

Firefly Femmes Fatales: A Case Study in the Semiotics of Deception

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Abstract Mimicry and deception are two important issues in studies about animal communication. The reliability of animal signs and the problem of the benefits of deceiving in sign exchanges are interesting topics in the evolution of communication. In this paper, we intend to contribute to an understanding of deception by studying the case of aggressive signal mimicry in fireflies, investigated by James Lloyd. Firefly femmes fatales are specialized in mimicking the mating signals of other species of fireflies with the purpose of attracting responding males to become their prey. These aggressive mimics are a major factor in the survival and reproduction of both prey and predator. It is a case of deception through active falsification of information that leads to efficient predation by femmes fatales fireflies and triggered evolutionary processes in their preys' communicative behaviors. There are even nested coevolutionary inter-

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actions between these fireflies, leading to a remarkable system of deceptive and counterdeceptive signaling behaviors. We develop here a semiotic model of firefly deception and also consider ideas advanced by Lloyd about the evolution of communication, acknowledging that deception can be part of the explanation of why communication evolves towards increasing complexity. Increasingly complex sign exchanges between fireflies evolve in an extremely slow pace. Even if deceptive maneuvers are played out time and time again between particular firefly individuals, the evolution of the next level of complexity—and thus the next utterance in the dialogue between species—is likely to take an immense amount of generations.

Keywords Communication · Deception · Semiotics · Firefly femmes fatales · Evolution

Introduction

Mimicry and deception are two important issues in studies about animal communication (Wickler 1965, 1968; Mitchell and Thompson 1986; Zabka and Tembrock 1986; Brower 1988; Mallet and Joron 1999; Komárek 2003; Kleisner and Markoš 2005; Maran 2007). The reliability of animal signs and the related problem of the benefits of deceiving in sign exchanges are rather interesting topics in the evolution of communication. In this paper, we intend to contribute to an understanding of deception by investigating the remarkable case of aggressive signal mimicry in fireflies, investigated by the entomologist James Lloyd. We will also consider some ideas advanced by Lloyd about the reasons for communication to evolve towards increasing complexity.

It seems indeed worthwhile to take fireflies as case studies about communication and its evolution. As Lewis and Cratsley (2008, p. 313) recently wrote, “Because of the complex interactions between chemical defenses, aposematic signals, and predation, fireflies provide an outstanding system for future studies to explore hypotheses about aposematism, Batesian mimicry, and aggressive mimicry”.

Our focus in this paper is deception in fireflies. In order to conceptualize deception in nonhuman animals, we should go beyond deliberate or intentional deception. Here, we take as a starting point Robert Mitchell’s (1986, p. 21) concept of deception:

- (i) An organism R registers (or believes) something Y from some organism E, where E can be described as benefiting when (or desiring that)
- (iia) R acts appropriately toward Y, because
- (iib) Y means X; and
- (iii) it is untrue that X is the case.

Notice, first, that this account of deception specifically considers a case in which ‘deception’ is characterized as a type of interaction between two organisms. In cases in which one describes situations in which inanimate objects produces ‘deception’ of an observer’s senses, no one to enact the deception is needed, and condition (i) can

be simplified to “an organism R registers something Y”, and the whole set of conditions describes a case where an organism is deceived by an ambiguous environment. Nevertheless, as we are analyzing here a case of interaction between different species of fireflies, we will focus on cases in which one organism acts as a ‘deceiver’.

It is also important to clarify the notion of ‘registering’, which Mitchell derives from Bennett (1976). Bennett meant by ‘registering’ that an organism had perceived and attended to stimuli relevant to its goals. Something which is registered can be said, then, to be ‘epistemically available’ to the animal, i.e., that something has been taken as relevant by the animal—in von Uexküll’s terms (1928), that something has been registered as a “perception sign” by the organism, facilitating a possible response in the shape of an “action sign”. As Bennett (1976, p. 47) writes, registration can be something that happens to an agent, rather than something it actively does. In lower animals without movable, orientable sense organs able to actively direct and focus attention, we may add, the distinction between activity and passivity is not as clear as among higher animals, and may, at least in some cases, disappear completely.

It is also clear that, if deception is to take place, Y has, in some sense, to mean something (X) to R. This just requires that there is a correlation between Y, R’s action, and X. To say that Y ‘means’ X is to say, in this case, that for R, Y is functionally associated with X. There is no need to engage with the difficult issue of whether we can ascribe conscious intentional states, such as beliefs, to some nonhuman animals or not. The intentionality required may be merely functional, that is, it may consist of the existence of a goal-oriented process. It is thus clear that part of the reason why deception works lies in the fact that R tends to act appropriately toward Y. In the case of a deception, the animal acts in this manner, but it is untrue—as clause (iii) in Mitchell’s definition states—that Y is objectively associated with X in that case.

Another important feature is that Mitchell’s account does not make it necessary to claim that E in some sense ‘intends’ or ‘desires’ to deceive R in order to explain the occurrence of deception. The difficulty of ascribing conscious intentional states to nonhuman animals is avoided by requiring only that E systematically benefits if R is deceived. Then, we do not need to claim that E intended to deceive R, but only that there is a correlation between E’s past events of benefiting from emitting Y to R and the fact that E in a specific circumstance emits Y. E does not seem, thus, to simply make a mistake when it emits Y; rather, E seems to be trying to benefit again from emitting Y to R—It seems to be trying to deceive R. To specify further what we mean by ‘benefit’, it is important to consider that, as Mitchell emphasizes, we as observers ascribe some benefits to an organism’s action, such as the benefits of enhanced survival and/or reproduction, of avoiding danger, etc. The notion of E’s benefits really refers, thus, to our well-founded ascription of benefits to E.

We believe that it is good advice to avoid intentional terms such as belief and desire when defining ‘deception’ in general terms, not in the particular case of humans, and also that one should be explicit about the role of signs in the mediation of deception. Based on Peirce’s theory of signs (see below), we take the usage of the term ‘sign’ here as not necessarily implying any kind of conscious intentionality.

Consequently, we will use in this paper the following modified version of Mitchell's definition:

- (i) An organism R registers a sign Y emitted by organism E, and E can be described as benefiting when
 - (iia) R behaves toward Y, as if
 - (iib) Y means that X is the case; but
 - (iic) it is untrue that X is the case.

In the next section, we will describe how male fireflies of several species pertaining to the genera *Photinus*, *Photuris*, *Pyraclonema*, and *Robopus* are predated by females of several species of *Photuris* fireflies, based on Lloyd's (1965, 1975, 1980, 1981, 1986) works. Subsequently, we will offer a semiotic analysis of firefly deception. And, finally, we will discuss the nature of firefly signs and Lloyd's proposal about the reasons for complexity increase in communication.

Firefly Femmes Fatales

Firefly femmes fatales are specialized in mimicking the mating signals of other species of fireflies with the purpose of attracting responding males, which become their preys. These aggressive mimics are a major factor in the survival and reproduction of both prey and predator. It is a case of deception through active falsification of information, less efficient than other variants of deception, such as concealment of information. But, despite the limitations of the mimicry at stake, it leads to efficient predation by femmes fatales fireflies and triggered evolutionary processes in their preys' communicative behaviors. Firefly femmes fatales are versatile and competent mimics, with fine-tuned deceptions. There are even nested coevolutionary interactions between these fireflies, leading to a remarkable system of deceptive and counterdeceptive signaling behaviors.

Typically, each species of firefly has its own signal code or signature, including a male flash pattern and a female flash response. The species' patterns vary in several parameters, including flash duration, flash number and timing in a pattern, as well as flash form. Although most patterns are simple, there are some species that show rather complex patterns. In a typical sexual communication sequence, a flying male exchanges flashes with a perched female in a simple pattern. There is intense competition among males for the females. Lloyd followed 199 individual males of a species of *Photinus* for a total of 10.9 miles and observed that they flashed all in all 7,988 patterns, but found only two conspecific females. These data suggest that males are much less successful in mating than one might expect. While a male would take, according to Lloyd's data, on average more than seven nights to find a mate, a female would require less than 6 min to attract a male, mate, and then turn to egg-laying. No doubt it seems much more exhausting to be a male than a female firefly! But things are even worse than that. Among Lloyd's observations, there were some unexpected findings: he noticed that the 199 males were answered by no less than 11 females of a different genus, *Photuris* fireflies, also known as femmes fatales. They were trying to attract the males to eat the latter by mimicking the mating signs of female *Photinus*. *Photinus* males play indeed a dangerous game of

sex and death. If we consider that only two males were answered by conspecifics during Lloyd's observations, it may be the case that a *Photinus* male is more than five times as likely to be answered by a femme fatale predator as by a female of their own species ready to mate.

This ability of predation has much to do with the fact that *Photuris* fireflies generally show the most complex flashing behavior of any fireflies studied so far. The females of this genus flash in many situations other than mating and courtship, including the usage of their light for illumination during take-off or landing, when walking on the ground ovipositing, at the moment they attack a flying, flashing firefly in the air, etc. These aerial attacks are used in conjunction with aggressive mimics, particularly when males hesitate to approach. Indeed, *Photuris* females use a number of tactical maneuvers in their aggressive signal mimicry. For instance, when a male is attracted and begins to approach, mimicking females perched in vegetation move down the stems to more concealed positions and then answer infrequently, with dim flashes. This behavior seems to be used to make it more difficult for a male to perceive the imposture. This also shows how the mimic of the *Photinus* pattern, although very good, is not perfect, since the *Photuris* female has to take some precaution to avoid that the male perceive it is not a mate that is waiting for him, but a luring predator. This also explains why their capture rate is not so high, only about 10–15% of the total number of attempts. Thus, aerial attacks are used to increase their rate of success.

Photuris females of many species mimic and prey on more than one species, and are thus capable of using varied repertoires of signs. Their versatility has been shown by experiments that indicated that individual females are capable of correctly answering the flash patterns of different prey species, and may even be able to adjust their signs during an attraction process. Thus, their mimicry is plastic enough to be improved through trial and error. If a partially attracted, but hesitating male begins to leave the site, a *Photuris* female can alter her time delay, flash duration, or flash intensity, attempting to lure him to serve as her next meal. As an example, females of *Photuris versicolor* are capable of mimicking the signs of four species, each with their own distinct flashing patterns, and can adjust their responses according to the male pattern present at a given occasion.

As we said above, the typical situation in fireflies is that each species has its own species-specific flash pattern. *Photuris* males, however, use multiple mate-seeking signs. While flying in courtship maneuvers, they switch patterns in the air. *P. lucicrescens*, for example, have been shown by Lloyd to exhibit two patterns: (i) a conspicuous, distinctive crescendo flash; and (ii) a bright, short flash, commonly emitted when flying among the treetops. Why do *Photuris* males have more than one flash pattern? Lloyd advanced a male mimicry hypothesis to explain this phenomenon. He noticed that there was a matching of the signals of *Photuris* males and two other firefly species of the genus *Pyraconema*, which he observed flying and luminescing together. Such a simultaneous occurrence in two species of a single luminescence pattern seemed to be rare, but Lloyd showed that in fact it is a fairly common and geographically widespread phenomenon. Consider, also, that the mimicry of signals of other species is likely to be a tactic for locating potential mates, since *Photuris* males fly during the evening to find mates and competition between them is quite intense. Indeed, there are data showing that the patterns

mimicked by the males are those of prey species that the females attract through deception. *Photuris* males are mimicking the prey, according to Lloyd's hypothesis, to find one of their own hunting females and mate with her.¹ Here, we see an interesting case in which a mimic is able to take advantage of another mimic, leading to a more complex situation than the usual picture in fireflies.

In one species of *Photuris*, an outstanding finding is that, instead of keeping their own signal and their mimicries, this species seems to have retained the mimic pattern only. In this case, a mimicry pattern seems to be the evolutionary origin of a species' 'own' pattern, while its former pattern simply disappeared. Lloyd (1986) reminds us that this finding lends support to Wickler's (1965) hypothesis that the signals of a species can be treated as having generally passed through an original mimetic stage.

Yet more astonishing is the fact that an evolutionary 'arms race' has been taking place between *Photuris* females and a firefly greatly influenced by their aggressive mimicry, *Photinus macdermotti*. The flash pattern of the latter is composed of two flashes emitted two seconds apart and is usually repeated each 4 to 6 seconds. *P. macdermotti* females answer with a single flash about one second after the second flash emitted by the male. When he receives an answer, the male flies closer and flashes again, but instead of landing near the responding lights, he usually lands a few to several centimeters away and then slowly walks towards the location of the response, now signaling at longer and irregular intervals. This can be interpreted as an evolutionary response to the predation pressure of *Photuris* fireflies that mimic the answer of *P. macdermotti* females.

As a result of their slow approach, often a small group of males gather nearby a responsive female, each attempting to become the first to reach her, while simultaneously attempting to avoid predaceous females. In this situation, a number of deceptive tactics are employed by the competing males. It is even observed that *Photinus* males answer other males with fake female flashes, emit flash patterns of other species, and employ a series of other signaling deceptive maneuvers to slow

¹ We should add, however, that this interpretation was controversial. Cf. the discussion between Copeland and Lloyd (1983). Copeland claimed, on the basis of laboratory findings, that Lloyd's interpretation of mimicry was not so secure, given that was based on a correlation study. He also argued that *Photuris* females completely change behavior from a virgin phase, where they signal for mating with conspecific males, to a post-mating phase, where their signal behavior changes to attract prey males from other species (see also Nelson et al. 1975). Then, how could mimicry by *Photuris* males be a reproductive strategy? Lloyd challenged these claims by considering, first, that the behavior of firefly communication, including aggressive mimicry, cannot be properly observed in fireflies confined in labs, as those studied by Copeland. By the way, we have here an interesting exchange about the relationship between lab and field studies of animal behavior. Secondly, he argued that Copeland had not been fair in the manner he addressed the quality and extent of his data about aggressive mimicry. Finally, he discussed Copeland's argument that other mechanisms than mimicry might be involved in the behaviors observed by him, calling attention to the fact that this was true, but Copeland did not put forward any hypothetical alternative mechanisms. Lloyd also considered different hypotheses about why male *Photuris* mimicry might be aiming at mating with females that were no longer virgins, having switched to predatory behaviour, such as female selection of male phenotype, paternal investment, and even forced insemination of the already-mated *Photuris* females. Despite the controversies, the existence of aggressive mimicry and its consequences to the evolution of communication in fireflies are widely accepted, as it can be seen, for instance, in a recent paper by Lewis and Cratsley (2008, p. 313), who offer an overview of a number of recent works that, in their terms, "... provided considerable evidence supporting the idea that *Photuris* predation represents an important force shaping the evolution of bioluminescent signals in North American fireflies".

down the rivals by misinforming them. One particular deceptive maneuver is quite remarkable, since it shows how complex and fine-tuned the communicative relationships between *Photinus* males and between them and *Photuris* females can be. Often, when one of the males (either already in the group around a female or still approaching) receives an answer from the female, other males inject an extra flash in his pattern so as to interrupt it; indeed, females usually do not answer to patterns with an injected flash. Furthermore, *P. macdermotti* males often land nearby the injected light, even though they did not see a female answer.

To make things even more complex, when *Photuris* females flash false signs to *P. macdermotti* males, they sometimes put 'extra' signs in the same position in the male's pattern, just as rival males do. Mimicry here goes both ways, since the injected flashes of *Photinus* males seem to be mimicking the injections made by *Photuris* females, and the injections of the latter, in turn, seem to be mimicking the injections of the males. The reason why rival males inject the extra flash to mimic the false injections of *Photuris* females is that they will then appear to be a predator to other approaching males, enhancing the former's chances of successful mating, as rivals may give up the disputed female. *Photuris* females, in turn, improve the chances of attracting their prey by adjusting their sequential signs so as to pretend to be both a female and a rival male. As Lloyd suggests, this seems to be an interesting case of a mimicry loop, in which a mimic is mimicking a mimic. Not surprisingly, the evolutionary question of how this mimicry loop began, with *Photuris* females or *Photinus* males, is a difficult one.

Aggressive signal mimicry in fireflies offers a compelling case study about how mimicry and deception can lead to the evolution of complexity in sign processes. The semiotic processes involved in such sophisticated deceptions obviously do not result from learning processes taking place in the individual's cognitive system, but from the fine-tuning of inherited capacities by natural selection among variants over thousands or millions of generations. Aggressive mimicry established an ecological circumstance in which natural selection favored changes in the mating behavior of *Photuris* spp. and *Photinus macdermotti* directed towards an increase of the complexity of the signs used to mediate courtship. The observations showing that *Photuris* are versatile and competent sign mimics, with well-tuned deceptions, indicate how their strategies to prey on other fireflies, *P. macdermotti* in particular, result from a long evolutionary arms race with their prey. Simpler *Photinus* signalers, in turn, have also been overcome in evolution by more complex signalers, due to the selective advantage of a more complex code, more difficult to copy with enough precision to deceive a male firefly looking for a mate.

Indeed, Lloyd claims that most of the complexity observed in firefly flash communication has resulted from selection pressures related to signal-tracking predators, which would more efficiently capture simpler signalers. He even advocates that complexity might be a universal countermeasure for, or consequence of, deception in all sorts of biological systems. Deception would be, therefore, a factor generally promoting complexity increase in the evolution of communication.² This highlights the importance of analyzing deception from a semiotic point of view,

² It is striking to note the formal similarities with the arms race between code makers and code crackers in military intelligence in the history of warfare, cf. Singh (1999).

in an attempt to build a proper understanding of the evolution of sign systems in the biological world. The firefly femmes fatales offer a good case study to pursue this investigation.

A Semiotic Analysis of Firefly Deception

Aggressive and related mimicries in fireflies can be modeled on the grounds of the modified version of Mitchell's account of deception discussed above:

- (i) An organism R registers a sign Y emitted by organism E, and E can be described as benefiting when
 - (iia) R behaves toward Y, as if
 - (iib) Y means that X is the case; but
 - (iic) it is untrue that X is the case.

If we consider, for instance, the attraction of *Photinus macdermotti* males by *Photuris* females, the latter will be modeled as emitters of a sign Y, which the former registers and then behaves toward Y as if it means or indicates an opportunity for mating, X. To understand the reason why *Photinus* males behave like this in the face of Y, there is no need of introducing any conscious intentional state in the picture. The reason simply lies in the fact that during evolution *Photinus* experienced several instances of correlation between the sign type Y and the act of mating, and such a correlation had an effect on the chances of successful reproduction of individual organisms in such a manner that those answering to Y were more likely to obtain the advantageous result X. Nevertheless, when a *Photuris* rather than a *Photinus* female is emitting Y, it is not really the case that Y means X. It rather means another result, Z, namely that the male will be probably eaten.

It is not that *Photuris* femmes fatales as individuals *intend* to deceive *Photinus* males, but simply that there is a correlation between the event at stake and past events in which *Photuris* females benefited from emitting that sign Y to *Photinus* males, and natural selection favored individuals showing that communicative behavior of emitting Y in the presence of flying *Photinus* males. *Photuris* females are just trying to benefit again from emitting Y to *Photinus* males.

Which kinds of signs are involved in these firefly interactions? From a biosemiotic point of view, this is an interesting research question, and a possible avenue to address it is provided by Peirce's theory of signs, as we explore in this paper.

Signs are, for Peirce, something that determines something else (its interpretant) to refer to an object to which it itself refers (its object) in the same way. The interpretant will become in turn a sign, and so on ad infinitum (CP 2.303), or, in some instances, a chain of sign processes can lead to a final action, which amounts to a termination of a semiotic process.³ The action of a sign, which Peirce calls

³ We will follow here the scholarly practice of citing from the *Collected Papers of Charles Sanders Peirce* by volume number and paragraph number, preceded by 'CP'; the *Essential Peirce*, by volume number and page number, preceded by 'EP'. References to the *Annotated Catalogue of the Papers of Charles S. Peirce* will be indicated by 'MS', followed by the manuscript number and pages. References to *Writings of Charles S. Peirce: a Chronological Edition* will be indicated by 'W', followed by page number.

semiosis, should be treated, in his framework, as a relation between three irreducibly connected terms (sign-object-interpretant, S-O-I) (Fig. 1).

In his later works, Peirce also defined a sign as a medium for the communication of a form or habit embodied in the object to the interpretant, so as to determine (generally speaking) the interpretant as a sign or (in semiotic systems) the interpreter's behavior (Queiroz et al. 2005; El-Hani et al. 2006):

[...] a Sign may be defined as a Medium for the communication of a Form. [...]. As a medium, the Sign is essentially in a triadic relation, to its Object which determines it, and to its Interpretant which it determines. [...]. That which is communicated from the Object through the Sign to the Interpretant is a Form; that is to say, it is nothing like an existent, but is a power, is the fact that something would happen under certain conditions (MS 793:1–3. See EP 2.544, n.22, for a slightly different version).

In short, a sign is both “a Medium for the communication of a Form” and “a triadic relation, to its Object which determines it, and to its Interpretant which it determines”. If we consider both definitions, we can say, then, that semiosis is a triadic process of communication of a form from the object to the interpretant through sign mediation (Fig. 1).⁴

But how should we understand the term “form” in this context? Peirce stresses that it is nothing like a “thing” (De Tienne 2003), but something that is embodied in the object as a habit, a “rule of action” (CP 5.397), a “disposition” (CP 2.170), or a “permanence of some relation” (CP 1.415). He also understands form as having the “being of predicate” (EP 2.544). It is also pragmatically formulated as a “conditional proposition” stating that certain things would happen under specific circumstances (EP 2.388).

In our view, it is particularly important to emphasize that the form communicated from the object to the interpretant through the sign has the nature of a regularity, a habit that allows a given semiotic system to interpret that form as being indicative of a class of entities, processes, phenomena, and, thus, to answer to it in a regular way. The communication of a form from the object to the interpretant constrains the behavior of an interpreter in the sense that it brings about a constrained set of effects of the object on the interpreter through the mediation of the sign. In these terms, the meaning of a sign can be conceived as the effect of the sign, as a medium for the communication of forms, on a given interpreter by means of the triadic relation S-O-I. A meaning process can be thus defined as the action of a sign, i.e., as semiosis.

Biology lacks up to now a unified theory of biological information (see, e.g., Jablonka 2002). As we argued in previous works (Queiroz et al. 2005; El-Hani et al. 2006, 2009; Stjernfelt 2007; Queiroz et al. 2009), Peirce's theory of signs brings a contribution to the building of such a theory, since it is quite helpful in addressing semantic and pragmatic aspects of information, which have not been properly treated by theories of information up to present day. Debrock (1996) comments that Peirce defined “information” at least ordinarily (CP 2.418), metaphysically (CP 2.418), as a connection between form and matter, and logically

⁴ It should be noted that “sign” here is ambiguous. It may refer to the sign vehicle specifically—in contrast to the object and the interpretant—or it may refer to the whole complex of sign vehicle, object, and interpretant. In most cases, the context makes it clear which use is intended.

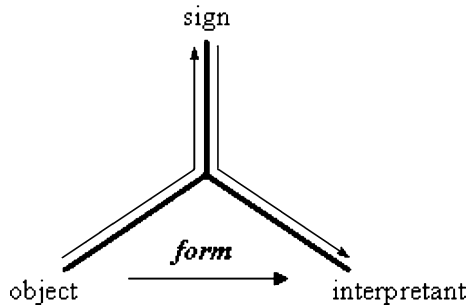


Fig. 1 Semiosis as the communication of a form from the object to the interpretant through the mediation of a sign. This triadic relationship communicates a form from the object to the interpretant through the sign (symbolized by the horizontal arrow). The other two arrows indicate that the form is communicated from the object to the interpretant through a determination of the sign by the object, and a determination of the interpretant by the sign

(W 1.276), as the product of the extension and intension of a concept. The definitions of sign mentioned above straightforwardly lead to a definition of information as the communication of a *form* from O to I through S (Queiroz et al. 2005; El-Hani et al. 2006; Queiroz et al. 2009).

According to our interpretation of Peirce's ideas, information has the nature of a process: it is a process of communicating a form to the interpretant that operates as a constraining influence on possible patterns of interpretative behavior. When applying this general semiotic approach to biological systems, information will most often be an interpreter-dependent objective process. It cannot be dissociated from the notion of a situated agent. It is interpreter-dependent in the sense that information triadically connects representation (sign), object, and an effect (interpretant) on the interpreter (which may be an organism or a part of an organism). A form or habit, as a regularity embodied in the object, acts through the mediation of the sign as a constraint on the interpreter's behavior, and this is why we refer to an objective interpreter-dependent process. In sum, information in a semiotic system depends on both the interpreter and the object (in which the form communicated in information is embodied as a constraining factor of the interpretative process).

To model the interaction between *Photinus* and *Photuris* fireflies, let us consider first the series of flashes produced by a *Photinus* male as the sign. It is a sign directed at the female of his own species, which will interpret that sign as indicating a male as its object. The effect of that sign on the female, the interpretant, will be the triggering of her predisposition to mate with that particular male (Fig. 2a). The female then answers the male with her own sign emission, which indicates to the male the position and existence of the female as its object, and has the effect of making him approach in order to mate (Fig. 2b). Both signs are local signs, indicating the existence of something at specific locations in space and time: "Here and now is a *Photinus* male (responsive female)". Thus these signs possess a primitive propositional structure, composed of an index indicating the existence of the proposition subject (the "here and now is"), on the one hand, and a rhematic symbolic predicate describing the object, on the other (the "*Photinus* male (responsive female)"). We shall return to this structure below.

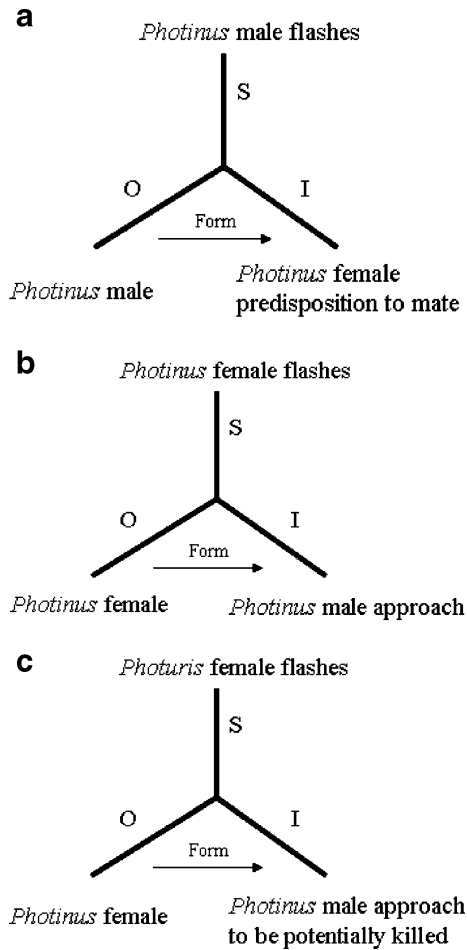


Fig. 2 **a** Signs emitted by a *Photinus* male indicate the male itself as an object to a female, having the effect (interpretant) of predisposing her to mate with that particular male. In this case, the interpreter is the *Photinus* female. The *Photinus* female is *informed* about the availability of a potential male to mate. **b** In response, signs emitted by a *Photinus* female indicate the female herself as an object, having on the male the effect (interpretant) of making him approach the female. The *Photinus* male is now *informed* about the availability of a potential mate at a specific position. In the second sign, the location is far more important than in the former, because of the (relative) motionless behaviour of the female. The flying male’s sign says: “Here is a male on the lookout for mating”, while the female’s answer says “There is a female located right here, responding to your call.”. This is the usual sequence of events, potentially leading to successful reproduction. **c** A *Photuris* femme fatale can answer the *Photinus* male, which will interpret the sign emitted by the *Photuris* female as indicating a *Photinus* female. The sign is not necessarily exactly identical to that of a *Photinus* female, but sufficiently similar to deceive the male in a sufficient ratio of cases for the female to be successful in feeding. If deception is successful, the interpretant will be that the male approach the femme fatale and may be killed, instead of successfully reproducing. Here, the *Photinus* male is *misinformed* about the availability of a potential mate, since what he finds is rather a potential predator

This is the sequence of communicative events that will take place when—so as to say—everything is just fine to the *Photinus* male. But consider then a *Photuris* female in the place of the *Photinus* female, sending an answer to a flying *Photinus* male. In this case, the sign seems to indicate a *Photinus* female as its object at the location of the flash, but in fact indicates a predacious femme fatale. The *Photinus* male's behavior is constrained by the interpretant so as to approach the *Photuris* female, and, if the deception reaches its goal, it will be the case that the male will perceive just too late, if at all, that he was deceived, that is, that the object of the sign at the location indicated is not what it seemed to be (Fig. 2c). It is clear that deception takes place through a disparity between sign and object (or in the sign-object relationship) that benefits the emitter of the sign, in this case, a *Photuris* female, by triggering in the receiver of the sign, a *Photinus* male, the interpretant that would be correct in the usual case, when Y indicates or means the presence of a female prone to mating. Deception relies upon the fact that this is the usual interpretant following the emitted sign. That is, a habitual relationship between sign and object must exist in order for an organism to act in such a way that it is deceived when a benefiting organism sends the same sign for indicating, however, a different object.

It is clear, also, that 'information' is communicated both in the typical case, in which a *Photinus* female is emitting the sign, and in the femme fatale case, in which a *Photuris* female is the emitter, but there are, obviously, important differences between these cases. In the former, information is the process of communicating the fact that there is, at the flash location, a female available to mating, and this process operates as a constraining influence on the interpretative behavior of *Photinus* males, so as to produce an effect (interpretant) on the males (as the interpreters) through the sign mediation. The latter is rather a misinterpretation event. By 'misinterpretation', we mean the interpretation of a sign that does not lead to a successful coping with a system's properties. *Photinus* males are deceived because they misinterpret the sign emitted by *Photuris* as a sign emitted by a female of their own species.

We may be tempted to say that this is a misinterpretation intended by the *Photuris* females, but in order to keep our explanation parsimonious, it is better just to say that the behavior of *Photuris* females that lead to that misinterpretation was selected for in past events, due to the fact that these females benefited from the misinterpretation. So the intention at stake lies in the selected action leading to benefits, not in any individual nor conscious intentional act. Therefore, natural selection so as to say "programmed" them to trigger that misinterpretation event. Accordingly, we can say that in this case "misinformation" takes place, that is, a process of communicating the fact that a female is present and available to mate so as to constrain the males' behavior in such a manner that they fall prey to *Photuris* females. They are misinformed: they were expecting sex, when all they got was death. Misinformation—and, consequently, deception—takes place because the sign communicates a form that does not really correspond to a habit embodied in the usual object (*Photinus* females), but, rather, in a different object (*Photuris* females). This is the heart of the deception.

A proper understanding of sign processes demands a typology describing the kinds of signs that can be involved in particular semiotic processes. Peirce

proposed several typologies, with different degrees of refinement and several relationships to one another. Here, we will just explore the fundamental differences between iconic, indexical, and symbolic processes within the framework of his theory of “dicisigns”, propositions. Our intention is to classify the signs mediating mating, courtship, competition, and predation in fireflies in accordance with the Peircean framework, which offers a proper, theoretically-informed and systematic avenue to pursue a more refined understanding of the diversity of sign processes and systems.

In his “most fundamental division of signs” (CP 2.275), Peirce characterized icons, indices, and symbols as matching, respectively, relations of similarity, contiguity, and law between S and O (the sign-object relation) in the triad S-O-I. It is important to underline that these relations are not mutually exclusive so that many actual signs and sign processes make use of more than one of these relations.

Icons

Icons are signs that stand for their objects through similarity or resemblance (CP 2.276), irrespective of any spatio-temporal physical correlation that S may have with an existent O (CP 2.299). If a determinative relation of the sign (S) by the object (O) is a relation of analogy, that is, if S is a sign of O in virtue of a certain quality that S and O share, then S is an icon of O. If S is an icon, then S communicates to I a quality of O:

An Icon is a sign which refers to the Object that it denotes merely by virtue of characters of its own, and which it possesses, just the same, whether any such Object actually exists or not (CP 2.247).

Among the examples of icons mentioned by Peirce, we find images, diagrams, metaphors, pictures, photographs, paintings, maps, ideographs, hieroglyphics—but icons are also taken to be responsible for the predicative aspects of symbols; in language, adjectives, common nouns, verbs will hence be symbolic icons. In terms of cognitive processes, icons are associated with all tasks dealing with the qualities of objects and, thus, play a central role in sensory tasks. They are present in the sensorial recognition of external stimuli of any modality, and in the cognitive relation of analogy. They constitute the predicative part of any dicisign, enabling it to describe (aspects of) the object it indicates. Icons may be similar to their object in widely differing respects and in highly variable granularity and stylization. According to Sebeok (1989, p.121), “iconic signs are found throughout the phylogenetic series, in all modalities as circumscribed by the sense organs by which members of a given species are able to inform themselves about their environment. Signal forgery, viz., the phenomenon of mimicry, in fact, all deceptive maneuvering by plants and animals, as well as humans, often crucially depends on iconicity”. In iconic semiosis, the form communicated from the object to the interpretant through the sign is a *general similarity* between the sign and the object. An iconic sign communicates a habit embodied in an object to the interpretant, so as to constrain the interpreter’s behavior, as a result of a certain quality that the sign and the object share (Fig. 3).

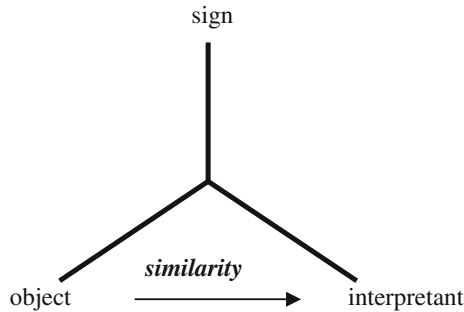


Fig. 3 Iconic semiosis as the communication of a general similarity or quality from the object to the interpretant through the mediation of a sign

Indices

In contrast, if *S* is a sign of *O* by reason of “a direct physical connection” between them (CP 1.372), then *S* is said to be an *index* of *O*. In that case, *S* is *really* determined by *O*, and both must exist as actual events: “An Index is a sign which refers to the Object that it denotes by virtue of being really affected by that Object” (CP 2.248). The notion of spatio-temporal *co-variation* is the most characteristic property of indexical processes. Indices may be reagents or designators. In the former case, they are causal effects of the object they signify. In the latter case, they are teleological ‘pointers’ directing the attention towards the object they indicate. The examples range from physical symptoms of diseases, photographs, weathercocks, thermometers to a pointing finger or a pronoun demonstrative or relative, which “forces the attention to the particular object intended without describing it” (CP 1.369)—the latter being examples of symbolic indices.

In indexical semiosis, the form communicated from the object to the interpretant through the sign is a *general correlation in space and time* between the sign and the object. An indexical sign communicates a habit embodied in an object to the interpretant as a result of a direct actual connection between sign and object (Fig. 4).

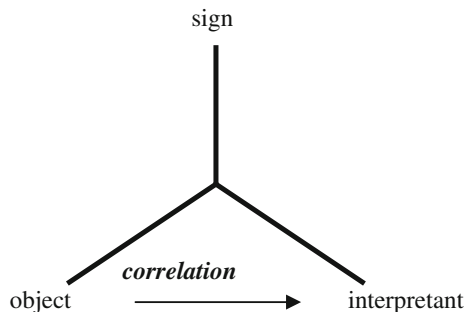


Fig. 4 Indexical semiosis as the communication of a physical correlation or connection between the sign and the object to the interpretant

It is important to notice that icons, indices, and symbols are sign *aspects*, not mutually *exclusive* classes of empirical, observable signs. Thus, photographs are both icons (resembling their objects to different degrees) and indices (being physically connected to their object by the photographic process). This does not mean all signs possess all aspects—but that the possession of one aspect—e.g. iconicity—does not preclude the same sign from being indexical or symbolic. In the context of deception, we must turn to Peirce’s theory of propositions—because propositions are the signs which may be true or false—, deception obviously being a case of a false proposition. The normal concept of proposition refers to linguistically represented signs claiming something about an object (e.g., “S is P”), but it is important to understand that Peirce’s theory of the proposition generalizes this notion to encompass also non-linguistic cases. The proposition forms part of the triad rhema-proposition-argument (or sumisign-dicisign-suadisign). The rheme is the skeleton of a proposition—but with one or more of its subject slots left blank. Thus “_ is blue” is a rheme just like “_ gives _ to _”. When one or more slots in a rheme are filled in by an index (a pointing finger, a demonstrative pronoun, a proper name, etc.), it becomes a proposition. When a proposition is inferred from one or more other propositions, it is an argument:

“An *argument* is a representamen which separately shows what interpretant it is intended to determine. A *proposition* is a representamen which is not an argument, but which separately indicates what object it is intended to represent. A *rhema* is a simple representation without such separate parts.” (CP 5.139)

The general notion of dicisign involves both symbolically and linguistically represented propositions—but it also comprises propositional structures which are neither symbolic nor linguistic. A recurrent example in Peirce is the portrait painting with a title—here only the indexical part of the dicisign is symbolic while the iconic part of it is not. The crucial structure uniting all dicisigns is that they refer twice to the same object, by means of indices and icons, respectively:

“The proposition conveys definite information like the genuine index, by having two parts of which the function of the one is to indicate the object meant, while that of the other is to represent the representamen by exciting an icon of its quality.” (CP 5.76)

In the proposition, the object dealt with must be indicated by means of an index (in the linguistic case: a proper name, a class name, a pronoun, etc.), thus constituting the subject of the proposition, while the predicate of the proposition is presented by means of an icon (in the linguistic case: an adjective or verb describing aspects of the object indicated by the index). Thus, a proposition forms a special type of syntactic combination between icon and index. The dicisign or proposition does not need, however, to be linguistically represented. A caricature accompanied by a pointing gesture towards a person is a proposition: the pointing functions as the index indicating the subject; the caricature drawing as the icon predicate part of the dicisign. This double reference of the dicisign is the reason why it may claim something (iconic) about something (indexical)—and this is why a proposition may be true or false,

depending on whether the iconic quality claimed actually exists in the object referred to. And this is why deceptive signs must necessarily be *dicisigns*.⁵

Symbols

In a symbolic relation, the interpretant stands for ‘the object through the sign’ by a determinative relation of law, rule or convention (CP 2.276), or, as Peirce most often calls it, a ‘habit’. According to Peirce (CP 2.307), a symbol is “a Sign (q.v.) which is constituted a sign merely or mainly by the fact that it is used and understood as such, whether the habit is natural or conventional, and without regard to the motives which originally governed its selection.”

We have claimed elsewhere that the alarm-call system used by African vervet monkeys (*Cercopithecus aethiops*), a well-known case of vocal communication in non-human primates, logically satisfies the Peircean definition of symbol (Queiroz 2003, 2004; Ribeiro et al. 2007). These primates possess a sophisticated repertoire of vocal signs used for intra-specific alarm purposes regarding imminent predation on the group (Seyfarth et al. 1980). Field studies have revealed three main kinds of alarm-calls, used to warn about the presence of (a) terrestrial stalking predators such as leopards, (b) aerial raptors such as eagles, and (c) ground predators such as snakes. Adult vervets produce these calls only in reference to the presence of specific predators. Such calls motivate whole-group escape reactions that are specific to predator type. When a ‘terrestrial predator’ call is uttered, vervets escape to the top of nearby trees; ‘aerial predator’ calls cause vervets to hide under trees; and ‘ground predator’ calls elicit rearing on the hind paws and careful scrutiny of the surrounding terrain. These are the interpretants of the calls, once the latter are explained as signs in a Peircean framework.

Field experiments in which predator-specific alarm-calls were played from loudspeakers to groups of wild vervet monkeys showed that adult individuals first responded to playbacks of alarm-calls by looking around in search of a referent (predator). Remarkably, even though this referent was always absent, adult animals consistently fled away to nearby refuges according to the specific type of alarm-call played. According to Peirce’s classification of signs, if the alarm-call operates in a specific way even in the absence of the external referent, it must be interpreted as involving a symbol of a predator class—the relation between the alarm call and the response forms the “natural habit” Peirce talked about. The alarm cry as a whole functions as a proposition: “There is a (specified) predator around.” Here, the indexical part of the *dicisign* refers to the location indicated by the location of the monkey uttering the call—while the iconic part of the proposition specifies and further describes the kind of predator. The iconic part, furthermore, is given by a symbolic icon (the call has no similarity to the predator). The transition from a sensory scan behavior after the alarm auditory perception to an escape reaction motivated solely by the alarm-call corresponds to the transition from indexical

⁵ Non-symbolic *dicisigns* may be—according to Peirce’s 10-fold sign classification—*Dicent Sinsigns* (e.g., the wind direction indicated by a weathercock, the object portrayed by a photograph) or *Dicent Indexical Legisigns* (e.g., a street cry whose tone and theme identifies the individual uttering it). (CP 2.254–265).

semiosis (interpretation by spatio-temporal coincidence) to symbolic semiosis (interpretation mediated by law or convention). The object of the sign, in the latter case, is not an object-token but rather a class of objects, i.e., an object-type, and therefore does not need to exist as a singular event, but the index part of the call individualizes this general predicate to indicate the presence of a particular object-token of the type. To say that an alarm-call is a symbol of a type of predator is equivalent to say that this call evokes a brain representation (of any modality) that stands for the class of predators represented in a law-like and specific way. The law at issue can be given by the inborn character of a sign, if the sign is not learnt by the animals, as we see in the case of fireflies, or, as we see in the case of vervet monkeys, the law can be a convention to be learned ontogenetically.

In symbolic semiosis, the form communicated from the object to the interpretant through the sign is a *lawful relationship* between sign and object. A symbolic sign communicates a habit embodied in an object to the interpretant as a result of a lawful or conventional relationship between sign and object (Fig. 5).

The Nature of Firefly Signs

The flashes emitted by a firefly act as composite signs, propositions, indicating both the presence and location of the emitting firefly, on the one hand, and describing its species and gender, on the other. The index aspect of the proposition concerns the fact that the flashes indicate the precise spacetime presence of these insects, because they are physically connected with these flashes: they are produced by the fireflies. The descriptive aspect of the proposition is provided by the specific signaling code used. In a basic sense, this code is iconic in so far as it characterizes the species to which the emitter belongs. It only constitutes a very specific and ‘small’ part of the different iconic qualities of the emitter, but (in the dark) a very pregnant one, and this is what facilitates its being copied by other species (just like the black-and-yellow pattern of certain wasps which may be copied by non-dangerous species to signal danger). The specific signaling code used by a firefly is a rhematic symbol in so far as it characterizes the species to which the emitter belongs. That is, it is an icon governed by genetic regularity so as to form a general sign describing the whole firefly species in question. The very ‘arms race’ discussed here is what has made

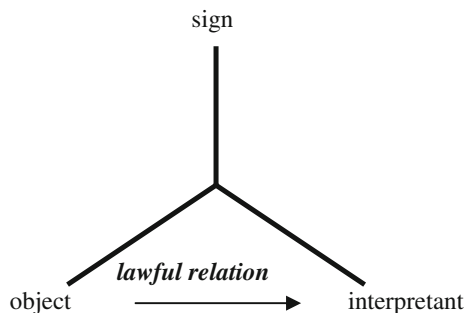


Fig. 5 Symbolic semiosis as the communication of a lawful or conventional relationship between the sign and the object to the interpretant

possible the ‘loosening’ of this rhematic symbol from one particular species to the use by other species, and, in this process, the icon becomes conventionalized so as to become a symbol of the species in question also readable for members of other species (just like the black-and-yellow wasp-like striping becomes a general symbol of poison and danger in the insect world).

Even though *Photuris* femmes fatales and their preys, *Photinus*, *Photuris*, *Pyraconema*, and *Robopus*, are involved in a mimicry arms race, their mimetic signs cannot be seen as simple icons. Here, we find a case of signal forgery that does not employ iconic signs only, *i.e.*, that is not in accordance with Sebeok’s emphasis on the role of icons in deceptive maneuvering. It seems to be the case, however, that, even though fireflies’ mimetic signs are not only icons, they crucially depend on iconicity, and, thus, a modified version of Sebeok’s argument can be correct.

If we describe the signs involved in firefly interactions as involving both indices and symbolic icons, they will offer us a telling and beautiful example of how indices are involved in lying. It is not, however, the indexical part of the signs that lies: the signs correctly indicate an existent at the specified point in space and time. It is rather the symbolic-iconic code indicating the character of that existent that does the lying.

If we examine the rather simple case of firefly communication mediating mating, and then the complex interactions resulting from deception, we are likely to agree with Lloyd that deception can act as a triggering factor in the evolution of communication complexity, as the several complex features of fireflies communication-mediated interactions show (see Fig. 6). Lies are only possible at the level of—ever so primitive—propositions, claiming that something is the case when it is not. Simple propositions can lie and, by lying, they can trigger increasingly more complex sign processes.

Lloyd’s arms race between the different firefly species is a good candidate case for a process of increasing sign complexity during evolution—one symbolic habit being taken as the basis for the formation of a more complicated habit at a higher level, involving the former as a possible—fallacious—interpretation of it. The firefly case thus points to Peircean symbols being present as soon as biological habits are formed—and hence it makes little sense to see the distinction icon-index-symbol as forming a biological scale of complexity.⁶ This complexity scale should be mapped by other means, *e.g.*, the number of nested levels of communication, the complexity of the sign vehicle, the complexity of the perceptive and cognitive processes necessary to interpret these signs, etc.

When considering the evolution of communication complexity in fireflies, it is also important to realize the extremely slow pace of the evolution of these more and more complex sign exchanges. Even if the deceptive maneuvers charted here are played out time and time again between particular firefly individuals, the evolution of the next level of complexity—and thus the next utterance in the dialogue between species—takes an immense amount of generations. While the single game is

⁶ Here, we disagree with Terrence Deacon’s (1997) attempt at characterizing animal semiosis as iconic and indexical only, while claiming that it is a human privilege to process symbols. The Peircean symbol notion refers to simpler semioses than human semiotics, the specificity of which must be characterized by other means.

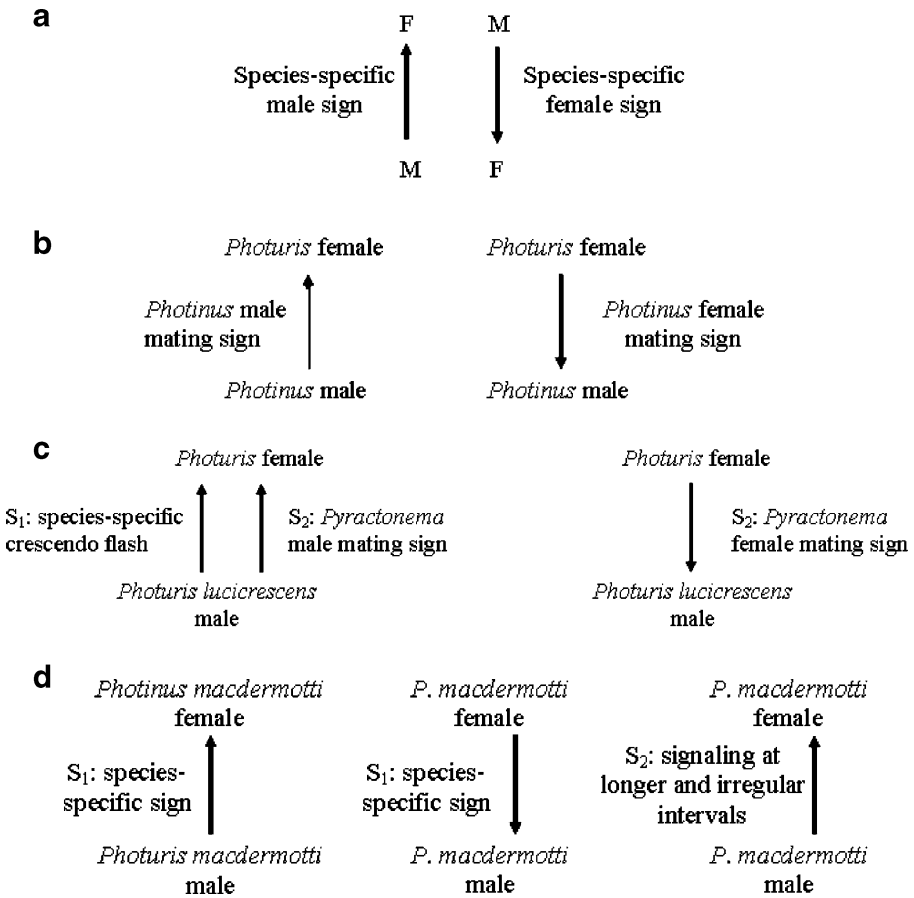


Fig. 6 **a** In its basics, firefly communication system is simple, involving a flying, flashing male (M) in search of a perched female (F), with exchanges of species-specific signs between them. **b** Aggressive mimicry by *Photuris* females, which answer to *Photinus* males, trying to lure them by mimicking the mating sign of female *Photinus*, in order to eat them. **c** Male mimicry in *Photuris lucicrescens*. Males exhibit both their species-specific patterns and the patterns of two *Pyraconema* species, since by mimicking the preys of *Photuris* females, they increase the likelihood of finding a female and successfully mating with her. **d** The cautious approach of *Photinus macdermotti*. After receiving an answer to its species-specific sign from a female, a *Photinus macdermotti* male approaches her cautiously, signaling at longer and irregular intervals. Thus, the male increases its chances of escaping predation by *Photuris* females. **e** Deceptive maneuvers by *Photinus macdermotti* males. In their cautious approach to the female, *P. macdermotti* males form a small group around the female and use a number of deceptive maneuvers in their competition for mating, such as emitting fake female flashes or other species signs. These maneuvers aim at misinforming other males, slowing down their approach. In the box, it is shown a deceptive maneuver in which a male injects an extra flash in the sign of a male which obtained an answer from the female, interrupting sign exchange between them. S₂, signaling at longer and irregular intervals that characterize *P. macdermotti* males' cautious approach; A, female answer to a male; I, injection of an extra flash by a *P. macdermotti* male; S₃, pattern with an injected flash, to which the female usually does not respond. F. A mimic mimicking a mimic. *Photuris* females sometimes put 'extra' signs in *Photinus* male pattern, in the same position that rival males do. Thus, the injected flashes of *Photinus* males mimic the injections of *Photuris* females, while the latter mimics males' injections

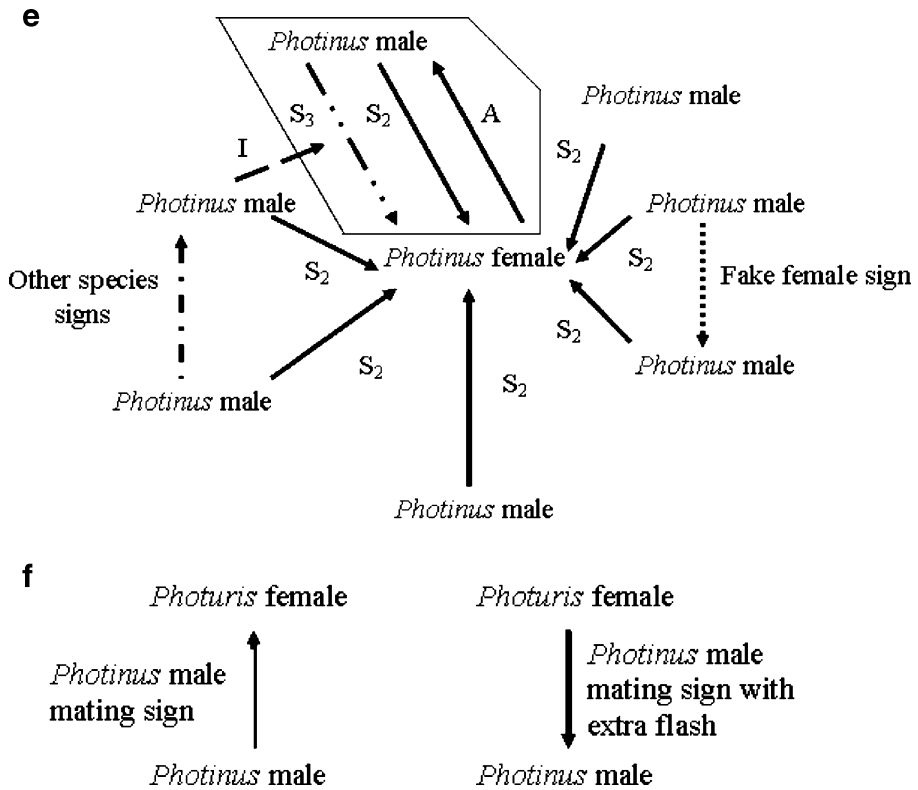


Fig. 6 (continued)

constantly acted out between particular insects out there, the ‘intelligent’ step taking us to the next level of deception in this fly-over-fly game is performed by the whole firefly populations subjected to natural selection. Whether any plastic interpretation behavior may be undertaken by the single firefly specimen is a further important issue that we have not investigated here.

Perspectives

To sum up, we consider that the analysis of firefly communication gives rise to the following conclusions:

- 1) It shows the necessity of considering even simple sign uses in biology as dicisigns, proto-propositions, displaying the duplicity of referring indexically and signifying iconically. These signs can be used to deceive because they propositionally claim that something is the case. At the same time, this analysis leads to doubt about the widespread assumption that the theoretical distinction between icon, index, and symbol may be mapped directly onto biological evolution so as to form three distinct phases. Rather, all three aspects of object reference are present in different combinations already in relatively simple

biological sign uses. Thus, firefly signal patterns seem to point to a continuous scale between simple icons at one end and symbolical stylizations of icons at the other end. Consider this continuum of cases: is the flash pattern an icon of a firefly? Is the stripe pattern an icon of a zebra? Are the two half circles of the breasts an icon of a woman? Is the outline of the body shape an icon of a man? In all these cases, the patterns mentioned have iconic qualities which permit conspecifics to recognize each other. But they do not display the same amount of stylization nor the same degree of arbitrariness in relation to other aspects of the animals' appearance. The flash pattern is evidently the most symbolic of these cases, because it is extremely stylized, can be repeated identically with a stable meaning, is used only for signifying mating behaviour and only at a specific time (night), and could, in theory, be substituted by another pattern. Moreover, it is the only sign facilitating the meeting between the firefly males and females in the dark. By contrast, each of the other three signs mentioned above are only one among many other possible iconic signs among conspecifics (smell, sound, other visual icons, etc.). Thus, the firefly flash pattern has acquired a specific signification—meaning the presence of a mate-seeking specimen of this particular firefly species. Nevertheless, as we saw above, it can be used in such a manner that fireflies are deceived by apt mimics of the species-specific flashes. They are deceived by different manners of using these proto-propositions that both refer indexically and signify iconically.

- 2) Our analysis also shows the need of considering two timescales: one of individual, highly routinized sign exchanges involving particular firefly specimens with relatively small interpretation plasticity, and one of the “arms race” between species leading to the evolution of nested deception strategies. This gives rise to the idea that such deceptive strategies in general—between predator and prey, between species competing for related ecological niches, between individuals or groups within the same species—constitute a major motor in the semiotic evolution of complex signs, to some extent analogous to the code maker-code breaker arms race in human military intelligence.

The study of firefly signal patterns presents, thus, wide perspectives for biosemiotics and calls for further comparative study, both empirical and theoretical, of the role of biological deception at different levels of evolution.

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