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John Maynard Smith's notion of animal signals

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Abstract. This paper explores John Maynard Smith's conceptual work on animal signals. Maynard Smith defined animal signals as traits that (1) change another organism's behaviour while benefiting the sender, that (2) are evolved for this function, and that (3) have their effects through the evolved response of the receiver. Like many ethologists, Maynard Smith assumed that animal signals convey semantic information. Yet his definition of animal signals remains silent on the nature of semantic information and on the conditions determining its content. I therefore compare three ways to specify the semantic content of animal signals. The first suggestion models semantic content on Maynard Smith's theory of genetic information. On the second proposal, semantic content is equated with a condition identified by conventional content ascriptions. The third suggestion is to explain semantic content in terms of consumer-based teleosemantics. I show how these accounts equate semantic content with distinct kinds of conditions and how they differ with respect to the kinds of traits that qualify as carrying semantic information.

Introduction

John Maynard Smith was interested in animal signals throughout his career. One of his very first studies was dedicated to the courtship displays of a small fly (Maynard Smith 1956). While this study was empirical, his major approach to animal signals soon became theoretical. In a paper that was to initiate evolutionary game theory, he sought to explain the ritualised nature of aggressive displays in terms of selection operating at the level of individual organisms (Maynard Smith and Price 1973). Among Maynard Smith's favourite topics in animal signals was the evolution of 'honest' or 'reliable' signals, i.e., signals that truthfully represent a condition. He initially rejected Zahavi's (1975) proposal according to which signals must be costly in order to be reliable (Maynard Smith 1976), but later accepted that costly signals can be evolutionarily stable (Maynard Smith 1991). However, he argued that costs are not the only mechanism to secure reliability (Maynard Smith 1991, 1994, Maynard Smith and Harper 1995).

Maynard Smith also had a conceptual interest in animal signals. He intended to clarify the confusions and disputes over how animal signals should be defined and categorised (see Dawkins 1995). Two works are prominent in this respect, both co-authored with the behavioural ecologist David Harper: the paper 'Animal Signals: Models and Terminology' (Maynard Smith and Harper 1995) and Maynard Smith's last book, *Animal Signals* (Maynard Smith and Harper 2003). In the opening pages of their book, Maynard Smith and Harper emphasise that many of the disputes are not merely about words. They helpfully distinguish purely 'semantic' questions from both 'theoretical' and 'empirical' issues (p. 2). Semantic questions, they say, concern the names given to certain types of signals; theoretical issues often turn on whether signals are distinct in kind, e.g., whether they require the same or different evolutionary mechanisms; and empirical questions typically ask what kind of signal occurs in a particular species.

In this paper I explore Maynard Smith's answers to one of the broadest questions he asked about animal signals: What are animal signals? Providing an answer to this question was for him, in one respect, a purely semantic exercise in defining clearly what he and others meant by 'animal signal'. However, Maynard Smith and Harper were not simply specifying how they would use the term. They also discussed the adequacy of various definitions in the literature and developed and defended their own definition against this background. As will become clearer below, they assessed adequacy primarily by asking whether a given definition applies, as it should, to various prima facie examples of animal signals and, conversely, whether it excludes apparent non-signals. Thus, for Maynard Smith and Harper, the question about animal signals is also a 'theoretical' one; it asks what it is for a biological item to be an animal signal. I believe they provide interesting answers to this question. However, I will argue that although they assume that animal signals carry 'semantic information' (information about an event or a state), they do not attempt to explain what it is for a signal to be *about* another thing. I then ask how Maynard Smith and Harper's definition might be extended into an account that also explains the apparent aboutness of animal signals. Three possible solutions are explored. The first draws on Maynard Smith's (2000a) account of the semantic information attributed to genes. The second solution is derived from examples of animal signals and takes its inspiration from consumer-based teleosemantic theories of mental content. As I will argue in the last section, the second solution is considerably more inclusive than the direct application of a teleosemantic theory like Ruth Millikan's to animal signals.

Maynard Smith's definition of animal signals

The starting point for Maynard Smith and Harper's (1995) analysis was the definition of animal signals proposed by Richard Dawkins and John Krebs. According to Dawkins and Krebs (1978, p. 283), animal signals are actions or structures which *change another organism's behaviour* and thereby *benefit the sender*. Consider roaring in red deer. Male red deer compete over groups of females during the rutting season by roaring at each other over prolonged periods of time (Clutton-Brock and Albon 1979). Usually, the less frequently roaring male will eventually give up and leave the females to his competitor. The winner has, through his roaring, changed his opponent's behaviour to his own benefit. Roaring is therefore a signal. Note that merely changing another organism's behaviour is insufficient for signalling. Take the camouflaged insect which moves its leg and so falls prey to an insectivorous bird. The insect's behaviour changes the bird's behaviour from searching prey to picking prey. But the insect's leg movement would not be interpreted as a signal to the bird, on the present definition, because the insect has not benefited from moving its leg (Dawkins 1995).

However, sometimes individuals change another organism's behaviour to their advantage even though we would not want to say that they have signalled anything (Hasson 1994). When the chasing fox abandons its hunt because the hare is fleeing with increasing speed, the hare changes the fox's behaviour to its own advantage. Nevertheless, the hare's increasing speed does not count as a signal to the fox; the hare simply outruns the fox.

Maynard Smith and Harper (1995) responded by adding a second condition (p. 306):[1] For an action or a structure to be a signal, it has to be a *specific adaptation* for changing another organism's behaviour. Signals have evolved because of their capacity to elicit behavioural responses. Accordingly, roaring in red deer is an adaptation for making rival males surrender their claims over groups of females. But why does the hare's running speed not satisfy this condition as well? After all, the hare's speed does not just so happen to change its predator's behaviour, it is also likely to have evolved as an adaptation to escape its predators. Maynard Smith and Harper's idea probably was that even though running is an anti-predator adaptation, it is an adaptation to *outrun* the predator, but not to change the predator's behaviour. Increasing running speed is not an adaptation to induce the predator to actively switch from one behavioural pattern (chasing) to another (abandoning the chase). Outrunning is not the consequence of the fox having abandoned the chase; the fox still chases, just not fast enough.

Maynard Smith and Harper (1995) emphasise both conditions in their definition of an animal signal:

> "We therefore define a signal as an action or structure that increases the fitness of an individual by altering the behaviour of other organisms detecting it, and that has characteristics that have evolved because they have that effect." p. 306 f.

But now consider red deer contests again. Most contests are settled by roaring and parallel walk displays, but not all. If these two kinds of displays do not settle the contest, then the two males will engage in a potentially debili-

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[1] This condition is explicit already in Dawkins and Krebs' (1978) paper when they define communication as involving an action "which appears to be the result of selection to influence the sense organs of another animal ...". p. 283.

tating fight, pushing against each other, head-on. Eventually, when the winning male has succeeded in pushing the opponent sufficiently backwards, the two disengage and the loser retreats. Maynard Smith and Harper (2003, p. 3) argue that pushing is an action increasing the winner's fitness by altering the behaviour of the loser, and pushing has evolved for that effect. Yet, although pushing conforms to the definition of a signal, we would not want to count the winner's pushing as a signal to the loser. According to Maynard Smith and Harper (2003), pushing lacks a third, crucial feature of signals. Signals like roaring have their effect on the receiver through an *evolved response* of the receiver, not through brute force: "If one stag pushes another stag backwards, that is not a signal but coercion. If it roars and the other stag retreats, it is a signal, because the response depends on evolved properties of the brain and sense organs of the receiver." By adding this third condition to their definition given in 1995, Maynard Smith and Harper thus arrive at their most recent formulation of animal signals:

> "We define a 'signal' as any act or structure which alters the behaviour of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved." (Maynard Smith and Harper 2003, p. 3)

Including the requirement that signals have their effects through evolved responses of the receiver excludes camouflage as signals. For although the motionless stick insect both changes the predator's behaviour (were it not camouflaged, the predator would detect and eat it) and is evolutionarily designed to do so, it does not achieve this effect by an evolved response of the receiver. The receiver could not possibly evolve a response to something it cannot detect (Maynard Smith and Harper 2003, p. 5). Excluding camouflage from the set of proper signals distinguishes Maynard Smith and Harper's (2003) definition from one other recent proposal (Hasson 1994) and can be regarded as an achievement.

Despite this success, I think the significance of the third condition is rather unclear. According to the definition, the presence of an evolved response makes the difference between roaring being a signal and pushing not being a signal. As Maynard Smith and Harper point out, being pushed backwards is not an evolved response on the part of the receiver; it happens by force. But if so, then the winner's push has not changed the loser's behaviour in the first place. The loser's moving backwards is not the result of a change in the loser's behaviour (from pushing to retreating), but rather a consequence of the winner pushing harder. The loser continues to push as hard as he can, just less effectively than the winner. So it seems that pushing fails to be a signal because it is not even an action that changes the receiver's behaviour as required by the first condition. On the other hand, if the loser finally retreats actively, the pushing has resulted in changing the opponent's behaviour. But that change is likely to have been effected by his evolved response. The loser has exhausted himself in a roaring contest, has measured up to the rival through parallel walking, and has engaged in a pushing fight which saw him forced backwards – his decision to retreat is likely to be an evolved response designed to make the best of a bad situation. It remains to be seen whether this difficulty arises only with regards to this example or more generally. For the rest of the paper, I accept Maynard Smith and Harper's (2003) definition and ask how it relates to the informational aspects of animal signals.

The missing content

One of the remarkable features of Maynard Smith and Harper's (2003) definition of animal signals is that it makes no mention of information, communication, instructions or the like. This is surprising given the colloquial sense of a signal as the means by which a sender conveys information about something to a receiver ('semantic information'). It is also the sense in which the term 'signal' is very often used in ethology, i.e. as a carrier of semantic information (e.g., Halliday 1983; Barnard 2004; McGregor 2005). In fact, one dimension along which ethologists categorise the variety of animal signals is the type of content or semantic information they carry. Two broad classes are frequently distinguished, although the terminology varies considerably (e.g., Halliday 1983; Krebs and Dawkins 1984; Hasson 1994; Maynard Smith and Harper 1995). The first class of animal signals carry information about some aspect of the sender ('self-reporting signals' in Maynard Smith and Harper's (1995) terminology; see their discussion of the terms used by other authors). Roaring in deer, for instance, conveys information about fighting ability. Other examples include the 'badges of status' like those of male Harris sparrows. The extent of their black plumage signals information about the bearer's social dominance (which also comes in degrees; e.g., Rohwer 1977; see also Wiley 1983, p. 172 f). The second class of signals carry information about neither the sender nor the receiver but rather about a third party ('other-reporting signals', Maynard Smith and Harper 1995). Perhaps the most remarkable example is provided by the three distinct types of calls given by vervet monkeys to other members of the group in response to three different kinds of predators (Seyfarth et al. 1980; see also Barnard 2004, pp. 580–582).

Given that the ethological literature ascribes semantic information to animal signals, why is this aspect missing in Maynard Smith and Harper's (2003) definition? In discussing some possible answers, my purpose in what follows is not to advocate any particular one, but rather to further explore the background and the nature of their definition. An initial thought might be that Maynard Smith and Harper modified Dawkins and Krebs' (1978) proposal and, therefore, endorsed the explicitly anti-informational framework advocated by Dawkins and Krebs. Perhaps Maynard Smith and Harper's (2003) definition is a deliberate attempt to transform the traditional notion of animal signal into a non-semantic concept. But this is unlikely, because Maynard

Smith and Harper fully embraced the informational view of animal communication. For example, they proposed three kinds of classifications of animal signals, all built on the premise of signals carrying semantic information: (1) 'self-' and 'other-reporting signals' carry semantic content about the sender and a third party respectively; (2) 'Minimal signals', 'cost-added signals' and 'indices' all convey true ('reliable') information and are distinguished by the mechanism guaranteeing their reliability; (3) 'Indices', 'icons', and 'symbols' are types of signals distinguished by how they relate to their semantic content (Maynard Smith and Harper 1995). More substantially, they argued that unless signals carry (true) semantic information, the receiver's response is not an evolutionarily stable strategy (Maynard Smith and Harper 1995, p 305; Maynard Smith and Harper 2003, p. 3). According to Maynard Smith and Harper, semantic information is even at the heart of evolutionary questions regarding animal signals in that the latter concern the origin and maintenance of a signal's 'reliability' (1995, p. 306). This issue became the main theme explored in *Animal signals* (Maynard Smith and Harper 2003).

A more plausible reason why semantic terms are excluded from Maynard Smith and Harper's (2003) definition of animal signals is that the authors aimed at a combination of conceptual analysis and operational definition. On this understanding, the definition is designed to clarify what the expression 'animal signal' means in ethology by proposing criteria ethologists should use to categorise an action or structure as a signal. In order to be operationally useful, these criteria should be easily assessable by ethological and evolutionary methods. Hence, the definition features behavioural changes and evolutionary functions, but avoids appealing to more diffuse concepts like semantic content.

There is, however, a philosophically more ambitious interpretation of the nature of Maynard Smith and Harper's (2003) definition. The absence of semantic terms might be taken to indicate an attempt at naturalising the concept of animal signal. That is, to make the reductive claim that what it is for a biological item to carry semantic information *is* for it to bear a complex behavioural and evolutionary relation to certain other items. More specifically, Maynard Smith and Harper may be understood as providing a 'teleosemantic theory' of semantic information. It would be inappropriate for such theories to employ semantic terms, because they seek to explain semantic norms (truth, falsehood, correctness and so on) through functional norms (e.g., achieving an evolutionary function; see Neander (2004) for a review of the teleosemantic project). This understanding is not so far-fetched given that Maynard Smith's (2000a) article on biological information has been widely received, and plausibly so, as providing a teleosemantic theory of *genetic* information (e.g., Godfrey-Smith 2000; Sarkar 2000; Sterelny 2000; Griffiths 2001).

We can certainly treat Maynard Smith and Harper's (2003) definition as a naturalistic theory of animal signals and then explore the explanatory claims of that theory. But it is readily seen that, as a naturalistic theory, their definition is rather incomplete as it stands. While Maynard Smith and Harper's proposal can claim to be a theory of what it is for a biological item to be the *carrier* or vehicle of semantic information (it is to change the behaviour of other organism, to have evolved for that effect and to be effective because the receiver's response has evolved), it has nothing explicit to say about the carrier's information itself. Suppose, for instance, the above condition is true of a certain biological item. Then, even though the item fully satisfies the condition for being a carrier, its content would nevertheless be undetermined. For the content could be either some property of the sender or some sort of external state. Thus, as a naturalistic theory, Maynard Smith and Harper's (2003) proposal fails to specify, in a general way, which entities are the contents of any particular signal. Furthermore, it lacks an account of what it is for something (e.g., a bird's territory, an eagle) to be the content of an animal signal.

All this is perhaps unsurprising given the philosophical strain I put on Maynard Smith and Harper's (2003) definition. But having exposed its shortcomings, I will now ask whether their definition can be elaborated into a fuller naturalistic account of animal signals. Ideally, there would be clues in Maynard Smith's own work how this might be achieved. His work on genetic information appears to be promising in this respect.

First solution: the content is a certain kind of effect

Maynard Smith's (2000a) 'natural history' of genetic information provides not so much a definition but rather a theory of genetic information. This theory features three criteria very similar to those we encountered in Maynard Smith and Harper's (2003) definition of animal signals. But in contrast to that definition, Maynard Smith's theory of genetic information provides also an account of the semantic content of an information carrier. It is therefore tempting to see whether his account of genetic content can be used to develop a satisfactory account of the content of animal signals.

In biology, genetic information is generally understood as information contained in the genetic material and directed at the effects the genetic material jointly produces with other factors, i.e. effects like proteins, development outcomes, and behaviours. In other words, the informational content of, say, a part of DNA is thought to be a certain kind of effect caused by this part of DNA. The philosophical debate regarding genetic information is over whether this idea of genetic information is legitimate and, if so, what it would mean for DNA to carry semantic information about its effects. Maynard Smith (2000a, p. 190) defended the claim that DNA carries semantic information about some of its effects, i.e. about the amino acid sequence of proteins and the development of organisms.

His account of genetic information proposes that DNA carries semantic information in virtue of several properties. Two of these are straightforward: A certain segment of DNA (1) causes (in concert with other factors) both the production of proteins and developmental processes and (2) it has the specific form (nucleotide sequence) it does because it has been selected in the past to produce these effects (p. 189 f.). Maynard Smith discussed two further issues, arbitrariness (p. 185) and evolved receivers (p. 193), and emphasised that both contribute in making DNA informational. Maynard Smith's (2000b) response to his commentators (Godfrey-Smith 2000; Sarkar 2000; Sterelny 2000) suggests that he sought to explain arbitrariness *in terms of* evolved receivers (see also Griffiths 2001, p. 402).[2] That is, molecular genes (and regulatory proteins) are arbitrary in that their effects are not determined and constrained by their chemical properties but rather by the evolved features of the receiver (the cell's translation machinery and regulatory sequences, respectively). On that reading, there is just one more, the third, condition for DNA carrying information: (3) DNA has its effect through the evolved response of a receiver. Together, these three features determine what it is to be a *carrier* of semantic (genetic) information: It is to have a causal, evolutionarily designed, effect in development, and to produce this effect through the evolved response of a receiver.

Maynard Smith's (2000a) theory of genetic information also specifies, in a general way, the informational *content* of any particular part of DNA. The content of a part of DNA is equated with a subset of the DNA's effects. That is, the content is that effect which (i) the piece of DNA is evolutionarily designed to cause and which (ii) is the consequence of the evolved response of the receiver (note that for something to be the informational content of DNA is for it to be such an effect). For example, the semantic content of the *eyeless* gene is 'make an eye here' (Maynard Smith 2000a, p. 188; *eyeless* specifies a transcription factor switching on other genes concerned with eye development). This is because (i) *eyeless* evolved in order to specify a protein that switches on genes controlling eye development, and because (ii) only eye development genes evolved regulatory sequences specific for the *eyeless*-protein. Similarly, any protein-specifying part of DNA contains information (about the primary structure of the protein it specifies, p. 190) in virtue of the fact that this part of DNA has the sequence it has because it evolved in order to specify the protein, and it helps to produce the protein partly because it relies on the evolved specificities and catalytic properties of enzymes. Hence, the semantic content of a protein-specifying part of DNA is the protein it helps to produce.

In short, a molecule has semantic (genetic) content on Maynard Smith's (2000a) theory in virtue of the fact that the molecule has an evolutionarily designed effect in development which is mediated through the evolved response of a receiver. And any such effect *is* the semantic content of that thing.

We can now use this account to attempt to specify the semantic content of animal signals. We only have to identify that element in the definition of animal signals which plays the same role as the thing that is the content in the account of genetic information. We saw that on Maynard Smith and Harper's (2003) definition, an individual's structure or action carries semantic content just in case it has an evolutionarily designed effect on the receiver's behaviour,

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[2] For example, in response to Godfrey-Smith's (2000) worry that arbitrariness is a consequence of focusing on 'distal' effects, Maynard Smith (2000b) insisted that arbitrariness "is not a matter of how far 'downstream' one must go, but of whether there is an evolved receptor" (p. 215).

and this effect arises as the evolved response of a receiver. Thus, both Maynard Smith's (2000a) account of genetic information and Maynard Smith and Harper's (2003) definition of animal signals appear to share the same general structure, featuring evolutionarily designed effects and evolved responses. They differ only as regards the kinds of effects and the kinds of entities producing them. More precisely, both accounts are consistent with the following claim about how an entity *X* must relate to another, *Y*, in order for *X* to be the carrier of the semantic content *Y*: *X* has an evolutionarily designed effect (*Y*) through the evolved response of a 'receiver'. *X* and *Y* can be different kinds of things. If *X* is a part of DNA and *Y* is a developmental effect, then *Y* is the semantic content carried by that part of DNA. If, on the other hand, *X* is an individual's action and *Y* another individual's behavioural response, then *Y* is the semantic content carried by the first individual's action.

In conclusion, if modelled along Maynard Smith's (2000a) account of genetic information, an animal signal *means* whichever behaviour the signal was designed to elicit in the receiver. Suppose the (eventually) winning male roars at a higher rate than its opponent. Then the winning male's higher-frequency roar would mean, to the opponent, the kind of behaviour this roar is evolutionarily designed to elicit in the opponent, i.e. the opponent's retreat. What one male signals to the other will therefore be 'Retreat!'.

This proposal has some appeal, because it suggests a unified account of the content of both animal signals and molecules. But it seems to identify the wrong kinds of entities as the content of animal signals. Ethologists take signals to be about either a property of the sender or about a third party, but not about how the receiver should respond (see section 'The missing content'). As far as I can see, the semantic content of animal signals is rarely, if ever, interpreted as the behaviour of the signal receiver.

However, there is a way to defend the implication that the semantic content of any given animal signal is the receiver's behaviour. Apparently, all kinds of content can be (re-)interpreted as the receiver's behavioural response. For there will be such a designed reaction to all signals carrying whatever content. Expressing the behavioural response in prescriptive form will then yield the proper content of the signal: Instead of meaning 'I am in good shape for a fight', roaring in red deer will mean 'Retreat!'; rather than meaning 'I am of high rank', an extensively black plumage in Harris sparrows will mean, perhaps, 'Wait until I have finished eating!'; and instead of meaning 'Leopard approaching', the leopard-alarm call in vervet monkeys would mean 'Climb up the nearest tree!'. But perhaps such reinterpretations are not a price worth paying.

Second solution: the content is a certain kind of circumstance

We may pursue a different strategy for supplementing Maynard Smith and Harper's (2003) account of animal signals; one not based on looking at another of Maynard Smith's theories. The alternative explored in this section is to take examples of animal signals and ask, in each case, whether there is something that unites all the contents customarily ascribed to them. If this common feature is some causal or functional relation, it might well be the kind of thing determining the contents of animal signals.

Consider an other-reporting signal like the leopard-alarm call of vervet monkeys. Its content is taken to be the approaching leopard. The leopard-alarm call has a certain behavioural effect on the receivers, i.e., they will climb up the nearest tree. There is also a certain environmental condition, a circumstance, in which this behaviour is beneficial to the receiver. This is the approaching leopard, and climbing up the nearest tree is the best strategy to survive. We can also plausibly assume that climbing up the nearest tree evolved *because* that behaviour was, on average, beneficial whenever leopards approached in the past. Of course, the presence of ripe fruits in the canopy is also a circumstance in which it pays to climb trees, but it is not the circumstance in virtue of which climbing evolved as the response to a leopard-alarm call.

Now take a self-reporting signal like roaring in red deer. Here, the content is supposed to be the sender's fighting ability, and the designed effect is that the opponent retreats. In line with Maynard Smith and Harper's (2003) definition we assume that the opponent's retreat is an evolutionarily designed response. Again, there is a circumstance in which retreating is beneficial to the receiver. It is the sender's superior fighting ability. For *if* he is superior, then the loser is better off retreating and saving his energy for a contest he is more likely to win.

It seems, then, that there is a common theme to all signal contents, whether other- or self-reporting. In each case, the content of a signal is the circumstance responsible for the evolution of the receiver's behavioural response. If that circumstance concerns a property of the sender, then that property *is* the signal's content (the thing the signal is about). Roaring *means* 'I'm in good shape for a fight' because the sender's *being* in good shape for a fight was the circumstance to which retreating evolved as an adaptation. If, on the other hand, the circumstance concerns a third party, then the third party is the signal's content. The alarm call *means* 'Leopard approaching' because the presence of leopards was the factor to which vervet monkeys adapted by climbing up trees.

The solution outlined here is inspired by consumer-based teleosemantic theories of mental content (e.g., Millikan 1989; Papineau 2003). One feature of these accounts is that they equate mental content with a certain kind of circumstance, rather than with an effect of a mental state (see Neander 2004 for a review). So if the solution proposed above is taken from teleosemantic theories, one might expect that applying these theories directly to animal signals would yield a very similar result. But I think doing so reveals significant differences.

Animal signals and Millikan's teleosemantic theory

One of the first consumer-based teleosemantic theories was developed by Ruth Millikan (e.g., 1984, 1989, 1995). On her account, signal producing mechanisms have the function to produce a signal in response to a certain environmental condition. For example, beavers are said to have evolved a mechanism which responds specifically to the presence of danger by tail splashing (Millikan 1989, p. 288). They also have a signal 'consuming' mechanism evolutionarily designed to elicit an escape reaction in response to hearing a tail splash. The tail splash represents danger, because danger is the condition with which the splash covaries such that the consumer mechanism can fulfil its function, i.e. to escape the predator by taking cover. More generally, the content of an animal signal[3] is that condition in response to which the signal producing device is designed to token a signal and whose correspondence with the signal is the normal condition[4] for the proper functioning of the consuming device (Millikan 1989, p. 287).

Millikan's account applies primarily to signals of limited duration and capable of being repeated many times within an individual's lifetime. These types of signals are highlighted by her examples, the beaver's tail splash and the dance of honey bees (Millikan 1995, p. 288). However, some animal signals are 'on' for a long time and others are permanent. For example, the 'badges of status' in birds often last throughout an entire season of the year (see Wiley 1983, p. 172). Some species identifying signals are permanent, like the facial colour patterns in a genus of African monkeys (*Cercopithecus*) who live in mixed species troops (Kingdon 1988, see also Bradbury and Vehrencamp 1998, p. 582). Moreover, rather than signalling transient events or states, as Millikan's account and examples would suggest, these signals often represent correspondingly permanent conditions. Thus, the Harris sparrows' dominance hierarchy lasts throughout the winter and species membership is permanent. Nevertheless, Millikan's theory is compatible with more permanent signals being produced in response to more permanent conditions.

However, many of those signals are not produced *in response to* the represented conditions. Badges in Harris sparrows are a function of both age and gender, but are not morphological effects triggered by the bearer's social rank (see Wiley 1983, p. 172). Similarly, it is difficult to see how species identifying features, like the facial colour patterns of African guenons, could be a reaction to species membership. Also, some of the less permanent signals can hardly be construed as responses to the represented conditions. Many territorial mammals, for instance, use scents and other means to mark off their territories (Bradbury and Vehrencamp 1998, p. 595), and these activities are a part of

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[3] Millikan's primary target is the explanation of mental content. But she uses external signal systems for illustration and believes that animal signals like the beaver's tail splash are signals in virtue of the very properties that also make inner, mental states representational (Millikan 1989, p. 288, footnote 14).

[4] A 'normal condition' is not a statistically normal condition but rather one that has to obtain if the mechanism is to perform its function in the way it was designed. The consuming device could achieve its function by accident, i.e., in the absence of a correspondence between danger and tail splash. But that would not be the normal condition for its functioning, because it was designed to be successful when danger and tail splash coincide (Millikan 1989, p. 285).

what it is to possess a territory. It appears then that these cases do not qualify as signals on Millikan's account. According to the proposed extension of Maynard Smith and Harper's (2003) definition, however, they are signals. A guanos' facial features represent the species to which it belongs in virtue of the fact that the behavioural responses (of both conspecifics and members of other species) to these features evolved, arguably, as adaptations to the sender's belonging to the represented species.

Another difference between Maynard Smith and Harper's (2003) supplemented definition and Millikan's theory concerns the evolved reaction of the receiver. Both theories require an evolved response. But whereas Millikan requires that the consuming mechanism has evolved its response specifically to the signal in question (because its proper function is to generate a certain behaviour in response to *that* signal), Maynard Smith and Harper (2003) demand only that the reaction evolved as a response to *some* features, but not necessarily to the signal. For example, Maynard Smith and Harper (2003) regard mimicking actions or structures as signals so long as they elicit *an* evolved response - the snapping of small fish after wiggling angler-fish lures is an evolved response, albeit not to angler-fish lures (p. 5). For this reason alone, angler-fish lures are not signals on Millikan's view.

More generally, it should be noted that Millikan's theory excludes all cases of mimicry as signals. For Millikan (1995), a signal needs to be produced and consumed by "biologically cooperating mechanisms" (p. 288; see also Millikan 2004, p. 73). It is part of this cooperation that the normal condition for the consuming mechanism's proper functioning is the proper functioning of the producing device (and vice versa). That is, the consuming mechanism is designed to achieve its function (a beneficial behavioural response to the signal) under the condition that the producing mechanism achieves its proper function (producing signals in response to a certain environmental circumstance). But mimicking actions and structures do not satisfy this condition. Lure-wiggling devices succeed in functioning properly when the lures elicit snapping responses in prey fish. Their success, however, is *not* the normal condition for the proper functioning of the consuming mechanisms of prey fish. For whenever that condition obtains, the consuming mechanisms *fail* to satisfy their proper function (detecting and catching worms). Since it is disadvantageous to the consumer to react to the lures by snapping, no consumer mechanism could ever have been selected for so responding to lures.

At this point one might think that the consumer mechanism's failure to react properly in fact explains why lures *mis*represent worms. Perhaps mimicking signals are exactly those which misrepresent because the consuming mechanism fails while the producing mechanism succeeds. Yet this idea is at odds with Millikan's account of misrepresentation. Misrepresentations are signal tokens that belong to a representational kind, and that are produced when mechanisms fail to fulfil their biological functions (Millikan 2004, p. 64). If a beaver splashes its tail in the absence of danger and other beavers take cover, then both the consuming and the producing mechanisms have failed to satisfy their biological functions. But this tail splash token still belongs to a representational *kind*. By contrast, angler-fish lures are not the type of item for which there is, or indeed can be, an evolved response satisfying both the consumer's and the producer's functions. Unlike tail splashes, mimicking signals are evolutionarily designed to occur in the absence of the represented condition.

Excluding mimicries as signals may strike one as an unwanted result. For mimicking items surely invite semantic descriptions. They appear to represent something as being the case which is not, i.e., they appear to *mis*represent. Moreover, Millikan's cooperation requirement also excludes all other types of actions or structures for which there are no cooperating producing and consuming devices. The ubiquity of conflicts of interest between distinct individuals (e.g., between parents and offspring, males and females, members of a group) suggests that many animal signals may belong to this group, and that they are not signals on Millikan's view. However, Millikan's account should not too easily be dismissed for being too restrictive. Apparently, ethologists disagree whether non-cooperative signals should count as signals. Some argue that at least the typical examples of signals benefit both the sender and the receiver (Bradbury and Vehrencamp 1998, p. 355), and this requirement excludes mimicking features as (typical) signals. Similarly, one might think that features not produced in response to a certain condition, like the facial colour patterns in monkeys, are signals of that condition only in some derived sense. But I do not want to assess whether these responses are convincing, or whether Millikan's account is better than Maynard Smith's. My aim was to show that directly applying Millikan's theory to animal signals will not yield the same results as supplementing Maynard Smith and Harper's (2003) definition with an account of content inspired by consumer-based theories such as Millikan's.

Conclusion

Maynard Smith and Harper's (2003) definition was stretched here to see whether a full account of animal signals might be developed from it. One possible worry against the second proposal to complement their definition should be mentioned. Suppose a given signal evolved to elicit different behaviours in different kinds of receivers, and suppose further that these responses evolved as adaptations to different, but co-occurring, circumstances. Then the signal had not one but several contents. I leave it open whether this constitutes a genuine indeterminacy problem or whether we may render a signal's content relative to a receiver.[5] There are other worries mentioned before; but despite these caveats, Maynard Smith's conceptual work on animal

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[5] Such relativity is advocated by so-called 'message-meaning analyses' of animal behaviour (e.g., Smith 1968; Bradbury and Vehrencamp 1998). Moreover, the idea that relativity of content is harmless for theories of content has been pursued by Papineau (2003) with respect to simple systems lacking a belief-desire psychology.

signals seems a rich and valuable source for philosophical approaches to the aboutness of biological entities.

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