

ISSN: 2641-1911

Archives in Neurology & Neuroscience

DOI: 10.33552/ANN.2021.11.000772



Research Article

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Compromise Between Individual Rationality and Collective Rationality in Decision-Making in *Schistocerca Gregaria* (The Desert Locust)

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Received Date: November 01, 2021

Published Date: November 18, 2021

Abstract

Animals living in groups interact with their environment and base their decision-making on the reliability of information sources such as the "personal information" and the "social information". As such, we studied the manner in which the information choice is made, within a simple nonsocial animal model, by assessing the compromise between individual and collective rationality in decision-making in the Desert Locust *Schistocerca gregaria* during the appearance of a predator. We analyzed the relationship between response times (jumping and freeze), the quality of required personal information as a function of group size and we checked the relationship between the choice of use of information (personal vs. social) and arrangement of locusts. Results show that, in small groups, locusts behave by individual rationality and use personal information regardless of its quality. As the group expands, and when personal information is sketchy, locusts tend to share information and behave by collective rationality. However, when personal information is accurate locusts tend again to avoid sharing information adopting an individual rationality. This observed effect is due to the quality of required personal information and access to the information through congestion and distance between conspecifics. Results underline a recurrent individual rationality in locusts in decision-making. Furthermore, the strong adaptation capacity of this insect could lead to a collective rationality in large groups when the required personal information is imprecise, unreliable, or difficult to access, to provide streamlined decision-making.

Keywords: Locusts; Predator appearance; Information quality; Group size; Personal vs social information; Decision-making

Introduction

Social animals living in groups interact between each other and with their environment by basing their choice of information for decision-making on the relative reliability on two sources of information such as the "personal information" and the "social information" [1,2]. "Personal information" is usually collected through environmental indices whereas "social information" comes

from the behavior of conspecifics [1,3] such as advanced "signals" or social "clues" [4]. "Signals" refer to intentional communication while indices refer to information produced incidentally by individuals as behavioral actions stating decisions of other group members or reflecting the indices on which such decisions are based [5-8].



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The flexible combination of these distinct sources of information is potentially the basis for adaptive decision-making. Because of the dangerousness of the environment, animals are often forced to make both fast and accurate decisions in their search of food, housing, mating, and moving. Therefore, such adaptability of decisions cannot be based on the selection of an arbitrary combination of personal and social information. King and Cowlishaw [5] argue that individuals are more likely to make correct decisions when they share personal information with other conspecifics and when information is of good quality. Furthermore, the size of the group may also affect the reliability of the personal and social information.

As the group expands, the probability that social information is correct is likely to decrease in conditions where personal information is poor [5]. Therefore, individuals would likely avoid relying on personal information as well as sharing it. In contrast, in cases of good personal information quality, individuals would promote the sharing of social information, which would properly inform the members of small groups and those less well-informed in major groups with the same probability of reaching a correct decision [9,15]. Through this compromise, animals in larger groups are able to minimize the investment in collecting personal information without affecting their ability to reach correct decisions. In other words, the social context significantly affects the reasoning and the manner in which information is acquired, transmitted and processed by the group members in social animals.

Reasoning in insects is cognitive processes involving inferences and conceptual models [10]. Previous studies on learning, that are close to reasoning (process of information processing as well as reasoning), have examined the ecological settings favoring social over individual learning [11,12,13]. Social learning is the ability to integrate new information coming from congeners. This learning affects all major insect activities including feeding, predator avoidance, sexual behavior, and social interaction [14]. The existence of parental care and overlapping generations in social animals largely contribute to the social learning [15]. However, the way of reasoning and learning in social animals could be different or absent in nonsocial insects.

To further understand the reasoning of nonsocial animal within a society we conducted a study on gregarious Desert Locust *Schistocerca gregaria* (*S. gregaria*). It is well known that *S. gregaria* can be gregarious or solitaries [16]. Through its polymorphism this animal model offers the opportunity to investigate different reasoning ways by keeping individuals living alone or in groups [17-19]. Such procedure will improve the understanding of rationality, which is the ability to make inferences and conceptualization, for *S. gregaria*.

To analyze the compromise between individual versus collective rationality in decision-making for this particular animal model, we designed a simple experimental setting in which we introduced a predator and observed the reaction of different locust groups. First of all, we studied how individuals adjust their use of personal versus social information in decision-making in various sized groups. We subsequently attempted to establish how the quality of the required personal information affects the choice of

use of information in decision-making.

Material and methods

Material

Insects

The study was performed on Desert Locusts *Schistocerca Gregaria* (Figure 1a). The oothecas originated from a colony maintained at Arbiothech (society of production of Inoculum, Rennes-France). After hatching, locusts were distributed in cages with a volume of $0.1 \, \mathrm{m}^3$. In each cage we placed a population of about thirty locusts. They were subjected to a circadian rhythm of 14h light / 10h dark. The lighting was provided by a 60W lamp placed in each of the cages. The room temperature was maintained around $30 \pm 2^\circ\mathrm{C}$ and at $45 \pm 3\%$ of humidity. Such conditions are close to the natural environment of the Desert Locusts. Locusts were maintained in these conditions until attaining the imago stage which is the last stage an insect attains during its metamorphosis including growth and development. For our experiments, we used 376 imagos (182 females and 194 males) having approximately the same age (8 weeks old ± 2 days).

Experimental setup

To study the reaction of locusts when facing a predator, we built a simple experimental setup in which we placed locusts and we introduced a predator. The experimental device comprises a box having dimensions of 1.20 m length, 0.80 m width and 0.80 m height, and illuminated with a 160 W spotlight (Figure 1b and c). An aperture is made at the front of the box to allow the entrance of the predator (Figure 1b). As predator, we used a remote cat with dimensions of 0.24 m of height and 0.19 m of length and having a speed of 0.27 m/s. We chose this type of predator because locusts are likely to react to large objects in slow motion since they consider them as potential predator [20]. Furthermore, a living animal is not easy to handle because of its unpredictable behavior during the experiments.

To study the effect of group size we created different groups. The individual number per group (i) was defined according to the relationship i = 3 N - 2 (with N the group number, $1 \le N \ge 16$ and $1 \le i \ge 46$) allowing to create sixteen various sized individual groups where the number of male and female is well known (Table 1). Locusts were fed fresh grass supplemented with wheat bran. Locust groups used during the experiment were deprived of food on the previous day. The reason for this is that when we put them in the experimental device on the day of the experiment, they fed and it became easier to observe freeze behavior. For each experiment the grass was replaced, and the walls of the box were cleaned after each test with another locust group in order to evacuate any remaining stress signal. After each experiment locust were replaced and never used again.

To collect the useful information, a camera (camera GO PRO high definition, very wide viewing angle "1080 p") was placed above the device to record the locust reactions (Figure 1c). Responses and behaviors of locusts facing predator's approach were analyzed based on the recorded videos using the software "Sony Vegas Pro 13.0".

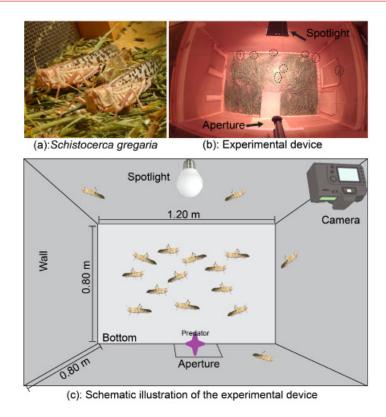


Figure 1: (a) Adult *Schistocerca gregaria*. (b) Picture of the experimental device used in this study. It contains 160 W spotlight and an aperture at the front for predator entry. The roof is made of movable glass. Grass was placed on the bottom. The location of some locusts is indicated by dashed circles. A camera was placed above the box to film the experiments. (c) Schematic illustration of the experimental device.

Table 1: Choice of use of information in each groups in unknown context (UC) and familiar context (FC). F: female; M: male.

C No	Locusts Number	Unknown Context			Familiar Context		
Group Number		Personal	Personal/Social	Social	Personal	Personal/Social	Social
1	1 (1M/0F)	1	0	0	1	0	0
2	4(2M/2F)	3	0	1	1	3	0
3	7(4M/3F)	2	3	1	3	4	0
4	10(7M/3F)	5	4	0	8	2	0
5	13(8M/5F)	8	3	2	4	7	1
6	16(9M/7F)	4	9	1	0	9	5
7	19(12M/7F)	1	7	9	2	12	5
8	22(11M/11F)	5	11	6	5	12	5
9	25(16M/9F)	5	12	7	5	9	11
10	28(15M/13F)	1	13	13	7	12	8
11	31(17M/14F)	3	16	12	4	8	17
12	34(17M/17F)	3	12	17	5	13	15
13	37(17M/20F)	2	12	22	3	25	8
14	40(18M/22F)	3	25	12	6	25	9
15	43(19M/24F)	10	12	20	0	30	13
16	46(21M/25F)	3	17	24	3	22	21

Methods

Unknown context vs. familiar context

For each group we established three experiments. As such we defined two different contexts: the unknown context (UC) and the familiar context (FC). The first experiment is considered as UC since the locusts were faced, for the first time, to the predator. To

familiarize locusts with the experimental protocol, we removed the predator and waited for five minutes before introducing it again to the same locust group. We sat exposition duration of five minutes including predator entry and time spent with the predator. For the FC, we repeated the experiment two times after the first experience. Based on preliminary experiments and previous studies [21,22], we assumed that locusts can retain information (arousing fear)

during an inter-trial interval of ten minutes when a stress factor is presented more than two times.

Observation and data collect process

Upon the appearance of the predator, locusts have the choice between two alternatives which are either to jump or freeze (Figure 2). Jump behavior is when a locust moves from point A to point B by jumping or remove by flying. Freeze behavior is noticed by an immobilization of the locust and a flexion of the legs. For each behavior, we measured the response-time, referred to as jump time (JT) and freeze time (FT), for the unknown and the familiar context. Sometimes locusts do not react, neither jump nor freeze and continue to feed without moving. We did not consider this

alternative in our study because it was very infrequent and the number of non-reacting locust was negligible comparing to the group size (one to two locusts in the larger groups). The locust decision is based on the choice of use of information picked up in its environment and in its field of view. Morphologically, *S. gregaria* has faceted eyes with binocular vision in the front, in back, and on the sides allowing horizontal vision field of 360° [16]. However, vertically they have a blind field in the bottom [16]. Locusts could have a limited field of view when there are obstacles or congeners around. To determine the choice of use of information in decision-making we analyzed all locusts' reaction through their responding times chronology for each group.

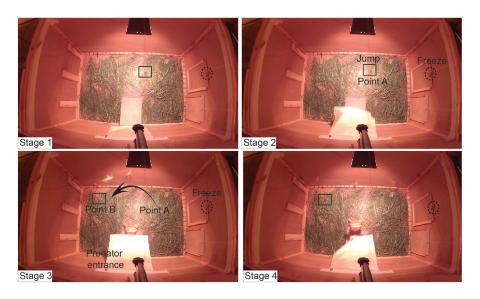


Figure 2: Example of experiment showing the behavior of locust during the entrance of predator. Four stages could be defined. Stage 1: just before predator entrance. Two locusts are indicated by circle and square. Stage 2: start of the entrance of the predator. The different behaviors of locusts are indicated. Locust freeze behavior is indicated by a dashed circle. Locust showing a flee behavior is indicated by a square. This behavior is characterized by the jump or flight of the locust. Stage 3: flying of the locust from point A to point B. Stage 4: end of the experiment.

First of all, we arranged group locusts depending on the chronology of their response times. Then, in the vision field of each locust, we noted the number of previous reacted congeners and the presence or not of the predator. By focusing on the synchronization of the locust with the different signals present in its vision field, we deduced if the subject consider or not the behavior of congeners and the entrance of the predator. By these analyzing procedures, we defined three potential locusts' information choices which are "Personal", "Social" or combined "Personal/Social".

The information is "personal" when the subject reacts solely after facing a predator (freeze and jump). None congeners in its vision field reacted before him. We considered the information used in decision-making as "social" if the subject reacted according to conspecifics only. In this case, some congeners in its vision field reacted before it froze or it jumped. The subject did not care about the entrance of the predator, even if he saw it. Finally, if the decision of the locust is based both; on the entrance of the predator (the subject freeze) and behavior of the conspecifics (the same subject jumps after the reaction of congeners in its vision field), we considered that the locust used combined "personal/social" information in decision-making.

To understand the manner in which locusts would optimize their use of personal vs social rationality in decision-making facing

the appearance of the predator, we compared the average response times for each group in the unknown and familiar contexts, then between the two contexts (Figure 3). Subsequently, we studied the choice of use of information depending on group size and context (UC and FC). For all groups, values of information choice are expressed as a percentage and reported in Table 1 and plotted in Figure 4.

Statistical analysis

We estimated the probability of the choice of use of information for Desert Locusts depending on the group size and the quality of personal information. We based all estimations on recorded video's observations and we accomplished a statistical evaluation using the R open source-software (version 3.0.2, Foundation for Statistical Computing, Vienna, Austria). We performed an analysis of variance using Fisher test applied on regressions between the predefined parameters such as the average jumping times, average freeze times, and the group size, in both unknown and familiar contexts. The analysis was additionally applied on regressions between information choices and group size in both contexts. Furthermore, we applied Welch test [23], which is a generalization of student t-test (assuming normality) for unequal variance and sample sizes, as in this case, to check any statistical difference in the mean between the different set of parameters. The determination of the p-value

allowed us to highlight any significant relationships between the studied parameters, and groups, i.e. test the statistical significance of the findings exhibiting the reliability of our results. We used a significance level of 5 %, i.e. p-value \leq 0.05, which represents a confidence level of 95 %.

Results

Response-time of the locusts facing predator

For the sixteen studied groups (Table 1), we measured the reaction times (expressed in seconds (s)) in terms of the average

freeze times (FT), and the average jumping times (JT) during the entrance of the predator in unknown and familiar context (Figure 3a and b). For the unknown context (Figure 3a), results show that the average FT ranges between 0.40 ± 0.13 s and 0.85 ± 0.13 s with a mean value of 0.55 ± 0.09 s. The average JT ranges between 0.56 ± 0.12 s and 1.10 ± 0.12 s with a mean value of 0.81 ± 0.08 s. The p-values show additionally non-significant difference between the FT (p = 0.22) and the JT (p = 0.16) values. This indicates clearly that the reaction time is not correlated with the average freezing or jumping times, hence, do not exhibit any dependency (Table 2a).

Table 2: Correlation test (a) and means	comparison test (b) for freeze and	iumping times in an uni	known and familiar context

(a)	Unknov	wn context	Familiar context		
	Freeze Time	Jumping Time	Freeze Time	Jumping Time	
Group size p	0.22	0.16	0.48	0.48	
(b)	Unknown context				
	Free	eze time	Jumping time		
Familiar context p	0	.027	0.0026		

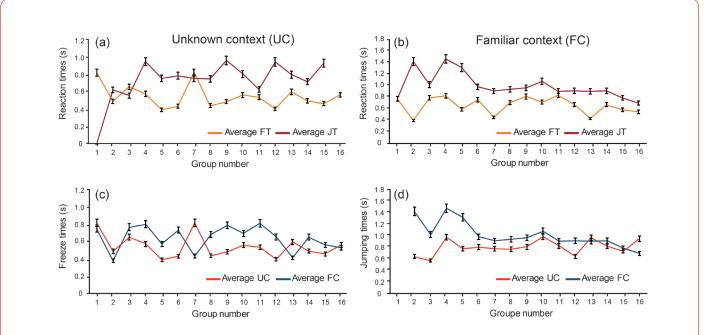


Figure 3: Average locust response times when facing the appearance of the predator depending on the group size in an unknown context (UC) (a) and familiar context (FC) (b). (c) Average locust freeze times when facing the appearance of the predator depending on group size in an unknown vs familiar context. (d) Average locust jumping times when facing the appearance of the predator depending on group size in an unknown vs familiar context. For each group, the number of individuals is indicated in table 1.

In a familiar context (Figure 3b), results show slightly higher response times that in the unknown context and the average freeze time values is about 0.64 ± 0.11 s (ranging between 0.39 s and 0.81 s). The average jumping time is about 0.98 ± 0.15 s and varies between 0.68 s and 1.44 s. The gender does not affect the reaction time with a p-value of 0.1 for freeze reaction and 0.9 for jump reaction. Similarly to the unknown context (Figure. 3a), the reaction times in the familiar context are almost constant, regardless of the group size (Figure 3b). No significant correlation could be noticed for the average JT and average FT (p-values higher than the significance level, Table 2 a). The group size does not seem to influence the time the locusts take before a decision is made. However, the reaction time seems to be affected by the gender for

freeze with a p-value of 0.03, but not for the jump reaction showing a p-value of 0.13.

Welsh's t-test was additionally performed to compare the average FT in both unknown and familiar context (Figure 3c). Interestingly, the average freeze time in the familiar context (mean average FT value of 0.64 ± 0.11 s) is slightly higher than in the unknown context (mean average FT value of 0.55 ± 0.09 s), however, the null hypothesis of equal means is not rejected as the p-value (0.027) is lower than the 5% significance level (Table 2b). Similar results were obtained when considering the average jumping time, (Figure 3d), showing no difference in the mean between the unknown and familiar context (p-value = 0.0026, Table 2 b).

Information choice and decision-making

We analyzed the behavior of locusts during the entrance of the predator in the two different contexts (Unknown and Familiar). We assessed the choice of use of information for decision-making (Personal, Personal/Social and Social) (Table 1) and plotted the choice of use of information (expressed in percentage) according to the group number (Figure 4). In the unknown context the use of personal information decreases significantly with group size while the use of social information increases significantly with the group size showing a confidence level of 99.9 % (p < 0.001, Table 3 a). For the combined personal/social information use, no important variation was noticed and the percentage is almost constant

(Figure. 4a). In small groups 1 to 5 (comprising 1 to 13 locusts, Table 1), locusts significantly prefer the use of personal information compared to the combined personal/social information (p = 0.013) and social information (p = 0.0026, Table 3b). In medium to large groups 6 to 16 (comprising 16 to 46 locusts, Table 1), locusts tend to prefer the use of social information and combined personal/social information rather than using the personal information before the decision is made (Table 3b). In the unknown context, the gender does not seem to affect the choice of use of information with p-values of 0.69, 0.23, and 0.19 for personal, social, and combined personal/social information, respectively. These values are higher than the 5% (i.e., 0.05) significance level.

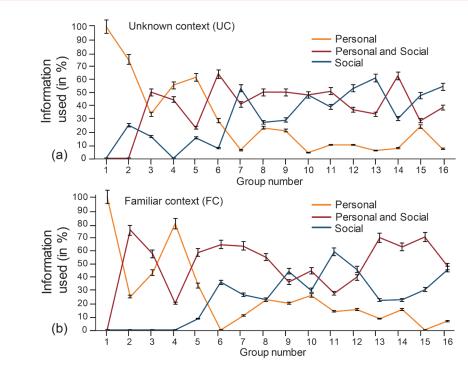


Figure 4: (a) Information choice (in percentages) when facing the appearance of the predator depending on the group size in an unknown context (UC). (b) Information choice (in percentages) of the locusts when facing the appearance of the predator depending on the group size in a familiar context (FC). For each group, the number of individuals is indicated in table 1.

Table 3: Correlations test (a) and Means comparison test (b) for the information choice in an unknown context.

(a)	Personal information Social information		Personal/Social information		
Group size p	< 0.001 < 0.001		0.14		
(b)	Personal/Social in	nformation	Social Information		
	Groups 1 to 5	Groups 6 to 16	Groups 1 to 5	Groups 6 to 16	
Personal information p	0.013	< 0.001	0.0026	< 0.001	

Similarly to the unknown context, the use of personal information significantly decreases with group size (p = 0.0036) while the use of social information significantly increases with the group size (p = 0.0017, Table 4a). For the combined personal/social information use, no difference was noticed and the percentage is almost constant (p = 0.33, Table 4a) (Figure 4a). Locusts significantly prefer the use of personal information (P) (p = 0.0094) and combined personal/social information (p < 0.001) compared to social information in groups 1 to 5 (comprising 1 to 13); whereas, in groups 6 to 16 (comprising 16 to 46 locusts) there is no preference for the information used for decision-making (Table

4b and Figure 4b). Nonetheless, we found a significant preference for usage of combined personal/social information compared to social information in groups 6 to 16 (comprising 16 and 46 locusts respectively) (p < 0.001, Table 4b), hence, the group size seems to influence the use of personal and social information. In the familiar context, the gender tends to affect the choice of use of information (p = 0.050) for personal and combined personal and social information (p = 0.045), however, no significant correlation was found for the use of social information (p = 0.12). As main results from this part, we found that locusts seem to preferably use personal information in small groups and social information in large groups. Whatever

the group size, locusts use more personal information in familiar than in unknown context. It suggests a significant influence of the

context (or quality of personal information required) and the group size on the choice of use of information in decision-making.

Table 4: Correlations test (a) and means comparison test (b) for the information choice in a familiar context.

(a)	Personal Information	Social Information	Personal/Social Information	
Group size p	0.0036	0.0017	0.33	
(b)	Personal/Social	Social Information		
	Groups 1 to 5	Groups 6 to 16	Groups 1 to 5	
Social information p	< 0.001	< 0.001	0.0094	

Effect of group size and collective organization in Decision-making

To study the effect of the group size on the decision-making process in the unknown and the familiar contexts, we analyzed in detail the behavior of locusts in a small-sized group (13 locusts), a medium-sized group (31 locusts), and a large-sized group (46 locusts). The grouping size is based on information choice and decision-making, where in small groups (groups 1 to 5 comprising 1 to 13 locusts) locusts prefer the use of personal information compared to the combined personal/social information and social information. In medium and large groups (groups 6 to 16 comprising

16 to 46 locusts), locusts tend to use the social information and combined personal/social information rather than using the personal information. For the different groups, we assessed the reactions of locusts during the entrance of the predator (Figure 5 and Table 5). We considered solely the first one second in our tests when the information choice was defined. The main reason was that one would expect that locusts may have chaotic behaviors (like jumping several times) after the first reacting individuals and the movements inside the group become random. This may alter our reasoning in analyzing the locust choice of information in decision-making.

Table 5: Information choice for small sized group (group five: 13 locusts), medium group (group eleven: 31 locusts), and large group (group sixteen: 46 locusts) in an unknown and familiar context. We consider the reacting locust only during the first second of the entrance of the predator. We noted P: Personal information choice; PS: combined Personal/Social information choice and S: Social information choice.

	Small Group		Medium Group		Large Group	
Subjects	Group 5 (13 locusts)		Group 11 (31 locusts)		Group 16 (46 locusts)	
	Unknown Context	Familiar context	Unknown context	Familiar context	Unknown context	Familiar context
1	P	Р	P	PS	PS	P
2	P	PS	P	PS	PS	P
3	P	PS	PS	PS	PS	PS
4	P	Р	P	PS	PS	PS
5	PS	PS	S	P	S	PS
6	P	Р	PS	P	S	PS
7	P	Р	PS	P	P	PS
8	PS	PS	PS	S	P	S
9			PS	S	PS	PS
10			PS	S	PS	PS
11			PS	S	PS	S
12			PS	S	PS	S
13			S	S	S	PS
14			S	S	PS	PS
15			S	PS	P	S
16					PS	S
17					S	S
18					S	S
19					S	S
20					S	PS
Major choice	P	P = PS	PS	S	PS	PS

For the small-sized group (13 locusts), Figures 5a and b show the locust position and the chronological reaction order in an unknown

and familiar context, respectively. We noticed that for both contexts, during the entrance of the predator, the first reacting locust is far

from the predator and its congeners. Successively reacting locusts are distant from each other and reacted randomly regardless of their fellows. Thus, we may conclude that the information on which a decision is made is personal (Table 5).

For the medium-sized group (31 locusts), the first reacting locusts are distant from each other and are surrounded by few congeners (Figure 5c and d). However, we noted in the unknown context that some locusts have reacted successively at very close distances (Figure 5c). This phenomenon is accentuated in a familiar context (Figure 5d). Observation showed that the first reacting locusts use combined personal/social information in the unknown context and seem to use more social information, picked up from their near neighbors, in a familiar context.

For the large-sized group (46 locusts), locusts have the tendency to be gathered in small groupings (Figure 5e and 5f). The first reacting locusts are located near the predator and close to some congeners. Successively reacting locusts are less distant than in medium groups. Furthermore, there are more locusts in close proximity to each other that are reacting successively. We noticed in both the unknown and familiar contexts that locusts utilize mainly social information and combined personal/social information in decision-making.

Discussion

The purpose of this study is to analyze how locusts adapt their use of personal vs social information when facing a predator. We analyzed several factors that may have an influence on decision making such as the group size effect and the quality of the required personal information in unknown and familiar contexts. To highlight the compromise of information use, we assumed that every individual decision based on social information is more accurate when many subjects are involved, hence their personal information becomes more accurate. Our results provide better constraints on the strategy of use of information in decision-making and the collective organization of these nonsocial insects.

Results also suggested that response times are not affected by group size and the average time is almost constant. Surprisingly, the average response times (freezing and jumping times) in a familiar context (Figure 3a), when personal information acquired is accurate, are higher than in an unknown context (Figure 3b), when personal information acquired is poor. The consistency of response times in each groups, and the delay in decision-making between the two contexts are likely due to the fact that locusts often base their response on the variability of information choice. This would reflect an adjustment in the decision-making strategy adopted by locusts (see Figure 4). Similarly to our results, numerous studies conducted on other animal models such as ants [9], honeybees [24] and monkeys [5] show that whatever the group size, the correctness of the decision is almost constant. To maintain this decision accuracy, animals do not use the same decision-making strategy in small and large groups.

Regardless the quality of personal information, locusts from small groups (group 1 to 5 containing 1 to 13 locusts) do not or rarely share the information and are likely to develop an individual rationality through the use of their personal information. In

medium to large groups (6 to 16 containing 16 to 46 locusts) locusts tend to share information and, thus, develop a collective rationality through the use of social information. Nevertheless, this penchant for social information is affected by the quality of required personal information. On one hand, when the latter is poor, locusts develop a stronger collective rationality through the preferential use of social information and combined personal/social information (Figure 4a). On the other hand, when the required personal information is accurate, locusts use information without preference (Figure 4b). We note, nonetheless, for large groups a significant preference for the use of combined personal/social information compared to social information (Tables 4b and 5, Figure 4b). Locusts seem to privilege individual rationality in decision-making and develop a collective rationality in a large group when it is necessary.

A conflicting use of social and personal information of varying reliability in decision-making has further been stated on social forager [25]. Van Bergen et al. [2], reported in a study of sticklebacks that when personal information is reliable, recently acquired and of good quality, sticklebacks ignore social information and based their decisions on personal information. Conversely, when the updated personal information is too old and conflicts with more recent social information or, if personal information is uncertain, sticklebacks lean towards recent social information. This antagonism in choice of information is strongly determined by the number of individuals holding information or present in the group [4,9,5,24,27]. However, according to our observations, other factors, than those cited above, seem to have an influence on the flexibility of use of information.

Moreover, the conflicting use of the information appears to be influenced by the distance between locusts which changes as a function of the group size (Figure 5). Locusts balance the choice of information regardless of the distance separating them from the predator, but depending on the number of individuals around them and the distance between each other. The greater the number of locusts is around and close to the subject, the more the latter interact with neighbors leads to better use of social information in decision-making [28]. This finding has been emphasized by King and Cowlishaw [29], according to which nonsocial animals are more inclined to despotic decisions in nature by a local communication. This phenomenon has been observed in other animal model such as sticklebacks [30]. In their study, stickleback tends to follow its surrounding neighbors and greatly increases the probability of following when more neighbors engage in a given direction. However, the emergence of sentinels, leader or leader group could arise from stochastic discrimination or predisposition factors.

Our results indicate that the first reacting locusts are distant from each other and are generally separated by several peers. For instance, in a large group size, locusts have the tendency to gather in small groups in which we can tentatively identify some monitoring locusts. These locusts, corresponding to the distant and first reacting individuals during the appearance of the predator, could be considered as "sentinels". Moreover, Cocroft and Hamel, Couzin and Fernandez et al. [4,30,31] suggested that in predation circumstances, the decision should be quickly reached. Accordingly, a subset of informed individuals (sentinels) regularly updates the members of the group through repeated signals on the level of

predation risk, including a decreased risk. This technique allows regulation of the response thresholds of the group members and reduces false alarms that lead to misinformation cascades consequent to a very rapid decision in which a positive feedback dominates. Furthermore, Cocroft and Hamel [4] suggested that animals belonging to large groups scrutinize their predators less frequently while maintaining their overall detection rate, which allows them more time to feed. King and Cowlishaw [29], stipulated that in nonsocial animals few individuals have relevant information for a current decision. Ultimately, this means that despotism

is common in this animal type and is essential in behavior coordination and decision process. However, other factors appear as actors in these rational patterns and should be checked. Rands & al. [32] state that in situation of predation, if the danger is weak the subject will base on his own energetic reserves to decision-making. But if the danger is high the subject will base on his energetic reserves and on those of congeners to decision-making [32]. Then, the emergence of collective vs individual rationality is monitoring by the subject energetic reserves and the danger level.

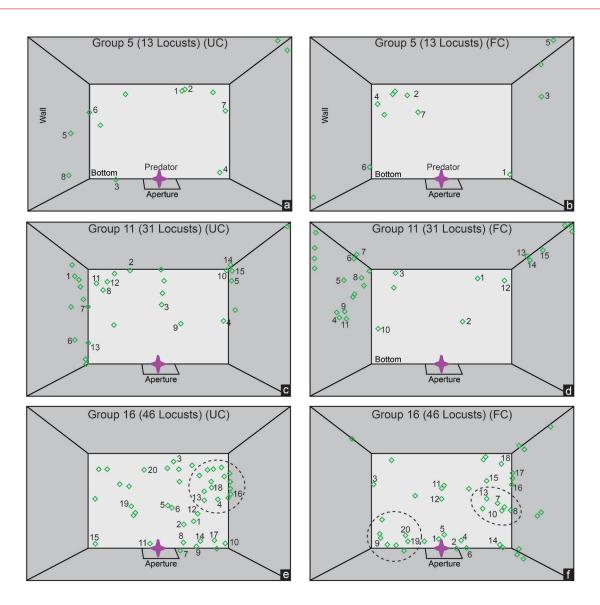


Figure 5: Examples of locust behavior in a small sized group (13 locusts), medium group (31 locusts), and large group (46 locusts) in an unknown and familiar context. The grouping size is based on information choice and decision-making, where in small groups (groups 1 to 5 comprising 1 to 13 locusts) locusts prefer the use of personal information compared to the combined personal/social information and social information. In medium and large groups (groups 6 to 16 comprising 16 to 46 locusts), locusts tend to use the social information and combined personal/social information rather than using the personal information. Locusts' location is indicated by the green diamond. We numbered the first reacting locust during the first second of the entrance of the predator. Dashed black circles indicate a small grouping within large group size.

Results from previous studies on other animal models showed good accordance with our findings which allowed us to propose testable hypotheses about the relationship between the group size, the quality of the required information and the streamlined decision-making. However, the lack of matters to control all signals received and processed by locust sense organs appears to be a limitation in this study and allows drawing upon a certain number of perspectives. It would be interesting to study how locusts

perceive their environment, process information, and make such a rapid and appropriate response called "paradigm of compromise between speed-accuracy" as reported by Lorenz et al. and Marshall et al. [26,33].

The gender seems to do not affect the response-time of locust and the choice of information in the unknown context. Whereas in the familiar context, our preliminary results show that the gender may have some effect. Such effect is not yet understood because the gender issues were not the focus of this study because this would complicate the problem. However, it would be interesting to conduct other studies by simplifying the problem and focusing solely on gender.

Conclusion

Desert Locust Schistocerca gregaria are nonsocial insects that can have gregarious or solitary nature. Our detailed study of this interesting animal model allowed us to bring better constraints to the behavior of such nonsocial insects. We, further, propose a simple protocol easily reproduced by any concerned researcher. Our results underline an individual rationality strongly developed and privileged in locusts in decision-making. Furthermore, and if it is necessary, the strong adaptation capacity of locusts could lead to a collective rationality in large groups. When personal information is sketchy or becomes unreliable or inaccessible, locusts search for acquired and low cost social information to improve personal information and to ensure a streamlined decision-making process. The group size and organization of the locust seems to have a direct effect on information choice in decision-making. In small groups, locusts behave by individual rationality and use personal information whatever the quality of personal information. As the group expands and when personal information is sketchy the locusts tend to share information and behave by collective rationality, whereas when personal information is accurate they again avoid information sharing. These observed rational patterns are not only due to the quality of required personal information or group size. They are also due to access to the information through congestion, distance between conspecifics and may be due to other multifactorial effects that it would be interesting to devote our attention to it in future research.

Acknowledgments

Funding for this work came from the ANR Chorus 2011 (project BTAF DOC) – France and from the Research Laboratory LR11ES31 – Biotechnology and Bio-Geo Resources Valorization, University of Manouba – Tunisia. SBG acknowledges ANR-17-EURE-0017 FrontCog. We used R open source software (version 3.0.2, Foundation for Statistical Computing, Vienna, Austria) to compile the different graphics and to perform the statistical analyses. We thank Wissal Dhifi and Hanna Jemaneh for reading and revising our corrected manuscript.

Conflict of Interest

No Conflict of Interest.

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