

Zebra stripes as an amplifier of individual quality?

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Amplifiers belong to a class of signals that alone do not indicate an individual's quality, but through design they improve the receiver's ability to assess pre-existing cues and signals. Amplifiers are cost free to produce and maintain, but may yield disadvantages to the individuals that are compelled to reveal their inferior quality. We suggest that zebra stripes, combined with the movement and proximity of other individuals with the same pattern, might function as an amplifier of the individual's escape potential. As a zebra flock is set in motion by predators, stripes may facilitate ascertainment of the quality of the moving individuals (i.e., their escape potential) relative to other individuals in the flock. We tested whether the suggested relationship between stripes such as that of the zebra and quality ascertainment might occur by constructing animations involving 5 moving objects, with one object moving differently from the others. A test panel was asked to identify the deviant object in 4 animations, each of the 4 animations having objects with a different color pattern (striped, black, gradient and spotted). This study lends support to the hypothesis as behaviorally deviant objects were easiest observed in "flocks" of zebra striped objects. Thus, zebra stripes may make odd individuals more visible rather than making them less distinguishable.

Introduction

A signal is an act or a structure that has evolved to alter the behavior of another organism, and which is effective because the receiver's response has also evolved (Harper & Maynard Smith 2003). It is likely that no single mechanism can explain the enormous variety of signals. Instead, several mechanisms are likely to function simultaneously. The main identified constraints resulting in honest signaling are handicaps (Zahavi 1975), design (Hasson 1990, 1991, 1997, Hasson *et al.* 1992) and conventions (Harper & Maynard Smith 1998, Silk *et al.* 2000). Conventional signals (symbols and icons) are supposed to be

honest in co-operative systems where signaler and receiver have a common interest, i.e., in systems where both signaler and receiver benefit if the receiver responds to the signal with an appropriate action. Therefore, deception is not beneficial to either participant. Reliability of handicaps, on the other hand, is based on the assumption of costs in the production or maintenance of the signal, and that the intensity of the signal is proportional to the resources possessed by the signaler (Zahavi 1975). Thus, when maximizing trade-offs between signaling and other components of fitness, high quality individuals can afford more intense signals as compared with low quality individuals. Finally,

signals constrained by design are ideally cost-free and honest due to a direct and incorruptible link between the signal and the quality signaled (Hasson 1997).

Amplifiers are a sub-group of design-based signals that alone do not indicate an individual's quality, but through their design they improve the receiver's ability to assess pre-existing cues and signals (Hasson 1990, 1991, 1997, Hasson *et al.* 1992). For example, the colors and patterns of the body that contrast with a background or with the rest of the body might increase the observer's power of resolution with respect to body size and body proportions (Hasson 1991, Berglund 2000, Taylor *et al.* 2000). Consequently, an amplifier will not make the body look bigger, it simply makes the actual size easier to ascertain. Amplifiers, in contrast to handicap signals, do not have costly trade-offs between their development and maintenance and other fitness components. For example, in cervids antler size might function as a handicap, indicating an individual's surplus of calcium and potassium (which are scarce minerals in cervids' natural habitat), whereas antler symmetry might function as an amplifier (Barber & Folstad 2000). For a given antler size the accrued symmetry would then be signaling and constrained by maximum ability, rather than maximized trade-offs. Instead of costly trade-offs, low-quality individuals incur costs due to how amplifiers reveal their lower quality. By definition (Hasson 1991), an amplifier is likely to evolve if, on average, the benefits to high-quality individuals outweigh the costs to low-quality individuals. Amplifiers, if not condition dependent (Hasson *et al.* 1992), can be fully expressed by all members of a population.

Amplifiers have usually been thought of as morphological characters, but they can also be behavioral traits (Barber & Folstad 2000). Within some spatially regular groups, for example fish schools and bird flocks, the ability to maintain accurate positions and perform movements in synchrony with the rest of the group may demand a minimum threshold level of behavioral ability (Barber & Folstad 2000). Thus, the level of participation in synchronous group maneuvers performed by an individual may indicate its locomotory and neurosensory capacity, characteristics that can be informative to both intra-

and interspecific observers. Individuals that fail to take up the optimal position in ordered groups can be described as individuals exhibiting 'positional oddity' (Barber & Folstad 2000). Taking up a deviant position can further lead to asynchronous movements with respect to the rest of the group (i.e., synchronal oddity). Certain morphological traits, as for example reflective body surfaces on fish, wing bands in birds, and pelt coloration in mammals, can facilitate such ascertainment, i.e., function as amplifiers of an individual's ability to perform behavioral synchrony (Barber & Folstad 2000).

The aim of this study was to investigate whether color patterns, such as zebra stripes, could function as an amplifier of an individual's ability to perform behavioral synchrony. However, as zebra stripes have fascinated biologists as well as lay people at least since Aristotle, there is a bewildering array of alternative hypotheses (e.g., Thayer 1909, Marler & Hamilton 1968, Vale 1974, Waage 1981). One of the most established hypotheses suggests that zebra stripes have a perplexing effect on predators, thus making it difficult for predators to distinguish a single individual from a flock. On the contrary, we suggest that zebra stripes, combined with the movement and proximity of similarly striped individuals, facilitate a predator's ability to estimate the differential locomotory abilities (i.e., escape potential) of individuals in a zebra flock. Individuals with deviant pace or speed will exhibit positional or synchronal oddity that will make them conspicuous because they do not conform to the structured background of moving patterns created by other group members (Barber & Folstad 2000). Zebra stripes are thus expected to facilitate a predator's ability to single out profitable prey, which would be beneficial for high quality individual zebras. A familiar example might illustrate the mechanism. In some marching tattoo bands, band members are trained to march in uniform pace and speed with respect to the rest of the group. Would some pattern in the uniforms facilitate pointing out the behaviorally deviant individual(s), and if so, what pattern would it be? One likely pattern is a stripe of contrasting color alongside the body (a pattern that is actually a quite common design feature on uniforms!). Stripes, in our opinion, would create

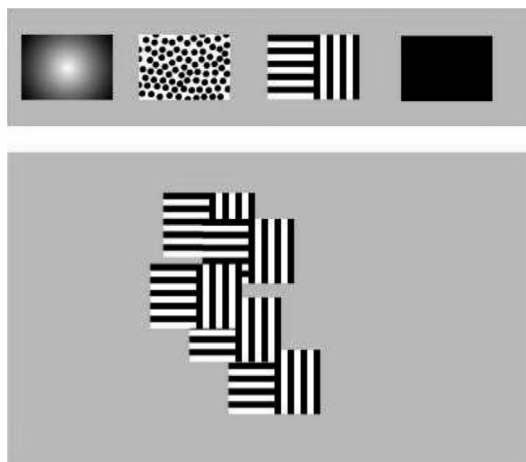


Fig. 1. Upper: The color patterns (and the background color) that were used in the animations. Lower: movie screen with striped objects. The animation can be seen at <http://zebra.darwinia.com/>.

a structured background of moving patterns, upon which deviant individuals would easily be distinguished. Contrasting colors would further facilitate distinguishing this abnormality.

In this study we addressed the following issue: May zebra stripes function as an amplifier of its carrier's positional and synchronal locomotory oddities in relation to its herd in a manner that reveals the individual's escape potential to predators? In order to answer this question, we investigated if, compared with spots, gradients and plain colors, stripes in particular facilitated identification of object(s) with positional and/or synchronal odd movements in a group of optically moving objects.

Material and methods

Simulations of a moving herd were performed by constructing animations using the software application Macromedia Flash 5. Each animation consisted of five rectangular objects with identical color patterning moving repeatedly across the screen. One of the objects was moving in a deviant manner with respect to the other objects (i.e., performing positional and synchronal oddity), and this behavioral oddity increased with time through the animation. Animations were showed to 173 students, and they were asked to stop the

animations after identifying the deviant object as soon as possible after starting the animations. The students were provided with identical written instructions. An erroneous identification was scored as 0, whilst a correct identification as 1. Sex and age of the students, as well as elapsed time and frames were recorded. Further, the sequence of shown animations and the relative position of the deviating object in each animation were recorded. Four animations were shown to each student. The four animations consisted of moving objects with either black, gradient, spotted or striped filling (see Fig. 1). A short standardized demonstration was given to students before performing the actual test, in order to smooth out potential learning effects. An example of the test experienced by a particular student can be viewed online at <http://zebra.darwinia.com/>.

Objects and background used in the animations

The striped (black and white) objects consisted of vertical stripes in the forepart and of horizontal stripes in the hind parts. This color pattern roughly resembles the color pattern in the most common zebra species, the plains zebra (*Equus quagga*, formerly *E. burchelli*). The three other color patterns (i.e., spotted, gradient and black) resemble the most common color patterns found in mammals.

Spotted objects were comprised of black spots on a white background (see Fig. 1). The diameter of the spots was the same as the width of the stripes in striped objects (i.e., 5 pixels). The black:white ratio in both spotted and striped objects was approximately 1.15. The background color of brownish yellow resembles the color of dry savanna, and as no white prey mammals are found in snow-free regions, plain objects were chosen to be black. Objects filled with gradient were constructed black in the margins, and to gradually whiten towards the middle. All the objects were of the same size (i.e., 50 × 70 pixels), with an approximate height:width ratio of 0.7. This ratio is, according to our subjective judgment, roughly the height:width ratio in zebras (when observed from the side). The

standard size of the movie screen in Macromedia Flash 5 was used (i.e., height 400 pixels, width 550 pixels).

Movements of objects

Objects used approximately 4.04 seconds when moving across the screen once, and for each time objects passed the screen a separate scene was constructed. In order to make sure that each student had enough time to judge between objects, 13 scenes were constructed in each animation. This resulted in an approximate time span of 52.5 seconds for each animation. A motion path with a saw blade pattern was constructed for each object in an animation. This resulted in a wave-like motion, simulating the undulating movement of a running mammal. Each motion path consisted of 10 or 10.25 waves, and this resulted in a motion path length of 400 and 410 pixels, respectively (with amplitude of 20 pixels and length of 40 pixels per wave). In each scene the number of waves in the deviating object's motion path increased with 0.5, starting with 11 waves in the first scene. The length of the motion path, however, remained the same (i.e., 400 pixels). This resulted in a motion with higher frequency of waves (i.e., shorter waves) in the deviating object's motion path as compared with that of the others. This deviation in frequency was assumed to simulate synchronal oddity in the deviant object. In order to accomplish positional oddity in the deviating object it was also accelerating and decelerating in speed in each scene. A Macromedia Flash 5 function 'easing in/out' for acceleration and deceleration could be adjusted between 0 and 100. In each scene this value was increased with 3, incrementing from an initial 10 in the first scene.

Study design

The four animations were shown to students in random sequence. Further, in order to randomize the position of the deviating object in the animations, 4 sets with 5 animations in each (since there were 4 color patterns and 5 objects in each animation) were constructed (a total of 20 ani-

mations). Apart from the color patterns of the objects, the 4 sets were identical. In each of these sets the deviating object took place in all the 5 possible positions (i.e., each set had five animations, and the deviating object was placed in a different position in each of them). Only one animation, picked at random, of each set was presented to a particular student. The sequence of animations and the position assigned to the deviating object in each animation were recorded.

Time measurement

In each animation the computer timer measured the elapsed time between the start and stop of the animation. In order to measure and eventually control for potential discrepancies in running speed of the animations, the number of elapsed frames was recorded. However, all the animations presented proceeded at the same speed, (gradient ≈ 4.03 , black ≈ 4.04 , spotted ≈ 4.05 and striped ≈ 4.06 seconds/scene) so the number of elapsed frames were not included in the statistical analysis. In order to avoid unnecessary disturbance both the timer and the frame calculator were hidden while the animations were running and they only appeared after the animations were stopped.

Statistical methods

We analyzed the proportion of correct *vs.* incorrect identifications with logistic regression models (i.e., assuming a binomial distribution for the response variable and a logit link; McCullagh & Nelder 1989). As we had repeated measurements at the individual level, we added "individual" as a random effect (i.e., a generalized linear mixed model (e.g., Diggle *et al.* 2002) was used, and fitted using Penalized Quasi-Likelihood). The random factor "individual" describes the variability among individuals on a logit scale, and is represented in the model as a normal distribution with standard deviation σ . The effects of the predictor variables "time", "color pattern", "position", "sequence", "age" and "sex" and their interactions were assessed using *F*-test, the variable of interest being fitted last (partial tests).

We investigated the goodness of fit of the generalized linear model ignoring the random effect “individual” using Pearson’s χ^2 -test (McCullagh & Nelder 1989). The latter was done to check if there was no large overdispersion indicating important missing covariates. Goodness of fit of the fitted models was assessed by considering a model fitted with time as a discrete variable (with 5 classes) and using proportions instead of binary observations (e.g. Cox & Snell 1989). The sum of squared Pearson residuals was then used to assess overdispersion (McCullagh & Nelder 1989). Fisher’s exact test for count data was used to analyze 2 subsets of data (i.e., the data obtained under ‘harsh’ conditions, *see Results*).

We analysed the time it took to get a correct identification using linear mixed models. Dependence among observations made on the same individual was taken into account by including “individual” as a random factor and the predictor variables “sex”, “age”, “position”, “sequence” and “color pattern” and their interactions were included as fixed factors. Effects of predictor variables (“color pattern”, “position”, “sequence”, “age” and “sex”) were assessed using partial F -test.

All analyses were done in R (R Development Core Team 2004), version 2.1.0. P values are reported two-tailed.

Results

Analysis of proportions of correct identifications

We obtained 692 observations, i.e. 173 for each color pattern group. The value of the Pearson χ^2 statistic was 14.68 on 16 degrees of freedom, i.e., there was no indication of overdispersion. There was no clear evidence against the null hypothesis of no effect of sequence ($F_{3,508} = 2.08$, $P = 0.102$) and no evidence against the null hypothesis of no effect of color pattern ($F_{3,508} = 1.54$, $P = 0.204$), age ($F_{1,170} = 0.651$, $P = 0.42$) and sex ($F_{1,170} = 0.293$, $P = 0.59$). However, there was strong evidence against the null hypothesis when assessing the effect of time ($F_{1,508} = 38.7$, $P < 0.0001$) and position ($F_{4,508} = 8.42$, $P < 0.0001$). There was, on the other hand, no such evidence when assessing

a non-linear effect of time (on a logit scale; effect of time²: $F_{1,507} = 0.97$, $P = 0.33$). Yet, there was evidence for interactions between position and color pattern ($F_{12,496} = 2.62$, $P = 0.0021$), showing that deviating striped objects were more often correctly identified, especially if positioned in the middle of the “herd” (*see Table 1*). Additionally, there was a significant interaction between time and position ($F_{4,504} = 2.79$, $P = 0.026$). Evidence for other interactions was not as strong (P varying between 0.06 and 0.57). The variability among individuals was relatively large ($\sigma = 0.91$).

Detecting the deviating object was most difficult if the deviantly moving object was assigned the uppermost or the lowest position, and the time elapsed was relatively short (*see Fig. 2*). In order to examine whether color patterns had effects on distinguishing between objects in these ‘harsh’ conditions, a subset of data, subset 1 (where only the observations where elapsed time was ≤ 10 seconds, and the deviant object took either the lowest or uppermost position) was considered (*see Table 2*). Further, another subset (subset 2) consisting of identifications where the elapsed time was ≤ 10 seconds, and the deviantly moving object was assigned to the relative upper, middle or lower position, was considered (*see Table 3*).

There was no evidence against the null hypothesis of no difference in correct and incorrect identifications between color patterns in subsets 1 and 2 (Fisher’s exact test: $P = 0.32$ and $P = 0.30$, respectively).

Analysis of the time used for the correct identifications

We registered 463 correct identifications. There was evidence for an effect of sequence on time

Table 1. Predicted proportions of correct identifications of the deviantly moving object within 5 seconds according to position and color pattern.

Position	Black	Gradient	Spotted	Striped
Lowest	0.21	0.23	0.18	0.34
Lower	0.36	0.44	0.50	0.62
Middle	0.45	0.53	0.72	0.80
Upper	0.33	0.64	0.75	0.31
Uppermost	0.45	0.23	0.17	0.29

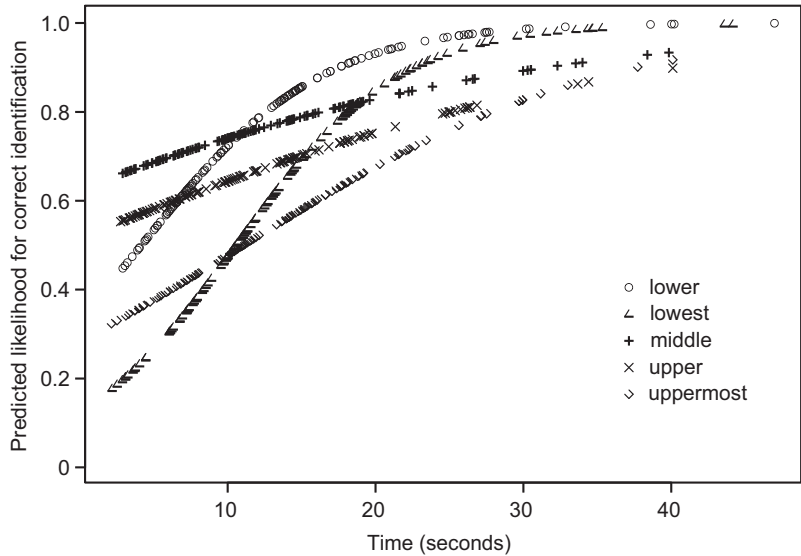


Fig. 2. Predicted probabilities of correct identification as a function of time and position. The different slopes of the curve express the interaction between position and time.

($F_{3,289} = 3.06, P = 0.029$): students used significantly less time on the last seen animations (differences sequence third-sequence first $\beta = -2.16$ s [SE = 0.79], and sequence fourth-first $\beta = -1.91$ s [0.80]). Male students used less time in watching the animations than female students ($F_{1,161} = 5.59, P = 0.019, \beta = -2.65$ s [1.12]). Further, there was evidence for an effect of position ($F_{4,289} = 3.78, P = 0.0051$): students used significantly less time (compared with reference level lower) when the deviating object was assigned to the upper position ($\beta = -2.04$ s [0.88]) or uppermost position ($\beta = -0.40$ s [0.98]), and more when it was in the lowest position ($\beta = 1.41$ s [0.98]). There was some evidence for a positive effect of age ($\beta = 0.17$ s/yr [0.087], $F_{1,161} = 3.69, P = 0.057$), but none for color pattern ($F_{3,289} = 0.262, P = 0.85$). However, this absence of a main effect for color pattern does not mean that

color pattern has no effect since there was strong evidence for an interaction between position and color pattern on time used for the correct identifications ($F_{12,277} = 2.63, P = 0.0024$). That is, deviating striped objects were faster identified, especially if positioned in the centre of the “herd”. There was no evidence for any other interactions (sequence:position: $F_{12,277} = 0.389, P = 0.97$; sequence:colour pattern: $F_{9,280} = 1.04, P = 0.41$).

Discussion

In the analysis of the whole data set, with identification (correct and incorrect) as a response variable, the results tended towards the predicted direction. That is, students were more likely to distinguish the deviantly moving object in

Table 2. Subset 1: distribution of correct and incorrect identifications when only the observations where the elapsed time was ≤ 10 seconds and the deviantly moving object was assigned to either the lowest or the uppermost position.

Identification	Black	Gradient	Spotted	Striped
Correct	10	3	6	8
Incorrect	10	11	14	20
Correct identifications (%)	50	21	30	29

Table 3. Subset 2: distribution of correct and incorrect identifications when only the observations where the elapsed time was ≤ 10 seconds and the deviantly moving object was assigned to the relative upper, middle, or lower position.

Identification	Black	Gradient	Spotted	Striped
Correct	28	34	29	24
Incorrect	25	20	15	9
Correct identifications (%)	53	63	66	73

animations where the objects possessed striped filling as compared with animations where the objects had other color patterns (i.e., spotted, gradient and black). Further, students were more likely to make an erroneous identification when the deviating object was assigned to the uppermost or the lowest position. It seems that in order to identify the deviating object, it is beneficial to have a comparison, or reference point (i.e., another object) on both sides of the deviantly moving one.

The initial hypothesis suggests that objects with certain color patterns, for example stripes (like those of a zebra) create a structured background of moving patterns upon which deviant object(s) would easily be distinguished. One would therefore assume that the structure that potentially facilitates identification would do so to a greater extent if the deviating object was assigned to a position in the middle of the group of objects. These assumptions are supported by the interaction effects between position and color pattern on the probability for correct identification and on the time used for correct identification. In both cases zebra stripes is the color pattern that, to the largest extent, eases the identification of odd behavior. In order to further investigate the effect of a structured background (i.e., the deviating object was assigned a position inside or in the periphery of the group of objects) two subsets of data were considered. In both subsets the time used in the animations was limited to 10 seconds. This was done in order to omit the potential observations where students used superfluous time in order to ensure their identifications. Further, limiting the time to 10 seconds allowed us to operate in the time-span where making the correct identification was most demanding, and thus where any visual amplifier of deviant behavior would be helpful. In the subset where the deviating object was assigned to a position in the periphery of the group no significant effects of color patterns were found, although the animations with black objects came out with most correct identifications as compared with the other color patterns. Further, in the subset where the deviating object was assigned to a position inside the group no significant effects of color patterns were found. However, the animations with striped objects came out

with most correct identifications as compared with those with the other color patterns (24 correct to 9 incorrect). The tendency in subset 2, where the deviating object was positioned inside the group, emphasize the importance of the position of the deviantly moving object, which, in order to achieve the hypothesized amplifying effect of color pattern(s), should be inside the group. Position inside the group would make an individual a part of the structured background, more so than if it was in the periphery of the group. Thus, as we narrow the conditions of the model down to situations where one can assume that the need for visual amplifiers become more acute, it seems that patterns in the predicted direction appear.

As zebra stripes follow the shape of the body, rather than run in random directions, it has been suggested that stripes therefore accentuate bodily features, i.e., signal shape and size of muscles (Zahavi & Zahavi 1997). Although we agree that stripes are not running in random directions, and that stripes accentuate individual's quality, we would rather suggest an alternative mechanism. The Zahavian handicap hypothesis is a very powerful explanation as most traits can be imagined to have a cost. However, the costs can actually limit the evolution of signals. As amplifiers bear no costs (per definition the benefits to high-quality individuals outweigh the costs to low quality individuals; Hasson 1991) they might actually evolve less constrained. We therefore suggest that zebra stripes run in their particular directions, i.e., vertical on the front part and horizontal on the hind part, because they amplify underlying behavioural traits when the zebras are running. Consequently, the hind parts horizontal stripes may amplify individual's ability to perform synchrony with the rest of the group in vertical motion i.e., altitude or frequency of steps or jumps. Accordingly, the vertical stripes in the front part may amplify the ability of individuals to adjust to the groups changing speed or direction, that is, the horizontal movement. The results of this study support these suggestions.

A method, like the one presented here, where artificial objects replace real performers (i.e., prey), and human observers replace real evaluators (i.e., predators) is not common, although some experiments have successfully exploited

this approach. An experiment performed on sex role reversed pipefish, where the males prefer mating with the largest females, used this method in order to investigate whether the pattern on the surface of the females facilitated distinguishing between females of different size (Berglund 2000). When students were asked to compare bar sizes, where bars differed in ornamentation, accuracy in estimating size was highest with heavily ornamented as compared with intermediate or not ornamented bars (Berglund 2000). Moreover, the bar size was more accurately judged with crosswise as compared with lengthwise striped bars, explaining why stripes run crosswise rather than lengthwise in females. Unlike in the method presented in our study, the evaluated objects were sessile. Including motion into a model increases the number of parameters, and thus complicates capturing the selective forces that are present in the real system. Further, in the human visual system, there are differences in the mechanisms that process the visual assessment of movements depending on whether the ones moving and observed are humans or objects (Pinto & Shiffar 2002). Including movement into a model like the one presented here, can therefore be difficult. However, as the moving individuals were an essential parameter in the initial hypothesis, movement had to be included.

The amount of variance explained by experimental and descriptive studies decreases from the fields of physiology over ecology to evolution, and biological studies will often only explain a very small amount of variance (Møller & Jennions 2002). Therefore, when evaluating the accomplishments of different fields of research these discrepancies should be taken into consideration. In evolutionary processes a minor difference in a trait can cause selective forces either to favor or to disfavor it. This is a serious problem when studies like the one presented here are designed. Even if zebra stripes have the suggested selective advantage, it is extremely difficult to set the initial parameters of the character in question and the other components in an experiment, in a manner that captures the selective forces that are present in the real system. Further, the human eye and the eye of a predator are not equally trained towards, nor are they equally selected for, observation of a

moving zebra flock. The level of observational capacity in an average human might function at a level of distinguishing oddities in tattoo bands, whereas lions, due to co-evolution between signaler and receiver, can potentially use the same mechanism in more complex systems. Therefore the simplifications made in the animations are partly justified.

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