumulative culture in which such a form of cultural propagation was not possible without what he then termed "true imitation" (Tomasello, 1999). Despite their considerable influence in this area of research, Galef and Tomasello did not succeed in imposing their terminological and theoretical points of view. The view linking true imitation and culture no longer holds. Forms of true imitation have been observed in other animals, including apes. Since then, the use of the animal culture concept has expanded considerably without really considering the requirement of a very specific (definitional) form of social learning. The presence of what amounts to a diversity of forms of imitative learning has also been established in chimpanzees. And both Galef and Tomasello have revised their initial positions on this matter (Tomasello, 2009; Galef, 2014).

To be clear, appeals to true imitation as a diagnostic sign of the presence of culture were not gratuitous, but were rather aimed at establishing a genuine natural kind based on the evolutionary study of behaviour. The search of nomothetic regularities, that is, meaningful generalizations across a broad range of phenomena, is at the heart of the program of capturing natural kinds. Part of the logic at work here was that if social learning was sustained by true imitation, then a series of nomothetic cultural dynamics should follow (for example what Tomasello called the "ratchet effect" of cultural propagation). The operation of the social learning mechanism of true imitation was thought to provide an inductive basis robust enough to characterize a natural form of culture, i.e., natural, in the sense that one could use the concept of culture to justify meaningful generalizations based on a causal account. This is not the place to discuss the specifics, but the empirical basis for the inductive generalizations premised on true imitation is not as strong now as it once was thought to be (Morin, 2015).

Another once relatively popular stance on the question of the naturalness of culture can be linked to the popularity of memetics, or if you prefer, to the belief in the existence of an entity that underlies culture, that is, a cultural substance (e.g. Lynch, 1996; Reader & Laland, 1999). The meme concept first coined by evolutionary biologist Richard Dawkins has proved immensely culturally successful, jumping to the internet and becoming quite a common term in everyday language. Although one can accept that modeling the causality of cultural propagation in this way can be useful in some instances, it does not result in a valid general characterization of culture (Claidière & André, 2012). The memetic approach to culture typically appeals to models provided by Mendelian genetics, population dynamics, and DNA replication. In this manner, culture is considered as a form of heredity that allows one to infer several nomothetic regularities and causal generalizations. According to other related accounts, those nomothetic regularities are supposedly derived from the nature of culture as "information" (Ramsey, 2013). The problem with these approaches is that, as a general theory of culture, they assume the background conditions and required processes and mechanisms that facilitate cultural resemblance at the group level. They place excessive focus on the general characteristics of so-called 'cultural information", thereby disregarding the specific diversity of mechanisms that drive social learning and propagation. "Information", as applied to the study of animal traditions, is a pre-Darwinian concept (Bevan, 1827). Contemporary accounts are certainly better equipped to provide useful insights in this domain (Calcott et al., 2020), yet also suffer from important limitations (Lewens, 2014). Moreover, however useful the culture as information approach might prove as a simplified model in some instances, if taken as a definition of culture in general, it hinders our ability to understand cultural phenomena in animals. Why? By appealing to the concept of information one may be presupposing exactly what deserves an explanation, namely the nature of social influence and the properties (both evolutionary and mechanistic) that make that influence relatively lasting and relatively widespread in a population. The inductive generalizations based on information might be solid on paper, but do not necessarily appear solid in the field. In fact, in the case of "animal

culture" reifying information is very much at odds with the current practice and methodology of most studies on the phenomena linked to this concept. In these studies, information as such is seldom invoked as an explanatory resource (if anything it serves as an explanandum more often than as an explanans). Information, it is true, is a concept that is frequent in the mathematical modeling approach to the evolution of cultural capacities. Such a use, however, may be easily considered to be one of the assumptions or simplifications at work in those models rather than as a very solid ontological statement regarding the reality that these models aim to describe. Nothing of this is to deny the value that mathematical models have in understanding the ecology of diverse traits, including culturally learned traits. The point is that the simplifications included in the models do not tend to capture the diverse spectrum of ways in which traits can be said to be cultural.

In this section we have seen how influential figures in the field of animal behaviour research considered that there was something very close to necessary and sufficient conditions for a species to be cultural in terms of specific social learning mechanisms, namely imitation and teaching. Others have made efforts to find the basis of nomothetic regularities in reducing animal culture to information or memes. Given the range of diverse social learning mechanisms by which a form of animal behaviour can be said to be cultural and given the lack of any general causal property or substance ("cultural information") that offers a solid inductive basis for making valid generalizations about all forms of culture, it seems legitimate to ask whether animal culture is a natural kind. And if not then how might we best describe it?

4.1. Homology

In order to tackle the naturalness of the concept of animal culture, there still remain other more promising strategies than the two already outlined. We might find inspiration in the way that other wide-ranging biological or psychological traits have been characterized as natural kinds. Two general strategies can be deployed to carve biological traits at nature's joints: the search for homologies, and the search for an evolved function.

The first approach relates to the quest for biological precursors to human culture in other animals. Since the publication of Darwin's 'The Origin of Species', homology has been considered the product of descent by modification. In the same way, from a natural kind perspective, it is descent by modification that might explain the resemblance between biological traits, and that guarantees the inductive generalizations which may derive from such resemblance (Brigandt & Griffiths, 2007). Thus, human dispositions toward culture may maintain certain homology relations with other traits or capacities present in primates, above all, our closest living relatives, the great apes.

What would a successful cultural homology look like? Scientists studying animal behaviour can approach the question of homology at different levels. Anatomical homology — at the anatomical level – tends to be seen as standing on more solid ground than the notion of functional homology, that is, at the level of behaviours or functions. As an illustration, gorillas, chimpanzees, and humans have thumbs, which are very similar and homologous or explained by common descent. Chimpanzees and humans also share approximately 98% of their genomes, pointing to our sharing of many homologous genes. Nonetheless, the notion of anatomical homology can also be problematic in the context of searching for precursors to a given type of behaviour such as cultural behaviour. Linking anatomy or genetics with behaviour is usually not a straightforward task (Fitch, 2018). Besides, the description of behaviour itself typically requires the use of finalistic or functional language. In practice, when faced with the lack of precise genetic or brain anatomical data needed for sustaining a comparative approach between human cultural capacities and those of other primate species, behavioural level functional homologies (Herrmann et al., 2007) have been the most intensively studied in the search for the naturalness of animal culture.

Behaviour, in turn, can be studied also at different levels when it comes to searching for the roots of culture. Andrew Whiten, for instance, has suggested that in the search for homologies between humans and the great apes, there are at least three ways in which these similarities could be cultural: at the level of distributed patterns of shared behaviours in a population (or whether our common ancestors also showed variation of traditions across time and space); at the level of social learning mechanisms that tend to produce shared behaviours (such as rational copying, or teaching); and at the level of functional cultural contents (such as different basic forms of 'tool culture', 'comfort culture' or 'hygiene culture'). These three categories of behaviour are good candidates in the quest for homologies among the great apes (Whiten, 2011).One way of framing the question of culture as homology is to ask whether the possible candidates are uniquely human traits or not. Are those traits an evolutionary innovation, what is referred in systematics as an apomorphy? Or do we share them with other primates by common descent, thus constituting a synapomorphy?. Our actual knowledge of the comparative study of behaviour shows that our species shares several behavioural synapomorphies with other species that are relevant to the description of social behaviour (Gomez, 2009). However, our species also presents a series of behavioural apomorphies that were probably not present in our common ancestors or with other great apes (see Carruthers, 2006, pp. 154–157 for a long list of plausible candidates). The existence of these apomorphies, many of which could have cultural significance, as well as the ubiquity of animal cultures in taxa as distant from each other as corvids, primates, or even fruit-flies (Lihoreau & Simpson, 2012; Logan et al., 2016) may suggest that the homological approach is of the utmost importance in studying our commonalities with other great apes in the cultural domain but that it is also limited in its ability to respond to the question of the naturalness of animal culture in general.

At least two possibilities remain in connection with the homology hypothesis. One is that specific animal cultures (the cultural properties instantiated in the shared behaviours of, for instance, bottlenose dolphins, or New Caledonian crows) might constitute individual historical entities (Ghiselin, 1981; Hull, 1980), rather than natural kinds with projectible properties allowing valid generalizations in connection with other taxa. The other possibility is that further study might reveal the presence of what are called "deep homologies". Sometimes deep homologies have been posited to play a possible role in the evolution of certain behaviours (e.g., vocal behaviour, Scharff & Petri, 2011). Were we to find that we share some deep homology with all these different taxa in relation to some aspects of cultural behaviour, then a homology concept of animal culture might be validated. In the absence of such deep commonalities, accounting for wide-reaching similarities should rely on other mechanisms.

4.2. General selection pressures

What about the other option of grounding a biological natural kind on its evolved function? This approach is linked to the quest for selection pressures that are strong and general enough to account for the emergence of cultural capacities. If such sufficiently strong and general selection pressures are detected, these could, in principle, inform us about the form and function of the adapted trait in a relatively wide range of environments, thus providing a causal basis for inductive generalizations.

The idea of convergent evolution supposes that given enough biological variation, natural selection can produce highly similar biological traits in fairly distant taxonomic lineages provided their evolutionary environments are sufficiently similar. Much in the same way dolphin fins and shark fins resemble each other by virtue of their common evolutionary environment, different forms of animal culture may resemble each other by virtue of the common evolved function of a trait or disposition.

The most frequent critique against this approach is certainly the limiting role of morphogenetic factors (Thierry, 2000). Not just anything can evolve from anything. Behavioural ecological theory is often just theory in search of empirical corroboration. To assume, for argument's

sake, that this is not an issue is to subscribe to the usual "phenotypic gambit" (Grafen, 1991), a working hypothesis that can be legitimately pursued as such. We should, therefore, judge this approach on its own terms.

Certain evolutionary models that are general enough in scope could in principle provide an anchor based on sufficiently strong and general selective pressures. For instance, the "costly information hypothesis" (Coolen et al., 2003; Kendal et al., 2011) links the evolution of a general form of social learning with the costs and benefits of exploring problems in the environment when these problems have already been tackled by other individuals. According to other general models linking cultural learning with certain forms of variability in the selective environment, the development of a cultural form of life would be closely linked with changing selection pressures and the need to adapt to a plurality of environments (see Potts, 1998 on the variability selection thesis). It follows that culture would be, in Robert Boyd and Peter Richerson and Boyd's (2000) felicitous phrase, "built for speed not for comfort". In other words, it is the capacity for acquiring adaptive solutions that have already been acquired by some other individual in response to problems in the environment. Such a disposition would be especially well-suited for changing selective environments.

However rich these general models might be in theoretical insights they also have obvious limitations when it comes to providing a general explanation for the vast domain of animal cultures. Some of these limitations are intrinsic. For instance, variability selection models are only valid within certain parameters of environmental variability, leaving aside other forms of social learning mechanisms that would be expected under different conditions (McElreath & Strimling, 2008). Moreover, *ceteris paribus*, cultural stability as such ("animal traditions") is not selected for in rapidly changing selective regimes.

But other limitations are extrinsic, almost by definition. Thus, in as much as certain forms of social learning could be an evolutionary accident or byproduct of other evolved characteristics, an evolved function — no matter how general— could not cover those cases that are not strictly functional. In this case, the developmental constraints that we had ruled out for the sake of argument, would return with a vengeance. They would do so not so much in the form of evolutionary constraints but rather as components and aspects of certain social learning processes not strictly covered by an approach that focused exclusively on evolutionary function.

4.3. Homeostatic cluster?

Another one of the most recently favored notions of what defines a biological natural kind points to yet another distinctive approach. This is the concept of a natural kind as a "homeostatic property cluster" (Boyd, 1991). A cluster concept is like that famous Wittgensteinian notion of concepts as based on family resemblance. According to this the concept of culture instead of being connected by one essential common feature could in fact be connected by a series of overlapping similarities, where no one feature is common to all of the things. A homeostatic cluster is not only based on conventional designation but also on natural mechanisms that give unity to the kind. According to this modern view of natural kinds, many natural kinds are not so much characterized by necessary and sufficient conditions that establish membership, but rather by a more flexible set of properties, some of which tend to cluster together following causal regularities. Thus, the presence of one or several of these characteristics may be considered a reliable indicator of the statistical co-occurrence of other properties. In order for the category to constitute a natural and not simply notional kind, this statistical co-occurrence must be established on a causal basis.

In recent years, certain wide-ranging biological categories whose naturalness was also disputed (the concepts of "species", "organism" or the concept of "life" itself) have been approached from this standpoint (Dieguez, 2013). The fact that the most common concept of animal culture is composed of what we called "cultural properties" may provide an idea of how to proceed. Suppose that in those species in which you observe certain forms of social learning or a larger fraction of behavioural variance which could be apportioned to social influences, you also tend to observe certain distributional patterns, and longer cultural stability. If the aforementioned cultural properties tended to cluster together on a sufficiently reliable basis, established from the causal properties of certain forms of social learning mechanisms perhaps, then it would make sense to talk of a homeostatic property cluster of culture. In other words, something like a cultural syndrome (a bundle of interrelated cultural properties) could be at play in certain animal species. Is this indeed the case?

The answer cannot be given on an a priori basis. A population of cultural agents can satisfy some of the properties of a cultural behaviour (social learning, stability, relative frequency in the population) to varying degrees without those properties being necessarily linked. Logical necessity is precisely the type of necessity that is invoked and rejected here. The empirical details depend on the specifics of the social learning mechanisms and the diffusion process (see Claidière & Sperber, 2010). The homeostatic property cluster of culture may be positively regarded as an ambitious but interesting working hypothesis in the search for a natural kind of culture. It is not, however, a hypothesis whose methodology appears straightforward. Louis Lefevbre, Simon Reader, and collaborators have shown how a related behavioural kind —the rate of behavioural innovation– can be evolutionarily associated with a cluster of biologically relevant characteristics such as rate of social learning or relative size of associated areas in the brain in both primates and birds (Lefevbre et al., 2004; Reader & Laland, 2002). The use of a similar methodology could test the foundations of some forms of homeostatic property cluster concepts of culture. It would imply operationalizing criteria to detect and measure the different cultural properties and investigate interesting ways in which these cultural properties covary. Success, however, is not guaranteed in advance.

4.4. Reduction

Considering the diversity of mechanisms and patterns of diffusion that potentially participate in the propagation of cultural behaviour, one might reasonably wager that if any clusters of properties are to be found, the most reliably co-occurring ones will be found at a specific rather than general level. This could either be because those properties reliably covary among certain taxa but not others (e.g., if for instance social learning is related to the stability of traditions in certain genera or families but not others), because the psychological mechanisms on which cultural transmission relies are finally more specific than simply any form of social learning (if, for instance, cultural transmission through teaching really opens up a distinctive form of animal culture (Loverdo & Viciana, 2018)), or because the biological substrates of the properties are rarer than previously thought (e.g., as could be due perhaps to evolutionary constraints in the neuronal organization of the neocortex in mammals or the nidoppallium caudolaterale in birds).

Were clusters of interesting causal properties to be discovered exclusively at a lower level, that could, in principle, also be a reason to reduce the original category. In this type of reductionism, the upper-level category is now absorbed by a narrower category. The loss of extension of the older term (i.e., the notion of culture that now refers to phenomena in vastly different taxa in the animal kingdom) could then be justified to the extent that the new category (i.e., culture as referring to a more restricted class) has a more robust inductive structure. The division of previously established biological or psychological categories into more natural categories (Grifiths 1997) —thereby resulting in the older categories' loss of extension — is not without precedent. "Rodents do not include guinea pigs", or "Fish is not a category which incorporates whales" were decisions taken at some point, in a similar fashion as the collective decision that a certain kind of animal culture does not include 'X' (where 'X' is a previously thought form of animal culture) could be taken in light of further considerations (LaPorte, 2004).

One possibility is that we may have one or various populational concepts of animal cultures that are deeply anchored in the existence of generally recognized case studies or prototypes (Driscoll, 2017). This general reduction strategy allows the proliferation of special models to explain different cultural dynamics. In such scenarios, considering the naturalness of culture, the bottle is half full. Were the reduction strategy to succeed, it opens up a related question. What explains how the different clusters have been linked together and why they have previously been thought to be grouped as a single kind? In the concluding section, this latter point will be dealt with more closely.

4.5. Elimination

A few years ago, asked to state one scientific idea whose time is due, several researchers in anthropology answered with the concept of culture (Brockmann 2015). As mentioned in the Introduction, this is not a radically new idea within that discipline. Their considerations, however, can be applied to the use of this concept in the study of animal behaviour. Consider anthropologist Pascal Boyer's argumentation, and how it can similarly be applied to the case of animal culture. Briefly, he argues that if culture is an overly encompassing concept there may be nothing of interest which can be said "in general" about it. In the same sense that there cannot be a science of trees —he claims— there can be no science of culture (Boyer, 2015). In the case of anthropology, group dynamics and social psychological models may allow for generalizations at a lower level, but not at the most general one. Pascal Boyer is calling for what philosophers of science call an "elimination" of the concept of culture. Based on this scenario, the bottle is empty.

Perhaps, in the field of animal behaviour, there is but a small step between the actual landscape in which culture is an articulated concept inside a network of other concepts, and an eliminativist landscape in which social learning occupies the large central node of the network, much as it does already. Consequently, the other properties associated with cultural phenomena (stability, distribution in a population, etc.) should be referred to in a more explicit fashion. In fact, "social learning[2]" does already play a larger articulating role than that of "culture", this latter being a term which tended to be avoided by some researchers (e.g., Fragaszy & Perry, 2003 considered the epistemological interest of the term "culture" to be too anthropocentric). A weaker version of this eliminative position may still accept the use of the concept in a descriptive fashion, as an explanandum, while proscribing its role as an *explanans*. Under such a view, the culturality of a trait is a feature in search of an explanation (not an explanation itself). The adjective "cultural" can thus survive easily, whereas the reference to culture would be unduly essentialist. The strongest eliminative version calls for a stricter use of language and proscriptions against the idea of culture altogether. This again raises the question of why the different phenomena have been viewed through a single lens.

In the previous section, we have surveyed different ways in which animal culture, understood as a broad phenomenon present in diverse taxa across the tree of life, could be seen as what philosophers have classically termed a natural kind. We have seen how those influential figures in the field of animal behaviour attempted to provide something very close to necessary and sufficient conditions for a species to be cultural in terms of specific social learning mechanisms, and how theoreticians have attempted to anchor the naturalness of animal culture in the concept of information or meme. We have examined how homology might provide a promising route towards anchoring specific forms of cultural characteristics among closely related taxa, but only improbably among all the different and often far related species which have been claimed to be cultural. The study of general selection pressures also provides clues to certain functional characteristics of cultural transmission in animals, but it does not cover the different properties which have been linked with cultural behaviour in a unified framework, nor all the different instances of cultural transmission. The homeostatic property cluster construal of natural kinds yields some fascinating hypotheses about the causal projectability of certain clusters of ecological and cognitive properties of cultural species. Although it is yet to be thoroughly investigated, it does not seem to positively link the three standard cultural properties across all the different taxa where animal culture has been claimed, which would at least call for a different cluster of properties to ground the naturalness of the kind. A reduction and loss of extension of the original concept has also been presented as an alternative. And we have seen some of the arguments presented by those who advocate for an elimination of the concept altogether. It is time to take stock and close by reappraising the value of animal culture as a classificatory concept.

5. Animal culture: an epistemic kind and a realist presumption

Ontology, the philosophical branch that questions the mode of existence of entities at its most fundamental level and studies how entities are grouped into basic categories, has often suffered a bad reputation. In the previous pages we have seen how a certain ontological question regarding the nature and classificatory status of culture in animals has tacitly guided productive work in animal behaviour research. Certain proposals tried to anchor culture either in necessary and sufficient mechanisms, in homology, in its evolved function, or in the investigation of interesting clusters of properties causally linked by evolutionary histories. As some of these investigative strategies still remain open avenues of research, the previous pages map out a terrain of possible solutions to the ontological question regarding animal culture.

As the previous sections contained arguments regarding how animal culture as a wide all-encompassing concept cannot plausibly be considered a natural kind in its present configuration, a reappraisal of the status of this concept is also in order. For this, it might be advisable to reject a "love it or leave it attitude" which has so often accompanied the culture wars in animal behaviour research (Langlitz, 2020), but also the understanding of natural kinds in philosophy (Khalidi, 2013). Even though, as currently conceived, animal culture might not be a very natural kind, the realism that has guided research in this area inserts it, so to speak, in a logic of discoverability. This has proved fruitful. Stated in the terms of a prominent textbook on the categories of the philosophy of biology, the naturalness of a kind is discovered "not through the construction of definitions at the beginning of inquiry, but, if we are lucky, as the culmination of inquiry" (Sterelny & Griffiths, 1999). Under this logic, "culture" in animals opened up a problem-agenda (Love & Lugar, 2013) in a way that other similar categories could not. The stronger realist presumption included in the concept of animal culture enables it to play a role that social learning (also a central node in the epistemological landscape of animal culture research) was perhaps less apt to play. Certain hypotheses could be tested, phenomena explored, and mathematical models devised because the notion of animal culture was the backbone which supported it. Questions regarding the stability of traditions, the diffusion dynamics of foraging techniques, mate choice, or social displays, could be connected, for instance, with the cognitive complexity of holding multiple traditions in a group, the specificity of learning mechanisms in relation to certain ecological outcomes or the study of the fitness landscapes of different types of social transmission. In this respect, this articulation might have operated in a way not so different from that in which the notion of cultural evolution has facilitated the articulation of a broad field, as investigated in a recent bibliographic analysis (Youngblood & Lahti, 2018). This indeterminate realism allows for structuring research activities and producing results that address both local and global questions in several related fields of study. All this could be achieved even if we are unable to confirm the most maximalist hypotheses grounding a broad concept of animal culture in a natural kind.

[2] Although the notion of social learning is not entirely without problems either, both from a mechanistic perspective (Reisman, 2007) and as a contender for a natural kind (Heyes, 2012).

Scientific practice does sometimes require central concepts that are not strictly natural kinds. Using bibliometric methods, Conix and Chi (2020) recently demonstrated that the notion of natural kind explicitly connects the work of researchers in the behavioural sciences with work being conducted in philosophy, mainly through the question of non-arbitrary classification. This scientific work can be fruitfully pursued even if the categories of study do not end up being prototypical natural kinds. Culture might be seen, in retrospect, to have played the role of an "epistemic object" (Rheinberger, 1997), a placeholder whose definition and conceptual range remain vague and yet nevertheless proves powerful enough to assemble a field of research and create wide meaningful connections deemed worthy of exploration due in part to the existence of available techniques. In the field of animal behaviour, a series of research methods and techniques have been deployed both in the lab and the field in the pursuit of this epistemic object that is culture (Sabater Pi, 1978; Whiten, 2021; Rendell & Whitehead, 2001; Horner & De Waal 2009; Hoppitt & Laland, 2013, Chapters 5–7). This has opened up a new space in which to build knowledge around a topic that was almost entirely ignored only a few decades ago. And yet these methods and tools come with their own array of limitations which have already been pointed out in the past (e.g., Koops et al., 2014; Laland & Janik, 2006; Langergraber et al., 2011). These limitations leave their own grey areas which must be cleared for epistemic progress to be achieved. As long as the broad research program remains productive, nothing of this should be reason to entirely discard the notion. If heredity has come to be seen as an epistemic kind by historians of biology (Müller-Wille & Rheinberger 2012), animal culture can also be seen as fulfilling a similar role in the past decades. This role has been accomplished partly because the notion is expected to some extent to reflect a "reality out there", an "objective" way of grouping things together. The notion of animal culture tends to embrace a realist presumption. Yet its boundaries are revisable in the light of empirical discoveries. This node that connects different research areas on common themes should be considered a rough rock from which to smooth and carve more specific causal models. It is acknowledging its relative unnaturalness that will be key to paving the way.

Declaration of competing interest

None.

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Appendix A. Supplementary data

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