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Using information theory to assess dynamics, structure, and organization of crayfish agonistic repertoire

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Abstract

Information theory measures provided useful quantitative tools for describing the transfer of information in interacting pairs of the eastern white-river crayfish, *Procambarus acutus acutus*, and furnished hints for deciphering the dynamics, structure, and organization of the agonistic repertoire in this species. As a confirmation of the predictive and heuristic potentials of the theory, results suggested hypotheses on the mechanisms underlying the formation and maintenance of dominance hierarchies in crayfish and indicated the directions that future developments of the research should follow.

Keywords: Agonistic behavior; Dominance hierarchies; Information theory; Freshwater crayfish; *Procambarus acutus acutus*

1. Introduction

Information theory, developed in the early 1950s (Shannon, 1948; Shannon and Weaver, 1949), revolutionized the field of communication by providing elegant methods for quantifying the amount of information that can be exchanged across a channel. Since the early years of its formulation, the theory "has perhaps been ballooned to an importance beyond its actual accomplishments" (Shannon, 1956), extending its application from the original field of communication engineering to a diverse range of disciplines, including biology, psychology, linguistics, fundamental physics, and economics. Despite the 'bandwagon effect' lamented by Shannon (1956), when the concepts and methods fostered from information theory have been properly applied, the predictive and heuristic values of the theory appeared to be high, as shown, for instance, within several biological disciplines (see, e.g. Reinagel, 2000; Weiss et al., 2000; Stone, 2001; Ulanowicz, 2001; Weinberger, 2002; Yockey, 2002).

The importance of measuring information has received considerable attention by ethologists and brought insights into the field of animal communication (for reviews, see Bradbury and Vehrencamp, 1998; McCowan et al., 1999). However, after a flourishing of studies in the 60s and 70s (e.g. Haldane and Spurway, 1954; Wilson, 1962; Altmann, 1965; Hazlett and Bossert, 1965; Dingle, 1969, 1972; Steinberg and Conant, 1974; Preston, 1978), the identification of both conceptual and technical pitfalls of the information analysis (Wilson, 1975) seems to have hampered a formal assimilation of information theory within the theoretical corpus of ethology.

The most serious difficulty lies in the observer's inability of recognizing all of the signals and their

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different sensorial components, as well as of correctly perceiving the other organism's response. Then, several large categories of signals, for instance graded signals, are hard to factorize into elemental messages and the amount of information transmitted by the same message sometimes changes with one animal's experience, age, and context (Wilson, 1975).

Furthermore, a large sample size is essential for the information theoretic approach to realize the full potential of its analytical capabilities (McCowan et al., 1999). Due to this limitation, few investigators (e.g. Chatfield and Lemon, 1970; Hailman and Ficken, 1986; Hailman et al., 1985, 1987; Ficken et al., 1994; Hailman, 1994; Da Silva et al., 2000) have been able to apply information measures to sequential signaling as a means for deciphering the structure and organization of communication systems at the individual, population, or species level.

One additional reason that might have tempered ethologists' enthusiasm towards information theory lies in that the original information measure (entropy) refers to the uncertainty resulting from the transmission of a message, and not to its significance for the receiver. Shannon was interested in answering the question as of how accurately the symbols that encode the message could be transmitted. His exclusive concern was 'the technical problem' (Weaver's introduction to 1962 edition of Shannon and Weaver, 1949). Therefore, the semantic content of the transmitted message and its efficiency in changing the receiver's behavior are both irrelevant to the characterization of communication systems. The actual message is the one selected from a set of possible messages (Shannon, 1948), no matter its meaning, and the information conveyed during this process is a mere measure of the average number of choices performed by the transmitter, that is Shannon's entropy.

Our purpose here is to identify some properties of information theory that make it a useful (even if not omnipotent; Losey, 1978) frame for the study of animal communication. We will show that the complexity of information transfer can be reliably measured in narrow, easily perceived communication systems, using as a case study the agonistic behavior in crayfish. Information analytical techniques appear feasible and desirable there in that they function as a unique tool for the description of the agonistic repertoire and the prediction of the temporal course of aggression.

2. Methods

2.1. Data collection and analysis

Data were borrowed from Gherardi and Daniels (2003), who analyzed the dynamics of agonistic interactions occurring during the formation of dominance hierarchies in the eastern white-river crayfish, *Procambarus acutus acutus*. This is a relatively common species occurring in moderately flowing streams or rivers and lentic waters (swamps, ditches, sloughs, and ponds) within an area extending between Maine and Georgia, Florida and Texas, and Minnesota and Ohio (Williams and Bivens, 1996).

Twenty-three symmetric pairs of crayfish, composed of form I, size-matched males, were observed for one hour per day during five consecutive days of cohabitation. Detailed description of the experimental protocol and of the rationale behind it can be found in Gherardi and Daniels (2003).

In the present study, an overall of 1654 agonistic interactions were analyzed, where an agonistic interaction was defined as the sequence of behavioral patterns (BPs) that started when one opponent approached the other and ended when one of the two crayfish retreated at a distance longer than one crayfish body length for at least 10 s.

On the overall, we distinguished 20 BPs (Table 1), following in part the ethogram provided by Bruski and Dunham (1987) for *Orconectes rusticus*. BPs were classified on the basis of their visual components only, but obviously we cannot exclude the simultaneous emission of urine-borne chemical substances that are known to contribute to the information transfer in hierarchies of decapods (e.g. Zulandt Schneider et al., 1999; Breithaupt and Atema, 2000).

If there was no visual 'response' on the part of one individual to an act of the other, the 'dummy act' (Rowe and Harvey, 1985), No Observable Change (NC), was recorded as a following BP. As discussed by Steinberg (1977), through the insertion of such an apparently neutral act, the danger of masking the order of BPs is far less than the danger of distorting data by ignoring a consistent part of the behavior. On the other hand, under the hypothesis that information transfer occurs also through chemicals, NC might correspond

Table 1
Codes and short description of the 20 behavioral patterns that form the agonistic repertoire of the crayfish *Procambarus acutus acutus*

Code	Behavioral pattern	Description: a crayfish ...
AF	Antennule Flicking	rapidly displaces one or both flagella of one or both antennules upwards and downwards.
BK	Moving Backward	walks backwards, away from its opponent, within a distance of less than one body length.
CA	Casual Approach	approaches a stationary opponent from behind or from the side.
CI	Interlocked	has both chelae open and interlocked with those of the opponent.
CS	Chela Strike	strikes its opponent's body using one, rarely both, chelae.
DA	Direct Approach	walks towards a stationary opponent that is more than one body length away.
FZ	Freezing	suddenly interrupts any action and assumes a body down posture.
GR	Grasping	grasps the opponent's body using one or both chelae.
HU	Hugging	uses its chelae to embrace the opponent's body.
MF	Moving Forward	moves towards its opponent within a distance of less than one body length.
MO	Motionless	remains motionless to an action of its opponent.
MS	Meral Spread	extends both chelae laterally and upwards.
NC	No Observable Change	continues the action, except Motionless, it was performing before the action of the opponent.
PU	Pushing	pushes the opponent's body using one or both chelae.
RT	Retreat	retreats from its opponent at a distance longer than one body length.
TF	Tail Flipping	is propelled backwards by a sudden contraction of the abdomen.
TO	Touching	touches the opponent's body using one or both chelae.
WB	Walking Below	walks below the opponent's body.
WO	Walking Over	walks over the opponent's body.
OT	Other	

to a burst of urine release; its identification appears, therefore, necessary for a realistic description of the agonistic communication.

We distinguished the identity of the transmitter (i.e. the crayfish that performed a BP), as opposed to the receiver, and its hierarchical rank. We deemed as dominants or alphas (as opposed to subordinates or betas) those individuals winning more than 50% of the interactions battled in the last day of cohabitation. The winner was the crayfish which did not retreat or which retreated after the opponent suddenly interrupted any action or remained motionless.

Every agonistic interaction was represented by a string, each element of which was a BP. We recorded strings of length between 2 and 103 BPs. Their sequence resulted from the regular alternation of the BPs performed by the two interactants. In the following, we will define as *n*-grams sub-sequences composed of *n* consecutive BPs (e.g. digrams, trigrams, tetragrams, and pentagrams if the sequence was composed of two, three, four, and five BPs, respectively). The subdivision of sequences into shorter units was the first step to compute transition probabilities for describing the information flow between the opponents and for analyzing the influence of the context on crayfish behavior.

2.2. Shannon's entropies

With the only exception of the Kullback–Leibler divergence, we refer here to some direct applications of the original information theory (Shannon and Weaver, 1949). In particular, to address the question of the organizational complexity in crayfish agonistic repertoire, we computed zeroth- to third-order entropies, while the second-order entropy was used to estimate the amount of information per behavioral pattern.

A zeroth-order model assumes that all the BPs in the repertoire are independent and equiprobable. The entropy per BP associated to this model (i.e. the zeroth-order entropy, the upper limit of the transmissible information) is measured as

$$H_0 = -\log_2 N \quad (1)$$

where N is the overall number of the BPs in the crayfish repertoire (in our case, $N = 20$). H_0 is therefore a measure of the repertoire diversity.

A first-order model takes into account the different probability of occurrence of each BP, which is however still assumed independent from the other BPs. The entropy per BP (i.e. the first-order entropy) associated

to this model is:

$$H_1 = -\sum_{i=1}^{N} p(i) \log_2 p(i) \quad (2)$$

where $p(i)$ is the probability of occurrence of the BP i, N is the overall number of BPs in the crayfish repertoire. H_1 is an estimate of the simplest degree of internal organization in the communication system.

A second-order model introduces conditional probabilities into the structure of the communication system. The entropy per BP associated to this model (i.e. the second-order entropy) is computed from Eq. (3):

$$H_2 = -\sum_{i,j=1}^{N} p(ij) \log_2 p(j|i) \quad (3)$$

where $p(ij)$ is the joint probability of occurrence of the BPs i and j (i.e. the digram ij); and $p(j|i)$ is the conditional probability of occurrence of j preceded by i; N is the overall number of BPs in the crayfish repertoire.

In general, nth-order models introduce conditional probabilities given the $n-1$ BPs in the observed sequence, and therefore examine how a BP is influenced by increasingly longer contexts.

2.3. Kullback–Leibler divergence

Hierarchical ranks were compared for their agonistic repertoire using the 'Kullback–Leibler divergence'. In 1951, Kullback and Leibler proposed a statistical theory of information (called 'discrimination function', and later referred to as 'cross entropy' or 'relative information'), involving two probability distributions associated with a discrete random variable, and introduced a measure of the distance between two probability distributions, the Kullback–Leibler (KL) divergence. This is defined by

$$\delta(p^1, p^2) = \sum_{i=1}^{N} p^1(i) \log_2 \left(\frac{p^1(i)}{p^2(i)} \right) \quad (4)$$

where N is the overall number of different events (here the BPs) within the analyzed repertoire; 1 and 2 refer to the first and the second probability distributions under analysis; and $p(i)$ is the probability of occurrence of the event (=BP) i.

2.4. Statistical analyses

We followed the procedures found in Sokal and Rohlf (1969) and Siegel and Castellan (1988). Non-parametric tests (i.e. Friedman two-way Analysis of Variance followed by a Multiple Comparisons test and Spearman rank correlation test) were used when the assumptions of normality of distribution and homogeneity of variances were not met. In the other instances, we utilized a one-way ANOVA, the Pearson correlation test, and an ANCOVA. Comparisons between observed and expected frequencies of n-grams were made through a G-test adjusted by William's correction. Probability values of less than 0.05 were considered statistically significant.

3. Results

3.1. Dynamics and structure of the agonistic repertoire

3.1.1. Information flow

A Markovian graph of the information flow within the agonistic communication of crayfish (Fig. 1) was generated by choosing the most likely digrams occurring in a set of 8984 digrams that resulted from 577

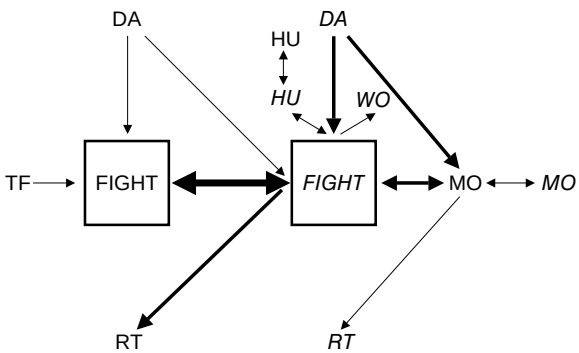

Fig. 1. Markovian graph showing the information flow in *Procambarus acutus acutus* agonistic communication, based on the most frequently observed digrams. Except "fight" (see Fig. 2), states are single behavioral patterns (for the correspondence between codes and behaviors, see Table 1). Behavioral patterns in italics and not in italics were performed by, respectively, dominant and subordinate crayfish. Sequences of states are depicted as arrows, their thickness being calibrated to the magnitude of probabilities (>50, 5–50, and <5%).

agonistic interactions analyzed in the first hour of cohabitation, when hierarchies are formed (Gherardi and Daniels, 2003). As shown for other taxa (e.g. three-spined sticklebacks, Losey and Sevenster, 1995; fruit flies, Chen et al., 2002) and in spite of the theoretical limitations listed by Losey et al. (2001), the estimated sequential relationships between behavioral acts can provide clues on the predictability of behavior. For example, after having approached the opponent, the dominant crayfish will enter the 'fight' state with a transition probability as low as 5%. Once the dominant has entered that state, there is a probability of 64% that, on its turn, the subordinate will enter the same state. The 'fight' state for the subordinate will be followed by the 'fight' state for the dominant in 68% of the times. Thus, fighting appears self-reinforcing and sequences 'fight'–'fight' only ended when the subordinate retreated, an event that followed the 'fight' state for the dominant with the probability of 5%.

The 'fight' state corresponds to a sequence of BPs that include physical contacts, such as Grasping, Pushing, and Touching. The most likely sequences that appear in the 'fight' state and the higher probability of transitions between BPs (Fig. 2) were obtained by the analysis of the highly recurring sub-sequences of two BPs (digrams) up to five BPs (pentagrams). The 'fight' state was assigned to the individual that moved forward for the most times, most often touched the rival, and made most frequent use of grasps and pushes.

3.1.2. Amount of information per behavioral pattern

The contribution that each behavior had to the information flow of crayfish aggression was estimated by computing a value $H_2(i)$ for each BP (with the obvious exclusion of Retreat that is followed by no BPs for its definition) (Table 2). This was obtained by decomposing H_2 in Eq. (5):

$$H_2 = -\sum_{i=1}^{N} p(i) \sum_{j=1}^{N} p(j|i) \log_2 p(j|i) = -\sum_{i=1}^{N} p(i) H_2(i) \quad (5)$$

Table 2
Probability of occurrence, $p(i)$ and contribution to the second-order entropy (in bits), $H_2(i)$, of every behavioral pattern

	$p(i)$	$H_2(i)$
*	0.106	1.07
AF	0.008	2.17
BK	0.091	1.44
CA	0.01	2.35
CI	0.005	1.68
CS	0.005	2.34
DA	0.047	2.19
FZ	0.006	2.03
GR	0.051	2.50
HU	0.037	2.35
MF	0.112	1.76
MO	0.060	2.61
MS	0.033	2.49
NC	0.224	2.42
PU	0.076	2.33
TF	0.011	0.14
TO	0.099	2.24
WB	0.004	2.62
WO	0.012	1.95
OT	0.003	1.97

(*) denotes the start of the sequence of BPs and is always followed by either CA or DA (in fact, its $H_2(i)$ is around 1). See Table 1 for the correspondence between codes and behavioral patterns.

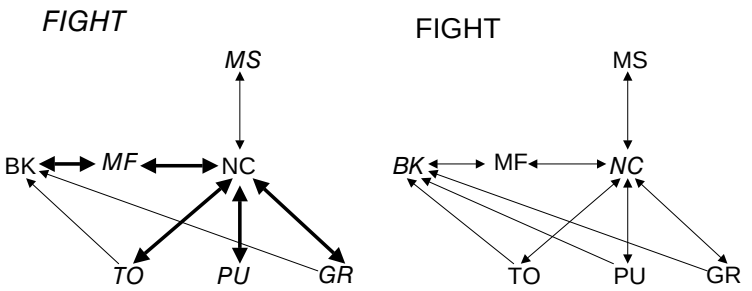

Fig. 2. Markovian graphs showing the information flow in the "fight" state, generated from the analysis of digrams–pentagrams. "Fight" (not in italics) is assigned to subordinates (left) or (in italics) to dominants (right). Other explanations in Fig. 1.

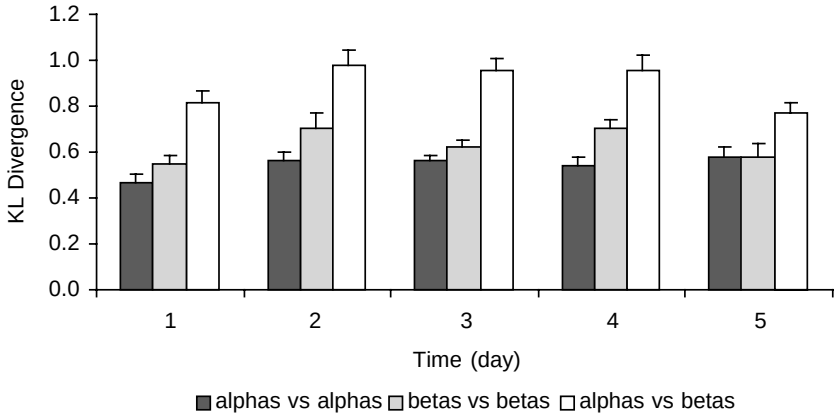

Fig. 3. Kullback–Leibler divergence (mean ± S.E.) computed for the agonistic repertoires of dominant and subordinate individuals and compared in the five days of cohabitation among: alphas of each pair (alphas vs. alphas), betas of each pair (betas vs. betas), and pairs of alphas and betas (alphas vs. betas).

If we exclude Chelae Interlocked (CI), Moving Backward (BK), Moving Forward (MF), and Tail Flipping (TF), $H_2(i)$ always ranged around the estimate of the overall second-order entropy for BP, i.e. 1.95 bits. A larger amount of information was transmitted by Grasping (GR), Motionless (MO), Meral Spread (MS), No Observable Change (NC), and Walking Below (WB) ($H_2(i) > 2.40$ bits).

3.1.3. Diversity of the repertoire between ranks

The Kullback–Leibler divergence was here applied to compare the probability distributions of BPs in the agonistic repertoire of alphas and betas and their eventual changes with time. For each day of cohabitation, we computed KL divergences among alphas of each pair (alphas versus alphas, $n = 23$), among betas of each pair (betas versus betas, $n = 23$), and among pairs composed of one alpha and one beta (alphas versus betas, $n = 23$). Agonistic repertoires diverged always to a greater extent between individuals of opposing hierarchical ranks than within dominants and within subordinates (after a one-way ANOVA, day 1: $F = 19.40$; day 2: $F = 13.35$; day 3: $F = 30.39$; day 4: $F = 18.34$; day 5: $F = 5.83$; d.f. $= 2, 66$, P at least <0.05; after Tukey test, $P < 0.05$: alphas versus betas $>$ alphas versus alphas $=$ betas versus betas) (Fig. 3). KL divergences remained constant with the time of cohabitation (after Pearson correlation test, alphas versus alphas: $r = 0.710$; betas versus betas: $r = 0.142$; alphas versus betas: $r = -0.183$, d.f. $= 3$, $P > 0.05$).

3.2. Organization of the repertoire

3.2.1. Effect of the opponent's behavior

We followed the methods of Hazlett and Bossert (1965), Dingle (1969), Losey (1978), Steinberg (1977), and Huber and Kzravitz (1995), but we limited our analysis to inter-individual sequences since our exclusive interest was to describe the exchange of information occurring between the two interacting individuals.

We constructed stochastic matrices in which the frequency of every digram *ij* (nonparenthetical numbers) is given in the *i*th row and in the *j*th column (Tables 3 and 4). The two matrices differ in that transmitters were alphas (and receivers were betas) in Table 3, and transmitters were betas (and receivers were alphas) in Table 4. Frequencies were obtained from 13,673 and 13,221 digrams for Tables 3 and 4, respectively. The parenthetical numbers in the matrices indicate the expected frequencies of occurrence for every digram *ij* under the assumption that the BP *i* and the BP *j* were independent, that is the transition *i*–*j* was random. Expected frequencies were obtained by multiplying the total of

Table 3
Matrix showing the frequency of every digram *ij* (nonparenthetical numbers), where *i* is the behavioral pattern that precedes (in rows) and *j* is the behavioral pattern that follows (in columns)

	AF		BK		CI		FZ		GR		HU		MF		MO		MS		NC		PU		RT		TF		TO		WO		*ni*
AF	25(1)	+	14(15)	=	0(0)		0(1)		2(4)		0(3)		7(7)		15(9)	=	1(3)		32(38)	=	4(6)		2(7)		0(2)		1(7)		0(1)		103
BK	4(4)		13(88)	−	1(2)		3(4)		2(24)	−	1(15)		348(39)	+	46(50)	=	15(18)	=	108(216)	−	9(32)	−	32(43)	=	0(10)		6(42)	−	3(3)		593
CA	0(1)		26(26)	=	0(1)		0(1)		1(7)		2(4)		5(11)		61(15)	+	11(5)		37(63)	−	1(9)		19(12)	=	5(3)		4(12)		0(1)		172
CI	0(0)		0(7)		22(0)	+	0(0)		2(2)		1(1)		1(3)		0(4)		2(2)		16(18)	=	2(3)		0(4)		0(1)		4(4)		0(0)		50
CS	0(0)		11(9)	=	1(0)		0(0)		4(2)		1(1)		1(4)		2(5)		1(2)		22(22)	=	0(3)		5(4)		9(1)		3(4)		0(0)		61
DA	1(6)		196(144)	=	5(4)		4(6)		2(39)	−	2(24)	−	29(63)	−	201(82)	+	31(30)	=	358(351)	=	11(53)	−	97(70)	+	10(17)	=	18(68)	−	0(6)		965
GR	8(6)		141(147)	=	5(4)		5(6)		75(40)	+	42(24)	+	19(65)	−	51(84)	−	41(30)	=	401(359)	=	54(54)	=	42(71)	−	46(17)	+	49(70)	=	0(6)		985
HU	3(4)		78(110)	−	1(3)		0(5)		40(30)	=	110(18)	+	17(48)	=	69(63)	=	30(23)	=	283(269)	=	51(40)	=	19(53)	=	6(13)		29(52)	−	0(4)		738
MF	3(15)		412(385)	=	1(9)		13(17)	=	35(105)	−	20(63)	−	71(169)	−	81(219)	−	36(79)	−	1605(942)	+	39(141)	−	181(187)	=	46(45)	=	41(183)	−	0(15)		2586
MO	8(4)		30(99)	−	0(2)		3(4)		12(27)	−	11(16)	=	78(44)	+	163(57)	+	6(20)	−	163(243)	−	33(36)	=	88(48)	+	0(12)		51(47)	=	21(4)	+	667
MS	3(3)		82(78)	=	1(2)		3(3)		17(21)	=	9(13)	=	29(34)	=	27(45)	−	26(16)	=	213(192)	=	37(29)	=	37(38)	=	16(9)	=	25(37)	=	1(3)		526
NC	19(13)	=	0(337)	−	2(8)		19(15)	=	286(92)	+	87(55)	+	191(148)	+	40(192)	−	130(69)	+	209(825)	−	403(124)	+	175(163)	=	60(39)	+	580(161)	+	37(13)	+	2264
PU	1(9)		426(236)	+	6(6)		19(10)	=	32(64)	−	31(39)	=	49(104)	−	139(134)	=	43(48)	=	607(577)	=	50(86)	−	102(114)	=	6(28)	−	54(112)	−	12(9)	=	1583
TO	6(12)		572(312)	+	5(8)		16(14)	=	45(85)	−	18(51)	−	49(137)	−	169(177)	=	35(64)	−	833(762)	=	43(114)	−	168(151)	=	32(36)	=	100(148)	−	1(12)		2092
WO	0(1)		31(33)	=	0(1)		3(1)		1(9)		0(5)		0(14)		88(19)	+	9(7)		60(80)	=	6(12)		15(16)	=	2(4)		3(16)		0(1)		219
nj	81		2037		50		90		557		335		896		1160		418		4980		747		987		238		970		80		

Frequencies were obtained from 13,673 digrams. Alphas execute the behavioral pattern *i* and betas execute the behavioral pattern *j*. The parenthetical numbers indicate the expected frequencies of occurrence of every digram *ij* under the assumption that the transition between *i* and *j* occurred randomly and exclusively depended on the relative frequencies of *i* and *j*. +, −, and = mean that observed frequencies are significantly higher or lower than, or are equal to, the expected ones using the *G*-test adjusted by William's correction. This analysis was not done for sample size smaller than 20 (empty cells). Behavioral patterns having a row/column total less than 50 were excluded from the matrix (FZ, OT, TF, and WB in rows, with a row total of 6, 1, 27, and 35, respectively; CS, OT, and WB in columns, with a column total of 30, 7, and 10, respectively). See Table 1 for the correspondence between codes and behavioral patterns.

Table 4
Matrix as in Table 3 with betas executing the behavioral pattern *i* (in rows) and alphas executing the behavioral pattern *j* (in columns)

	AF		BK		CI		CS		FZ		GR		HU		MF		MO		MS		NC		PU		RT		TO		WO		*ni*
AF	28(1)	+	3(4)		0(0)		0(0)		1(0)		1(6)		1(5)		7(16)	=	13(4)		0(3)		21(14)	=	2(10)		1(4)		3(13)		0(1)		81
BK	11(17)	=	43(101)	−	0(8)		0(10)		0(9)		17(167)	−	22(125)	−	1634(439)	+	113(113)	=	56(89)	−	151(388)	−	18(269)	−	130(105)	=	41(355)	−	8(37)	−	2246
CA	0(1)		3(4)		0(0)		1(0)		0(0)		2(6)		2(5)		21(16)	=	21(4)	+	8(3)		12(14)	=	4(10)		3(4)		7(13)	=	0(1)		84
CI	1(0)		0(2)		30(0)	+	0(0)		0(0)		3(4)		0(3)		3(10)		1(3)		1(2)		11(9)	=	0(6)		0(2)		0(8)		0(1)		50
DA	0(3)		50(19)	+	0(2)		0(2)		0(2)		7(32)	−	4(24)	−	105(85)	=	91(22)	+	28(17)	=	101(75)	+	9(52)	−	25(20)	=	12(69)	−	1(7)		433
FZ	1(1)		0(4)		0(0)		1(0)		46(0)	+	1(7)		1(5)		9(18)	=	5(5)		2(4)		6(16)	=	13(11)	=	0(4)		4(14)		1(1)		90
GR	13(4)		31(25)	=	4(2)		8(3)		0(2)		91(41)	+	37(31)	=	37(109)	−	23(28)	=	20(22)	=	200(96)	+	34(67)	−	9(26)	−	43(88)	−	0(9)		557
HU	2(3)		11(15)	=	0(1)		1(2)		0(1)		31(25)	=	115(19)	+	10(66)	−	14(17)	=	11(13)	=	89(58)	+	28(40)	=	2(16)		20(53)	−	0(6)		335
MF	0(7)		100(41)	+	2(3)		1(4)		1(4)		25(68)	−	23(51)	−	79(179)	−	35(46)	=	18(32)	=	486(158)	+	41(109)	−	52(43)	=	46(145)	−	1(15)		914
MO	8(9)		40(52)	=	0(4)		2(5)		0(5)		33(86)	−	40(65)	−	189(227)	=	151(59)	+	13(46)	−	127(200)	−	161(139)	=	201(54)	+	139(184)	−	50(19)	+	1160
MS	1(3)		13(19)	=	3(2)		0(2)		0(2)		24(31)	=	32(23)	=	30(82)	−	15(21)	=	35(17)	+	149(72)	+	51(50)	=	22(20)	=	35(66)	−	4(7)		418
NC	27(37)	=	77(214)	−	0(18)		45(22)	+	1(19)	−	659(355)	+	366(266)	+	323(933)	−	31(241)	−	273(190)	+	0(823)	−	1109(571)	+	73(224)	−	1621(755)	+	135(79)	+	4771
PU	3(6)		103(34)	+	4(3)		0(3)		1(3)		41(56)	=	45(42)	=	55(146)	−	47(38)	=	28(30)	=	268(129)	+	61(89)	−	34(35)	=	41(118)	−	14(12)	=	747
TF	0(2)		1(11)		0(1)		0(1)		0(1)		0(18)		0(13)		2(47)	−	0(12)		0(9)		234(41)	+	0(28)	−	0(11)		0(38)	−	1(4)		238
TO	8(8)		105(44)	+	7(4)		2(4)		2(4)		42(72)	−	48(54)	=	75(190)	−	76(49)	+	30(39)	=	388(167)	+	44(116)	−	62(46)	=	76(153)	−	2(16)		970
WO	0(1)		10(4)		0(0)		0(0)		0(0)		0(6)		0(4)		3(16)		31(4)	+	1(3)		22(14)	=	7(10)		4(4)		1(13)		0(1)		80
nj	103		593		50		61		52		985		738		2586		667		526		2282		1583		621		2092		219		

Frequencies were obtained from 13,221 digrams. Behavioral patterns having a row/column total less than 50 were excluded from the matrix (CS, OT, and WB in rows, with a row total of 30, 10, and 7, respectively; OT, TF, and WB in columns, with a column total of 1, 27, and 35, respectively). Other explanations in Table 3.

the *i*th row by the total of the *j*th column and dividing it by the total number of digrams.

A comparison was made between the observed and the expected frequency distributions of digrams using a *G*-test adjusted by William's correction (we set 20 as the minimum sample size that allowed for reliable comparisons). This analysis furnishes suggestions on whether the BP *i* influenced the BP *j* that followed, addressing the question of whether the behavior performed by one crayfish had an effect on the subsequent behavior of the opponent. The influence can be either 'directive' or 'inhibitory' (in a statistical sense without any implication of causation, see Hazlett and Bossert, 1965 and Dingle, 1969), when the observed frequency is significantly higher or lower than the expected one, respectively.

Motionless (MO) and No Observable Change (NC) appeared to be more influential BPs in that they had an effect on more than 70% of the crayfish agonistic repertoire, as opposed to Hugging (HU), Meral Spread (MS), and Pushing (PU) that affected less than 50% of the repertoire (Fig. 4). We used the non-parametric Spearman rank correlation test to answer the question whether a BP had a different effect on the receiver in function of the hierarchical rank of the performer. For this analysis, the influence of every BP was ranked in two ordered series, one for alphas and one for betas. The precise correspondence of positions within the two series (i.e. the highly significant correlation between series; $r_s = 1$, $n = 7$, $P < 0.001$) suggests that the relative influence of every BP was independent of the rank of the performer.

3.2.2. *Effect of the context*

We hypothesized that the influence exerted by a particular BP on the BP that followed might depend on the previous behavior or on the behavior before that, that is it might depend on a context longer than one BP. For example, what crayfish No. 1 does (BP *j*) in 'response' to a given BP by crayfish No. 2 (BP *i*) might be also influenced by what crayfish No. 1 did before (BP A_1) or even by the behavior (BP A_2) previously performed by crayfish No. 2 itself. Therefore, the next step in the analysis was to work with trigrams of the type A_1–*i*–*j* and/or with tetragrams of the type A_2–A_1–*i*–*j*. The frequency distributions of BPs *j* following A_1–*i* and of BPs *j* following A_2–A_1–*i*, were compared with the frequency distribution of BPs *j* following *i* regardless of the preceding BPs (see, also Hazlett and Bossert, 1965, and Dingle, 1969).

One example was that, when one crayfish moved forward (MF), the interactant most often displayed a No Observable Change (NC) (in 55.11 and 49.21% of the times when the moving crayfish was alpha and

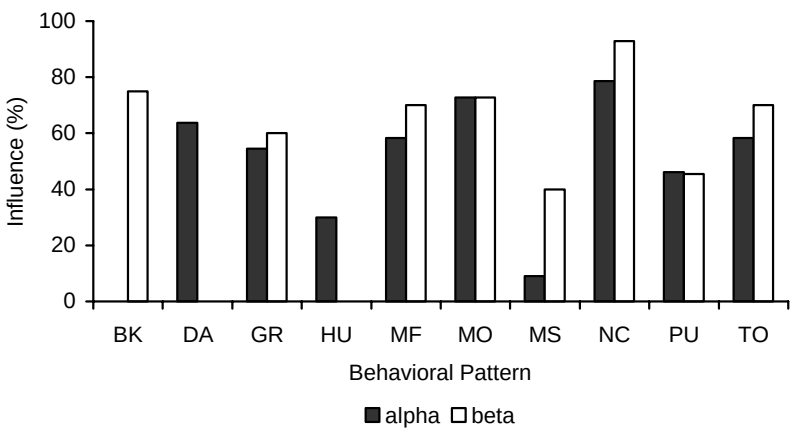

Fig. 4. Influence of the behavioral patterns in crayfish agonistic repertoire (distinguished on the basis of the hierarchical rank of the executor). This was computed as the frequency of the behavioral patterns that follow (in percent on the whole repertoire), the execution of which was significantly influenced by that particular behavior, as estimated by comparing observed and expected frequencies of digrams *ij* (see Tables 3 and 4) using the *G*-test adjusted by William's correction. Only those behavioral patterns are shown, in which the *G*-test was applicable for at least 15 cells of the matrices.

beta, respectively) or less often moved backward (BK) (in 19.20 and 12.57% of the times). As a second example, when one crayfish moved backward (BK), the most frequent BPs performed by the interactant were, in decreasing order of occurrence, MF (in 58.68 and 72.75% of the times), NC (in 18.21 and 6.72% of the times), and MO (in 7.58 and 5.03% of the times). For the first example, comparisons were made between the distribution of BPs *j* following MF and the distributions of BPs *j* following A_1–MF (here A_1 was either BK or MO or NC); for the second example, we compared the distribution of BPs *j* following BK with the distributions of BPs *j* following A_1–BK (here A_1 was either DA or MF or NC or PU or TO or BK). As shown in Table 5, no significant differences were found. That is, in both the analyzed cases (we set 100 as the minimum number of sequences that allowed for reliable comparisons between samples), when one crayfish moved forward or moved backward, independently of its hierarchical rank, the interactant performed NC or MF, respectively, no matter which its previous behavior was. In other words, a one-BP long context had no apparent effect on the informative value of either MF or BK and this was independent of the hierarchical rank of the crayfish executing those BPs.

Table 5
Effect of the context composed of one behavioral pattern (in rows) on the digrams MF-*j* and BK-*j*

	Alpha	Beta
Digram: MF-*j*		
BK-	21.941	23.331
MO-	21.783	11.429
NC-	22.168	11.494
Digram: BK-*j*		
DA-	5.492	18.954
MF-	22.748	18.456
NC-	13.241	10.195
PU-	7.739	10.922
TO-	12.817	14.466

See Table 1 for the correspondence of codes and behavioral patterns. *j* is one behavioral pattern in the agonistic repertoire of *Procambarus acutus acutus*, obviously excluding CA and DA that start agonistic interactions. MF and BK were either performed by the dominant or the subordinate crayfish. Cells provide the statistic of the *G*-test adjusted by William's correction that was used to compare the distribution of BPs *j* at the end of digrams with the distribution of BPs *j* at the end of the corresponding trigrams. In no case a significant difference was found; d.f. = 14.

Table 6
Effect of the context composed of one (left) or two (right) behavioral patterns on the digram NC-*j*

	Alpha	Beta
Analysis of trigrams		
BK-	365.542	234.105
DA-	86.989	98.348
GR-	98.62	121.675
HU-		93.829
MF-	309.719	343.586
MO-		226.423
MS-	50.213	65.205
PU-	109.3	234.105
TF-	532.195	
TO-	124.9	136.129
Analysis of tetragrams		
NC-GR-	71.23	90.032
NC-PU-	98.798	114.113
NC-TO-	138.345	34.434

See Table 1 for the correspondence of codes and behavioral patterns. NC was either performed by the dominant or by the subordinate crayfish. Cells provide the statistic of the *G*-test adjusted by William's correction that was used to compare the distribution of BPs *j* at the end of digrams with the frequency distribution of BPs *j* at the end of the corresponding trigrams or tetragrams. We excluded from the analysis (empty cells) the instances in which sample size was smaller than 100. Differences were always significant ($P < 0.001$); d.f. = 14. Other explanations in Table 5.

We were curious about the informative content of No Observable Change (NC). To understand whether NC was on its part influenced by the context, we conducted the same analysis as explained above and thus compared the distribution of BPs *j* following NC with the distribution of BPs *j* following A_1–NC. In all the analyzed cases (again 100 was set as the minimum number of sequences that allowed for reliable comparisons between samples) and in both ranks, significant differences were found after a *G*-test adjusted by William's correction (Table 6), suggesting that in this case the informative content of NC depended, at least in part, on the BPs that the other crayfish had performed before.

The analysis of tetragrams helps understand whether the informative value of NC is influenced by a context longer than one BP. For example, we identified tetragrams A_2–A_1–NC–*j* where A_2 was NC, A_1 was a grasp or a push or a touch, and NC was displayed by alphas or betas; then we compared the distributions of BPs *j* at the end of tetragrams

with the distributions of BPs *j* at the end of the corresponding trigrams and digrams. We found that the former significantly differed from the distributions of BPs *j* obtained from the analysis of digrams (e.g. in the case of A_1 = GR: $G = 71.230$ for alphas executing NC and $G = 90.03$ for betas executing NC; d.f. = 14; $P < 0.01$); they were different among themselves ($G = 84.997$ and 97.914; d.f. = 28; $P < 0.001$), but not from the distributions of BPs *j* obtained from the analysis of trigrams ($G = 4.884$ and 3.364; d.f. = 13; $P > 0.05$). Fig. 5 (for alphas executing NC, but similar results were obtained for betas) shows that differences among the three sets of distributions depended on the frequency of GR, PU, and TO, respectively. A GR (or PU or TO) as a BP *i* was less frequent at the end of digrams than at the end of trigrams and tetragrams, while its probability of occurrence was equal in these latter two cases. In other words, the probability of grasping (or pushing or touching) by a crayfish is independent of its rank and is affected by a previous grasping (or pushing or touching) by the same individual that was followed by doing nothing on the side of the interactant, no matter which the behavior previously performed by this latter crayfish was.

3.2.3. Entropic slope

The structural organization of the agonistic repertoire of crayfish and its temporal change can be estimated by applying the method developed by McCowan et al. (1999, 2002). Entropic slope was obtained by regressing *n*th-order Shannon's entropies against their corresponding entropic orders. As said above, Shannon's lower entropic orders furnish estimates of the repertoire structure, whereas higher entropic orders measure the importance of dependencies among signals in sequences. The more dependency between signals at each sequential level results in a communication system that has less entropy or fewer degrees of freedom in signal choice given that certain signals have already occurred (McCowan et al., 1999). Therefore, as the importance of signal sequential dependencies increases, entropic values for each subsequent entropic order progressively drop. A more negative entropic slope would indicate a higher degree of dependency and, thus, less statistical information or fewer degrees of freedom or lower entropy. On the one hand, this would mean more organizational complexity, as shown for the acoustical repertoires analyzed in bottlenose dolphins and squirrel monkeys by McCowan et al. (1999, 2002). On the other hand, an extremely negative entropic slope would result from a reduction in the number of different signals; therefore almost all degrees of freedom or choices in selecting signals are lost since there are few signals to choose from; this corresponds to a low, rather than a high, degree of organizational complexity or, in other words, to an increased stereotypy in the communication system.

Table 7 presents the estimates of zeroth- to third-order entropies as computed for the whole period of cohabitation and for every day taken separately (in this case each number was a mean of 20 pairs of crayfish; we excluded from the analysis three pairs where we did not record any agonistic interaction for at least one day of the whole period of cohabitation). Table 7 shows also the slopes (i.e. entropic slopes) and other parameters of the linear fit of entropic values against their entropic orders.

Entropies of every order (obviously excluding H_0) significantly differed among days (after the non-parametric Friedman two-way analysis of variance for related samples, H_1: $X_r^2 = 9.634$, d.f. = 4, $P < 0.05$; H_2: $X_r^2 = 21.320$, d.f. = 4, $P < 0.001$; H_3: $X_r^2 = 27.560$, d.f. = 4, $P < 0.001$). The decrease with time of first third-order entropies always occurred after the first day of cohabitation as shown by a Multiple Comparisons test (a modified Newman–Keuls test) ($P < 0.05$). After an ANCOVA, we found that entropic slopes for the second-fifth days of cohabitation were significantly steeper than the slope for the first day ($F = 4.219$, d.f. = 4, 390, $P < 0.01$).

4. Discussion

This study shows that information theory formalism can provide an excellent framework for the analysis of a relatively simple communication system. A number of quantitative tools developed by diverse authors showed to have a great potential in describing the transfer of information between interacting crayfish and provided hints for deciphering (a) dynamics, (b) structure, and (c) organization of the agonistic repertoire in *P. acutus acutus*. In addition, our results suggested hypotheses on the mechanisms

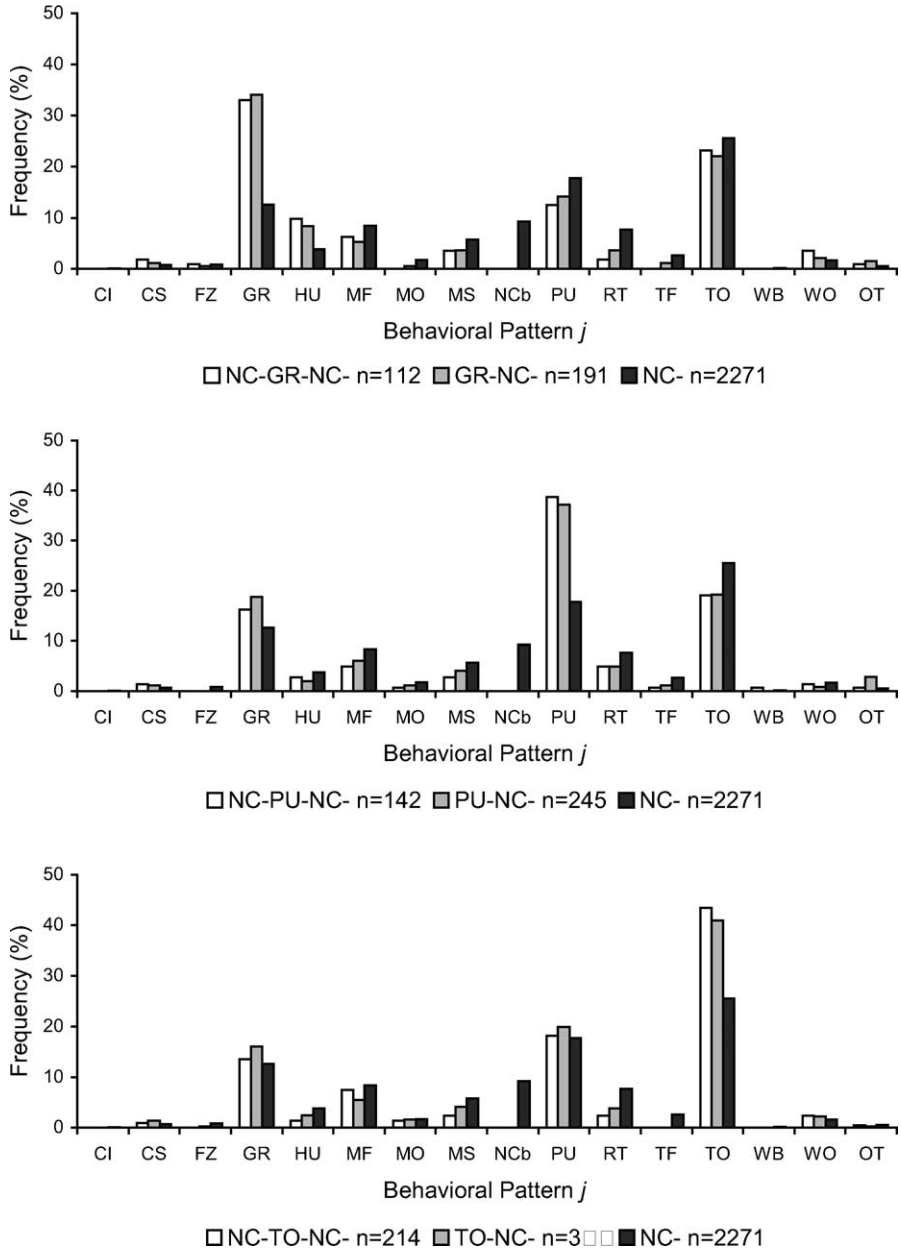

Fig. 5. Effect of the context on the informative value of No Observable Change (NC), when it was executed by alphas. Comparisons were made among frequency distributions of the behavioral patterns j that follow NC–A_1–NC, A_1–NC, and NC. In this example, A_1 was a tactile behavior, i.e. either Grasping (GR) (top), or Pushing (PU) (middle), or Touching (TO) (bottom).

underlying the formation and maintenance of dominance hierarchies in crayfish and indicated the directions that future developments of the research should follow.

First, we found that the 'fight' state is the core of the information flow, at least during the first hour of cohabitation when hierarchies are formed (Gherardi and Daniels, 2003). An analysis of *n*-grams showed that

Table 7
Zeroth-, first-, second-, and third-order entropies, slopes and other parameters of the linear fit of entropic values against their entropic orders for the agonistic repertoire in *Procambarus acutus acutus*

	H_0	H_1	H_2	H_3	r	d.f.	Slope	Elevation
Overall	4.17	3.38	1.95	1.25	−0.991	2	−1.019	4.215
Day 1	4.17	3.42 (0.02)	2.09 (0.06)	1.36 (0.06)	−0.977	78	−0.977	4.226
Day 2	4.17	3.29 (0.07)	1.67 (0.08)	0.95 (0.07)	−0.964	78	−1.127	4.211
Day 3	4.17	3.32 (0.03)	1.70 (0.09)	0.99 (0.07)	−0.966	78	−1.116	4.219
Day 4	4.17	3.36 (0.03)	1.74 (0.06)	1.01 (0.06)	−0.976	78	−1.111	4.236
Day 5	4.17	3.29 (0.04)	1.69 (0.08)	0.96 (0.08)	−0.968	78	−1.125	4.214

Figures are provided for the whole period of cohabitation and for every day taken separately. Entropic values for every day are means (S.E. in parenthesis; sample size = 20). Correlation coefficients r are always significant ($P < 0.01$).

'fight' was composed of a highly repetitive sequence of behavioral patterns, mostly resulting from an alternation between tactile behaviors and moves forward or backward. Although transition probabilities from other behavioral states to this state were low, 'fight' appeared self-reinforcing and sequences 'fight'–'fight' only ended when the defender retreated. Future studies should clarify whether the ability to endure in this state is an uncheatable prerogative of dominant individuals and/or this is a reliable cue adopted by the subordinates to assess their rival's agonistic superiority. Using a similar approach, Huber and Kzravitz (1995) showed that agonistic interactions in juvenile American lobsters escalated through various levels of intensity from meral spread displays to unrestrained combat using the claws and pass through periods of restrained physical combat, in which combatants were likely to receive direct information about each others vigor.

To describe the structure of the agonistic repertoire in *P. acutus acutus*, we estimated the contribution that every behavioral pattern had to the overall transmission of information, similarly to the attempt made by Steinberg and Conant (1974) for grasshoppers. This was nearly uniform in the crayfish repertoire and for all the behavioral patterns remained near the amount of the overall information delivered, with the exceptions of, for instance, Chelae Interlocked and Tail Flipping at the lowest levels and Grasping and Motionless at the highest levels.

Then, we examined the relative diversity between dominant and subordinate individuals for several aspects of their communication potential. Behavioral patterns seemed to influence to the same extent the opponent's response, that is the 'meaning' of every behavior was independent of one individual's status. On the other hand, the probability distributions of behaviors significantly diverged between the two ranks and this divergence was established since the first hour of cohabitation. This suggests that *P. acutus acutus* hierarchical ranks differed in the quality of their behavioral repertoire since the very start of combating, when also a significant decline in both the number of interactions battled and the agonistic level displayed was recorded (Gherardi and Daniels, 2003). Further studies are needed to understand whether this marked divergence is related to previous subtle constitutional differences between individuals other than body size and claw dimensions (Vye et al., 1997) or else it resulted from a quick definition of individual ranks as a possible consequence of chance events (Landau, 1951). Then, one intriguing question is whether the observed divergence in behavior is simply an epiphenomenon resulting from the formation of a dominance hierarchy or it functions as a reliable symptom of the rank and therefore is used by *P. acutus acutus* for recognizing the status of the rival (Zulandt Schneider et al., 2001).

The dynamics of *P. acutus acutus* agonistic communication was explored by measuring transition probabilities between two acts within inter-individual sequences through the analysis of digrams and examples of trigrams and tetragrams; these probabilities were compared with the probabilities expected under the assumption that transitions occur randomly. Some patterns in the crayfish repertoire, such as Motionless and No Observable Change, appeared to have a higher informative value than others (for instance, Hugging, Meral Spread, and Pushing) in that their positive or negative influence on the receiver's behavior was significantly higher. In addition, we assessed the role

exerted by the context to the expression of particular behavioral patterns. For instance, we found that the informative value of either Moving Forward or Moving Backward was independent of the context. On the contrary, no apparent changes in the behavior of one crayfish, if preceded by, for instance, a blow inflicted by the opponent, most likely induced the repetition of a blow by the same individual.

It seems apparent that the above applications of information theory provided clues on the structure of displays, as well as on the complexity of their sequential use, notwithstanding that the behavioral data examined cannot be said stationary and the sequence lengths are not infinite (for a discussion on the analytical limitations of information theory applied to animal behavior, see Rowe and Harvey, 1985). Both the 'semantics' and the 'effectiveness' problems are viewed as extraneous to Shannon's theory (Warren Weaver's introduction to 1962 edition of Shannon and Weaver, 1949) and it is a cliché to admit that informational analyses cannot directly measure the type of information transmitted. However, a dissection of the crayfish agonistic repertoire onto its elemental components indirectly gave insight into the meaning of the signals emitted, the amount of information being often linked to the type of information transmitted (McCowan et al., 2002; for review, see Bradbury and Vehrencamp, 1998). We have learnt from these analyses that there are some behavioral patterns, including 'doing nothing' (see, also Hazlett and Bossert, 1965), that show a high informative value since they exert a strong influence on the opponent's behavior and contribute to a large extent to the information exchange.

One limitation of our analysis is that we did not discriminate among sensory modalities that likely act in conjunction during information transfer. Evidences are in fact accumulating that support the idea that communication "goes multimodal" (Partan and Marler, 1999) also in decapods (e.g. Hughes, 1996; Acquistapace et al., 2002).Tactile signals may have a role in crayfish agonism, as suggested in *O. rusticus* (Bruski and Dunham, 1987). Besides, since Thorp and Ammerman's (1978) definition of an 'agonistic pheromone' in *P. acutus acutus*, the hypothesis that urine-borne chemical cues function as "badges of status" and/or backup signals in 'assessment' hierarchies (Barnard and Burk, 1979) has been consolidated within the crayfish literature (Zulandt Schneider et al., 1999, 2001), even if recently their role has been revised by Breithaupt and Eger (2002) under the viewpoints of 'confidence' hierarchies (Barnard and Burk, 1979) and 'winner and loser' effects (Issa et al., 1999; Goessmann et al., 2000). As a consequence, to provide a more realistic picture of communication systems in crayfish, future information analyses should lead to a dissection of the multiple sensory channels operating in conjunction within agonistic behavior by relying, for instance, upon methods for making visible urine release (Breithaupt and Eger, 2002). Aims will be to analyze the different contribute of each sensory modality to the agonistic communication and the potential advantage of multimodality to provide more reliable information for receivers (Rowe, 1999).

Our third attempt was to define the organization inherent to the agonistic repertoire of crayfish by computing the slope of Shannon entropies. This measure was introduced by McCowan et al. (1999) as an efficient tool for comparing the organizational complexity of diversified communication systems both within and across species. As it is generally true of information measures, it allows for "apples and oranges" comparisons (Beecher, 1989). If confronted with the only values at the moment available in the literature (from -0.50 and -1.33 for human languages, dolphin whistles, and squirrel monkey chucks; McCowan et al., 2002), an entropic slope of -1.019 might signify that the aggressive communication in crayfish contains a certain organized structure. The degree of organization does change with the time of crayfish cohabitation, since after the first day we obtained a significant drop in first-, second-, and third-order entropies and more negative entropic slopes. Since previous studies (Gherardi and Daniels, 2003) had shown that, with the exception of retreats and strong tactile patterns, the relative frequency of the other behavioral categories did not change with the time of cohabitation, these results could demonstrate that the formation of a dominance hierarchy is not accompanied with a substantial impoverishment of the repertoire, but on the contrary with an increase in the organizational complexity of the agonistic communication system.

Even though our analysis is bringing more questions than answers, one final remark is that, when the examined signals are sufficiently sampled, well quantified, and appropriately classified into discrete categories (Pierce, 1980), the investigators on animal

communication should benefit from the insights that information theorists have gained within the past 50 years.

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