# A Consumer-Based Teleosemantics for Animal Signals

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Ethological theory standardly attributes representational content to animal signals. In this article I first assess whether Ruth Millikan's teleosemantic theory accounts for the content of animal signals. I conclude that it does not, because many signals do not exhibit the required sort of cooperation between signal-producing and signal-consuming devices. It is then argued that Kim Sterelny's proposal, while not requiring cooperation, sometimes yields the wrong content. Finally, I outline an alternative view, according to which consumers alone are responsible for conferring representational status and determining content. I suggest that consumer-based teleosemantics reconstruct the content of both cooperative and noncooperative signals and explain how a given trait can mean different things to different consumers.

**1. Introduction.** According to standard ethological theory, animals can exchange information in order to mutually influence their behavior (Allen and Hauser 1992; Bradbury and Vehrencamp 1998; Seyfarth and Cheney 2003). They often use specifically evolved morphological and behavioral traits (signals) for this purpose. Some signals are false or 'dishonest': roosters sometimes send food calls in the absence of food (Gyger and Marler 1988), great tits (*Parus major*) emit more than half of their alarm calls in winter flocks without the presence of predators (Møller 1988), and mantis shrimps perform their threat display even when they have just shed their hard exoskeleton, rendering them defenseless (Barnard 2004), and so on. In fact, with its concern for cheaters and dishonest signaling, much theoretical work on signal evolution presupposes the possibility of misrepresentation (Sober 1994; Maynard Smith and Harper 2003).

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‡Ruth Millikan, David Papineau, Nicholas Shea, and Peter Godfrey-Smith provided valuable comments on the manuscript. I am also thankful for the responses of audiences at Pittsburgh, Bristol, Hannover (Germany), and Leeds, where different versions of this article were given. The generous support of the British Academy (PDF and OCG), the PSA, and the Arts Faculty of the University of Bristol is gratefully acknowledged.

Philosophy of Science, 76 (December 2009) pp. 864–875. 0031-8248/2009/7605-0033$10.00
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https://doi.org/10.1086/605820 Published online by Cambridge University Press

In short, a rooster's food call is taken to mean something like "here is food" irrespective of whether there actually is food. The possibility of misrepresentation and error is the hallmark of what philosophers of mind call representational content or 'semantic information'. Thus, mainstream ethology attributes representational content to animal signals, not just the possession of 'natural information' (which is commonly taken to disallow errors). This raises the question of how we should account for the representational content of animal signals.

Among the theories of content on offer, teleosemantics is a particularly promising candidate. Animal signals exhibit all the ingredients a teleosemantic theory would need to succeed; that is, an appeal to representation and evolutionary functions. Moreover, making sense of the content of animal signals is a desideratum for several teleosemantic theories. One prominent account has already been found wanting in this respect. Dretske (1988) suggested that an item represents some fact just in case it has the function to indicate (carry the natural information) that this fact obtains. Critics rejected this suggestion because it fits ill with many animal signals. Animal signals rarely indicate facts in Dretske's demanding sense (Godfrey-Smith 1989; Millikan 1989). Nor do they indicate in a weaker, correlational sense of natural information (Godfrey-Smith 1992): some types of alarm calls, for example, are tokened more often in the absence of danger than in its presence (see the example of *Parus major* above). If the calls indicated what they most strongly correlate with, then, if anything, they would indicate the *absence* of danger. This is an oddity to be expected for theoretical reasons. The fitness contribution of a signal depends on its overall success rate, that is, the proportion of cases in which it is critical for survival or reproduction. But this rate depends only partly on a signal's reliability. If factors like low costs dominate in determining the success rate, selection may favor less reliable over more reliable signals.[1]

In the face of these difficulties, some teleosemantic approaches have abandoned any appeal to natural information, opting instead for purely functional views (a trend opposed by Shea 2007). One of the most influential, purely functional, versions of teleosemantics is Ruth Millikan's (e.g., 1984, 2004).

In this article I argue that Millikan's version is too demanding for animal signals. The theory requires that sender and receiver cooperate, which is at odds with findings in behavioral ecology. Research over the past 40 years has seen a wealth of evidence that individuals pursue opposite (evolutionary) interests in many contexts. Noncooperation has

1. This argument was originally developed for internal sensory states ("prey-detectors"; Godfrey-Smith 1992). But it generalizes to animal signals.

https://doi.org/10.1086/605820 Published online by Cambridge University Press

turned out to be the norm in communication, rather than the exception. Nonetheless, teleosemantics still offers the conceptual resources to explain the representational content of animal signals. I will argue that consumers alone can confer representational status and determine content. Consumer-based teleosemantics generates content for both cooperative and noncooperative signals, and it generates the ethologically appropriate kinds of contents. Furthermore, it explains why a given signal may represent different things to different consumers.

The plan of this article is as follows: The next section briefly explains Millikan's cooperative theory, which is then rejected in Section 3. Section 4 discusses Kim Sterelny's (1990) 'modest' teleosemantics. Section 5 sketches a purely consumer-based version of teleosemantics, and Section 6 considers two major implications.

**2. Cooperative Teleosemantics.** At the core of Millikan's view is the distinction between signal-producing and signal-receiving ('consuming') mechanisms (e.g., Millikan 1984, 2004). These are biological mechanisms belonging to one and the same organism or, as in animal signals, to different organisms (Millikan 2004, 79). Both mechanisms have specific evolutionary functions. The function of the producing mechanism is to issue signals that correspond to the world according to a certain mapping, and the function is achieved just in case signal tokens do in fact map to the world according to the mapping (2004, 76, 80). The function of the consuming mechanism is to react to the signal in a way that benefits both the sender and receiver (2004, 80). For reasons that will become clear later, I use the mating signals of fireflies to explain how this framework is intended to apply to animal signals.

Fireflies are a group of closely related beetle species that use their luminescent abdomina to emit light flashes in order to attract and locate mating partners (e.g., Lloyd 1975). The flashes' physical properties (e.g., their duration and intensity) are both sex and species specific. Males fly about in their habitat, emitting their typical light flashes. Stationary females respond with their own specific flash if they are willing to mate. A dialogue of flash signals ensues, eventually guiding the male to the female. The signals are taken to convey information about the sex and the species of the sender and its willingness to mate. The flash of a *Photinus macdermotti* male, for instance, is taken to mean something like "here is a *P. macdermotti* male ready to mate."

From Millikan's point of view, the function of the flash-producing mechanism is to issue flashes that map to a set of conditions comprising the sender's sex and species identity and its willingness to mate. For example, the function of the flash-producing mechanism of a *P. macdermotti* female is to emit her specific flash (in response to a conspecific

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male's signal) when and where she is willing to mate.[2] On the other hand, the flash-consuming mechanism in a male *P. macdermotti* has the function to help in locating a female conspecific by prompting the male to move toward the location of a female-*macdermotti*-type flash and emit a flash in turn. Such behavior was usually rewarded with a mating.

Of course, approaching a female-*macdermotti*-type flash was rewarded with mating only when it was actually emitted by a female *P. macdermotti* willing to mate. Otherwise, the consuming mechanism did not achieve its function, for example, when the female was not ready to mate or when she was not a conspecific. To be precise, the mapping of a flash to a conspecific female is not a necessary and sufficient condition for the male's consuming device to achieve its function. It is, rather, what Millikan would call the 'normal condition'. The normal conditions for a biological trait to achieve its function are the conditions that obtain when the trait achieves its function by the historically predominant or 'normal' mechanism (Millikan 2004, 69).[3] The normal condition for signal-consuming devices is that a signal token co-occurs with that circumstance in the world the mapping of which (to signals of this type) is the function of the signal-producing mechanism (Millikan 1989, 286–287; 2004, 76).

In a nutshell, the (descriptive) content of a signal is that circumstance in the world the mapping of which (to signal tokens of this type) is (*a*) the function of the producing device and (*b*) the normal condition for the consuming device to achieve its function (Millikan 2004, 76–80). This account yields the right content for some firefly flashes. Flashes of a female *P. macdermotti* mean "here is a female *P. macdermotti* ready to mate" because the function of the female's producing device is to map its flash to the presence of a *P. macdermotti* that is willing to mate, and this mapping is also the normal condition for the male's consuming device.

One noticeable feature of Millikan's account of signals is the mandatory cooperation between signal-producing and signal-consuming devices (Millikan 1984, 97–98; 2004, 79). We already encountered one aspect of cooperation: achieving the producing device's function is the normal condition for the consuming mechanism. The reverse also holds according to Millikan; that is, the normal condition for the producing device is that

2. Female *P. macdermotti* that succeeded in mapping female-*macdermotti*-type flashes to their presence were selected because the males' response (approaching the light source) tended to result in a mating just in case such a mapping obtained.

3. Talk of 'normal mechanisms' replaces earlier talk of 'normal explanations' for the performance of a function (Millikan 2004, 69, and note 5). Initially, Millikan characterized normal conditions in terms of "Normal" explanations for the performance of a trait's function (Millikan 1984, 33–34; 1989, 285): 'normal conditions' were defined as the "preponderant explanatory conditions under which [a given] function has historically been performed" (Millikan 1984, 34).

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the consuming device achieves its function. This is Millikan's technical notion of cooperation: the two devices depend on each other's success in order to achieve their respective functions in the historically predominant way.

In what follows I will argue that many signals are exchanged between *noncooperative* producing and consuming devices.

**3. The Problem of Noncooperation.** Among the fireflies are some species that prey on other fireflies. Females of the species *Photuris versicolor*, for example, prey on the males of several *Photinus* species. Predation involves the deceptive use of mating signals (Lloyd 1975). The aptly named 'femmes fatales' lure the males by sending the sort of mating signals that the males' conspecific females would send. So, for instance, if a predator perceives the flashes of a male *P. macdermotti*, and if she's hungry, then she will emit the sort of flash that a female *P. macdermotti* would emit if she were willing to mate. Similarly, if a male *P. tanytoxus* passes by, then the predatory female will emit the kind of flash with which female *P. tanytoxus* respond. From an ethological point of view, the *predator's* female-*macdermotti*-type flash carries the information that there is a female *P. macdermotti* willing to mate. In other words, the flashes of both a female *P. macdermotti* and its mimic have representational content and the same one, at that. Furthermore, the flashes' having this content explains why male *P. macdermotti* respond to them in the way they do.

However, producing and consuming devices do not cooperate in this example. Recall one of the elements of cooperation: the normal condition for the consuming device to achieve its function is that the producing device achieves its function. The function of the predator's producing device is to token female-*macdermotti*-type flashes that map to the presence of a hungry predator (in response to perceiving the flash of a male *P. macdermotti*). The device achieves its function when its flash indeed co-occurs with these circumstances. But the co-occurrence of a female-*macdermotti*-type flash with the presence of a hungry predator is clearly not the normal condition for the male's consuming device to achieve its function. When males responded in the past to flashes emitted by predators, they typically located a predator instead of a conspecific female. The co-occurrence of a female-*macdermotti*-type flash with the presence of a hungry predator is therefore not the kind of circumstance that obtained when the consuming device achieved its function (let alone when it achieved its function by the predominant mechanism). In other words, the predators' flashes are not of a type where producing devices cooperate with consuming devices in the required sense. They therefore lack representational content on Millikan's account.

Noncooperation is not restricted to signal mimicry. Over the past de-

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cades, research in behavioral ecology has revealed that conflicts of interest drive a large number of communication-based interactions between animals. Parent-offspring relations, mate choice, resource defense, and predator-prey contexts are four broad fields of animal life where selection pressures may give rise to 'deceiving' signaling strategies (e.g., Krebs and Davies 1993; McGregor 2005). Signals produced by a deceiving mechanism will never be consumed by devices whose normal condition is that the producing device achieves its function. Therefore, they all lack representational content on Millikan's account.

One response is to embrace Millikan's theory despite this consequence and to accept that some traits were wrongly endowed with content. This response would be in line with Allen and Bekoff (1997, 106–107), who seem willing to revise ethological attributions of content in the light of Millikan's account. This is a sensible strategy where there is the occasional mismatch between philosophical theory and ethological practice. But the sheer ubiquity of noncooperative signals makes this move unattractive.

Another line of response is to deny that Millikan's view has the consequence of rendering noncooperative signals devoid of content. For instance, Millikan's (2004, 86) brief discussion of systems designed to produce false signals seems to imply that such signals are representational. Such systems need to "ride piggyback on" systems designed to produce true signals, she says. The latter are needed to establish the mapping against which the deceivers' signals count as false. This response will not do, however. Deceiving signaling systems may well depend for their evolution on a cooperative signaling system. But in order to misrepresent, the deceiving signals still need to be of a representational kind. And in order to be of a representational kind, the respective producing and consuming devices must cooperate.

Might the predators' flashes have content because they inherit it from the cooperative flashes they mimic? The notion of a copy or 'reproduction' plays a significant role in Millikan's (1984) account. The predators' flashes, however, do not qualify as 'reproductions' in her technical sense. 'Reproductions' share properties with the model due to the fact that the model is *directly* causally responsible for the reproductions' properties (Millikan 1984, 20). Imitations like a parrot's "hello" are reproductions in this sense. But there is no such direct causal link from cooperative to mimicking flashes. Nor do the predators' flashes form a 'higher-order reproductively established family' together with the females' flashes. For this would require that either all flashes are produced by the same device or, if produced by distinct devices, the devices are reproductions of one another (Millikan 1984, 24–25). Neither is the case.

It may be possible to devise ways in which noncooperative signals could inherit their content from cooperative signals, perhaps by refining the

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notion of 'reproduction'. But such moves would be premised on the assumption that cooperation is somehow essential for conferring and determining content. No argument has been given to support this assumption. That cooperation is part of Millikan's account may have much to do with the purpose for which it was originally developed, that is, to understand *mental* content. It is plausible to assume that producing and consuming devices cooperate when they are parts of the same individual organism.

My conclusion is that cooperation should not be a feature of a teleosemantic account. I believe that consumers can do all that is needed to confer and determine representational content. But before defending this line, it is instructive to consider the opposite suggestion, which is to tie content to the producer. Sterelny's (1990) 'modest proposal' exemplifies this approach.

**4. Producer-Based Teleosemantics.** According to Sterelny (1990, 124), signal tokens represent correctly when they are caused by the circumstances responsible for the existence of the type, and they misrepresent if they are caused by other circumstances. At first blush, the firefly scenario is a case in point: female-*macdermotti*-type flashes produced by predators misrepresent exactly because they are not caused by the circumstances responsible for the existence of signals of this type. For, in those circumstances, the flashes do not co-occur with predators.

Suggestive as it is, this proposal appears to deliver the wrong content for fireflies. To see this, consider first Sterelny's own example of how content is determined. A frog's internal fly representation means "that's a fly" (1990, 125) irrespective of whether it was elicited by a fly or a small black spot on a computer screen. This is because the circumstance responsible for the existence of fly representations is the presence of a fly, rather than a flicker on a screen.

Now, the presence of a fly is hardly the only circumstance responsible for the existence of fly representations—some standing conditions also contributed to their existence; for example, the fact that frogs were nourished well enough for their visual system to be responsive. From this example it seems that Sterelny identifies a signal's content specifically with the *trigger* that is part of the circumstances responsible for the existence of signals of this type. Flies are such triggers; screen flickers are not.

Here is the difficulty in applying Sterelny's account to fireflies. The trigger that is part of the circumstances responsible for the existence of female-*macdermotti*-type flashes is the flash of a male *P. macdermotti*. So if a signal's content is to be identified with these types of triggers, female-*macdermotti*-type flashes would be about the flashes of males. They would mean something like "there was a male-*macdermotti*-type flash," and they

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would have this (correct) content whether produced by females or predators. They would not represent the presence of a conspecific female either correctly or incorrectly.

**5. Consumer-Based Teleosemantics.** In this section I argue that appealing to consumer functions suffices to account for both representational status and content determination. The proposal can be stated as follows:

1. Representational status. An item (token) has descriptive representational content (for a consumer) just in case it is consumed by a mechanism whose normal condition to perform its function is that items of this type correspond to something other than themselves according to a mapping. The normal condition is understood in Millikan's sense (see above).
2. Content determination. The representational content of a (type of) item is the circumstance in the world the mapping of which (to the item) is the normal condition for the consuming device to achieve its function. If a token does correspond to something other than itself according to the mapping, it correctly represents that circumstance; if it does not, then it misrepresents.

The first condition endows female-*macdermotti*-type flashes with representational content irrespective of whether they were generated by females or predators. The flashes have content simply in virtue of the fact that there are consuming mechanisms (in male *P. macdermotti*) whose normal condition is that such flashes map to the presence of female *P. macdermotti* willing to mate. The second condition determines the content of female-*macdermotti*-type flashes. The content is something like "here is a female *P. macdermotti* willing to mate," because the presence of a female *P. macdermotti* willing to mate is the circumstance the mapping of which (to such a flash) is the normal condition for the males' consuming device. Consumerist teleosemantics thus endows both cooperative and noncooperative signals with content, and it attributes the ethologically plausible sort of content.

For present purposes signals must not be individuated in terms of their content. Their representational content and status is what the account aims to explain. Nor can they be classified as forming Millikanian 'reproductively established families' (see above). What then makes it the case that, say, light flashes emitted by different kinds of producers belong to the same type (e.g., a female-*macdermotti*-type flash)? There seem to be at least two viable options, both of which avoid classifying the flashes in terms of their overt physical similarities, or merely in terms of their effects, or indeed their content. The first is to individuate flashes in virtue of their biological function (in an etiological sense): all flashes that have the func-

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tion to attract male *P. macdermotti* willing to mate are female-*macdermotti*-type flashes. The second option is in terms of causal properties: all flashes with properties $P_1, \ldots, P_n$, which are causally relevant for attracting male *P. macdermotti*, are female-*macdermotti*-type flashes.

Note that an entirely consumer-based version of teleosemantics has been developed for internal sensory states by David Papineau (2003). Papineau identifies the representational content of certain sensory states with the success condition of a consumer's function. This mode of content determination is similar to the present account. But the two accounts were developed for different target systems. Papineau is concerned with sensory-motor mechanisms in modular systems of behavioral control. Consequently, the representational items in his account are internal states, whereas animal signals are external features. Furthermore, since a given sensory-motor mechanism is part of an individual, the senders and receivers of its sensory states belong to the same organism. The receiver systems of animal signals, by contrast, belong to individuals other than the sender. Most important, sensory states are rigidly linked to specific types of receiver mechanisms in modular systems, whereas animal signals are not linked with specific consumers in this way. An item may have evolved to convey semantic information to several different consumers simultaneously. Moreover, communication systems are intrinsically 'open' insofar as some species can eavesdrop on the signals of others. Signals can be employed as cues by species that are not the (evolutionarily) intended receivers.

**6. On Cues and Consumer Relativity.** One implication of the present account concerns the bearers of representational content. In the first instance, consumer-based teleosemantics seeks to explain why animal signals have representational content and how their content is determined. But it is not limited to animal signals, as opposed to cues or items that are not biological traits. Consider this example. Mosquitos locate their targets by the $CO_2$ mammals exhale (Maynard Smith and Harper 2003). For mosquitos, a local, higher-than-average concentration of $CO_2$ is an olfactory cue meaning something like "here is a mammal." This is also the content that consumer-based teleosemantics attributes. For the function of the mosquito's $CO_2$-response system is to locate a mammal, and so the normal condition for achieving this function is that $CO_2$ maps to the presence of a mammal. As a corollary, signals are not distinguished from cues by the kind of information they carry (i.e., semantic vs. natural information). Rather, as current biological science suggests, signals are evolved for the purpose of representing and carrying information, whereas cues are not (Maynard Smith and Harper 2003; Barnard 2004).

Another feature of consumer-based teleosemantics is that representa-

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tional status and content are relative to a consumer. Consequently, a signal may represent different things to different consumers.

A signal's content will differ between receivers just in case their consuming mechanisms have different normal conditions. Here is an example. The ground-alarm call of chickens is said to warn conspecifics of imminent danger but also to drive away predators by communicating that the sender has already discovered the predator and could escape (Marler and Evans 1996). Accordingly, the call carries something like the content "there is a predator" for conspecifics and "I could easily escape" for the predator. In this example, the two kinds of consumers differ in both the function of their behavioral responses and the corresponding normal conditions. The conspecifics' reaction to run for cover is advantageous if there really is a predator. On the other hand, the predator's reaction to retreat and hunt elsewhere is advantageous if the sender could indeed escape easily. Consumer-based teleosemantics not only attributes dual content, as it should, it also attributes the right sort of content in each case.

Not all signals with several consumers have multiple contents. There are also instances in which a given signal means the same thing to different consumers. This could happen in either of two ways. The first is where the consumers share both the same function and normal condition. For instance, the flash of a male *P. macdermotti* has at least two kinds of consumers, female conspecifics (*Photinus macdermotti*) and female predators (*Photuris versicolor*). The function of the consumers' behavioral responses is the same, that is, to attract the signaling male. Also, the normal condition for achieving the function is the same, that is, that the source of the flash is a male *P. macdermotti* willing to mate (because only then do the consumers' responses attract a mating partner/prey). Thus, the meaning of the flash is the same to both consumers.

The second case in which one signal represents the same content to different consumers is where the consumers merely share the same normal conditions, while their evolutionary functions are different. The mating call of territorial male songbirds is received by at least two kinds of consumers, male and female conspecifics (Slater 1983). Females respond to the song by flying toward the source in order to assess the potential mating partner more closely; males respond by flying away from it in order to avoid competition. Hence, the consumers' behaviors have distinct functions, that is, locating a mating partner and avoiding competition, respectively. Nevertheless, the normal conditions for these functions are identical. The source of the song was a male conspecific in those historical circumstances in which the behavioral reactions had beneficial effects. Therefore, the song means "here is a male conspecific" to both males and females.

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**7. Conclusion.** This article identified a difficulty in applying Millikan's teleosemantic account of representational content to animal signals. In response, I outlined a consumer-based teleosemantics. Throughout this article I took it for granted that the informational framework of mainstream ethology is legitimate. Furthermore, like many other teleosemantic theories, my suggestion presupposes that multiple functions, and possibly multiple normal conditions, do not lead to indeterminacy of content. There is also an open question about exactly which are the relevant traits. Considering these issues is beyond the scope of this article, as is a defense against the danger of explanatory vacuity (Godfrey-Smith 1996; Shea 2007).

However, one objection can be addressed here. It is Shea's (2007) worry that on a purely consumer-based teleosemantics, randomly generated internal states would need to count as representational although they stand in no systematic relation to states in the world: such states may prompt certain types of behavior, which in turn would have success conditions. And further, if the success conditions constituted the content of the states, then the latter would be representational. However, this worry does not threaten the present account, because it licenses the attribution of content to states only if the consumer has a function to react to those items in a certain way. And consumers are unlikely to have acquired such functions with respect to randomly generated states.

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