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TELEOSEMANTICS AND ANIMAL COMMUNICATION

Teleosemántica y comunicación animal

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Abstract

This paper proposes a hybrid teleosemantic account of meaning in (non-human) animal-to-animal communication. I consider two families of cases: signals about events external to the sender, and signals about the sender's identity or current condition. On the most influential teleosemantic approach to animal communication, such signals represent the conditions in the world required for their receivers' signal-guided behavior to be beneficial. I argue that, taken on its own, this benefit-based approach yields implausible ascriptions of content, diverging both from ethological practice and from what the view is advertised as delivering in cases of animal communication. To address this problem, I draw on a teleosemantic framework I previously developed for simple perceptual representations, which I here extend to the case of animal signals. In particular, I supplement the benefit-based approach with a signal-production condition that constrains content to what causally elicits the sender's signaling. The resulting hybrid delivers plausible contents for signals about both events in the external world and a sender's identity or current condition.

Key words: Animal Signals; Ethology; Functional Reference; Misrepresentation.

Resumen

Este artículo propone una explicación teleosemántica híbrida del significado en la comunicación entre animales (no humanos). Distingo dos familias de casos: señales sobre acontecimientos externos al emisor y señales sobre la identidad o la condición actual del emisor. Según el enfoque teleosemántico más influyente sobre la comunicación animal, tales señales representan las condiciones del mundo requeridas para que la conducta del receptor guiada por la señal resulte beneficiosa. Sostengo que, considerado por sí solo, este enfoque basado en el beneficio conduce a atribuciones de contenido poco plausibles, que se apartan tanto de la práctica etológica como de aquello que la propuesta se presenta como capaz de ofrecer en casos de comunicación animal. Para abordar este problema, recurro a un marco teleosemántico que desarrollé previamente para representaciones perceptivas simples, el cual aquí extiendo al caso de las señales animales. En particular, complemento el enfoque basado en el beneficio con una condición de producción de la señal que restringe el contenido a aquello que causalmente provoca la emisión de la señal por parte del emisor. El

híbrido resultante asigna contenidos plausibles tanto para señales sobre acontecimientos del mundo externo como para señales sobre la identidad o la condición actual del emisor.

Palabras clave: Señales animales; Etología; Referencia funcional; Representación errónea.

1. Introduction

Biologists routinely treat non-human animal signals as meaningful. Some signals are explicitly said to denote external events or objects; these signals are described as functionally referential and as instances of semantic communication (Macedonia & Evans, 1993; Marler, Evans & Hauser, 1992). But even cases not given those labels are regularly described as encoding information and conveying messages, with receivers extracting content and adjusting behavior accordingly (Bradbury & Vehrencamp, 1998; Smith & Harper, 2003). Many signals are about events external to the sender (such as the presence of predators or food), while others are about the sender (such as species identity, sex, readiness to mate, or hunger) (Smith & Harper, 1995). Ethologists treat both kinds as having correctness conditions: they can convey accurate information and be honest, yet they also sometimes involve classificatory mistakes or deception. These explanatory practices seemingly regard animal calls, displays, and pheromones as representations, not as mere natural signs. The question, then, is how such signals can be about other affairs—and depict them correctly or incorrectly. This is a philosophical question about content determination.

Among the principal philosophical accounts of content determination, *teleosemantics* offers a particularly plausible fully naturalistic explanation of how misrepresentation is possible—a phenomenon other naturalistic approaches have struggled to explain. It is well suited to simple animal signals largely shaped by natural selection, since it relies on a biologically inspired notion of *function* anchored in what mechanisms have been *selected for* doing. Teleosemantics is often presented as a theory exclusively of mental content. Many of its advocates focus on thought or perception (e.g., Papineau, 1984, 1993; Neander, 1995, 2017; Price, 2001). However, Ruth Millikan (1984, 1989, 2004, 2017)—a leading proponent and founding figure alongside David Papineau—has always applied her version equally to "inner" mental representations and to "outer" animal signals and even human language. Here I focus on animal signals, for which her account is the most influential teleosemantic treatment. On Millikan's sender–receiver framework, signals are taken to represent those conditions in the world under which the receiver's signal-guided behavior brings about the

beneficial effects it has the function of producing—benefits that account for the selection of the signaling system.

While providing much of the basis for the account I propose, Millikan's theory, taken on its own, does not yield adequate results. As Karen Neander (1995, 2017) and Paul Pietroski (1992) showed for "inner" perceptual representations, tying content (exclusively) to beneficial conditions assigns contents that do not match animals' perceptual abilities. Their objections align with ethological criteria for attributing recognitional capacities. I have argued that benefit-based accounts deliver contents that do not match ethologists' independently supported content ascriptions—invoked in explanations of goal-directed behavior—which provide proper *explananda* for theories of content determination (Withrington, 2024). Extending the point to animal communication, I here show that the benefit-based account of signals—about the world or the sender—faces the same Neander–Pietroski problems and actually delivers contents that diverge from ethologists' independent ascriptions—including the ascriptions the view is presented as accommodating in canonical cases of animal communication. In order to overcome these problems, I supplement the benefit-based approach, formulated in sender–receiver terms, with a signal-production condition—adapted from Neander's stimulus-based teleosemantics—according to which, in the relevant circumstances, what a signal represents must also be among the causes that elicit the sender's signaling. This applies and extends my previously developed proposal for simple "inner" perceptual representations in non-human animals (Withrington, 2024) to "outer" signals, generalizing its production condition beyond perceptual causes to include any normal cause of signaling, such as physiological or developmental mechanisms that are neither perceptual nor cognitive.

Combining the benefit and causal requirements yields contents that track what senders can recognize or what normally elicits their signaling, and that cohere with ethological practice. In what follows, I introduce the benefit-based teleosemantic approach, focusing on Millikan's account of "outer" animal signals. Afterward, I show that the counterexamples identified by Neander and Pietroski for simple "inner" representations have real-world counterparts in "outer" signals about both the external world and the sender, and that in these cases the benefit-based view assigns contents that diverge from the contents ethologists independently ascribe in explaining signaling behavior in terms of what signals convey. Finally, I argue that supplementing the benefit requirement with a causal one results in a version of teleosemantics for animal signals that avoids these problems and delivers adequate meanings that match those ascribed by ethologists.

2. The Benefit-Based Approach

Teleosemantics offers a framework for naturalizing representational content. The view posits that content is determined by the *functions* of the mechanisms involved in generating or utilizing representations. Central to this approach is an *etiological* notion of function, according to which the function of a trait or mechanism is defined by what it has been *selected for doing* through evolutionary processes, typically the *beneficial effect* that historically explains its existence (Millikan, 1984; Neander, 1991). While *natural selection* serves as the paradigm for such processes, the framework is often extended beyond innate biological mechanisms to cover representations that result from experience, learning, and cultural inheritance. Among the different teleosemantic proposals, Millikan's version has been the most influential and the one most directly applied to animal communication.

2.1. Millikan's framework

In addition to relying on an etiological notion of function, Millikan (1984, 1989) employs the notions of a "normal explanation" and a "normal condition". A *normal explanation* describes how the relevant functions of a trait were *historically performed* on occasions of *successful* performance. These instances benefited the animals involved, aiding their survival and reproduction, and thereby explaining selection for the trait and its transmission to descendants. A normal explanation characterizes how the mechanism operated on selectively relevant, function-conferring occasions—when it did what it was selected for doing. A *normal condition* is one that obtained on those occasions and must be included in the normal explanation of the mechanism's performance of its function.

Millikan's teleosemantics distinguishes between two primary types of mechanisms crucial to content determination: *producers* and *consumers* of representations (1989). In the context of simple mental representations, the producer is typically a sensory mechanism that generates a representational state, while the consumer is a motor mechanism that utilizes this state to guide behavior. However, in cases of animal signals used for communication, the roles of producer and consumer are distributed across *different animals*: the sender of a signal acts as the producer, and the receiver as the consumer. A signal acquires its representational status through its role within this sender–receiver system.

In simple systems, the *consumer's function* is to bring about certain *beneficial behavioral effects* under certain external circumstances, and those

circumstances—the crucial *normal conditions* for the performance of that function—constitute the content of the representational state (Millikan, 1989, p. 287).[1] The *producer's function* is then to token that state precisely when those normal conditions obtain, which is itself beneficial insofar as it enables the consumer to perform its function.

Consider the familiar example of frog prey detection and capture. The frog's tongue-snapping mechanism (the consumer) has the function of capturing prey. Millikan (1990a, p. 154) suggested that the internal state produced by a frog's prey detector (the producer) is supposed to covary with "the presence of an edible bug". This would be the normal condition required for the consumer mechanism to perform its function, and would thus constitute the content of the frog's representation. On Millikan's teleosemantic account, a frog that snaps at a prey dummy *misrepresents*. This is consistent with the seminal study by Lettvin et al. (1959, p. 1940), which characterized frogs as having *bug detectors* and as being "fooled easily […] by any moving small object". By contrast, purely causal/informational accounts (Dretske, 1981; Fodor, 1990) struggle with error: if a state's content is fixed by whatever reliably causes it, then prey dummies count among what it represents. These accounts have a serious problem of error (Godfrey-Smith, 1989).

2.2. Application to signals about external events

We can now turn from the "inner" frog case to the "outer" signals used in animal-to-animal communication, beginning with signals about events external to the sender. A signal of this kind is what Smith and Harper (1995, p. 307) classify as an "other-reporting signal", which "conveys information about an object or organism other than the signaller". A classic example is the vervet's predator-specific alarm-call system. Vervet monkeys give acoustically distinct calls for mammalian carnivores (standardly called "leopard" alarms), large raptors ("eagle" alarms), and various snakes ("snake" alarms). Playback experiments show corresponding, qualitatively different receiver responses: on "leopard" alarms, monkeys run into trees; on "eagle" alarms, they look up and move into cover; on "snake" alarms, they look down and inspect the surrounding vegetation, often standing bipedally (Seyfarth, Cheney & Marler, 1980a, 1980b). Each call type applies to more than one species within a predator

[1] The relevant normal conditions are those identified in the *least detailed* normal explanation (Millikan, 1984, pp. 33-34). Fully detailed normal explanations also list background enabling conditions, but those factors are not represented.

class, e.g., mainly but not exclusively leopards among mammalian carnivores, martial or crowned eagles among raptors, and several snake species (Seyfarth, Cheney & Marler, 1980a, p. 1071). These responses are relatively insensitive to contextual variation in the field: different alarm types typically elicit different behaviors even when produced in the same setting, consistent with the idea that the calls designate predator kinds rather than merely broadcasting arousal; as the authors of the seminal research on vervet alarm calls put it, the calls "function to designate different classes of external danger" (Seyfarth, Cheney & Marler, 1980a, p. 1070). The authors explicitly frame these calls as instances of *semantic communication* and conclude that the calls "designate particular external referents" (Seyfarth, Cheney & Marler, 1980a, p. 1091). Many ethologists regard such signals as paradigms of "functional reference"—that is, as somewhat word-like signals that stand for objects or events external to the sender and are taken as such by receivers, without requiring the kinds of cognitive production mechanisms characteristic of human language (e.g., Macedonia & Evans, 1993; Marler, Evans & Hauser, 1992; Cheney & Seyfarth, 1990).

Millikan takes the vervet calls in precisely this way: they "tell what kind of predator is near and direct the response appropriate to that predator" (Millikan, 2004, p. 81).[2] She writes that "the location of a Normally true vervet monkey's leopard call is an intentional sign of the rough space-time location of a leopard" (Millikan, 2017, p. 162), that "communicative signals used by non-human animals are intentional signs" whose effects serve the purposes of both senders and receivers—and that "the vervet monkey's snake call tells when and where there is a snake […] and tells other monkeys when to take to the trees" (Millikan, 2017, p. 163). What Millikan (2017) calls an "intentional sign" is specifically a sign that has *intentionality* in Brentano's sense: it is *about* something and can be *true* or *false*. Animal signals are intentional signs, belong to reproductively established families—a broad category encompassing phenomena like biological organs, innate behaviors, and culturally transmitted patterns—and their proliferation is shaped by various selective forces such as genetic,

[2] Millikan describes animal signals as "Pushmi-pullyu Representations". These representations are characterized as "two-faced" because they inherently combine both *descriptive content* (what is the case about a situation) and *directive content* (what actions are afforded or required in response) (Millikan, 2004, ch. 13). For example, a vervet monkey's call not only describes the presence and location of a snake but also directs other monkeys to climb trees (Millikan, 2017, p. 163). While Millikan discusses animal signals as having this dual nature, this paper's discussion focuses exclusively on their descriptive content.

learning, and cultural selection. They proliferate because they serve communicative purposes that benefit both senders and receivers (even when the benefit comes largely from the receiver's behavioral response).

On a Millikanian sender–receiver analysis, the consumer side here is the receiver's predator-avoidance mechanism. For each alarm type, the behavior that mechanism is selected to bring about is beneficial only under a matching environmental condition: running up into trees is adaptive in the presence of terrestrial carnivores but increases vulnerability to raptors; conversely, leaving the trees and moving into dense cover is adaptive in the presence of eagles but not for terrestrial predators. Hence, the normal condition for the consumer's successful performance in each case is the presence of the corresponding predator kind. By the lights of the theory, that condition is the *representational content* or meaning of the signal and, on the producer side, senders are selected to emit the call precisely when that condition obtains. Thus "leopard", "eagle", and "snake" calls represent the presence of a leopard-type, eagle-type, and snake-type threat, respectively, while also directing the appropriate response (Millikan, 2004, p. 81; 2017, pp. 162-163, p. 189). As the classic studies emphasize, younger vervets often misclassify—e.g., giving eagle alarms to many non-raptor birds and snake alarms to snakelike objects—but improve with age (Seyfarth, Cheney & Marler, 1980b), providing straightforward cases of mistakes that the benefit-based teleosemantic treatment can readily treat and characterize as errors. In parallel with the frog case, as described above, this alignment with ethological ascriptions and error patterns initially seems to count in favor of the approach; however, I argue below that without further constraints it does not, by itself, secure these very contents.

2.3. Application to signals about the sender

I now turn to signals about the sender's identity or current condition—what Smith and Harper (1995, p. 307) classify as "self-reporting signals", which "provide information, positive or negative, about some property of the signaller". A clear kind of case is that of mating dances or displays. On Millikan's view, these courtship displays are *intentional signs* whose content includes, minimally, species, sex, and the readiness of this particular individual. She explicitly lists "the mating dance of the stickleback fish and of the Canadian goose" among "intentional signs" (Millikan, 2004, p. 103). More specifically, she treats them as self-signs. She says the goose's display is performed "to sign that he himself is ready to mate" (Millikan, 2017, p. 131), and she makes the self-signing meaning explicit: "Greygoose's mating dance is a sign that Greygoose is ready to

mate; Whitegoose's mating dance is a sign that Whitegoose is ready to mate" (Millikan, 2017, p. 163). The stickleback case fits the same pattern: the dancing male, she writes, "indicates to the female that that very male is now ready to mate with her—not some indeterminate male, but that very male! […] the dancing male stickleback clearly functions as a reflexive intentional sign of himself" (Millikan, 2004, p. 148). In short, the message the receiver is meant to pick up is something like: *I am a stickleback male (or a male goose) and I am ready to mate.*

How, on Millikan's teleosemantic framework, is this content fixed? Very briefly: by the *normal conditions* that figured in the historically successful producer–consumer coordination that explains why these signals and the sender and receiver mechanisms involved were selected. In her terms, an intentional sign's content is determined by "what the sign needs to correspond to if the consumer is to perform its tasks in its normal way" (Millikan, 2004, pp. 79-80). Applied here, the consumer side (the female's recognition and mating response) has its function satisfied when the state of affairs actually is that a conspecific male—the very individual dancing—is presently ready to mate; correspondingly, the producer side (the male's dance) fulfills its function when produced on precisely those occasions. Crucially, the behavior elicited by the dances was *beneficial* only when it led to successful mating and reproduction—*only then* were the relevant traits passed along to future generations—so those are the function-conferring conditions that historically fixed the content. Just as with the vervet case, Millikan's suggested contents for these self-signs look initially adequate: they line up with standard ethological characterizations of courtship displays as instruments of mate recognition and pre-copulatory coordination (Tinbergen, 1948; Johnsgard, 1965). However, I show below that the teleosemantic machinery she relies on does not, in fact, secure these plausible contents.

A natural worry is whether such self-signing displays can ever be wrong. But they surely can be. An immature goose may "practice" a precopulatory routine while not yet capable of copulation; in that circumstance, the display misstates present readiness. A creepier case is that of the "zombie cicadas": infection by the fungus *Massospora* induces male periodical cicadas to give the female-typical wing-flick mating signal, drawing in conspecific males and thereby spreading the pathogen (Cooley, Marshall & Hill, 2018). The fungus is not a puppeteer; it surely hijacks and triggers a species-specific signaling mechanism that exists but is normally inactive in males. Another example involves the well-known "femme fatale" fireflies: females of *Photuris* mimic the mating flash-reply code of *Photinus* females to lure *Photinus* males close enough to capture and eat them

(Lloyd, 1965).[3] On Millikan's account, none of these tokens count as *true*, which is the right outcome.

3. Problems with the Benefit-Based Approach

Before turning to communication, it is important to consider the difficulties that arise for Millikan's account in the domain of simpler "inner" representations—perceptual states guiding behavior within a single animal. I will therefore begin by reviewing some well-known objections to her treatment of such cases, focusing on prey recognition in frogs, mate recognition in hoverflies, and Pietroski's kimus thought-experiment. These examples show that the benefit-based approach delivers contents that outstrip the recognitional capacities of the animals themselves and diverge from ethological practice. After considering these cases, I will turn to Millikan's account of animal signals and argue that the same concerns apply there as well.

3.1. Inner representations

Millikan originally described the frog's prey state as representing "the presence of an edible bug". But since the content is tied exclusively to the condition whose obtaining makes the consumer's performance truly beneficial, the account actually slides from "edible bugs" towards "food": catching such things matters because they are *nutritious*. In fact, Millikan later writes that "the firing [of the frog detector] means frog food" (Millikan, 1991, p. 163). Carolyn Price likewise concludes that frogs represent "nutritious objects", since the relevance of flies derives merely from their biochemical properties (Price, 2001, p. 80). Nicholas Shea's more recent version of teleosemantics departs in several ways from Millikan's, yet it also counts being nutritious among the represented properties of frog prey (Shea, 2018, ch. 6). The trouble is that this pushes content beyond the animal's recognitional capacities.[4] Frogs do not discriminate the nutritious from the non-nutritious as such; ethologists treat them as

[3] There is some debate over whether, on a Millikanian sender–receiver cooperation account, such heterospecific mimics can count as sending *false* signals to deceived receivers with the *same content* as those sent by conspecifics, given the absence of a cooperative producer–consumer history (see Artiga, 2014).

[4] I use "recognition" here and throughout in its standard ethological sense, to mark content-involving ascriptions employed in explanations of animal behavior (e.g., prey recognition, predator recognition, mate recognition). This usage does not presuppose any particular philosophical account of content, nor does it preclude other uses of the word.

recognizing moving prey animals. The classic study noted that a frog "can be fooled […] by a bit of dangled meat" (Lettvin et al., 1959, p. 1940). The meat is nutritious, yet the frog responds to it as if it were a moving prey animal. Benefit-based contents therefore part company with the contents ethologists independently ascribe for explanatory purposes in their accounts of prey recognition and capture. On my view, those ethological ascriptions provide proper *explananda* for a theory of content; features like nutritiousness belong in an "ultimate explanation" of why the system was selected, not in the representational content attributed to the perceptual state to explain behavior (Withrington, 2024, pp. 9-11).

Neander's well-known objection points to the same underlying difficulty. Millikan (1990b) treats the male hoverfly's mate detector as representing "female hoverflies", since successful matings explain the trait's selection. But, as Neander objects, only matings with *fertile females who survived to reproduce* really explain it—so under Millikan's own criterion, the detector would implausibly represent something like "fertile females that will not be eaten soon" (Neander, 1995, p. 127). That is not the content attributed in the empirical studies on hoverfly mating behavior (Collett & Land, 1978). Millikan resists by insisting that the detector would represent such females only if it were sensitive to "recurrent natural signs" of fertility or of not being eaten soon—yet, she argues, no such signs are available to the detector (Millikan, 2004, p. 85). This supplements her earlier benefit-based account with a constraint on what the producer is sensitive to. However, her notion of sensitivity does not go beyond mere correlation and does not suffice to solve the problem, since the detector was indeed correlated with fertility and with conditions under which females survived long enough to reproduce in the relevant circumstances. Martínez (2013) shows that these correlations can indeed be worked out probabilistically. So Neander's diagnosis stands: the contents Millikan's theory actually delivers are more fine-grained than the perceptual capacities support (Withrington, 2024, pp. 17-18).

An analogous problem arises in Pietroski's *kimus* case. His fictional creatures avoid *snorfs*, their predators, by moving toward a red hilltop; on a benefit-based reading, their internal state would therefore represent "snorf-free areas". Millikan herself accepts this result and treats it as unproblematic (Millikan, 2000, p. 236). But the kimus lack any capacity to discriminate snorfs or their absence: they climb the hill simply because they are attracted to a red stimulus located at its top. As Pietroski remarks, "all the behavioral evidence is going to tell against the claim that kimus represent snorfs" (Pietroski, 1992, p. 276). Real-world analogues exist (Withrington, 2024, pp. 16-17): many "indirect" anti-predator defenses,

such as microhabitat selection, reduce encounters with predators without involving any recognition of predators or of their absence. Ethologists explicitly deny that predator-related recognition plays any role in explaining such adaptive behaviors (Kruuk, 1964; Caro, 2005).

Millikan herself shifted between different attributions: frogs were first said to represent "edible bugs" but later "frog food"; she accepted that kimus represent "snorf-free areas" and regarded this as unproblematic; yet she rejected Neander's verdict that male hoverflies represent "fertile females that will not be eaten soon", or even simply "fertile females". But on what grounds are some of these results treated as acceptable and others dismissed as implausible? This points to a serious methodological problem in debates about teleosemantics and the naturalization of content. Philosophers' preferred contents often track their theoretical principles or intuitions about what must be represented. Ethologists' content ascriptions, by contrast, are empirically grounded and play indispensable explanatory roles in accounts of animal behavior. That gives us independent reason to treat them as picking out real contents, which therefore constitute properly identified *explananda* for a theory of content. In the simple perceptual cases at issue, benefit-based approaches ascribe the representation of properties like nutritiousness, predator absence, or fertility—none of which ethologists would ascribe as what the animals involved recognize in explaining their behaviors. That divergence is a serious flaw, since these approaches fail to account for how the explanatorily crucial recognitional contents identified by ethology are determined.

It is important to stress that nothing in this methodological appeal to ethology presupposes that ethologists are infallible or that they always agree in their ascriptions. However, there is a remarkably stable and widespread pattern across ethological practice. Recognitional capacities are routinely attributed to explain how animals respond in appropriate, goal-directed ways to behaviorally significant objects or events: prey recognition guides prey-catching behavior, predator recognition often guides predator avoidance, and mate recognition guides mating, for example. In these explanations, what is recognized are typically objects—prey animals, predators, conspecific mates—that are the very targets of the goal-directed behaviors, even though the same behaviors are also explained in terms of other features of those objects. Proximate explanations specify how recognition is achieved, often by identifying sign stimuli or releasers that serve as means of recognition, while ultimate explanations appeal to the fitness benefits that explain why the relevant capacity evolved. These two explanatory dimensions are not in competition with one another: sign stimuli explain, for example, *how* prey is recognized, while fitness benefits

such as nutrition explain *why* prey recognition evolved, without displacing prey animals as *what* is recognized.

The anuran case consistently fits this general pattern, despite some philosophical misreadings. Neander (2006, 2017) and Peter Schulte (2012) appeal to ethological work on anuran prey-catching behavior by Jörg-Peter Ewert and David Ingle, respectively, in order to ground teleosemantic content ascriptions in independently supported *explananda.* I agree with this methodological aim. Yet they misinterpret the relevant studies as ruling out recognition of prey animals and as favoring sign stimuli as what anurans actually recognize. This reading is mistaken. The studies by Ewert and Ingle are consistently framed as investigations of prey recognition, even while focused on specifying the sign stimuli—roughly small moving stimuli—and the neural mechanisms involved. Ingle describes his object of study as the mechanisms "by which food is recognized", where "food" stands for prey, as he immediately clarifies that this concerns "the discrimination of appropriate prey" in frogs (Ingle, 1976, p. 437); the relevant tectal neurons are described as having "prey-detecting […] functions" (Ingle, 1976, p. 449). Similarly, Ewert characterizes activation of certain tectal neurons as indicating that an object is "recognized as prey" (Ewert et al., 1983, p. 459), and describes the toad as interpreting an artificial stimulus "as a prey animal" (Ewert, 1980, p. 72). In other words, frogs and toads are described as recognizing small moving stimuli *as prey animals,* not as recognizing prey animals *as small moving objects.*[5] To my knowledge, there is no independent practice in the ethological literature on anurans of ascribing recognition of nutritional properties as such.

In the cases just reviewed, benefit-based teleosemantics assigns contents that diverge from the recognitional contents ethologists invoke to explain animal behavior. Those ethological ascriptions are empirically supported and play crucial explanatory roles, which gives us reason to treat them as real contents whose nature a theory of content must account for. Taken on its own, the benefit-based approach fails to do so. In the next section, I show that the same difficulty arises for Millikan's account of animal signals, both those about external events and those about the sender.

[5] Nothing in my argument rules out that additional contents—e.g. contents corresponding to sign stimuli—may be posited for other explanatory purposes, such as characterizing perceptual processing at an algorithmic level. My claim is only that ethology primarily attributes recognitional contents of the sort discussed here, and that these are contents a theory of content determination must account for.

3.2. Animal signals

The same methodological considerations apply once we turn to animal communication. Here too, there is a need for independent identifications of content to assess the adequacy of philosophical theories, rather than mere reliance on philosophers' disputed principles or intuitions. I suggest again that ethological content ascriptions provide such identifications. Absent specific empirical reasons for doubt—such as genuine ethological disputes about a signal's meaning—the contents identified by ethologists should be treated as genuine *explananda* for theories of content determination.

Ethologists routinely describe calls, displays, and pheromones as signaling predators, mates, or other behaviorally significant entities, and the contents thus ascribed play key explanatory roles in accounting for receivers' behavior. These semantic characterizations are often reflected in the labels used for signals themselves (e.g., "leopard alarm call")—and sometimes made even more explicit through talk of meaning or reference. As in the case of recognition, the contents attributed to signals are closely tied to the objects or events toward which the receiver's behavior is directed. Signals said to mean or signal *X* guide behavior appropriately directed at *X*. In cases involving signals about external events, there is a further alignment with recognition: a signal signaling *X* to others is typically produced in response to the sender's prior recognition of *X*. However, this breaks down in many cases of signals about the sender, which may convey information about its identity or condition without requiring any corresponding act of self-recognition. Even in such cases, the signal functions as a means for the receiver to recognize the sender's identity or condition.

It is worth noting that Millikan herself, while not articulating this as a methodological point, presents her account as delivering the very meanings attributed by ethologists in canonical cases of animal communication, including vervet alarm calls and courtship or mating displays. This plausibly contributes to the appeal of her account and to its apparent adequacy in these cases—even though, as the frog case already illustrates, Millikan is willing to revise content ascriptions when theoretical pressures arise. As I argue in what follows, however, Millikan's theory does not in fact deliver the advertised meanings for signals. I will first show that there are analogues of the frog "nutritiousness" problem in cases of signaling. I will then argue that Neander's worry about overly fine-grained contents also reemerges, both for signals about external events and for those about the sender. Finally, I will point out that there are real-world analogues of Pietroski's kimus case in the domain of animal signals.

In all of these cases, the meanings delivered by the benefit-based approach systematically diverge from—and thus fail to account for—the meanings postulated in ethological explanations.

To see an analogue of the "nutritiousness" problem in signaling, consider a food call whose ethological content is a specific prey category. Among the food calls of common marmosets, a New World monkey species, ethologists isolate an insect-specific signal—"Call C"—that they classify as *functionally referential,* and they explicitly state that "Call C […] has specific meaning, signaling the availability of insect food" (Rogers, Stewart & Kaplan, 2018, p. 1). On the sender's side, Call C is "produced only in response to seeing insects, and not fruit"—that is, the emission is elicited by the sender's prior visual detection of insect prey (Rogers, Stewart & Kaplan, 2018, p. 1). On the receiver's side, playback of the call prompts a targeted search for insects in a location previously associated with such prey, even when no insects are present (Rogers, Stewart & Kaplan, 2018, p. 1). Therefore, the calls satisfy the criteria of functional reference: (1) "they are emitted reliably in response to a specific external event" and (2) "those hearing the calls (the receivers) react in a way that is consistent with the external event, even in its absence" (Rogers, Stewart & Kaplan, 2018, p. 2). Finally, the authors note that, although marmosets also eat fruit, insects are "an important source of protein" in their natural diet, which helps explain why there is a dedicated signal for insect availability (Rogers, Stewart & Kaplan, 2018, p. 15). Notice that under a strictly benefit-based Millikanian approach, the advantage of eating insects lies precisely in their high protein content. By the same reasoning that led Millikan to move from "edible bugs" to "frog food" in the frog case, or Price to argue that flies matter to frogs only in virtue of their nutritious biochemical properties, Call C would come out as representing "the availability of protein-rich objects" instead of nutritious objects in general, since this is a dedicated signal that plausibly evolved to help marmosets secure proteins rather than any other nutrient. (If one insisted on including the perceptual features guiding receiver behavior, the full content might be something like "small moving protein packs here!") Yet marmosets have no capacity to recognize protein value as such. Ethologists, in contrast, are explicit: the call signals *the availability of insect food*—closer to Millikan's initial "edible bugs" characterization in the frog case. So, the benefit-based approach again delivers an intentional content that diverges from the one that figures in ethological explanations and is supported by the empirical evidence. Notice that, while on the benefit-based view the *causes* that elicit signaling play no role in fixing content, ethologists do rely on them in identifying what a signal *refers* to: it matters that senders produce the call in response to the presence of insects.

There are analogues of Neander's objection concerning overly fine-grained contents in animal signals. I begin with signals about external events, such as vervet alarm calls. The predator-avoidance behaviors of receivers were genuinely beneficial only when the relevant predators were actually motivated to hunt. A fully satiated leopard, unless it had cubs to feed, posed no immediate danger; vervets climbing trees on such occasions were not escaping a real threat. Much the same holds for snakes like pythons, which after a large meal may move toward cover or to drink water but do not actively hunt until hunger returns, and for raptors that attack only when driven by need. Those instances in which vervets reacted to predators lacking motivation to hunt cannot count as function-conferring occasions, since the avoidance behavior was unnecessary and conferred no selective advantage. By the lights of a benefit-based approach, then, the normal conditions that explain why the alarm system was selected must be narrowed to occasions when predators were motivated to hunt. The result is that the "leopard" call would actually mean something like "mammalian carnivore that is hungry or has cubs to feed", with parallel refinements for the other alarm types. Yet vervets have no capacity to discriminate predators with such motivational states from those without, and ethologists do not ascribe any such contents to their calls. As with Neander's hoverfly objection, Millikan is likely to reply that producers are not sensitive to any recurrent natural signs of predator hunger or parental status, and so these properties are not represented. But her supplementary appeal to sensitivity is purely correlational, and in the relevant function-conferring occasions the "leopard" call was in fact correlated with mammalian predators that were hungry or provisioning offspring. *Input sensitivity* understood in terms of mere *correlation* does not block the objection here any more than it does in the hoverfly case. Moreover, ethologists themselves describe the senders as *responding* to the presence of predators (Seyfarth, Cheney & Marler, 1980a, p. 1071), not to predators with particular motivational profiles, and it is precisely this observable responsiveness that anchors their ascriptions of content. So again, the benefit-based account delivers a content that diverges from what ethologists actually ascribe and from what vervets can recognize.

Overly fine-grained contents arise also for signals about senders. Consider the courtship displays of male geese and male sticklebacks. The responses of females to such displays are genuinely beneficial only when the displaying male is fertile. Displays given by infertile males contribute nothing to reproduction, even if receivers respond to them. On a strictly benefit-based account, then, the normal conditions that explain why these signaling systems were selected would narrow to occasions involving

fertile and reproductively successful males. The resulting content would be something like "fertile male conspecific", rather than the simpler "male conspecific ready-to-mate" content (i.e., male conspecific in breeding condition) that ethologists ascribe. Millikan might again reply that the signal's production is not sensitive to any recurrent natural signs of fertility. But here too the reply is unconvincing: fertility was correlated with the displays in all the function-conferring occasions, even though the mechanisms that elicit these displays are not selectively responsive to fertility status as such. Infertility, arising from factors such as genetic anomalies or disease, can impair sperm viability without disrupting the hormonal and neural systems that drive display behaviors. It is therefore reasonable to suppose that some male geese or sticklebacks would still display even when infertile, with the result that the benefit-based theory delivers contents that exceed what the underlying mechanisms can possibly respond to. In any case, it generates contents that differ from what ethologists actually attribute.

Finally, there are Pietroski-style cases in animal communication as well. Imagine a modest variant of the kimus story: callers produce a signal when in red zones that happen to be snorf-free; receivers approach the red patch. The trait evolved because it contributed to snorf avoidance. On a benefit-based account, the call would mean "snorf-free area here!", but what is actually signaled—given what elicits production of the signal and what guides responses to it—is the location of a red patch (cf. Pietroski, 1992). A real case with the same structure occurs in Spix's disc-winged bat. These bats roost in sparse, ephemeral tubular leaves, and roosting individuals emit a call from within a suitable leaf that guides group-mates to that site; ethologists explicitly characterize the bats as using these "cooperative signaling behaviors to convey information about roost location" (Chaverri & Gillam, 2010, p. 600). The fitness benefit of this behavior is straightforward: "finding and securing suitable roosting sites is […] important, as roosts provide protection from predators" (Chaverri & Gillam, 2010, p. 599). Consequently, by the same reasoning that leads a benefit-based teleosemantics to treat frogs or kimus as representing objects or locations by their fitness-relevant properties—such as prey being nutritious or areas being snorf-free—these bats' calls should represent the roost, at least in part, as a place *affording predator protection*. Yet what is signaled, as ethologists themselves emphasize, is *the location of the roost (a tubular leaf)*, determined by what elicits the call (being inside such a leaf) and by the receivers' approach behavior—not by the ultimate benefits that properly belong in an explanation of why the signaling system evolved. One may wonder why this ascription should be preferred over the benefit-based

one, given that both alternatives may seem equally plausible. The answer is methodological: content assessments should rely on identifications specified independently of the philosophical theories under debate and of the diverging intuitions of their advocates. In the case of animal communication, ethological content ascriptions are empirically grounded and play indispensable explanatory roles in accounting for behavior. These are contents whose nature a theory of content ought to explain, rather than revise in light of theoretical commitments.

4. A Hybrid Approach

The cases discussed above suggest that benefit alone does not fix the right meanings for animal signals. I propose adding a causal condition on production—inspired by Neander's (2017) stimulus-based teleosemantics—to overcome this problem. The proposal extends the hybrid view I previously defended for simple "inner" representations (Withrington, 2024), which I here apply to account for the meanings of outer signals used in (non-human) animal-to-animal communication. I first outline the core features of the proposal, briefly illustrating how it works in cases of animal perception, and then show how it applies to the signaling cases discussed above, where it yields determinate contents that align with ethological practice and avoid the overly fine-grained results of purely benefit-based views.

4.1. Causal-behavioral teleosemantics

My hybrid proposal—which I call "Causal-Behavioral Teleosemantics" (CBTS)—combines two central ideas drawn from Millikan's and Neander's approaches, respectively. It adopts Millikan's suggestion that the content of a representational state is among the *normal conditions* for the performance of its consumer's functions: bringing about certain beneficial behavioral effects. From Neander (2017), it borrows the requirement that what is represented must stand in the right causal relation to the state—specifically, that it be among the state's normal causes, understood as causes that the producers respond to on *function-conferring occasions*. According to CBTS, content is both a normal condition for consumption and a normal cause of production of a representational state. But consumers typically have multiple functions, associated with different normal conditions, and producers respond to several normal causes. This generates more than one candidate normal condition that is also a normal cause. CBTS selects as the content of a representational state the *most crucial* normal condition for its consumption—roughly, the one tied to the benefits most directly relevant to

the trait's selection—that is also a normal cause of its production. In what follows, I spell out the notions required to make the commitments of this proposal clear.

In much of the discussion so far, I have spoken loosely of *the* normal condition associated with the consumption of a given representational state. In reality, however, there are *several* normal conditions involved in the normal explanation of how a trait performs the functions for which it was selected. This is partly because traits typically have various *hierarchically nested functions* (Neander, 1995). Consider the simplified frog case, suggested by Fodor (1990), who imagines that frogs eat only flies. The tongue-snapping mechanism contributed to the frog's survival *by:*

catching nutritious objects
by
catching flies
by
catching small moving objects (SMOs)
by
snapping at small moving retinal images (SMIs).

Each item in this hierarchy corresponds to a genuine function of the mechanism, and must be cited in a full explanation of why the trait was selected. But notice that each function has its own associated normal conditions for successful performance: respectively, the presence of nutritious objects, the presence of flies, the presence of SMOs, and the presence of SMIs. These functions are hierarchically related because each is performed by means of performing the next lower one. While the successful performance of any of these functions is beneficial, the benefits associated with the higher-level functions are the most crucial—and most directly relevant—for explaining why the mechanism exists at all: catching small moving objects is beneficial only because it contributes to catching flies, which in turn is beneficial only because it contributes to catching nutritious objects. Accordingly, a normal condition is more crucial than another just in case it is involved in the performance of a higher-level function.

In addition to normal conditions for consumption, I appeal to the notion of a *normal cause* of a representational state, inspired by Neander's (2017) stimulus-based constraint on content. By this I mean a cause of the producer's tokening of the state that must be cited in a normal explanation of the successful performance of the representational system's functions. Normal causes are thus causes that actually triggered the state on those function-conferring occasions in which the coordinated operation of producer and consumer performed all of their respective functions and thereby contributed to selection. So understood, normal causes are events

to which the producer is supposed to respond, given its selective history—namely, events involved in function-conferring occasions.[6] Importantly, what such function-conferring occasions typically reveal is not a single cause of a representational state's production, but a *causal chain* leading to its activation. In perceptual cases, the producer's activation is normally caused by proximal sensory events, which are in turn caused by distal environmental events; those distal events may themselves have further causal antecedents. All of the causes in such a chain that must be cited in a normal explanation count as normal causes in the present sense. As a result, a single representational state may have several normal causes, just as it is associated with several normal conditions for its successful use.

With these notions in place, it should be clear what the proposal sketched above amounts to. According to CBTS, the content of a representational state must be both a normal condition for the successful performance of the consumer's functions and a normal cause of the state's production—one to which the producer is supposed to respond, given its selective history. Since consumers have hierarchically ordered functions and producers typically respond to several normal causes, more than one candidate will usually satisfy these constraints. CBTS therefore claims that content is fixed by the *most crucial* normal condition for consumption—namely, the one associated with the highest-level consumer function—that is also a normal cause of production.

Consider the frog case again. The normal conditions associated with the successful consumption of the prey-detector state include the presence of nutritious objects, flies, SMOs, and SMIs. Being nutritious is not a normal cause of the detector's activation, since the producer is not causally sensitive to nutritive properties. SMOs and SMIs are normal causes of the detector's activation, but I contend that the presence of flies is as well. Since the presence of flies is the most crucial normal condition that is also a normal cause, CBTS yields the result that the state represents flies.

A natural worry concerns the notion of causation presupposed by CBTS. On a very permissive understanding, nutritious objects might be said to cause the activation of the prey detector, since flies are nutritious and flies do cause the detector to fire. Following Neander (2017), CBTS relies on a more restrictive, property-specific notion of causation to block this move. Nutritious objects do not cause the detector's activation *qua* nutritious: the frog is not causally sensitive to nutritive properties, as illustrated by

[6] This broad characterization of normal causes—as what the producer is supposed to respond to, given its selective history—is shared with Neander's (2017) account, though there are important differences in how the notion is further constrained and applied. See Withrington (2024) for discussion.

the fact that a frog can starve in the presence of abundant stationary food (Lettvin et al., 1959, p. 1940). By contrast, SMOs and SMIs do cause the detector to fire *qua* SMOs and SMIs, and hence qualify as normal causes. This much is shared with Neander's use of property-sensitive causation. However, contra Neander (2017), this principle does not exclude flies.[7] In function-conferring occasions, the relevant SMIs are produced by moving SMOs, whose movements in turn result from the activity of living flies—by their self-propelled locomotion, sustained by their physiology and behavior. The causal explanation of the detector's activation therefore does not stop at the level of SMOs or SMIs. Rather, the presence of a fly figures in the causal chain leading to activation on those occasions that mattered for selection. Accordingly, CBTS treats flies as normal causes of the prey detector's activation.[8]

This way of understanding causal sensitivity is also in line with standard ethological practice. Ethologists routinely characterize animals as *responding* to prey, predators, mates, or conspecifics, and these characterizations play a central explanatory role in accounting for their behavior. The operative notion of "responding to *X*" in such explanations presupposes a conception of causality that is neither the maximally permissive one (on which any merely correlated beneficial factor would count) nor the overly restrictive one (on which only sign stimuli or even just proximal stimuli would qualify). CBTS is designed to capture this moderately constrained causal notion already operative in ethological explanations of animal behavior.

It is worth situating CBTS with respect to other hybrid proposals that combine consumer-side benefits with producer-side constraints. Millikan's later work explicitly gestures toward such a combination by supplementing her benefit-based account with a requirement on the *sensitivity* of the producer (Millikan, 2004). Shea (2007; 2018) develops this kind of idea more systematically by adding an *input condition* to teleosemantics. These moves are well headed: they acknowledge that benefit alone is insufficient

[7] Schulte (2018) notes that, on Neander's account, the underlying causes of detectable cues may themselves count as normal causes, thereby allowing contents involving deeper properties that her view is meant to exclude, although he does not include being a fly among such deeper properties. See Withrington (2024, pp. 14-15).

[8] This appeal to deeper causal explanations is broadly compatible with Martínez's (2013) proposal to treat biological kinds such as flies as homeostatic property clusters whose presence explains the co-instantiation of detectable features, as well as with Artiga's (2021) extension of this strategy to non-homeostatic cases. For comparison between these views and CBTS, see Withrington (2024). I believe that insights from these proposals and from CBTS can be fruitfully combined, though discussion of this will have to wait for another occasion.

to fix content, and that constraints on production are needed. However, the constraints they introduce are correlational rather than causal, and for that reason they still deliver contents that are more fine-grained than the recognitional and signaling capacities standardly attributed in ethological explanations. By their own analyses, these approaches assign to frogs' prey-detection states contents that include properties such as being nutritious, and to kimu detectors contents involving snorf-freeness—results that diverge from the sorts of contents appealed to by ethologists when explaining recognition and signaling behavior. CBTS likewise supplements a benefit-based approach with a production-based constraint, but replaces correlational input conditions with a causal one, thereby yielding contents that align more closely with ethological practice.[9]

4.2. Signals and the production constraint

I now extend CBTS to animal signals. The cases in section 3.2 exhibited several problems for the purely benefit-based approach: the "nutritiousness" problem (marmosets' Call C signaling protein-rich objects instead of insects); overly fine-grained attributions in signals about external events (vervet alarms signaling motivated predators rather than simply predators), with a parallel over-refinement in signals about the sender (courtship displays pushed toward signaling fertility rather than breeding condition or readiness to mate); and Pietroski-style cases, both fictional (kimus signaling snorf-free areas instead of red ones) and real (disc-winged bats implausibly signaling predator safety rather than just roost location). On CBTS, a signal's content is fixed by the most evolutionarily crucial normal condition for the receiver's behavior to be beneficial that also normally causes its production on function-conferring occasions. This prevents drift to ultimate-level benefits that producer mechanisms cannot respond to and realigns contents with ethological practice, which anchors

[9] In a recent paper, Millikan (2023, p. 9) tentatively suggests that the frog's state may not represent an SMO, a fly, or food, but rather a "no-choice affordance" of "catching and swallowing", adding that "there is no consumer that uses information about what that something is […] [so] *what* it is would not be represented". It is unlikely that she intends this to entail that the state would be true in cases involving prey dummies, even when these are catchable and swallowable. If the relevant affordance is instead constrained by normal conditions involving nutrition, then the content again appears to involve food. If she were now effectively denying contents involving the presence of prey or food, this would mark a significant departure from her earlier analyses, as well as from the contents appealed to in ethological explanations. Insofar as the latter are properly identified, her new view would fail to account for their nature. I set this suggestion aside in what follows, which continues to engage with Millikan's standard teleosemantic framework.

content ascriptions in what elicits signal production and how receivers characteristically respond. In what follows, I apply CBTS case by case.

The "nutritiousness" problem—Marmosets' Call C: On CBTS, the most evolutionarily crucial normal condition for the receiver's behavior to be beneficial that also normally causes production is the presence of insects. Senders produce Call C "only in response to seeing insects", and receivers mount a targeted search for insects; ethologists explicitly characterize the call as signaling "the availability of insect food" (Rogers, Stewart & Kaplan, 2018, pp. 1-2). Insects do not cause Call C *qua* objects with high protein content. As in the anuran case, producers are not causally sensitive to nutritional properties as such. Rather, insects cause Call C *qua* insects. In the study, the relevant elicitors include particular insect prey such as crickets and mealworms. According to CBTS, the presence of these insects is causally responsible—via the developmental, physiological, and behavioral mechanisms that give rise to their characteristic morphology and self-propelled locomotion—for the instantiation of the perceptual features that trigger call production. CBTS's inclusion of insects among the normal causes of Call C coincides with what ethologists explicitly describe marmosets as responding to when they give this call. Proximal stimuli and sign stimuli for such insects are also themselves among the normal causes of production and among the normal conditions for successful use by receivers. However, they are not what is represented, because they are not the most crucial normal conditions that are also normal causes of signaling. Nutritional properties figure instead at the level of ultimate explanation: Rogers and colleagues explicitly note that insects are "an important source of protein" in the marmoset diet (Rogers, Stewart & Kaplan, 2018, p. 15), but they treat this fact as explaining why there is a dedicated insect call, not as part of what the call means. In line with this explanatory practice, CBTS prevents drift to "protein-rich objects" and treats the signal as representing the presence of insects.

Overly fine-grained contents for signals about external events—Vervet alarm calls: For the alarm call system, the receiver's responses are beneficial under predator encounter conditions; among those, the most evolutionarily crucial normal condition that also normally causes call production is simply predator presence of the relevant kind (several carnivorous mammals for the "leopard" call, martial or crowned eagles for the "eagle" call, and several species of snakes for the "snake" call). Callers are described as responding to the presence of the predator (Seyfarth, Cheney & Marler, 1980a, p. 1071). Predators do not cause alarm calls *qua* hungry or provisioning individuals. Rather, they cause alarm calls *qua* the kinds of animals they are, through the perceptual features by means of which vervets detect

them; the presence of these animals is causally responsible—in virtue of the biological mechanisms that underlie their characteristic appearance and behavior—for the instantiation of the detected features that elicit call production. Proximal stimuli and distal sign stimuli for these predators are not what is signaled, because they are not the most crucial normal conditions that are also normal causes of signaling. Properties such as hunger or provisioning young are relevant to explaining why avoiding certain predators is beneficial in particular circumstances, but they are not among the properties to which the producer mechanisms are causally sensitive. CBTS therefore prevents motivational states from entering the signaled content and treats the alarm calls as representing only the presence of the relevant predator, which coincides with the contents ethologists ascribe, and with the contents Millikan presents her account as delivering in this case—though, as argued above, it does not in fact secure those results.

Overly fine-grained content for signals about senders—Courtship displays: Here the receiver's responses are beneficial when the male goose or stickleback is fertile, and reproduction will succeed, but what normally causes display production in senders is their being a male goose or stickleback entering the hormonally primed breeding condition, not fertility status *per se*. As already noted above, infertility can arise from genetic anomalies or disease without disrupting the hormonal and neural mechanisms that elicit display behavior. CBTS does not require that breeding condition be causally independent of fertility, nor does it deny that both may share upstream hormonal causes. Rather, the relevant question is which properties of the sender the display-producing mechanisms are causally sensitive to in the normal explanation of signal production. On function-conferring occasions, displays are elicited by the sender's entering the characteristic breeding condition—via hormonal priming and related physiological processes—whether or not reproduction will in fact occur. By contrast, fertility as such does not play this causal role: variation in fertility that does not affect breeding condition does not systematically affect display production, whereas variation in breeding condition does. CBTS therefore yields the familiar ethological characterization—something like "male conspecific ready to mate"—rather than "fertile male conspecific". The benefit-based pressure toward fertility is halted because fertility does not figure among the properties to which the display mechanisms are responsive.

Notice that in these display cases the production mechanism is not purely perceptual or cognitive. Although display is typically facilitated by perceiving a female conspecific, the proximate trigger is the male's

physiological state (hormonal priming and related processes), not plausibly a matter of inner perception. A natural worry is that, since perceiving a female is itself a normal cause, the display should also represent her presence. This, however, is not problematic—courtship routines are interactive, and the signal is naturally read as "I am a male conspecific, ready to mate (with you)". This result is in line with standard ethological characterizations of courtship displays as signals involved not only in mate recognition but also in coordinating mating behavior (Tinbergen, 1948; Johnsgard, 1965).

Pietroski-style real cases—Disc-winged bats' roosting calls: Receivers benefit when they locate a suitable roost; the most evolutionarily crucial normal condition for the receiver's behavior to be beneficial that also normally causes production is the sender's being inside a suitable roost, *qua* tubular leaf. Roosting individuals emit the call from within such leaves, and field experiments show that the bats use "cooperative signaling behaviors to convey information about roost location", with "response calls […] emitted by roosting individuals […] to aid conspecifics in finding the roost" (Chaverri & Gillam, 2010, pp. 599-600). The presence of a tubular leaf is causally responsible—via the biological and developmental processes of the plant that give rise to the leaf's characteristic shape and structure—for the instantiation of the perceptual features that elicit call production on function-conferring occasions. The case can be situated within a well-known ethological class of *indirect anti-predator defenses,* in which protection from predators is achieved without any response to or recognition of predators themselves, but rather through behaviors directed at other environmental features (Kruuk, 1964; Caro, 2005, p. 2). One of the ultimate fitness benefits of this signaling system is predator avoidance: "finding and securing suitable roosting sites is […] important, as roosts provide protection from predators" (Chaverri & Gillam, 2010, p. 599). A purely benefit-based approach therefore invites drift from roost location to "place affording predator protection". CBTS blocks this drift. Predator protection helps explain why the signaling system evolved, but it is not among the properties to which the production mechanisms are causally sensitive. What normally causes call production is being inside a tubular leaf, and what receivers are guided to is that location. CBTS therefore assigns the content "roost location (tubular leaf) here!", in line with the explicit ethological ascription of what information the call conveys.

Pietroski-style thought-experiment—Signaling Kimus: If callers signal from red patches on the hilltop, and receivers home to them, the normal cause of production is being in a red area, since the caller is responsive to that area *qua* red. The area does not elicit signaling *qua*

snorf-free, even if snorf-freeness figures among the higher-level conditions under which the signaling system performs its ultimate function. Given the property-sensitive character of causation assumed by CBTS, such higher-level normal conditions do not qualify as normal causes of production. The content is fixed by the most crucial normal condition that is also a normal cause—here, being in a red patch—yielding the content "red-patch here", rather than "snorf-free area here" (cf. Pietroski, 1992). Importantly, what is represented in such cases depends on the causal structure of the environment. Suppose, for example, that the hilltop is red because a distinctive species of red grass grows only there, and that it is the physiology of this grass that causally explains the relevant surface coloration to which callers respond. In that case, signaling would be elicited by being in red grass *qua* red grass, and the most crucial normal condition that is also a normal cause would be the presence of that grass itself. Here, red grass would count as more crucial than redness alone, since kimus would reach snorf-free areas *by* homing to red-grass areas, and do so *by* homing to red areas. CBTS would yield the content "red-grass here". Hierarchical relations among normal conditions, together with property-sensitive causation, determine content.

In some of these cases, CBTS yields disjunctive contents. For Call C, what normally elicits production across function-conferring occasions is the presence of particular insect prey; the resulting content is therefore, roughly, "cricket or mealworm or…"—in short, the insects the system was selected to detect. Likewise, the "leopard" alarm call represents the presence of one of the historically relevant mammalian predators of the population ("leopard or hyena or…"), with parallel disjunctions for the "eagle" and "snake" calls. These disjunctions are principled: they reflect families of normal causes that actually figured in the system's selective history and that continue to elicit signal production under normal conditions. This disjunctive treatment draws on Marc Artiga's (2021) proposal.

5. Conclusion

The cases discussed show that a purely benefit-based teleosemantics of animal communication inherits the same difficulties that arise for inner representational states. In signaling systems, as in animal perception, appeal to ultimate benefits alone pushes contents toward properties to which the relevant mechanisms are not responsive, yielding overly fine-grained attributions that diverge from those employed in ethological explanation.

Focusing on animal signals, I have argued that these failures can be avoided by extending to communication a hybrid teleosemantic framework

previously defended for inner states. On this view, contents are fixed not only by the benefits of successful use by receivers, but also by the normal causes that elicit signal production on function-conferring occasions. Applied to animal communication, this production constraint blocks drift to ultimate-level benefits, preserves the possibility of misrepresentation, and delivers contents that coincide with ethologists' independently grounded ascriptions. In this way, the hybrid account offers a unified treatment of inner representations and animal signals, while respecting the explanatory practices of ethology.

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