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Knowledge, Information, Biases and Signal Assemblages

OREN HASSON

P.O. Box 11598, Ramat-Gan 52015, Israel

E-mail: ohasson@hotmail.com

Abstract

*Information has been usually treated by Information Theory that provides tools to measure the capacity of signals to store data. However, it often makes more biological and empirical sense to measure information stored in a signal by the changes it induces on the recipient's knowledge. Knowledge is defined here as the individual's estimate of the mean values and variances of the variables that affect its decision about its future actions, relatively to their true values when it acts. Given this definition, knowledge, hence also information, are best estimated by using tools that are derived from Signal Detection Theory, rather than those provided by Information Theory, because the former measures the precision of decision making. In order to improve their knowledge, organisms have developed tools that improve their perception of the relevant parameter values, and corresponding biases that improve performance. Because knowledge is required on many different variables, it only makes sense that so are biases for certain estimated values of these variables. Each bias can lead to the evolution of at least one signal. It can lead to an exaggeration of a trait, which becomes either Fisherian or a handicap, and/or to signals that function as amplifiers and improve its perception. Hence, if organisms evolve multiple biases in response to the assessment of different variables, we should expect that these biases will lead to assemblages of multiple co-existing signals. I present here an analysis of an observation on pursuit-deterrent signals of the spur-winged plover, *Hoplopterus spinosus*. I use it to explore some of the possible parameters, detectable in prey, which might be important to predators. Predators that evaluate these parameters may evolve*

biases, to which prey are likely to respond by evolving assemblages of signals. Indeed, we often find that a prey sends to its predator several types of signals that operate in concert, and include behavioral displays (such as chronologically oriented head-bobs, described here), color patterns that improve spatial orientation, alarm calls, or even duetting.

The Trollveggen fallacy

Not too far from Kongsvoll, there is a cliff called Trollveggen. It is the tallest vertical wall in Europe. It is over one kilometer high, with a hangover of about 50 m (see: <http://www.stud.ntnu.no/~olegram/Romsdalen.html>, for interesting photographs). If you think of jumping over the rim of Trollveggen, your intuition will tell you that you are bound to fall down and get killed. You can, if you like, be more specific and build a detailed verbal description of everything that might happen to you along the long way down. You can describe how the wind would blow through your hair, the feel of your shirt flapping in the wind on your skin and stroking it, while its sound is dimmed by the sound of the wind in your ears. You can go on and on describing all the possible little details of your fall. Some of these details, especially the qualitative ones, might be accurate. Some other details, especially the quantitative ones, might be false. If you remember a few elementary equations in physics, you can probably build a simple mathematical model that will accurately predict the moment you hit the ground, and the speed of your fall at that moment. If you are very good in mathematical modeling, you will be able to also construct the precise recursive equations that describe, for example, the movements of your shirt in the wind and your exact position at each moment. This model will also inform you how sensitive are your predictions to the exact angle and momentum of each of your limbs, as you start falling down. One thing is certain, however. In order to build a full mathematical model of your fall, you need a detailed verbal description. The verbal model will list all the possible options for you, and will guide you in constructing the model's equations. When you are done, you will be able to know exactly how it would be falling down from Trollveggen. The conclusion is an empirical one: you don't want to do it.

Despite the (seemingly) undoubtable consequences of such a fall, a number of people, each year, used to leap over the rim of Trollveggen. In fact, there is even a ledge, near the top of Trollveggen, which is marked with the word 'Exit', pointing at a convenient leaping point. However, this sign was not intended for people who wanted to commit suicide. Instead, it marks the exit point for skydivers. People who leaped there were parachuting their way down (a practice now forbidden by the Norwegian authorities). The interesting lesson from this little story is that the thinking method that we used had no effect on our conclusion. We used intuition, we used a verbal description and we used a mathematical model, and all gave us the wrong conclusion. This is because we were imprisoned by a certain conception, and our initial assumptions were wrong or incomplete. So, let us give homage to Trollveggen, and call the fallacy of using a wrong or incomplete set of assumptions, the 'Trollveggen Fallacy'.

A few years ago I received a manuscript to review. It was based on a mathematical model and it was written by an excellent modeler. The math was a bit over my head, but I thought the model was pretty good and presented an interesting point, so I sent it back to the editor, recommending its publication. Something bothered me, though. A couple of days later I realized what it was. It was the Trollveggen fallacy, or so I thought. In mathematical models assumptions are more explicit than in verbal ones because one must give them a certain value, either a variable or a constant. Often, at least some assumptions in mathematical models are clearly unrealistic. We nevertheless use them because we need solutions. Unrealistic assumptions simplify models enough to give us solutions. However, it is important for a modeler to make sure that unrealistic assumptions will not result in solutions that are the opposite of what one expects from realistic ones. And this is what I felt happened in that particular model. Hence, I rushed an e-mail letter to the author. I told this modeler that it seemed to me that by making one of the assumptions more realistic, the model's conclusion would be reversed. In reply, the modeler told me that my intuition was correct.

The manuscript was, eventually, turned down by the editor on the ground of being too mathematical for that particular journal. However, the important point about this case is that it shows us that the Trollveggen fallacy can be fairly common. Take the saga of the handicap idea, for example. Amotz Zahavi first published it in 1975 (Zahavi 1975), and since then it was crucified by modelers for almost 15 years. Zahavi presented it as a verbal model. In response to the strong criticism, he later expanded and explained it further in a number of additional papers, using other verbal descriptions of the handicap mechanism. The first mathematical models did not agree with Zahavi's conclusions (Davis & O'Donald 1976; Maynard Smith 1976), and only at about the turn of the 90's theorists have finally and fully accepted it (Maynard Smith 1991). What went wrong? There are two possibilities: either Zahavi's verbal model was erroneous, and the mathematical models explored options beyond Zahavi's description until they found those assumptions that made it work, or, alternatively, Zahavi made the correct assumptions in his verbal description, though these were not included in the early mathematical models. The truth leans toward the second possibility. After receiving the first wave of criticism, in 1976, Zahavi modified and clarified his assumptions (Zahavi 1977). The main core of the handicap mechanism, i.e., the assumptions that made it tick in the genetic models 10 years later (Pomiankowski 1987), were already found in his verbal description in 1977.

The complexity of the mathematical models of the handicap mechanisms increased over time. Assumptions of the first models were simple, and their solutions were mathematically neat. Indeed, the assumption that a handicap is condition-dependent complicates the model. It was an assumption that was ignored in the first models. When it was used, in later models, it was first assumed that condition or the handicap or both vary, but also that they were not heritable (Kirkpatrick 1986). Pomiankowski (1987) was the first modeler who put together, in genetic models, all the assumptions that made the handicap mechanism work. Simple optimization models of Andersson (1982), and of Nur and Hasson (1984), or game theory models starting with Grafen (1990), made the same assumptions, and arrived at the same conclusions.

What we should learn from the saga of the handicap mechanism is that we cannot rely exclusively on mathematical models. They alone will not prevent us from sinking again into the abyss of the Trollveggen fallacy. It is in the hands of naturalists, empiricists and modelers to put forward verbal explanations that cover all the reasonable options. The role of mathematical modelers is to use their models to explore the logic of these explanations. It is their duty to expose hidden assumptions of the verbal models, and to make sure their own assumptions do not remain hidden. It is their duty to explain, as much as they can, what unrealistic assumptions do to the model's conclusions. And it is in the hands of us all to use our intuition, each of us based on his or her own knowledge and skills, and ensure the conclusions make sense. Given the appropriate assumptions, they must, at least as an aftermath, make intuitive sense, or we do not fully understand the theory.

Signal diversity

Signals refer to traits (such as behavioral, acoustical, chemical or structural patterns) whose specific evolutionary benefit stems from their potential to change the behavior of others (Hasson 1994, 1997; Maynard Smith & Harper 1995). However, to make decisions, organisms use, in addition to signals, also characteristics, termed 'cues', which are found in living organisms or in non-living objects, and which have evolved (in living organisms) for other reasons. In fact, they may have evolved despite their effect on recipients (in such cases, organisms might evolve attenuators that hide these cues; see Hasson et al. 1992). In signaling theory, because we are interested in understanding signals rather than cues, we often tend to ignore the perception and assessment of cues. Most of this paper is dedicated to the argument that we should not.

The potential of signals to coexist is a relatively new topic which, in my opinion, has already slipped a few times into the Trollveggen fallacy. Evelyn Hutchinson gave a famous plenary lecture in the annual meeting of the American Society of Naturalists, 1959, entitled 'Homage to Santa Rosalia, or why are there so many kinds of animal?' He talked mainly about competition and limiting similarities, and ended his lecture with the sentence: 'And this is where solutions may be found to questions ecologists should ask, such as: How similar can species be, yet coexist? and Why are there so many kinds of animals?' This is the kind of questions we should ask today about assemblages of signals found in gene pools (Hasson 1997).

The study of signal diversity may benefit from the parallelism between communication and community ecology. This analogy hints upon competition that occurs between signals over a certain resource or resources. Like species in ecological communities, signals may be arranged in 'guilds' according to their contexts and recipients. Furthermore, some signals are generalists and exploit perceptions and biases of several recipients, or in several contexts, whereas others are specialists and exploit perceptions and biases of only a single recipient at a very specific context. By way of analogy, perceptions and biases are the resources upon which signals compete, and they exist mainly because potential recipients of signals need information.

Information and knowledge

What is information? The answer is not as trivial as it may sound. Information is described, by Information Theory (Shannon & Weaver 1949), as the capacity of a signal to store data, which is a positive function of the number of bits that one can put in it. Given that signals store and transmit information, recipients make judgements of how many perceived bits in a signal are turned on or off. Note, however, that according to Information Theory, information is not an asset of recipients. According to Information Theory information is not even an asset of signalers but, instead, it is an asset of signals. Other than in the context of Information Theory, however, information has been used for both signals and individuals. In contrast, ‘knowledge’ is a term assigned for individuals only. To improve clarity, I use the term ‘information’ for signals, and ‘knowledge’ for individuals.

Hence, according to Information Theory, a signaler fills signal’s bits with zeros and ones. This information, however, is only as efficient as its perception by recipients. It makes a practical sense, therefore, to handle this by using perceived bits rather than submitted bits (e.g. Bradbury & Vehrencamp 1998). Another difficulty with Information Theory is that the mathematical treatment it offers cannot handle negative values of information stored in signals. This is important, because signals can change recipients’ knowledge either positively (improving their performance) or negatively (diminishing their performance). Although it is theoretically possible to assume, a priori, that a signal is a cheating signal, and then measure its potential to deceive by measuring its capacity to store ‘cheating units’ in cheating-bits, filled with zeros and ones, this would be rather cumbersome. Information Theory does not handle well cheating signals. Hence, it makes more intuitive sense to measure information by its effect on the performance of recipients (Hasson 1994, 1997; Maynard Smith & Harper 1995). By using the above distinction between ‘information’ (of signals) and ‘knowledge’ (of individuals), we can define reliable signals as signals that induce a positive change in the recipients’ knowledge. As a result, recipients of reliable signals make better judgements about their future actions, and their fitness increases. Similarly, cheating signals are defined as signals that decrease recipients’ knowledge, thereby decreasing their fitness (Hasson 1994). We can use this distinction to also improve the definition of signals (Hasson 1994, 1997; Maynard Smith & Harper 1995) as characters that evolve because they change the recipient’s knowledge, hence, their behavior.

Although both Maynard Smith and Harper (1995) and I (Hasson 1994, 1997) thought that the information content of a signal should be evaluated by the signal’s effect on its recipients’ knowledge, this approach was made on the intuitive level only. Neither Maynard Smith and Harper, nor I, defined ‘information’ and ‘knowledge’. We know that the more knowledge individuals have, the more ‘precise’ their behavior would be. In other words, additions to existing knowledge increase fitness. Hence, knowledge refers to the values an individual assigns to all variables that affect its decisions about its future actions. The better the correspondence between the estimate of these values with their real values, the more knowledge an organism has about its environment, and the more precise its behavior would be. Consequently, cheating signals decrease correspondence of the relevant set of variables with their true values, and reliable signals improve this correspondence.

Most of the time, knowledge is not complete. For some variables, for example, when features of the environment or the individuals' qualities that are sought by recipients fluctuate, knowledge can never be complete. Hence, knowledge is better defined as the individual's estimate of the mean values and variances of variables that affect its decision about its future action, relatively to their true values when it acts. Knowledge does not necessarily imply consciousness, but it determines performance. Hence, by observing an individual's performance, we can make inferences about its knowledge. I hereon restrict the term 'information' to the potential of cues and signals to change their recipients' knowledge.

Although this definition is new, it can be treated within a framework of an already existing theory. However, this is not the framework of Information Theory, but that of Signal Detection Theory. In a review on pursuit deterrent signals (Hasson 1991a), I introduced an approach, which I thought was new, to explain communication. It was, in my mind, the simplest way to explain why a predator should respond to a pursuit-deterrent signal. It recognized that when a predator makes a decision of whether or not to pursue an individual prey, it can make two types of errors. One is the error of being too anxious, pursuing prey that it should not pursue, the other is the error of being too cautious, namely, not pursuing a prey that it should pursue. When a prey estimates that the predator is committing or is about to commit the error of being too anxious, it should benefit by increasing the predator's knowledge. Consequently, it sends reliable signals that improve the predator's estimate of the prey's alertness, health and vigor. Hence, in order to deter predators, prey benefits by informing the predator of its alertness and strength, minimizing the predator's error of being too anxious. Later, I realized that the same logic applies to other communication systems, though, if they are aimed to attract rather than to deter (e.g. courtship signals), they are targeted to reduce the recipient error of being too cautious (Hasson 1994). In terms of Signal Detection Theory, to which I was introduced only a short time before the latter paper was published, overanxiousness is a 'false alarm' and overcautiousness is a 'miss'.

Signal Detection Theory is founded on these two types of errors. It also recognizes two types of correct choices: 'a correct rejection' and a 'hit'. Unlike Information Theory, which is concerned with the capacity of signals to store data, Signal Detection Theory is interested in choices individuals make based on their current knowledge. Signals change knowledge by either increasing it (if reliable) or decreasing it (if cheating). Both of these effects can be easily included, as different parameter values, in Signal Detection Theory (see Getty et al. 1987, for the use of Signal Detection Theory, with examples of cheating signals).

The most appropriate way to measure knowledge is probably indirectly, by measuring the precision of an individual's choice of actions. This can be done by calculating the relationships between the individual's choice of hits and false alarms, relative to the expected or to the empirical choice of actions the individual makes when it is fully informed. Signal Detection Theory provides mathematical tools for describing the relationships between hits and false alarms. The actual information content of a signal, as it is perceived by recipients, is therefore defined as the change in knowledge it induces in the recipient (which may be either positive or negative). It can be measured by monitoring the average change in the relationships between hits and false alarms induced by the signal.

The role of multiple biases

By definition (Hasson 1997), signals survive or perish because recipients' perceptions and biases change fitness of signalers, and give direct benefits or losses to alleles that code for signals. These perceptions and biases are the evolutionary resources of signals upon which they compete. The more efficient are signals in exploiting biases of recipients, the more likely they are to eliminate competing signals. Hence, in order to understand signaling, we must study the evolution of perceptions and biases, where perceptions are the tools that organisms use to gather information (from cues and signals), and biases are tendencies of organisms to make certain choices based on different values of parameters in their knowledge space. It seems to me that the role of the animal's quest for information, especially via modifications of biases and perceptions, was heavily undermined in the theory of communication. The source of this negligence is probably the fact that the theory of communication developed mainly through studies of sexual selection. Sexual selection theory, including handicap models, is mainly based on the (Fisherian) genetic linkage between choice and male trait, which results in a simultaneous evolution of both signals and biases. With, perhaps, one exception (Hasson 1994), such a linkage does not exist in other communication systems. The study of the evolution of biases independently of signals has been, nevertheless, ignored too frequently.

This negligence is probably limited to studies of communication. Take, for example, studies of foraging behavior. It is a trivial assumption in optimal foraging models that animals are capable of gathering information based on many different cues. It is an assumption based on a plethora of empirical studies. Similarly, animals were found to be capable of using many environmental cues in order to navigate in it. Yet, if we look into theoretical studies of communication, either verbal or mathematical ones, we find that most of them assume that recipients are incapable of receiving information in the absence of signals. Relative to studies of animal behavior in other fields, this is a naïve assumption. Worse, it hinders our understanding of signaling.

I should give credit here to Amotz Zahavi. It was from him that I absorbed, as a young student at Tel Aviv University, the concept that communication is based on information recipients need. Although, as far as I can appreciate it, this was his working assumption, he has never explicitly published it. Since then, this concept has guided my understanding of communication (admittedly, at first unconsciously). The possibility that signals function as amplifiers (Hasson 1989, 1991b), for example, is based on the assumptions that individuals need information, are capable of perceiving it, though not perfectly, and make choices regardless of the existence of signals. I show, below, why this assumption matters, and how multiple biases can lead to multiple signals.

Alertness and chronological orientation

Predators need information about several prey characteristics, such as alertness, escape potential, nutritional value and defense mechanisms. Let us focus on alertness alone. One

way of perceiving it is by looking at the prey facial symmetry. If a prey is vigilant and knows where the predator is, its face would appear symmetric to the predator, at least significantly more so than expected by a random distribution of facial orientations. This can lead to the evolution of symmetrical facial color patterns that function as amplifiers of the previously perceived symmetry (Hasson 1991a). Sometimes, however, prey does not use binocular vision. This is often the case in birds and in some mammals such as hares, rabbits and other Lagomorpha. In such cases, other cues may be used, such as, for mammals, the orientation of their ears. Cues refer to characteristics upon which biases are based, but which are not signals (Hasson 1994). Organisms use cues, such as daylength, light or prey movements because, on the average, they add information. In contrast with signals, however, if they are found in living organisms, they have not evolved because they change information but, sometimes, despite the fact that they add information. Hares and other mammalian prey must be attentive to their predators, hence, just like facial orientation of antelopes and deer, their ear orientation is a cue predators can use for detecting alertness in such prey. Ear markings, such as colored ear tips or margins that are found on many mammal's ears, are amplifiers of the ears' orientation. Because they better reveal the ears' orientation, the predator's knowledge of their prey's attentiveness, increases: the predator knows better when its prey is alert, but also when it is not.

Both facial symmetry and ear orientation can be categorized as 'spatial orientation'. Predators detect alertness by perceiving orientation of the prey attentiveness in space. However, there is more in vigilance than spatial orientation alone. Predators can use cues such as prey movements and flight distance. If prey respond to the predator's attempts to stalk them by moving away to maintain safe distance between them, predators should be able to learn that they have been spotted. Hence, they should pay attention to their prey's movements. In other words, they should respond to their prey's 'chronological orientation' in addition to their spatial orientation. For species, such as many small birds, whose face may be too small for its orientation to be perceived by a mammalian predator, and their head lacks conspicuous appendages, signals that use chronological orientation make more sense. For example, alarm calls and head-bobbing, which are common in birds, such as waders, may be chronologically oriented if given at a higher frequency immediately following their predator's movements.

Head-bobbing as chronological orientation

I tested this possibility by approaching the spur-winged plover *Hoplopterus spinosus*, in Israel, in September 1989, following the bird's breeding season. When approached, it uses both sharp alarm calls and head-bobs. Upon further approach, the plover walks away from the observer while continuing head-bobbing and calling and, eventually, it escapes by flying away. This sequence of behavioral displays is a typical response of spur-winged plovers toward human and natural predators alike (Simmons 1955; Cramp 1983; Walters 1990). To test the chronological orientation of the spur-winged plover's head-bobs I recorded the birds' reactions to my movements, which included only alternate walking toward the birds, and standing. Chronological orientation of head-bobs was measured by their proximity in time to the initiation of my walking.

To collect data I used a Casio PB-1000 hand-held computer (435 g), which I programmed to perform two operations: (i) to instruct me, by beeps given at random intervals of 3 to 15 seconds, to start walking toward the plover, or to stop, and (ii) record the timing of the plovers' head-bobs and, based on the numbers I pressed on the key-pad, also the estimated distance between me and the bird in units of ten meters.

Randomizing my walking movements ensured that I was not responding to the birds' behavior. By dividing each recording session into five equal time intervals, I found that the total number of bobs significantly increased as the recording session proceeded ($x_1=69$, $x_2=113$, $x_3=124$, $x_4=129$, $x_5=172$; Spearman rank-order correlation coefficient, $r_s=1$, one-tailed test, $P<0.01$, Siegel & Castellan 1989). This indicates that the spur-winged plovers were bobbing in response to my approach (see Appendix for other technical details).

During each uninterrupted walk, i.e. after beginning walking and before stopping, the spur-winged plovers bobbed more than once. After they bobbed, they waited a little, and bobbed again. Such a response that was not related to my change of behavior peaked at the third second (Fig. 1). This confirms that head-bobbing is not exclusively used for chronological orientation, and shows that head-bobbing is given periodically. My test of chronological orientation of head-bobs therefore considered only the first head-bobs made after each initiation of walking.

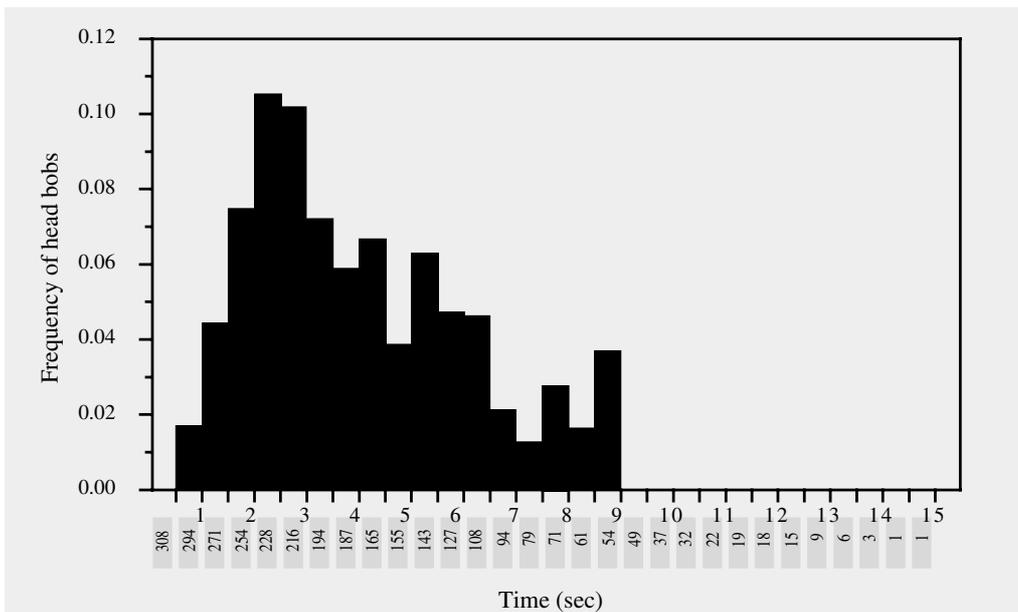


Figure 1. Distribution of head bobbing intervals between two successive head bobs while I was walking uninterruptedly toward the plovers. Because long intervals were less available than short intervals (e.g. 5 sec or longer intervals were not available if only 4 sec remained between a head bob and the next beep) frequencies were calculated as the number of times each interval between two successive head bobs occurred, divided by the number of times this time interval was available (given by vertical numbers at the bottom).

To make sure the analyses created no bias (see Appendix), Figure 2 presents two identical analyses. The first is the frequency of first head-bobs that were given forward in time, starting at the moment I heard the beep (0 to 15 sec) and while I was approaching the plovers (Fig. 2A), and the second is the frequency of first head-bobs that were given backward in time (0 to minus 15 sec), prior to the beep, while I was standing (Fig. 2B). Figure 2A shows a significant change over time, not seen in 2B, which indicates a response to my initiation of walking. Furthermore, the frequency of head-bobs during the first or second seconds, respectively, were significantly higher than the frequency of bobs during most or all other seconds (Fig. 2A). The second second was significantly different from any later second at a level of at least $P < 0.05$ (Pearson chi-square), and the first second from all but the seconds marked with crossed squares. The first and second seconds were not significantly different from each other. Considering that I was slow to respond to the beep, and had a small delay of about three tenth of a second in pressing the key in response to the plover's head-bobbing, I was responsible for a delay of about a second between time zero (beep time) and the recorded first bob (Appendix). As a result, if the plovers use chronological orientation, their peak response is expected, indeed, to be found at around the beginning of the second second. In addition, the null hypothesis (no chronological orientation), given periodical head-bobs with a mode during the third second, and beeps that were given at intervals that were never shorter than three seconds, predicts no difference among the first three seconds. However, bobbing at the third second was significantly lower than that at the second second, indicating chronological orientation of head-bobbing.

Assemblages of signals

This little field study is hardly a breakthrough. It shows that signals can be chronologically oriented at predators, which is an interesting point, but one that hardly justifies its presentation in this forum. I present it here, nevertheless, in order to make a point. In order to understand communication, such as the plover's communication with its predator, we must follow such studies by taking a broader view and look for the signal's place in the community of signals given in the same context. Hence, we should ask: what is so special about head-bobbing and its chronological orientation, and why does the spur-winged plover also send other signals to its predator in addition to head-bobbing?

The spur-winged plovers responded to my initiation of walking by head-bobbing. However, they also continued to head-bob, periodically, in a non chronologically-oriented pattern. This must have diminished my perception of chronological orientation. Why do the plovers bob more than seems to be both necessary and most efficient for advertising their alertness toward a particular predator? Moreover, why do the plovers bob at all if, at the same time, they emit sharp, loud alarm calls? Alarm calls seem to be perfect for the job because, by being more conspicuous they are more informative about alertness. Also, as vocal rather than visual signals, they are less informative about the plover's exact location, hence they are also less risky.

The answers to both questions probably lie in the type of information that is transferred by these signals. True, repeating head-bobs in the absence of further changes in the

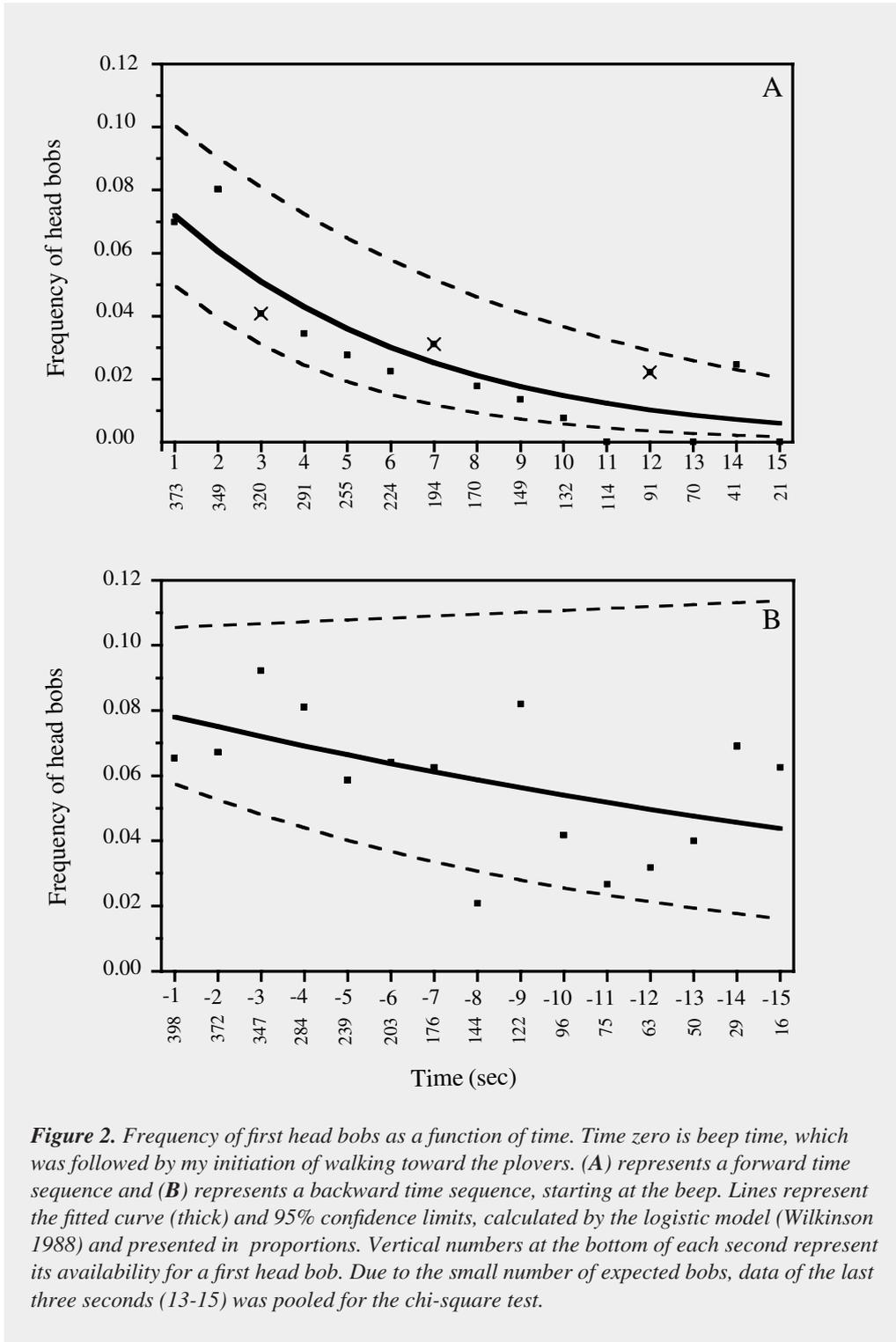


Figure 2. Frequency of first head bobs as a function of time. Time zero is beep time, which was followed by my initiation of walking toward the plovers. (A) represents a forward time sequence and (B) represents a backward time sequence, starting at the beep. Lines represent the fitted curve (thick) and 95% confidence limits, calculated by the logistic model (Wilkinson 1988) and presented in proportions. Vertical numbers at the bottom of each second represent its availability for a first head bob. Due to the small number of expected bobs, data of the last three seconds (13-15) was pooled for the chi-square test.

predator's behavior decreases perception of the signals' chronological orientation. As a result, prey impairs the information it adds to the predator about its knowledge of the predator identity and location. However, it gives more information about the prey's overall state of alertness, especially if the predator does not keep an eye contact with its prey throughout its approach. Head-bobs that are given only in response to changes in predator behavior may often be left unnoticed by the predator. Thus, the actual rate of head-bobbing may represent a trade-off between decreased perception of chronological orientation and increased perception of overall alertness. The two variables in the predator's knowledge space are therefore: the probability that prey is aware of a predator's presence (given by head-bobs), and the probability that it actually sees the predator and knows where it is (given by chronological orientation of the head-bobs).

In contrast, vocal alarm signals are less constrained by such tradeoffs. They are very effective at indicating the prey's overall alertness, but where several prey individuals are present, they are ineffective in allowing the predator to single out the individual prey that is alert (i.e., that has identified the predator and uses chronological orientation), because it is more difficult to identify callers. Hence, at least for prey that is occasionally found in groups, vocal signals are less useful for chronological orientation. Consequently, by increasing the rate of alarm calls, prey does not lose much in decreasing the predator's perception of its chronological orientation, whereas it may significantly increase the predator's perception of its overall alertness. Indeed, vocal alarm calls of the spur-winged plover are given at a much higher rate than head-bobs.

A predator may not quit stalking unless it is certain that all prey individuals have detected it. This can explain two observations. The first observation is that all the plovers that were present were signaling. The second is that the plovers used both alarm calls and head-bobs. If predators need information about alertness of all prey individuals, vocal alarm signals alone may fail to deter predators. The visual head-bobbing is useful because it adds information about the identity of the alert prey. Visual signals are probably used, therefore, not only to aim the signal at a specific predator, via chronological orientation, but also to aim the predator at a specific alert prey.

Finally, unlike vocal signals, visual displays may be conspiratorial, especially when prey is cryptic to its predator. A weak vocal signal may not be perceived by predators regardless of whether they have spotted their prey. In contrast, an weak and inconspicuous visual signal can be used as a private message of alertness received only by a predator that has already established an eye contact with its prey. Such a signal decreases the prey's risk of exposure to predators that are unaware of its presence or location.

Wilson (1975) wrote that if there is one thing that is certain about signals, it is their redundancy. If we recognize the limitations and advantages of different types of signals, we may find they are not redundant. We should also recognize that repetition of signals is itself a signal if it evolves, like head-bobbing and calling, to change the predator's behavior. Hence, instead of seeing redundancy, we may see that each signal, including signals' chronological orientation or repetitiveness, specializes on providing a different piece of

information that is important to the predator. Each signal changes a variable, or sometimes several variables in the recipient's knowledge.

Duetting

It is mentioned above that predators may not quit unless they are certain that all prey individuals are fully alert. Some prey species are found, almost always, in pairs. Predators may learn that if they see and hear only one individual, the other individual may be in a vulnerable state. This is the case, for example, for klipspringers *Oreotragus oreotragus*, who inhabit little rocky islands in the African savanna. Sometimes they feed in the open, but when a predator approaches, they flee to the rocky hills where they are safe. It is there, on the rocky hill, that they make their alarm calls. The interesting twist here is that they duet. The male gives a call, and the female immediately follows. Why duetting? What additional information is given by duetting? The answer to this puzzle first occurred to me when I looked at spectrograms of the alarm duetting of the klipspringer (Tilson & Norton 1981). These spectrograms show that the calls of the male and the female are about one and a half tenths of a second apart. I suddenly realized that, considering the speed of sound, there is no way they could duet like this if they were more than 50 m apart (assuming the predator is at equal distances from both). This is because, in order to duet, the female has to first hear the male call before she responds with hers (note that if the female responds to a certain visual signal given by the male then, depending on the actual distances from each other and from the predator, her call might overlap or even precede that of the male; since the female call consistently follows the male call, then they must call only when close to each other, or use a very sophisticated calculation method). The time interval between her call and that of the male gives the predator an estimate of the maximum distance they are from each other. It is an efficient way of informing the predator that both of them are together on the hill, attentive and safe. Hence, there is no reason for the predator to stay.

By considering the selective forces that operate on duetting, i.e., the potential responses by recipients, we can identify its signal type. If predators, such as hyenas, have a bias to quit if the klipspringers' alarm calls are synchronized, then klipspringers always benefit by minimizing the interval between their alarm calls. The result, duetting, should therefore be classified as an index (Maynard Smith & Harper 1995; Hasson 1997) of the actual distance between pairs of klipspringers.

Conclusion

Perceptions and biases play a crucial role in the evolution of signals. Perceptions evolve for the purpose of gathering information about specific variables, and biases as appropriate, adaptive responses to certain values of these variables. However, biases may also exist as a result of side-effects and constraints. We know something about the latter (Ryan & Keddy-Hector 1992), although there are reasons to think that biases of this type play only a minor role in the evolution of signaling, at least in a stable state (Hasson 1997).

However, in studies of signaling we have not even scratched the surface of the understanding of what is the kind of information that interacting individuals (hence, potential signal recipients) need and, especially, how they gather it: what cues are they using, what is the role of signals in adding or subtracting knowledge, and how do signals do it? Instead, we have focused on signals and signalers. This might change if we acknowledge that knowledge is important to interacting individuals or to individuals that consider interacting, and that the major selective force that drives the evolution of signals is their power to change it.

The second point is that we must give more credit to verbal models. We need them to explore possible solutions. My purpose here is not to undermine the role of mathematical models, but to give more room for people who know their system and use their intuition to understand it and bring about reasonable options. Then, such options or assumptions should be rigorously tested using both mathematical models and experiments. While exploring all these options, we should remember that there is more in communication than handicaps and Fisherian traits alone. Take for example a female preference for a long tail and the elongated male tail that corresponds with this bias. The tail could be either a handicap or a Fisherian 'aesthetic' trait. One way or another, at least two possible amplifiers may evolve and coexist as a result of the bias for a long tail: one is conspicuous tail colors, and the other is behavioral displays, such as tail fanning, that expose the tail to females. Both are signals, because their sole benefit stems from the fact that they change the female's behavior, and they do it by improving the female's perception of differences in tail length. On average, males with short tails lose by adding information to females, males with long tails benefit by doing so. By definition, such signals are amplifiers. Hence, a single bias can lead to the evolution of not only one signal, but to an assemblage of at least three signals.

Pursuit-deterrent signals are examples of a relatively simple communication system. It is simple, because there are relatively few variables for which predators need to make an estimate, perhaps because the interaction between predators and prey is usually very short. As a result, predators evolve relatively few biases, to which prey respond by evolving only small assemblages of reliable signals that correspond with them. Add to these a few possible cheating signals such as camouflage (a response to the perception of prey's presence), attenuators (of cues that reveal information useful to predators but harmful to prey), or mimicry (a response to biases regarding prey recognition), and we can see that a prey-predator communication system, despite its relative simplicity, can maintain a number of coexisting signals aimed by prey at their predators.

In other systems, such as sexual selection, recipients often need to fit values to a larger array of variables. Hence a female should find information about male features such as the accumulation of his deleterious mutations, his resources, his resource holding power, his feeding efficiency, his health etc., using many different cues. Some of her biases may operate simultaneously, others sequentially. She might find a provider, and then look for a sire, she might put more emphasis on some cues under some conditions, and on other cues at different conditions. We should be very naïve to think that females cannot assess males in the absence of signals, or that all these biases will not create many different signals.

Finally, if signals evolve in response to biases and not biases in response to signals, then another term might be obsolete. It is the alleged recipient's 'cost of communication'. This concept was probably inspired by two ideas. One is the underlined traditional assumption that perceptions and biases follow the evolution of signals. The other, and maybe the dominant one, is Information Theory that assumes information is accumulated in signals in distinct bits, and should, therefore, be extracted the same way. Hence, it follows that 'The amount of information also affects the costs of communicating. Usually the greater the amount of information, the more it costs senders to encode it into signals and receivers to extract it from signals.' (Bradbury & Vehrencamp 1998, p. 388). The second argument is often false. There is no a-priori reason to believe that it is more difficult to make a distinction between two tails, one is 70 cm long and the other is 72 cm long, than it is for a similar pair of tails of 70 and 72 mm long. However, this is only a minor criticism on the concept of the recipient's 'cost of communication', based on empirical grounds. The other comes from a much more fundamental difference in the understanding of communication. It challenges the assumption that perceptions and biases only follow the evolution of signals. This assumption is often subtle, but its effect on the understanding of signals is dramatic. By being more conscious to it, we may avoid yet another Trollveggen fallacy.

Indeed, recipients make a costly investment. However, they would make such an investment regardless of the existence of signals. Their cost is not the cost of signaling, but the cost of information. It costs to gather information, and they would pay this cost if benefits, by the new choices they make as a result of the additional knowledge, exceed costs of gathering the information that changed it. If this is how it works, then reliable signals which, by definition, add information, can only decrease this cost. If it costs more to add a given piece of information via signals than it does via other cues, then biases for such signals will be eliminated by natural selection. After all, if biases evolve largely independently of signals, then the use of signals, from the recipient point of view, is only an option. Hence, the role that the search for information plays in determining recipients' perceptions and biases should not be ignored. Without perceptions and biases as selective agents, signals cannot endure.

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Appendix: Techniques and additional data

This appendix adds some information about the field study of head-bobbing of the spur-winged plover.

Techniques

Observations were made in September 1989, following the end of the plovers' breeding season, near kibbutzes Ma'agan Michael and Ma'ayan Zvi's artificial fish ponds, along dirt roads, most of which were surrounded by short shrubs and annuals. I focused on birds that were alone or in small groups (of five or less; mean 2.13, SD=1.04, $n=48$) and that appeared to be isolated from other groups (apparently, still in territories).

For each observation I focused on an individual bird, the one closest to me. I slowly approached it, alternating walking and stopping until the bird flew away. As a result of the apparent territorial behavior of the birds that I chose to watch, and of my chosen path in the large study area during the entire field study, it is highly unlikely that a plover was recorded more than once.

The numbers pressed on the key-pad indicated the estimated distance between myself and the bird, truncated to the nearest 10 m. The times (in tenths of seconds) of beep instructions and of keys pressed, as well as the estimated distances, were automatically filed. These files were later transferred to an MS-DOS computer for data analysis. However, although the use of a computer in the field improved data handling, it also introduced a measure of imprecision due to my inability to immediately respond to stimuli. To take this into account, I estimated my average delay in initiating walking in response to the beep, and in pressing keys in response to a visual stimulus. Based on daily measurements in the field, using a similar program modified to simulate and measure my response, I found the average delay in my initiation of walking to be 0.66 sec ($SD=0.17$, $n=82$). I also measured a delay of 0.30 sec ($SD=0.03$, $n=40$) in my key-pressing response to a visual signal that appeared on the computer screen at random intervals of 2 to 6 sec, approximating the plover's maximal bobbing rate (see below). The recording procedure therefore resulted in a total estimated delay of almost a full second, independently of the plover's behavior.

When head-bobs are given periodically, the statistical conclusions of the experiment may be seriously biased. For example, if, regardless of my behavior, head-bobbing is given every n seconds, any movement of mine will be followed by a head-bob within the next n seconds (with an equal probability for each second smaller or equal to n). Thus, if n is small, periodical head-bobbing will indicate an apparent response even if none exists.

To overcome this difficulty I used two statistical procedures: one compared the timing of head-bobs given immediately following my initiation of walking with that given immediately before my initiation of walking (expected to have the same bias). This analysis is shown in Figure 2. The other tested for a difference in response among seconds fewer than n (the cycle of periodical head-bobbing). For the first procedure, the null hypothesis (no chronological orientation) predicts no significant differences between the frequency of head-bobbing expressed backward or forward in time, starting with my initiation of walking. For the second procedure, it predicts no significant difference in the frequency of head-bobs among seconds that are equal to or smaller than n , following my initiation of walking.

One final complexity that I needed to take into account is the availability of time intervals: long intervals are not available for head-bobbing as often as short intervals. Furthermore, once a first head-bob is given following my initiation of walking, the rest of that interval is no longer available for a first head-bob. Thus, the frequency of head-bobs at each time interval (either a half or full second) was calculated as the number of times head-bobs were given at that interval divided by the number of times that interval was available for first head-bobs (which are given as vertical numbers at the bottom of the figures). Available intervals in Figure 2B were similarly calculated, using intervals of standing prior to initiations of walking.

Figure 2B is useful to ascertain there were no other hidden statistical or procedural biases in Figure 2A. For example, to construct Figure 2A, I have pooled data of 48 different individuals, each had 1 to 11 observations. This might create a bias, if between-subject variance exceeds intra-subject variance (Leger and Didrichsons 1994). However, we are interested here in distributions of timing of head-bobs rather than in their averages, and there is no sufficient data for each individual to compare between-subject variations in skewness. Luckily, all potential biases, including this one, if it exists, should be included in Figure 2B. Hence, any pattern that is found in both Figures 2A and 2B may be attributed to such biases. In contrast, patterns that exit in Figure 2A but are not found in Figure 2B could only be attributed to my initiation of walking toward the plovers.

Additional data

The average estimated distance at which I detected the plovers was 45.3 m (range 25-65, SD=9.49, $n=48$), and the flight distance, 34.5 m (range 18-55, SD=9.34). The difference between detection and flight distances was small because the plovers usually walked away from me during the observations (many observations ended when the plovers seemed to have reached the border of their territory and flew above or around me, to land behind me). The average duration of recording sessions was 2 min 26 sec (SD=1 min 42 sec), and the number of head-bobs per session, 12.9 (SD=10.8).