JARQ 46 (4), 339 – 345 (2012) http://www.jircas.affrc.go.jp

Field Observations of the Sheltering Behavior of the Solitarious Phase of the Desert Locust, *Schistocerca gregaria*, with Particular Reference to Antipredator Strategies

Koutaro OULD MAENO[1]*, Cyril PIOU[3], Sidi OULD ELY[1], Sid'Ahmed OULD MOHAMED[1], Mohamed EL HACEN JAAVAR[1], Mohamed ABDALLAHI OULD BABAH[1] and Satoshi NAKAMURA[2]

[1] Locust control and research team, The Mauritanian Desert Locust Centre: Centre National de Lutte Antiacridienne (CNLA) (Nouakchott, Bp: 665, Mauritania)

[2] Japan International Research Center for Agricultural Sciences (JIRCAS) (Tsukuba, Ibaraki 305–8686, Japan)

[3] CIRAD, UPR Bioagresseurs analyse et maîtrise du risque (F-34398 Montpellier, France)

Abstract

Solitarious phase locusts are cryptic animals and usually seek shelter in plants. This trait was thought to be a specific antipredator strategy associated with the solitarious phase. However, information on preferences for particular shelter plants and sheltering behavior remains limited. In the present study, small-scale field observations were conducted to investigate the sheltering behavior of the solitarious phase of the desert locust, *Schistocerca gregaria,* in relation to plant species and size. A spiny plant, *Fagonia arabica*, and two spineless plants, *Nucularia perrini* and *Stipagrostis plumosa*, were identified at the survey site. Although the size of *F. arabica* did not differ significantly from that of the two other plant species, almost all the solitarious locusts used *F. arabica* for shelter. Locusts were found on a majority (78%) of the individual *F. arabica* examined, but the number of sheltering locusts varied. The *F. arabica* plants with locusts were significantly larger than those without. A positive correlation was found between the total number of sheltered locusts (nymphs and adults) per individual plant and the plant size (m^3). The same tendency was observed for nymphs and adults alike. The local densities (no. of sheltered locusts / plant size (m^3)) remained constant over a range of plant sizes. These results might indicate that solitarious locusts selected their shelter plant based on its species and size. Because *F. arabica* is a spiny plant, we concluded that solitarious locusts use not only visual but also physical defense mechanisms as antipredator strategies.

Discipline: Insect pest
Additional key words: behavior, density-dependent phase polyphenism, morphology

Introduction

Antipredator adaptations in animals have evolved to maximize the prey's probability of survival. Locusts and grasshoppers have developed visual, chemical and physical defenses against predators to reduce the risk of mortality[29,38,39]. Desert locusts, *Schistocerca gregaria* Forskål, show density-dependent phase polyphenism in behavioral, morphological and physiological characteristics[28,29,37]. These density-dependent changes are commonly assumed to be adaptations[29]. In *S. gregaria*, phase-related differences are also found in antipredator strategies, which are closely linked to host plants. When gregarious 3rd-instar nymphs feed on a toxic plant, *Hyoscyamus muticus*, their conspicuous body coloration functions as a warning coloration[34,35]. Due to the uniform body coloration of gregarious locusts and the fact that they move in dense groups during the day, their visual and chemical defenses are probably advantageous in serving to decrease the rate of attack by predators[15,29,34,35]. In contrast, solitarious-phase nymphs show body color polyphenism[21,36]. They display various body colors, including green, yellow, brown, beige and black, and varying black

---

*Corresponding author: e-mail otokomaeno@yahoo.co.jp

Received 11 January 2012; accepted 30 March 2012.

patterns that serve as camouflage in their natural environment. In general, polymorphic preys suffer less predation than single-morph species at a particular density[7]. Furthermore, solitarious locusts are nocturnal and shelter in plants during daytime[19,38]. These cryptic morphological and behavioral characteristics related to the shelter plants used by solitarious locusts undoubtedly reduce the risk of detection by predators. Although the visual and physical roles of shelter plants have been frequently mentioned[12,18,32], little is known about the relationships between the sheltering behavior of solitarious locusts and shelter plants[38].

Although *Schistocerca gregaria* is well known as a polyphagous insect, its host plant preference is phase-dependent[10,14,22]. The host plant preference of gregarious locusts is also broader than that of solitarious locusts. Gregarious locusts form aggregations. In contrast, solitarious locusts avoid one another and may therefore find it difficult to locate a suitable unoccupied host plant. If solitarious locusts have a strong preference for particular shelter plants and are attracted to the same high-quality (e.g. size, toughness, structure) shelter, their local density would increase and produce gregarization, even at a low population density. Indeed, if food plants are patchily distributed, the local locust density increases, which then leads to gregarization[8,13,15,17,18,25,32]. Accordingly, we hypothesized that solitarious locusts utilize a specific plant species as a shelter and are more strongly attracted to a shelter of high rather than low quality. This hypothesis should be tested in the field at a site where several palatable plant species co-occur within the plant community. During a field survey in one of the major breeding and recession areas of the desert locust in Mauritania[2,3], we found a site suitable for addressing this problem within a natural desert locust habitat. In this study, we investigated the shelter utilization pattern of solitarious locusts on a fine scale after identifying the locust behavioral phase. The purpose of the investigation was to understand the relationship between solitarious locusts and the plant community.

Materials and methods

1. Study area

Mauritania, in West Africa, represents an important area in which gregarization occurs within the recession zone of the desert locust[2,3]. The study site (N20°36', W15°36') is located in northwestern Mauritania near Taziast. It is a vast plain with various cover types, including dunes and rocks, relatively inaccessible and with no permanent human population. The area's three dominant plant species include a spiny plant, *Fagonia arabica* (Zygophyllaceae), and two spineless plants, *Nucularia perrini* (Chenopodiaceae) and *Stipagrostis plumosa* (Poaceae). The plant species included in this study were identified according to Barry and Celles[5,6] as perennials, occurring in discontinuous patches. A field survey was conducted in April 2011.

2. Sampling regime

Overnight observations were conducted from 22:00 to 02:00. The survey sites were randomly chosen from the area where the three dominant plant species co-occurred and a total of twenty-five belt transects (2 × 50 m) were conducted within the survey area. In the present study, locust perching or moving inside plants was regarded as using a sheltering behavior, according to Uvarov[38]. To determine the relationship between plant size and the number of locusts sheltered, all three dominant plant species present within the belt transects were observed. The locusts found on each plant were recorded and collected by hand. Body coloration of the nymphs collected was recorded, as will be described later. To determine the plant size, the maximum length, width and height was measured for each bush (maximum length x width x height, m^3) with a tape measure. The percentage of ground surface covered by plants within the belt transects was calculated from data derived from twenty-five belt transects. These coverage for *F. arabica*, *N. perrini* and *S. plumosa* at the survey site were 10.56%, 6.22% and 3.63%, respectively.

3. Nymphal body coloration

The nymphs of *S. gregaria* show body color polyphenism[21,36]. To determine the phase state of the locusts observed at this site, the body coloration of all collected nymphs was examined. The collected nymphs were then assigned to green, brown or yellow color types based on the background color of the body. The insects were also categorized in three grades based on the intensity of the black patterns on the head and according to the classification of Maeno and Tanaka[26].

4. Behavioral phase state

It has frequently been argued that solitarious locusts are nocturnal and avoid each other[29,38]. To quantify the behavioral phase, two factors in particular, grouping behavior and the distance between locusts, are frequently used[1,17,20]. Based on this information, we categorized the position of the locusts on a plant in terms of two classes: 1) the locusts remained within one body length of one another or 2) the locusts remained multiple body length from one another.

5. Statistical analysis

Chi-squared, Wilcoxon rank sum and Fisher PLSD tests were performed with Stat View software (SAS Institute, Inc.) to analyze significant differences among locust colors, locust instars, plant species and plant sizes. To analyze the relationship between *F. arabica* plant size and the number of sheltered individual *S. gregaria*, we used Poisson regressions with the R software[31]. We then wanted to evaluate if some specific plants had higher or lower numbers of locusts than a random Poisson process dependent on plant size. To do so, we drew 10,000 replicates of Poisson random numbers according to the adjusted regression models and compared the distribution of these random points with the observed data.

Results

A total of 137 locusts (45 adults, 78 last-instar nymphs, 12 L-1 (one instar before the last nymphal instar) nymphs, 2 L-2 nymphs (two before the last instar)) were found on plants at the study site. No individuals were found within a distance of one body length of other individuals ($n = 137$). This result indicated that the behavioral traits of these locusts were not typical of the gregarious or transient phase. In nymphs, a significant difference in the frequency of background color was found between the females and males (χ^2-test; $P < 0.001$), but almost all the nymphs displayed either the green or brown body color typical of the solitarious phase (Table 1). No nymphs developed the high-intensity black patterns characteristic of the typical gregarious phase (Table 1). Based on body coloration and inter-individual distances, the nymphs observed at this survey site were identified as being in the solitarious phase.

Although *F. arabica* did not differ significantly in size from the two other plant species (Fig. 1; Fisher PLSD test, $P > 0.05$), almost all the nymphs and adults were found on *F. arabica* (Fig. 2). No locusts were found on *S. plumosa*, No significant difference between the nymphs and adults was found in the percentage of locusts occurring on *F. arabica* (χ^2-test, $P > 0.05$). Among the *F. arabica* surveyed, a majority of plants (78%) sheltered locusts.

The number of locusts per individual *F. arabica* varied from 0 to 16 (Fig. 3). Interaction between the plant size and the number of locusts was also observed on individual plants. Bushes with locusts were significantly larger than those without (Fig. 4; Wilcoxon rank sum test, $z = -5.704$, $P < 0.001$). A significant positive correlation was also found between the size of an *F. arabica* plant and the total number of locusts on it (Fig. 5a; $n = 54$; Poisson regression: z value = 17.98, $P < 0.001$). The same ten-

Table 1. Percentages of different background colors and black pattern grades of the heads of different nymphal instars in field-collected *Schistocerca gregaria*

Nymphal	Female				Males			
instars	Background body coloration				Background body coloration			
	Green	Brown	Yellow	n	Green	Brown	Yellow	n
Last	33	4	1	38	11	25	4	40
L-1	3	0	0	3	5	4	0	9
L-2	2	0	0	2	0	0	0	0
Total	38	4	1	43	16	29	4	49
(%)	88.4	9.3	2.3		32.7	59.2	8.2	
	Black pattern grades				Black pattern grades			
	1	2	3		1	2	3	
Last	35	3	0	38	32	8	0	40
L-1	2	1	0	3	7	2	0	9
L-2	2	0	0	2	0	0	0	0
Total	39	4	0	43	39	10	0	49
(%)	90.7	9.3	0.0		79.6	20.4	0.0	

Grade 1, no or few black patterns; grade 3, intensive black patterns; grade 2, intermediate between grades 1 and 3 (Maeno & Tanaka, 2007). The nymphal instars are designated as L-1 and L-2 and indicate one and two instars, respectively, before the last nymphal instar.

dency was observed for nymphs alone (Fig. 5b; n = 54; Pearson regression: z value = 12.11, P < 0.001) and less strongly for adults alone (Fig. 5c; n = 54; Pearson regression: z value = 1.75, P = 0.08). The local densities on each individual *F. arabica* plant (number of sheltered locusts / plant size (m^3)) were unrelated to the plant size (Pearson correlation; r = -0.034, n = 42, P = 0.829).

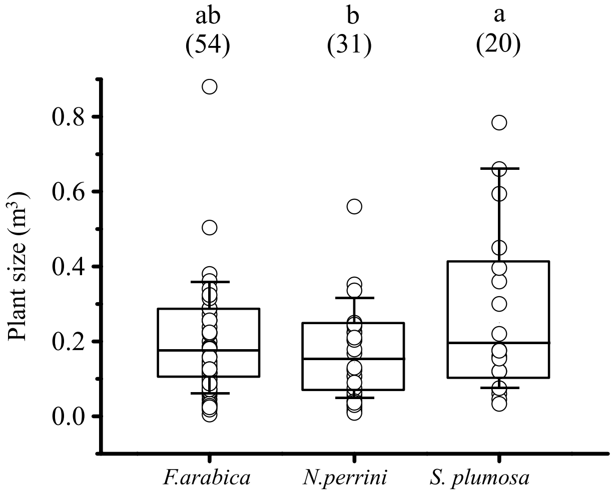

Fig. 1. Plant size of the three dominant plant species, *Fagonia arabica*, *Nucularia perrini* and *Stipagrostis plumosa*, at the study site

Each box plot displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentile values respectively. Each circle shows the individual data points. Different letters indicate significant differences at P < 0.05 (Fisher PLSD test). Numbers in parentheses indicate sample sizes.

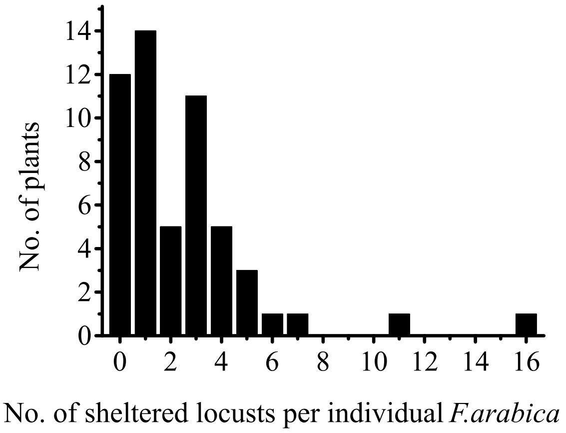

Fig. 3. Frequency of individual *Fagonia arabica* with different numbers of sheltered *Schistocerca gregaria* individuals

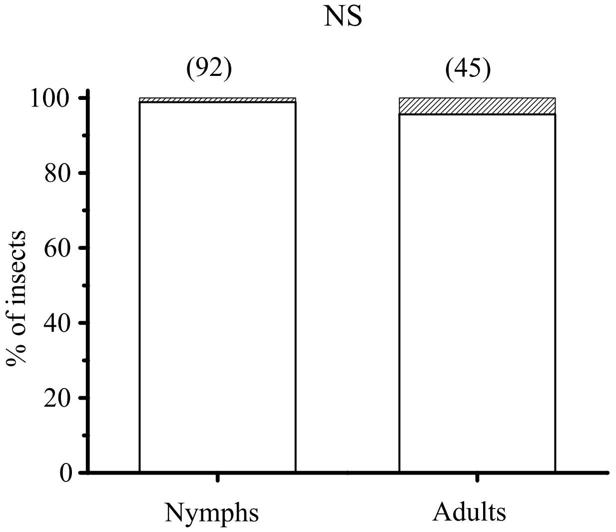

Fig. 2. Percentage of nymphs and adults of *Schistocerca gregaria* sheltered by *Fagonia arabica* (open) or *Nucularia perrini* (slash)

No locust was found on *Stipagrostis plumosa*. Numbers in parentheses indicate sample sizes. NS indicates no significant difference between nymphs and adults based on an χ^2-test at 5%.

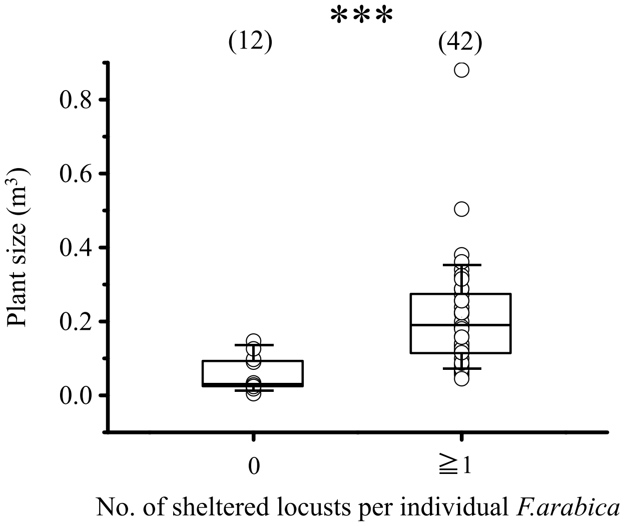

Fig. 4. Plant size of *Fagonia arabica* without or with multiple locusts

Each box plot displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentile values respectively. Each circle shows individual data points. Wilcoxon rank sum test; ***, P < 0.001. Numbers in parentheses indicate sample sizes.

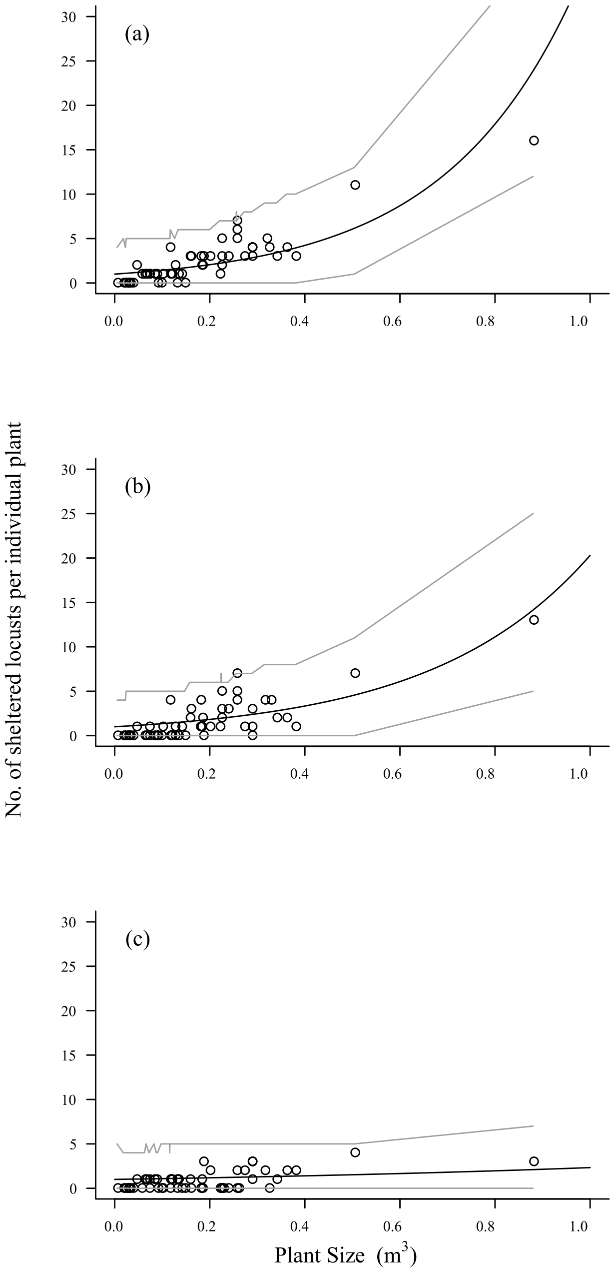

Fig. 5. Relationship between *Fagonia arabica* plant size and the number of sheltered individual *Schistocerca gregaria* (a), only nymphs (b) or only adults (c)

Black lines are Poisson regression lines adjusting a log (No.) ~Size model passing through the origin. Gray lines are 99% confidence intervals from 10,000 replicates of Poisson random numbers according to the adjusted models. No point falls outside these intervals. A random Poisson process influenced by plant size is therefore sufficient to explain the numbers of individuals occurring on each *F. arabica*. See text for detailed statistical results.

Discussion

Solitarious locusts are camouflaged and show polymorphic body coloration in their habitat and in the host plants that they use for shelter. These cryptic characteristics have been widely recognized as a visual defense used to avoid detection by predators[7,23,24,30]. The present study focused on the use of shelter by solitarious locusts and identified another aspect of the physical antipredator strategy in terms of a link between plant species and quality.

The host plant preference of solitarious locusts has been considered narrow relative to that of gregarious locusts[10,14]. The present field survey confirmed that the solitarious locusts showed a strong shelter plant preference, although the use of all three dominant plant species for food has been known[27]. Although the morphological characteristics of the *N. perrini* and *S. plumosa* bushes apparently made these plants suitable for use as shelter and food[5,6], *F. arabica* was exclusively chosen by the solitarious locusts. In the present study, environmental factors, such as weather and the abundance of predators, were not considered as playing a role in the shelter choice, because the observations were conducted at the same place and time. Because *F. arabica* has many spines on its stems, the solitarious locusts are likely to have used *F. arabica* as shelter against predators. In this area, jerboas (*Jaculus jaculus*), lizards (*Acanthodactylus dumerili*) and birds (*Cursorius cursor*) are the main potential predators of the solitarious locusts. The spines of *F. arabica* apparently prevent predators from foraging within these bushes. In fact, it was difficult to collect locusts without using thick gloves. A physical rather than a visual antipredatory strategy appears advantageous for nocturnal solitarious locusts. In addition to cryptic body coloration and behavior, shelter preference can be advantageous to solitarious locusts. By choosing *F. arabica* as a food plant, these locusts decrease the probability of attack by predators. It is possible that the strong host plant preference of solitarious locusts reflects not only palatability but also sheltering behavior. However, no information about this hypothesis is currently available.

The understanding of the biological factors involved in outbreaks and swarm formation in locusts requires studies on different spatial scales, from micro to macro[4,8,11,12,33]. The current study was performed on a macro scale, ranging from individual plants to a limited area of natural habitat and revealed a detailed examination of the relationship between solitarious locusts and plant quality. Although the survey area was very limited, the study results suggested that the plant size influenced the sheltering behaviors of the solitarious locusts. The observations made during the study indicated that relatively small *F. arabica* bushes were randomly distributed at the site but that such bushes were avoided by the locusts, whereas the larger bushes attracted more locusts. During the day, solitarious locusts seldom walked on the ground and tended to remain within the shelter of an *F. arabica* bush if approached by observers. It was difficult to find and collect locusts if their shelter plant was relatively large. The importance of shelter quality has been documented in arthropods[16]. Based on these observations, we speculated that the small *F. arabica* could not function as a shelter. Solitarious locusts might therefore select their shelter plants not only according to plant size but also according to plant species. It is interesting to note how solitarious locusts determine the quality of a potential shelter plant. Knowledge of the mechanism controlling the sheltering behavior of the desert locust not only allows us to predict the distribution pattern of locusts but also to attract them to a particular place to facilitate the application of control measures. Such information can be a key factor in developing novel methods to control locust outbreaks.

A patchy distribution of vegetation often causes local gregarization[8,13,17,18,25,32]. Based on previous observations, we hypothesized that high-quality shelter plants also attracted more solitarious locusts than poor-quality plants. As expected, large shelter plants attracted more locusts than small plants. However, the solitarious locusts adjusted their local population densities to maintain low densities at each bush, regardless of the size of the shelter plant. The maximum number of sheltered locusts found on a single bush was 16. However, this bush was also the largest found to contain locusts, hence the local density of locusts remained low. This ability to regulate the local population density might function to maintain the characteristics of the solitarious phase. The shift from the solitarious to the gregarious phase might begin beyond a critical threshold in population density[9]. Although it is highly probable that such shift may begin within the host plants, it remains unknown whether it occurs in high- or low-quality shelter plants. This type of information is important to gather for understanding the process of gregarization.

In Mauritania, several species of *Fagonia* are distributed over the recession area, but these plants do not occur in certain areas. Additional large-scale surveys are necessary to better understand the relationship between desert locusts and plants.

Acknowledgements

We would like to thank Mrs. Tijany, Lemine and Mohamed for their assistance with the field survey. Thanks are also due to Drs. S. Tanaka (NIAS, Japan), D. Whitman (Illinois State Univ., U.S.A.), K. Cressman (FAO), J.-M. Vassal (CIRAD) and Mr. Hiroshi Azuma (The Japanese Ambassador to Mauritania) for encouragement and stimulating discussion. This study was funded by the Japan Society for the Promotion for Science through a research abroad fellowship for PD (No. 128 ・2011) and Inoue Zaidan to K.O.M. and supported by Grants-in-Aid for Scientific Research (KAKENHI) Grant Number 24405027 from Japan Society for the Promotion of Science (JSPS). Two anonymous referees significantly improved the manuscript.

References

1. Anstey, M. L. et al. (2009) Serotonin mediates behavioral gregarization underlying swarm formation in desert locusts. *Science,* **21**, 627–630.
2. Babah, M. A. O. (1997) Strategy for controlling the desert locust in Mauritania. *In* New strategies in locust control, eds. S. Krall, et al., Birkhaeuser Verlag, Basel, Switzerland, 487–492.
3. Babah, E. M. A. (2010) *Biogéographie du Criquet pèlerin en Mauritanie*. Hermann, Paris, pp. 286.
4. Babah, M. A. O. & Sword, G. A. (2004) Linking locust gregarization to local resource distribution patterns across a large spatial scale. *Environ. Entomol.,* **33**, 1577–1583.
5. Barry, J. P. & Celles, J. C. (1991a) *Flore de Mauritanie.* Tome 1. Université de Nice/ ISS de Nouakchott, pp. 359.
6. Barry, J. P. & Celles, J. C. (1991b) *Flore de Mauritanie.* Tome 2. Université de Nice/ ISS de Nouakchott, pp. 550.
7. Bond, A. B. (2007) The evolution of color polyphenism: crypticity, searching images, and apostatic selection. *Annu. Rev. Ecol. Evol. Syst.,* **38**, 489–514.
8. Bouaïchi, A. et al. (1996) The influence of environmental microstructure on the behavioural phase state and distribution of the desert locust *Schistocerca gregaria*. *Physiol. Entomol.*, **21**, 247–256.
9. Buhl, J. et al. (2006) From disorder to order in marching locusts. *Science*, **312**, 1401–1406.
10. Chapman, R. F. (1990) Food selection. *In* Biology of Grasshoppers, eds. Chapman, R. F. & Joern, A., J. Wiley & Sons, New York, 39–72.
11. Collett, M. et al. (1998) Spatial scales of desert locust gregarization. *Proc. Natl. Acad. Sci. USA,* **95**, 13052–13055.
12. Culmsee, H. (2002) The habitat functions of vegetation in relation to the behavior of the desert locust *Schistocerca gregaria* (Forskål) (Acrididae: Orthoptera): a study in Mauritania (West Africa). *Phytocoenologia*, **32**, 645–664.
13. Despland, E. et al. (2000) Small scale processes in desert locust swarm formation: how vegetation patterns influence gregarization. *Oikos*, **88**, 652–662.

14. Despland, E. & Simpson, S. J. (2005a) Food choices of solitarious and gregarious locusts reflect cryptic and aposematic antipredator strategies. *Anim. Behav.*, **69**, 471–479.
15. Despland, E. & Simpson, S. J. (2005b) Surviving the change to warning colouration: density-dependent polyphenism suggests a route for the evolution of aposematism. *Chemoecology*, **15**, 69–75.
16. Eggleston, D. B. & Lipcius, R. N. (1992) Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology*, **73**, 992–1011.
17. Ellis, P. E. (1963) The influence of some environmental factors on learning and aggregation in locust hoppers. *Anim. Behav.*, **11**, 142–151.
18. Ellis, P. E. & Ashall, C. (1957) Field studies on diurnal behaviour, movement and aggregation in the desert locust (*Schistocerca gregaria* Forskål). *Anti-Locust Bull.*, **25**, 1–94.
19. Ely, S. O. et al. (2011) Diel behavioral activity patterns in adult solitarious desert locust, *Schistocerca gregaria* (Forskål). *Psyche*, **2011**, 1–9.
20. Heifetz, Y. et al. (1996) Factors affecting behavioral phase transition in the desert locust, *Schistocerca gregaria* (Forskål) (Orthoptera: Acrididae). *J. Chem. Ecol.*, **22**, 1717–1734.
21. Hunter-Jones, P. (1958) Laboratory studies on the inheritance of phase characters in locusts. *Anti-Locust Bull.*, **29**, 1–32.
22. Husain, M. A. et al. (1949) Studies on *Schistocerca gregaria* (Forskål) XIII. Food and feeding habits of the desert locust. *Indian J. Entomol.*, **8**, 141–163.
23. Isely, F. B. (1938) Survival value of acridian protective coloration. *Ecology*, **19**, 370–389.
24. Joern, A. (1981) Importance of behavior and coloration in the control of body temperature by *Brachystola magna* Girard (Orthoptera: Acrididae). *Acrida*, **10**, 117–130.
25. Kennedy, J. S. (1939) The behaviour of the desert locust (*Schistocerca gregaria* (Forsk.) (Orthopt.) in an outbreak center. *Trans. R. Ent. Soc. Lond.*, **89**, 385–542.
26. Maeno, K. & Tanaka, S. (2007) Effects of hatchling body colour and rearing density on body colouration in last stadium nymphs of the desert locust, *Schistocerca gregaria* (Forskål)(Orthoptera: Acrididae). *Physiol. Entomol.*, **32**, 87–94.
27. Mamadou, A. et al. (2009) Diet effects on the number of egg-laying and water loss in the desert locust (*Schistocerca gregaria* Forskål 1775)(Orthoptera: Acrididae). *Zool. Baetica*, **20**, 85–95.
28. Pener, M. P. (1991) Locust phase polymorphism and its endocrine relations. *Adv. In Insect Physiol.,* **23**, 1–79.
29. Pener, M. P. & Simpson, S. J. (2009) Locust phase polyphenism: An update. *Adv. In Insect Physiol.*, **36**, 1–272.
30. Pick, F. E. & Lea, A. (1970) Field observations on spontaneous movements of solitarious hoppers of the brown locust, *Locustana pardalina* (Walker), and behavioural differences between various colour forms. *Pbytopbylactica*, **2**, 203–210.
31. R Development Core Team. (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, http://www.R-project.org.
32. Roffey, J. & Popov, G. B. (1968) Environmental and behavioural processes in a desert locust outbreak. *Nature*, **219**, 446–450.
33. Roffey, J. et al. (1970) Outbreaks and recession populations of the desert locust, *Schistocerca gregaria* (Forskål). *Bull. Entomol. Res.*, **59**, 675–680.
34. Sword, G. A. (2003) To be or not to be a locust? A comparative analysis of behavioral phase change in nymphs in *Schistocerca americana* and *Schistocerca gregaria*. *J. Insect Physiol.***,** **49**, 709–717.
35. Sword, G. A. et al. (2000) Density-dependent aposematism in the desert locust. *Proc. R. Soc. Lond. B Biol. Sci.*, **267**, 63–68.
36. Stower, W. J. (1959) The color patterns of hoppers of the desert locust *Schistocerca gregaria* (Forskål). *Anti-Locust Bull.*, **32**, 1–75.
37. Uvarov, B. P. (1966) *Grasshoppers and Locusts*, Vol. 1. Cambridge: Cambridge University Press, London.
38. Uvarov, B. P. (1977) *Grasshoppers and Locusts*, Vol. 2. London: Centre for Overseas Pest Research, London.
39. Whiteman, D. W. (1990) Grasshopper chemical communication *In* Biology of Grasshoppers, eds. Chapman, R. F. & A. Joern, J. Wiley & Sons, New York, 375–391.