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Adult Desert Locust Swarms, *Schistocerca gregaria*, Preferentially Roost in the Tallest Plants at Any Given Site in the Sahara Desert

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Abstract: The desert locust, *Schistocerca gregaria*, is a major migratory pest that causes substantial agricultural damage. Flying adult swarms disperse widely during the daytime, but they densely roost on plants at night. Swarm control operations are generally conducted during the daytime, but night-time control is a significant potential alternative. However, the night-roosting behavior of swarms is poorly understood. We determined night-roosting plant preferences of migrating sexually immature swarms of *S. gregaria* at four different sites in the Sahara Desert in Mauritania during winter. The night-roosting sites were divided into two types based on presence or absence of large trees. Swarms tended to roost on the largest trees and bushes at a given site. Swarms used medium-sized plants when large trees were not locally available, but the same medium-sized plant species were hardly used when large trees were available. Plant choice influenced roosting group size—large locust groups roosted on larger plants. Night-roosting locusts rarely fled from approaching observers. These results suggest that swarms of *S. gregaria* exhibit plasticity in their utilization patterns of night-roosting plants depending on the plant community encountered and they selectively use larger plants. We propose that this predictable plant-size dependent night-roosting can be used to particularly ease locust swarm control and to generally adopt anti-locust night control strategy.

Keywords: aggregation; density-dependent phase polyphenism; migration; night-roosting site choice; *Schistocerca gregaria*

1. Introduction

The desert locust, *Schistocerca gregaria* (Forskål, 1775), is one of the most destructive migratory pests in the world [1–3]. Locust outbreaks are irregular and can cause serious agricultural damage over a wide range across West Africa, the Middle East, and southwest Asia [4–8]. Understanding the biology and ecology of wild locusts can help improve locust management [9,10].

Locusts are polyphenic grasshopper species that show density-dependent phase polyphenism in behavioral, morphological, and physiological characteristics [11–13]. Solitarious locusts occurring at low densities are usually dispersed across the landscape, while gregarious locusts at high densities aggregate together and migrate over long distances as a group [14,15]. Nymphal and adult groups are traditionally called "bands" and "swarms", respectively. Swarm sizes vary greatly and sometimes cover several hundred square kilometers [7,15]. Preventive control has been promoted, where the nymphal stages are treated before they reach adulthood and can fly as swarms to agricultural areas, because control of highly mobile, gigantic swarms is costly and ineffective [1,5,9,10,16]. Although desert locust management systems have been developed by the Food and Agriculture Organization of the United Nation (FAO), locust affected countries, and researchers by using chemical pesticides and biopesticides, swarms often occur at remote and inaccessible habitats due to geography and insecurity issues and then invade cultivated areas near human activity [17]. This may be one of the reasons why we still face desert locust problems in 2020 [18,19]. Therefore, improving control techniques and methods against swarms is important.

Surveys and control operations are usually conducted during the daytime and consider environmental factors such as wind, temperature, plant community, time of day, and locust behavior [20]. Swarms show various diel-cycling behavioral activities such as migratory flying, settling on the ground for basking, feeding, and resting during the daytime, and roosting on plants at night [15]. Aerial spraying using aircrafts is one of the few control techniques against flying swarms [21–23], but the flying locusts become hazardous to low-flying aircraft. When swarms settle on the ground, ground control measures can be used, which involve less pesticides than control measures against actively flying swarms [23]. However, the settling period is relatively short and irregular during the daytime [20,22]. Therefore, the efficacy of night-time control as an additional management strategy should be explored. As a first step, knowledge of night-roosting behaviors of swarms is essential.

Swarms roost for the night in trees or bushes. Locust densities in roosting swarms are much higher than that in migrating swarms [15]—the ratio between the area taken up by a swarm in flight and that by a swarm when settled can range from 12:1 to 900:1 [22]. Therefore, night-roosting swarms may be a suitable target for control. However, little is known about the night-roosting plant preference of swarms at a fine scale [24]. Our previous studies observed that both solitary adults and small-grouped gregarious adults selectively roosted on large trees [25,26]. Habitats of *S. gregaria* are diverse in terms of topography and plant communities, including vast plains with a variety of soil types such as rocky dry soils, dunes, and playas [27–29]. Some areas lack large trees and only have small bushes [30,31]. Highly mobile swarms of *S. gregaria* could encounter a variety of plant communities during migration [6,21,32], thus it is likely that they sometimes cannot reach favorable plant communities until night. However, they can access favorable plants by flying within the local areas. Accordingly, we hypothesized that migratory swarms of *S. gregaria* exhibit plasticity in their night-roosting plant utilization patterns depending on local plant communities and preferentially use relatively large plants. Previous studies have suggested that night-roosting plant choice influenced locust group size—gregarious nymphs selectively roosted on the largest plants and formed large groups [33]. Accordingly, we also tested the hypothesis that night-roosting swarms of *S. gregaria* form larger groups on larger plants.

Mauritania is a major breeding and recession area for the desert locust [27,30,34,35]. In 2013, swarms invaded the Banc d'Arguin National Park in Northwestern Mauritania, where plants are abundant and natural conditions are preserved. This ecological Park is nationally strictly protected from any chemical pesticides or alternative pest control strategies, only mechanical methods are allowed. We used this opportunity to test our hypotheses. We investigated the night-roosting plant preference and group formation of migratory swarms of *S. gregaria* at a fine scale. This work will contribute to developing better locust swarm survey and control methods.

2. Materials and Methods

2.1. Study Area

Mauritania, in West Africa, is an important area for desert locust outbreaks [27,30,34]. Our study sites were located in the Banc d'Arguin National Park, midway between Nouakchott and Nouadhibou, in north-western Mauritania. The area is a vast plain with a variety of soil types including rocky dry soils, dunes, playas, and small hills along the coast of the Atlantic Ocean. The primary plant community of the survey sites were identified according to Duranton et al. [28]. Sparse, low-growing desert annuals (grasses, herbs, vines, etc.) grow between the bushes and trees. We conducted field surveys from December 22–25 and 29–31, during the winter of 2013, when we encountered migrating sexually immature swarms. At this time, rain was rare and desert annuals were still partially green but starting to dry. Sunrise and sunset occurred at about 07:30 and 18:30 h local time, respectively. The mean temperature during the observation period (21:00–07:00) was 13.6 °C (SE: 0.2 °C, range: 8.6–19.5 °C) and the mean humidity was 44.4% (SE: 0.6%, range: 24.1–71.4%) at 50 cm above the ground, measured using a thermo-hygro recorder (TR-72wf, ONDOTORI, Tokyo, Japan).

2.2. Study Species

We studied migratory swarms of sexually immature adult desert locusts, *Schistocerca gregaria* (Forskål, 1775). Classical morphometric characteristics (hind femur length/head width) of locusts [36] confirmed their gregarious-phase status. During our study, locusts moved and fed in a daily cyclical rhythm—during the colder night and dawn period they roosted in trees and large bushes. After dawn they warmed by solar basking, moved to the ground, and began alternatively feeding, migrating, and resting, often on relatively bare ground. Near dusk, they flew or climbed into trees and large bushes for nocturnal roosting. They mainly fed on low-growing annuals and used the bushes and trees as refuges. Sexually mature gregarious locusts become yellow in body coloration [37]. Our population were dark red in body coloration and no sexual behaviors were observed, indicating that our population were sexually immature.

2.3. Sampling Regime

We followed migratory swarms encountered within the survey site without disturbing them until they roosted at night (17:00–19:00). Field surveys were conducted at night (21:00–07:00). We established 25 × 2-m belt transects and recorded information on night-roosting plants (species and abundance) and locust group size within each transect. We recorded the aggregation level of locusts on each bush and tree based on visual estimation. At least 30 transects were surveyed during each sample period and transects were separated by at least 10 m.

2.4. Night-Roosting Plants

Plants were patchily distributed at the study site. In our previous studies we measured all the plants within transects to examine plant size and locust group levels [31,33], but this was time consuming. In the present study, we determined the maximum length, width, and height of individuals of the dominant plant species at four survey sites within a strait belt transect until obtaining enough sample size, according to Maeno et al. [31]. At least 35 individuals or, whenever possible, all plants were measured and all data were pooled and analyzed to calculate mean size. The volume (m^3) of each plant species was calculated as maximum length × width × height. The abundance of each plant species was calculated from the transects (50 m^2). Maeno and Ould Babah Ebbe [33] reported that maximum plant height rather than width and volume was the most important factor for night-roosting site choice by gregarious late instar nymphs. Accordingly, we categorized relative plant size based on mean plant height: small, <1.0 m; medium, 1.0–2.0 m; large, >2.0 m. At Site 1, some trees *Euphorbia balsamifera* and bushes *Nucularia perrini* had started to dry out. Therefore, we also recorded plant states (green vs. dry) based on leaves from the two plant species to test whether green plants attracted more locusts and formed larger groups than dry ones.

2.5. Locust Group Size

We estimated the number of adults roosting on each plant by directly counting them after 20:00 when locusts were inactive. Each plant was given a score based on the number of roosting locusts (i.e., group size): 0 (0 locusts), 1 (<10), 2 (10–100), 3 (100–1000), 4 (1000–10,000) and 5 (>10,000), following the estimation method described by Maeno et al. [38].

2.6. Defensive Response

To determine defensive behaviors of the swarms at night, their response to an approaching observer carrying a light was recorded according to modified methods by Maeno et al. [39]. We carried a low-intensity wide-angle headlight (Gentos, DPX-233H, Delta Peak) and walked within 1 m from roosting locusts, filming their behavior with a video camera (Panasonic, HC-V520, Tokyo, Japan). This was only done for locusts in groups of size 5 and was repeated for seven night-roosting groups (i.e., >70,000 individuals). This observation was conducted on 30 December 2013.

2.7. Statistical Analysis

The effect of plant species on the percentage of plants roosted by locusts were determined using a post hoc Fisher's exact test after Bonferroni correction. To analyze differences in plant size (maximum length, height, and volume) and abundance between different plant species, Tukey–Kramer HSD tests were conducted. Percentages of plants roosted by locusts were arc-sine transformed and analyzed using Tukey–Kramer HSD tests. Two-way analysis of variance (ANOVA) was used to analyze the effects of plant species and presence of trees on locust group size. Differences in plant sizes between green and dry plants were analyzed using *t*-tests. The proportions of different group sizes were analyzed using a χ^2-test. Statistical analyses were conducted using the software package R, version 4.0.1 [40] and JMP (SAS Institute, Cary, NC, USA).

3. Results

3.1. Plant Characteristics

In the present study, only Site 4 had three large tree species (Figure 1a,b, Table 1). Large trees were relatively scarce (Tables 1 and 2: Tukey–Kramer HSD test, $p < 0.05$). Smaller plants were more abundant than trees (Tukey–Kramer HSD test, $p < 0.05$).

3.2. Daily Cyclical Movement and Night-Roosting Plant Preference

During our study, swarms migrated, fed, settled and roosted on plants in a daily cyclical rhythm. During the colder night and dawn periods, they roosted in relatively large plants including trees and bushes (Figure 1c–e). After dawn they displayed solar basking on the plants or ground by orientating perpendicular to the sun's rays to maximize the body surface (Figure 1f,g). They began alternating between feeding and resting, often on relatively bare ground (Figure 1h). At mid-day they usually migrated downstream (Figure 1i) and sometimes settled on the ground (Figure 1j). When swarms reached the coast, they avoided the ocean and returned inland. As a result, migrating locust density apparently increased (Figure 1k). Near dusk, they flew or climbed into trees and larger bushes for nocturnal roosting. No locusts were observed on the bare ground at night during any of the 150 belt surveys conducted, suggesting that locusts avoid habitats that lack plants. Locusts roosting on large trees rarely flew away from approaching observers with lights (i.e., when we tested their defensive response) (Figure 1l).

Plant utilization patterns by swarms varied. Figure 2 summarizes the percentage of each plant species roosted by locusts at our four survey sites. Large trees, such as *Capparis decidua*, *Acacia tortilis* and *Maerua crassifolia*, were relatively scarce, but most of them were roosted by locusts (post hoc Fisher's exact test after Bonferroni correction, $p < 0.00091$). More than 50% of *Euphorbia balsamifera* trees (medium-sized), *Panicum turgidum* bushes (medium-sized), and *Salsola imbricata* bushes (small-sized) were also utilized by locusts. The other small-sized plants (*Stipagrostis plumosa*, *Crotalaria saharae* and *Hyoscyamus muticus*) were rarely used, except for *Nucularia perrini*.

Table 1. Abundance of 11 dominant plant species in four survey sites. Mean (±SE) number of plants per belt transect (50 m^2).

			ID	**Site 1**	**Site 2**	**Site 3**	**Site 4**
			Data **Location**	**2013/12/22** **19°55′ N, 16°14′ W**	**2013/12/23** **19°53′ N, 16°18′ W**	**2013/12/24** **19°53′ N, 16°18′ W**	**2013/12/29** **19°24′ N, 16°13′ W**
Plant Species	**Family**	**Types of Plant**	**Plant Form**				
Capparis decidua	Capparaceae	Perennial	Tree	-	-	-	0.2 ± 0.3 a
Acacia tortilis	Fabaceae	Perennial	Tree	-	-	-	0.2 ± 0.3 a
Maerua crassifolia	Capparaceae	Perennial	Tree	-	-	-	0.2 ± 0.3 a
Euphorbia balsamifera	Euphorbiaceae	Perennial	Tree	4.2 ± 0.9 b	-	-	1.2 ± 0.3 a
Calotropis procera	Poaceae	Perennial	Bush & tree	-	-	-	0.2 ± 0.3 a
Panicum turgidum	Apocynaceae	Perennial	Bush	-	2.0 ± 0.9 a	6.6 ± 0.8 b	-
Stipagrostis plumosa	Poaceae	Annual	Bush	-	-	-	6.8 ± 0.3 b
Salsola imbricata	Amaranthaceae	Annual	Bush	2.7 ± 0.9 ab	10.5 ± 0.9 b	3.7 ± 0.8 ab	-
Nucularia perrini	Amaranthaceae	Perennial	Bush	17.0 ± 0.9 c	10.8 ± 0.9 b	6.3 ± 0.8 b	0.3 ± 0.3 a
Crotalaria saharae	Fabaceae	Perennial	Bush	-	2.0 ± 0.9 a	1.2 ± 0.8 a	-
Hyoscyamus muticus	Solanaceae	Annual	Bush	0.7 ± 0.9 a	-	-	-
			No. of transects	30	30	30	60

Different letters after values indicate significant differences within each survey site (Tukey–Kramer HSD test, $p < 0.05$). "-" indicates the absence of the plant species at the study site.

Night-roosting plant choice varied depending on plant community structure, i.e., the presence of relatively large trees (Figure 3). Our survey sites could be roughly divided into either areas with trees (Site 4) or without trees (Sites 1–3). For example, at Site 1, *E. balsamifera* trees, which are medium-sized, were locally the largest plants and most of them were roosted by locusts, while the percentage of *E. balsamifera* trees roosted by locusts was lower at Site 4. A similar tendency was also observed for *N. perrini* between Site 2 and 4. The relatively small-sized plant, *C. saharae*, was rarely used by locusts even at sites without trees. We could not analyze *H. muticus* due to a small sample size.

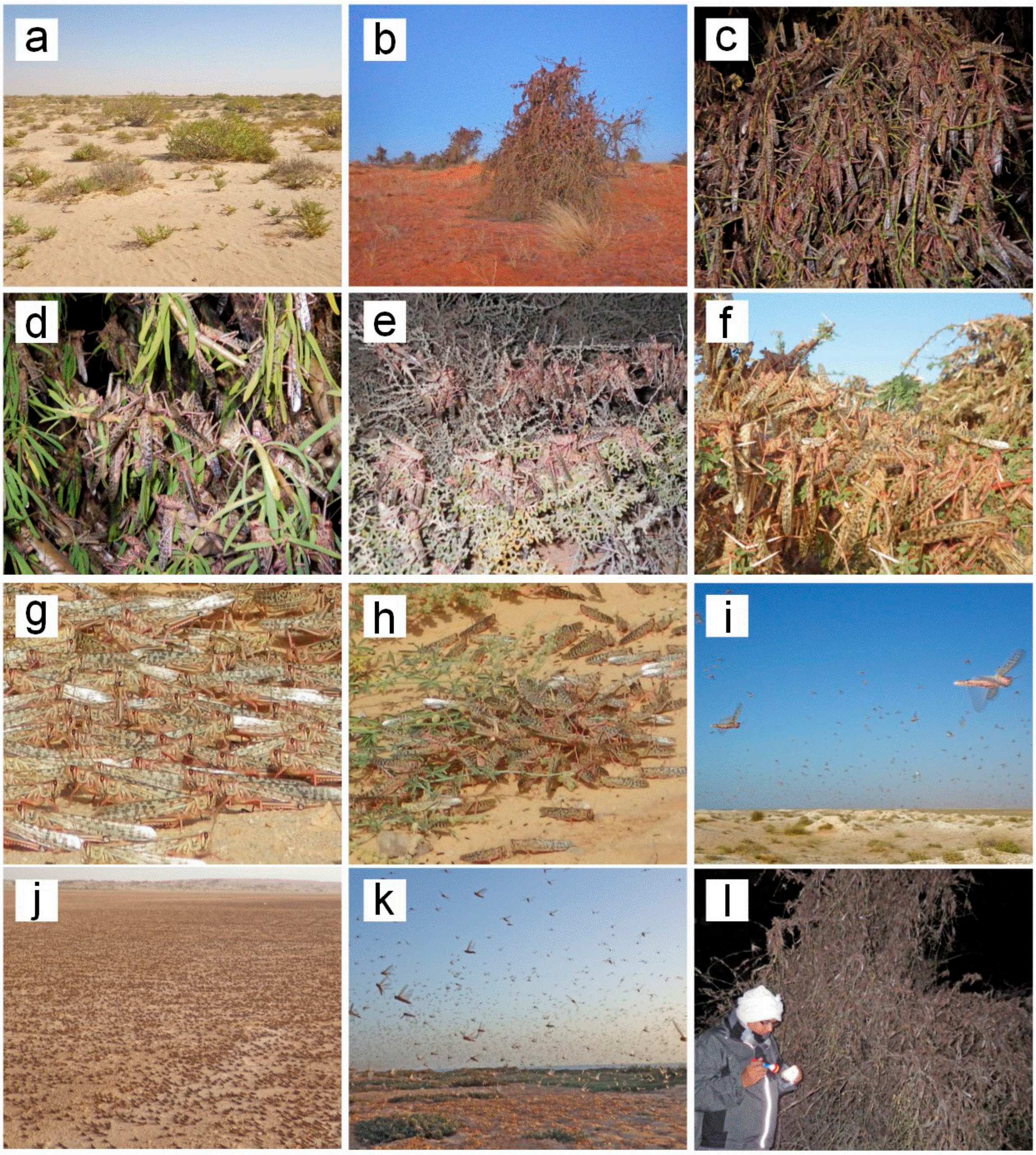

Figure 1. Habitats used by sexually immature swarms of *Schistocerca gregaria* for night-roosting sites and various diel behaviors in a population in Northwestern Mauritania during winter. (**a**) Habitats without trees and (**b**) with trees. (**c**) At night, locusts roosted on large trees (*Capparis decidua*), (**d**) medium-sized trees (*Euphorbia balsamifera*) and (**e**) small bushes (*Salsola imbricata*). (**f**) In the morning, locusts moved to the top of night-roosting trees or (**g**) to the open bare ground for basking. (**h**) Swarms feeding on low vegetation, (**i**) flying swarms, (**j**) settled swarms on the bare ground, (**k**) flying swarms along a coast, and (**l**) an observer staying near night-roosting swarms on a tree at night.

Table 2. Mean (±SE) plant sizes of 11 dominant plant species in the four survey sites.

Plant Species	Relative Size	Maximum Width (m)	Maximum Height (m)	Volume (m^3)	*n* Plants Measured
Capparis decidua	Large	9.34 ± 0.23 h	3.71 ± 0.08 h	331.5 ± 13.2 d	18
Acacia tortilis	Large	7.08 ± 0.20 g	2.84 ± 0.07 g	117.5 ± 11.2 c	25
Maerua crassifolia	Large	5.03 ± 0.25 f	2.29 ± 0.08 f	55.7 ± 14.0 b	16
Euphorbia balsamifera	Medium	2.20 ± 0.11 e	1.26 ± 0.04 e	5.9 ± 6.0 a	87
Panicum turgidum	Medium	2.10 ± 0.12 de	1.18 ± 0.04 e	4.9 ± 6.7 a	70
Calotropis procera	Medium	0.71 ± 0.26 abc	1.03 ± 0.09 de	0.6 ± 15.0 ab	14
Stipagrostis plumosa	Small	1.53 ± 0.17 cd	0.74 ± 0.06 dc	1.5 ± 9.5 ab	35
Salsola imbricata	Small	1.23 ± 0.09 bc	0.54 ± 0.03 bc	0.8 ± 5.3 a	110
Nucularia perrini	Small	1.00 ± 0.08 abc	0.43 ± 0.03 ab	0.5 ± 4.5 a	157
Crotalaria saharae	Small	0.76 ± 0.12 ab	0.32 ± 0.04 a	0.2 ± 6.6 a	71
Hyoscyamus muticus	Small	0.41 ± 0.22 a	0.34± 0.08 ab	0.1 ± 12.5 ab	20

Different letters after values indicate significant differences within each survey site (Tukey–Kramer HSD test, $p < 0.05$). Relative plant size was based on mean plant height: small, <1.0 m; medium, 1.0–2.0 m; large, >2.0 m.

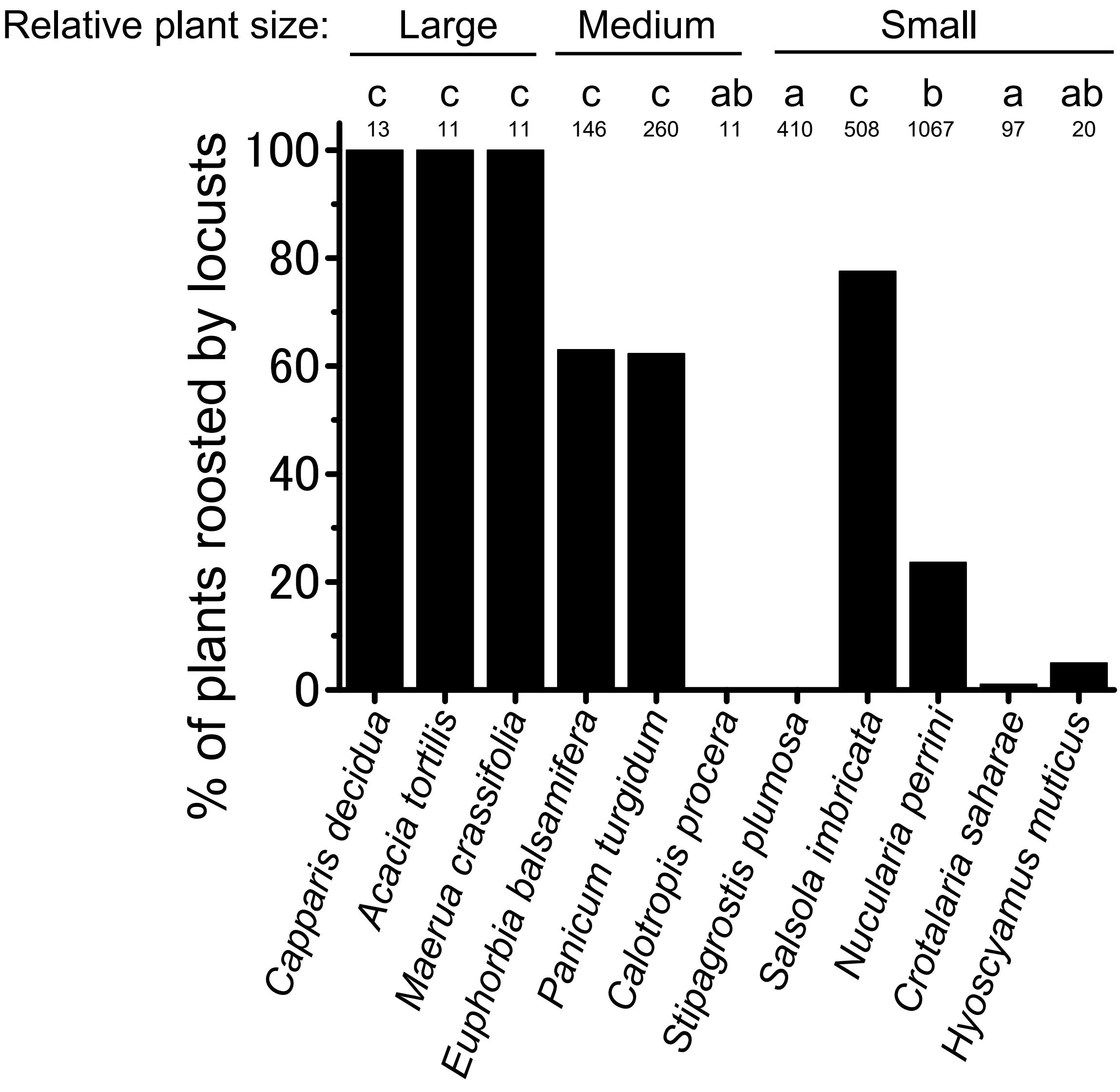

Figure 2. Percentage of plants from 11 plant species roosted by swarms of *Schistocerca gregaria* at four survey sites at night. Numbers above bars indicate sample sizes. Different letters above bars indicate significant differences at $p < 0.00091$ (post hoc Fisher's exact test after Bonferroni correction).

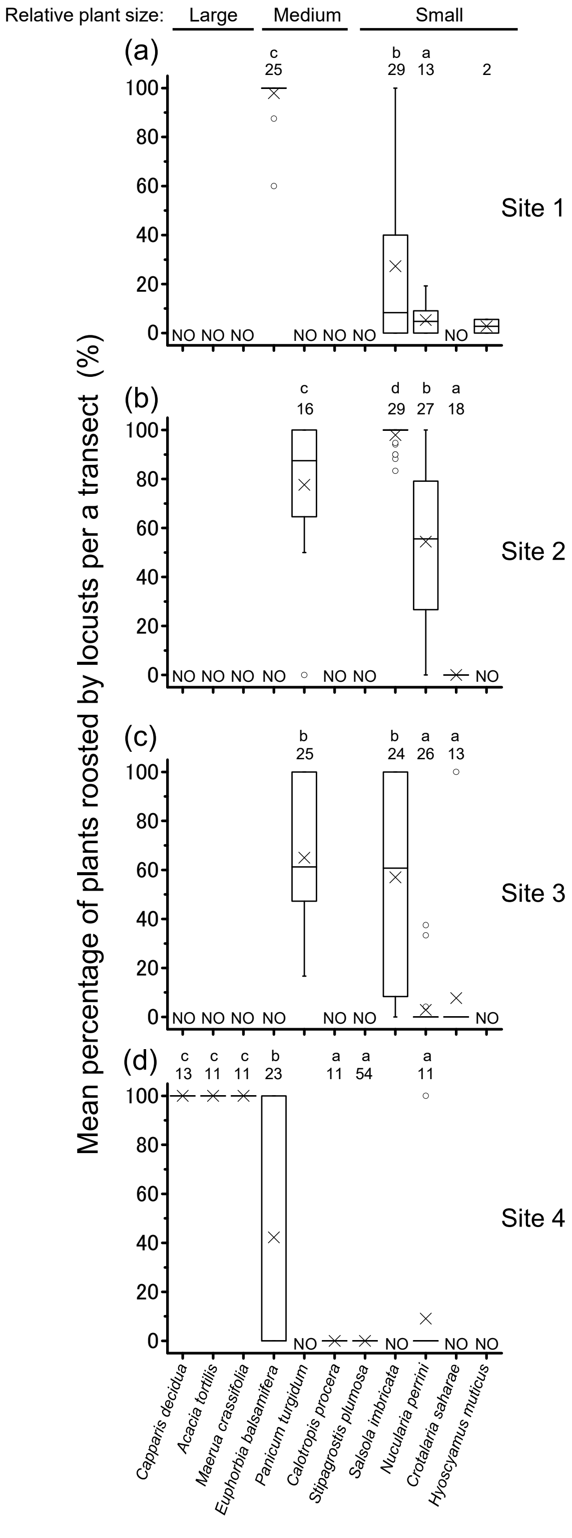

Figure 3. Mean percentage of plants from 11 plant species roosted by swarms of *Schistocerca gregaria* at night at four survey sites [Site 1: (**a**), Site 2: (**b**), Site 3: (**c**), and Site 4: (**d**)]. Each box plot displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentiles. Crosses indicate mean values and open circles are outliers. Different letters above each bar indicate significant differences at $p < 0.05$ based on a Tukey-Kramer HSD test after arc-sine transformation. Numbers above bars indicate sample sizes (numbers of transects which certain plant species were recorded). "NO" in the figure indicates absence of the plant species at the study site.

3.3. Group Size on Roosting Plants

At night, locust groups were rarely observed on the ground or on grass; they mainly aggregated on relatively large plants. Figure 4 summarizes the different group sizes observed for 11 plant species across the four survey sites. Group sizes ranged from size 0 to 5 for each plant species. Larger groups (>10,000) tended to be formed on large trees, and medium-sized groups (3, 100–1000 locusts; 4, 1000–10,000 locusts) on medium-sized trees and bushes, while large-sized group was not formed on small bushes. The 11 plant species differed significantly in the proportion of group sizes that roosted on them (Figure 4: $\chi^2 = 3861.814$, d.f. = 10, $p < 0.01$).

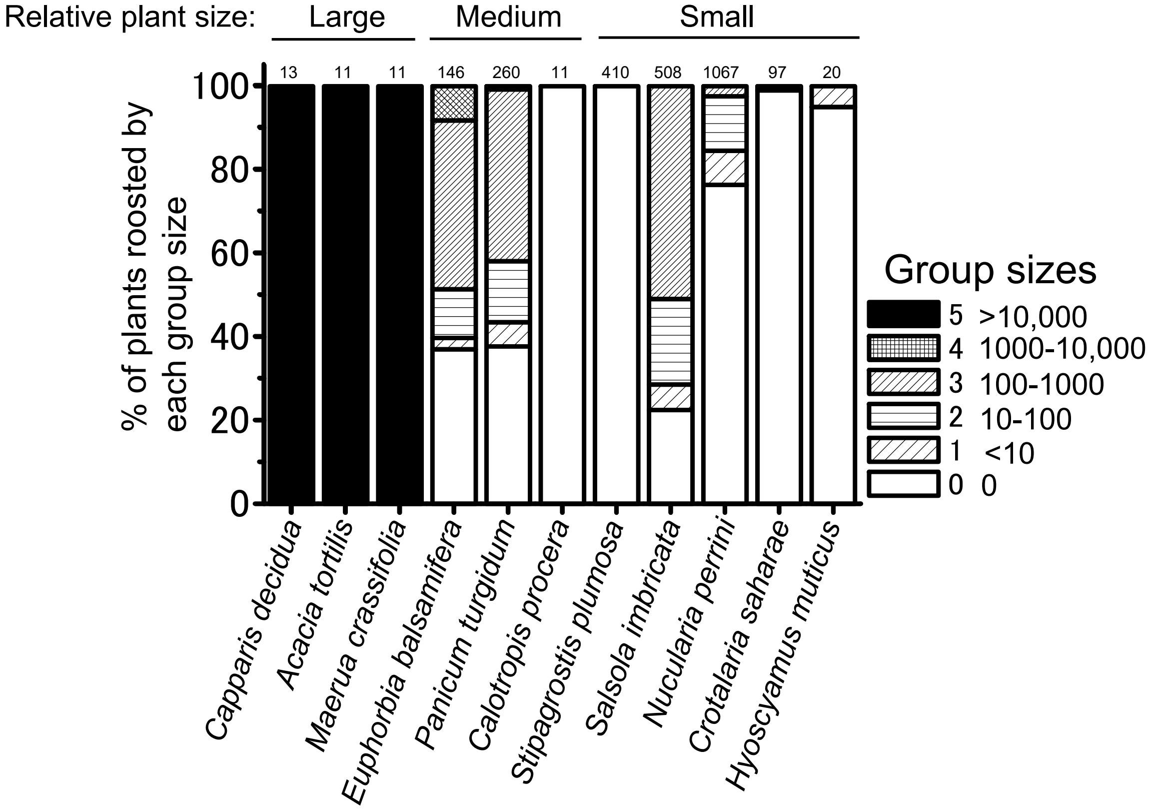

Figure 4. Percentage of plants roosted by each group size of *Schistocerca gregaria* swarms for the 11 dominant plant species at the four study sites. Numbers above bars indicate sample sizes (numbers of plants observed).

Plant community structure also influenced group size (Figure 5). The largest groups (>10,000 locusts per single plant) were observed at Site 4, where there were trees, but not at Sites 1, 2 and 3.

Group sizes on night-roosting plants varied depending on local plant community structure. For example, the size of *E. balsamifera* plants did not differ significantly between Site 1 and 4 (Figure 6a; Wilcoxon rank sum test, $z = -0.598$, $p > 0.05$), but significantly more large locust groups were observed on this species in Site 1 than in Site 4 (Figure 6b: $\chi^2 = 121.170$, d.f. = 4, $p < 0.001$).

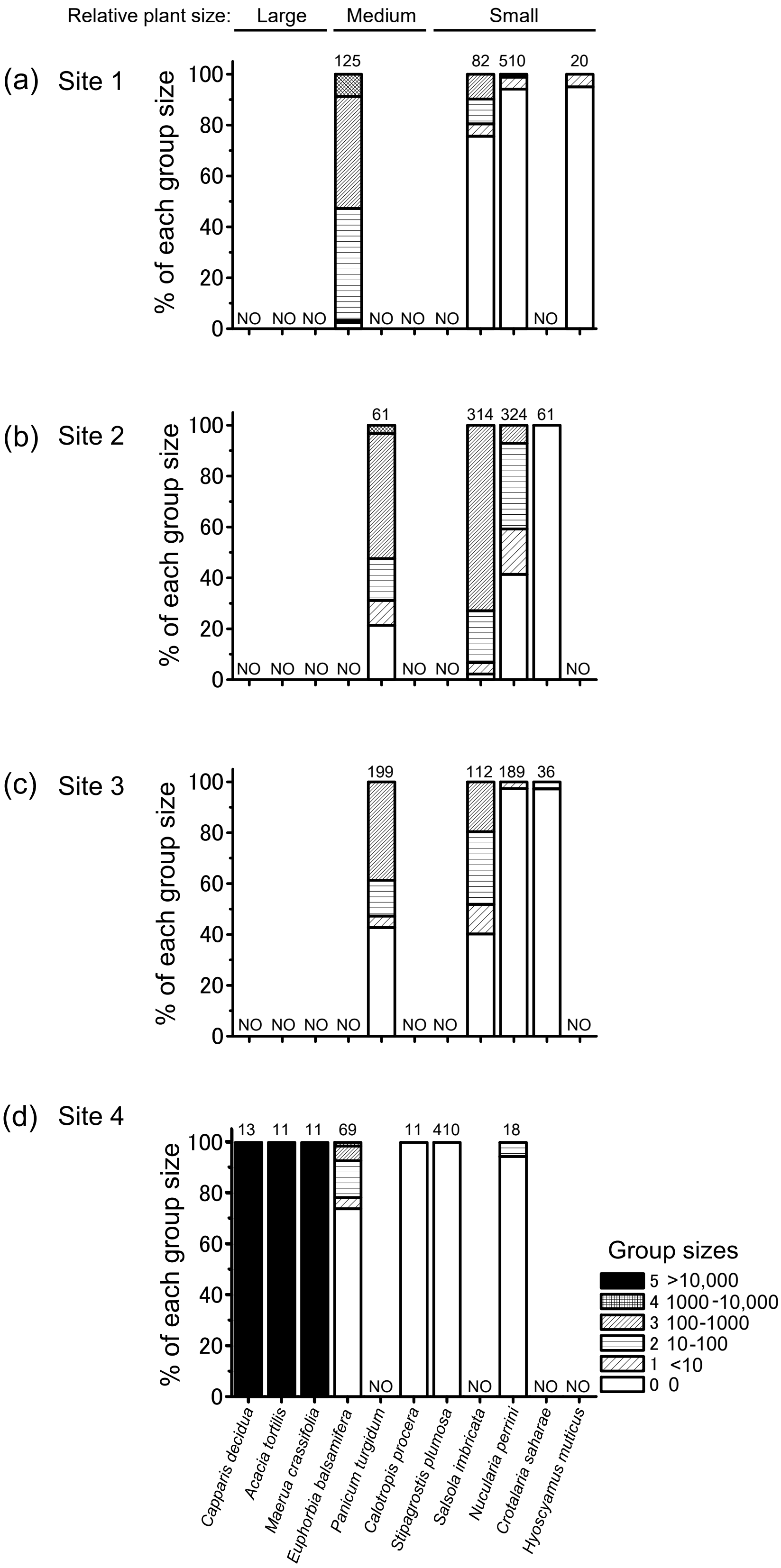

Figure 5. Percentage of plants roosted by each group size of *Schistocerca gregaria* swarms for the 11 dominant plant species at the four study sites [Site 1: (**a**), Site 2: (**b**), Site 3: (**c**), and Site 4: (**d**)]. Numbers above bars indicate sample sizes (numbers of plants observed). “NO” in the figures indicates absence of the plant species at the study site.

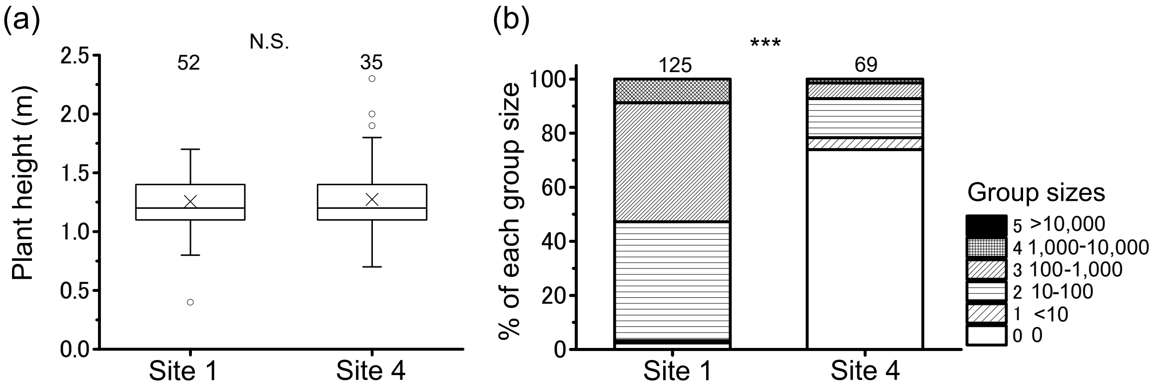

Figure 6. Height of *Euphorbia balsamifera* plants (**a**) and the percentage of *E. balsamifera* plants roosted by each group size of *Schistocerca gregaria* swarms (**b**) at a site without trees (Site 1) and one with trees (Site 4). Each box plot displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentile values. Crosses indicate mean values and open circles are outliers. N.S. indicates no significant differences at $p > 0.05$ according to a Wilcoxon rank sum test. Numbers in figures indicate sample sizes. ***, significant differences between the two groups (χ^2-test, $p < 0.001$).

3.4. Plant Conditions: Green vs. Dry

At Site 1, some *E. balsamifera* and *N. perrini* plants were still green but others were dry. We examined whether greenness of plants influenced night-roosting plant choice of swarms. The utilization of green and dry plants by swarms was compared for each species. Plant size did not differ between green and dry plants for either plant species (Wilcoxon rank sum test, $p > 0.05$ for both). For *E. balsamifera*, greenness did not affect roosting. Conversely, for *N. perrini*, green plants were roosted by locusts significantly more than dry plants (Figure 7a; Wilcoxon rank sum test, $z = -3.573$, $p < 0.01$). Plant greenness did not influence group size composition on *E. balsamifera* (Figure 7: $\chi^2 = 0.8731$, d.f. = 4, $p > 0.05$). Conversely, for *N. perrini*, there were significantly more large locust groups on green plants than on dry plants (Figure 7: $\chi^2 = 24.5$, d.f. = 4, $p < 0.01$).

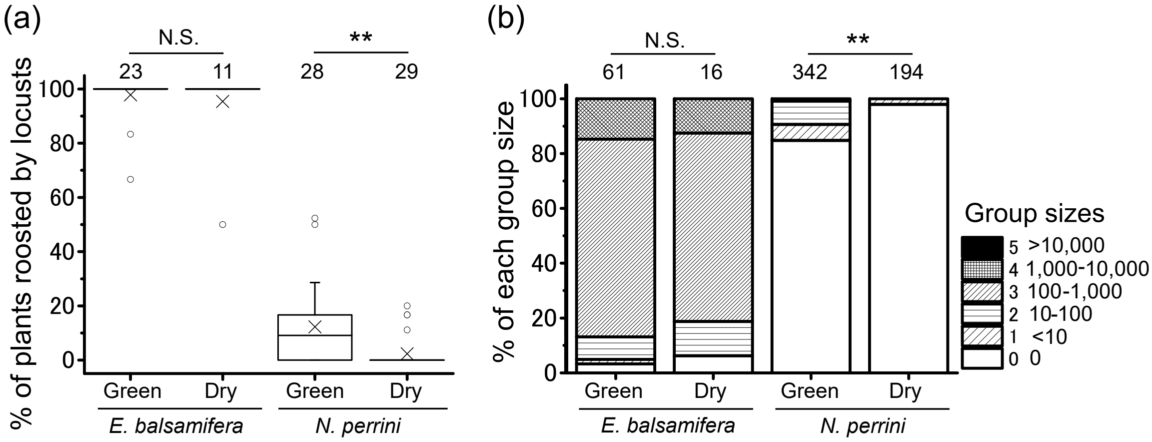

Figure 7. Percentage of green and dry plants roosted by *Schistocerca gregaria* swarms for *Euphorbia balsamifera* and *Nucularia perrini* at Site 1 (**a**) and the percentage of each locust group size on each plant (**b**). Each box plot displays the median value with the ends of the boxes representing the 25th and 75th percentiles and the ends of the lines representing the 10th and 90th percentiles. Crosses indicate mean values and open circles are outliers. Numbers in figures indicate sample sizes. (**a**) **, $p < 0.01$; N.S. indicates no significant differences between the two groups at $p > 0.05$ according to a Wilcoxon rank sum test. (**b**) **, $p < 0.01$; N.S. indicates no significant differences between the two groups at $p > 0.05$ according to a χ^2-test.

4. Discussion

The present results support our hypothesis that migratory swarms of *S. gregaria* exhibit plasticity regarding their utilization patterns of night-roosting plants depending on the plant community encountered and they selectively use larger plants. Furthermore, we found that their night-roosting plant choice influenced locust group size—larger groups were formed on larger trees, and night-roosting locusts rarely fled from approaching observers. This knowledge not only aids our understanding of night-roosting behaviors of swarms, but is also important for effective and easier locust control by night. In the following, we will discuss night-roosting plant preference and group formation by swarms of *S. gregaria* and how to apply this knowledge for improving locust control operations.

4.1. Night-Roosting Plant Preference

Many grasshopper species are known to roost on plants overnight [15]. In *S. gregaria*, swarms are known to roost on large trees or bushes at night [15,22,24]. The present study confirmed this trend for sexually immature swarms in Northwestern Mauritania during a winter season. Further, we found plasticity in their night-roosting plant utilization—they preferentially used relatively larger plants within local plant communities, but they used medium-sized trees and bushes as refuges when large trees were not available. For example, swarms were observed on most of the *E. balsamifera* trees, which are medium-sized, at Site 1, where this plant species was locally the largest. Conversely, the percentage of *E. balsamifera* trees roosted by locusts at Site 4 was less than half that at Site 1, as large trees were present in Site 4. Height of *E. balsamifera* trees was not significantly different between the two sites, thus swarms might use relative plant size to select night-roosting plants. Swarms also occupied medium-sized bushes at Site 2 and 3 where large trees were not available. To our best knowledge, we are the first to report that swarms of *S. gregaria* change their night-roosting plant preference depending on the local plant community, preferentially using the largest plants within the local area. We have previously observed that marching gregarious nymphs of *S. gregaria* also selectively roosted on the largest trees in the local plant community and plant height rather than width and volume was the primary cue for night-roosting plant choice [33]. Solitarious adults and gregarious adults at relatively low densities, and even solitarious nymphs, used relatively larger plants as their night-roosting sites [25,26,31]. These results suggest that *S. gregaria* tend to use relatively larger night-roosting plants irrespective of population density, developmental stage, and phase.

Plant height seems to be a useful criterion not only for ground-dwelling locust nymphs but also for flying adults, likely because they can visually recognize tall plants from all directions and they are comparable and available in all locust habitats. In fact, plant height is frequently used by insects as a cue for selecting aggregation sites, known as a "hill-topping" behavior [41]. At Site 3 where the ground was almost flat and there were no large trees, our car (TOYOTA, Land Cruiser, 5 m × 2 m × 2 m) was the largest object at the site. We observed that some flying locusts tried to land on our car around dusk (18:20–18:50). This observation also suggested that locusts preferred relatively large plants (or objects) within the local area and provided a hint for developing an artificial trapping system which can be used as an environmentally friendly control option. The simple criterion of plant height seems to be useful for migratory locusts as they encounter various habitats characterized by different vegetation cover, plant species, and plant sizes [24,27,28].

Plants are frequently used as a refuge by prey animals [42]. Greenness, i.e., the amount of leaves on refuge plants, may influence detectability by predators [42]. In the present survey sites where trees were not available, greenness of medium-sized plants such as *E. balsamifera* did not influence night-roosting site choice by swarms of *S. gregaria*, but more green plants of small-sized plants (*N. perrini*) were used than dry ones. Plant size of *N. perrini* did not differ depending on greenness, thus this may suggest that greenness is an important factor for small-sized plants. These plants are mainly used as a shelter rather than as food during a night. However, larger dry *E. balsamifera* plants attracted more locusts than green *N. perrini* plants, thus attraction of greenness could be masked by plant size. Although plant height was almost similar between the small bushes *S. plumosa* and *S. imbricata*, the former were rarely used by locusts. The stem and leaves of *S. plumosa* are thin and soft, thus they seem to have an unstable structure. This observation suggests that morphological characteristics of plants could be another factor for night-roosting plant choice.

Anti-predatory strategies are usually associated with microhabitat selection [42]. In the present survey area, ambient temperature can fall below 20 °C at night. Because escaping performance is temperature-dependent in grasshoppers [43,44], adult locusts cannot escape quickly from approaching predators below 20 °C [39]. This is most likely why locusts roost in large trees and bushes at night, away from nocturnal ground-foraging mammals. Morphological structures of medium-sized *P. turgidum* bushes and small-sized *N. perrini* bushes, which locusts used in the present study, were complex and apparently prevented access of relatively large predators. Some smaller plants such as *S. plumosa* and *C. saharae* had enough space for many locusts to roost, but the percentages used by swarm were small, probably because they did not provide shelter. Furthermore, aggregation with conspecifics could reduce the risk of predation through a dilution effect, or the "selfish herd effect" [45], as suggested for lubber grasshoppers, *Romelea guttata* [46], and Mormon crickets, *Anabrus simplex* [47]. Therefore, using refuges and grouping on the night-roosting plants might jointly serve as an anti-predator strategy. Interestingly, night-roosting locusts sometimes responded to an approaching observer by dropping and moving their hind legs, but they usually remained in place. It remains unclear how darkness (i.e., intensity of moon light) and low temperature influence escaping behaviors of night-roosting locusts, but this reduction of escaping performance may be useful, because sprayers can closely approach swarms.

4.2. Local Locust Group Size on Night-Roosting Plants

The present results supported our hypothesis that migratory swarms of *S. gregaria* would form larger groups on larger night-roosting plants. We found that larger locust groups (>10,000 individuals) roosted on large trees (>2 m tall), while medium- and smaller-sized locust groups (10–10,000 individuals) roosted on medium- and small-sized trees and bushes. This variation cannot be explained by plant size as a capacity of roosting space alone. Of course, large trees have more roosting space than small bushes, but the presence of large trees influenced the locust group size on other roosting plants. Locust group size on medium-sized plants significantly decreased when large trees were nearby, as observed for the medium-sized tree *E. balsamifera* at Site 1 and 4. This suggests that larger trees attracted more locusts from surrounding smaller plants. This spatial pattern was similar to that observed in gregarious late instar nymphs of *S. gregaria*—marching bands formed one large group on the largest plant with several smaller groups scattered at the local level [33]. This trend could be associated with plant distribution patterns and sizes in the semi-arid area. In the desert plant community, resource competition for water often results in heterogeneous patchy distributions [48], as was observed in the present survey area. The largest trees in a local area were conspicuous, because no other large plants existed near them. This may allow swarming locusts to see the roosting tree from afar without the need to evaluate other potential roosting plants.

In *S. gregaria*, it has been reported that heterogeneous plant distributions promote local crowding leading to gregarization, whereas a uniform distribution promotes scattering [29,30,49–53]. Cisse et al. [29] reported that vegetation cover and greenness influenced the threshold of gregarization in adults—low vegetation cover and dry vegetation led to a low density threshold of gregarization. Drying or dry vegetation forces locusts to meet on the few usable resources of a given area. Ould Babah and Sword [30] showed that specific plant communities promoted gregarization in nymphs. The present results suggest that not only plant distribution, communities, greenness, and cover, but also relative plant size, particularly the presence of large trees, and plant community structure played an important role in aggregation and local locust density.

Physical contact with conspecifics is the primary factor inducing gregarization in locusts [54–57], but flying locusts stay at a distance from conspecifics [15]. This raises the questions of when and where swarms aggregate and maintain gregariousness during migration. Microhabitat preferences are critical to recruit scattered conspecifics to a particular site [58], and individual attraction, group basking behavior and microhabitat preferences jointly lead conspecifics to concentrate within a limited area [49]. In *S. gregaria*, some scattered swarming members were also attracted to the large roosting trees, suggesting that scattered swarms can fuse to form an aggregation via night-roosting behaviors. Local crowding in the habitat has been observed on discrete resources such as host plants, basking, or shelter sites [49,59]. It is reasonable to assume that night-roosting plant preference of gregarious locusts may concentrate them in limited areas where they would receive physical contact while roosting and ground basking, leading to the maintenance of gregariousness.

4.3. Applications and Future Directions

The present study suggests that future locust control methods could also target night-roosting swarms for the following reasons: (1) night-roosting was a regular event and predictable, (2) locusts densely aggregated on large plants, which were patchily distributed, instead of on the ground or in the air, (3) roosting locusts were relatively immobile and escaping performance was low, thus sprayers could approach roosting locusts even using lights, (4) large trees or bushes are easily located in the habitat. Conversely, it may be difficult to conduct aerial spraying of night-roosting locusts due to the following: (1) a large proportion of the locusts were often inside trees and so would be sheltered if spraying was done from the air, (2) locusts roosted so densely that they would shield one another from aerial spraying, and (3) night-roosting locust swarms are not easily visible from aircraft in addition to the spatial dispersion of trees which make full coverage spraying not rational. To overcome these disadvantages, we suggest the following: (a) ground survey teams should follow migratory swarms until roosting time to determine roosting areas, (b) spraying should be done from the ground by car or by man with backsprayers, (c) sprayers should target night-roosting locusts and control them directly. (d) an eventual trapping system based on high similar object of the trees could be created to attract swarm before they roost, (e) although night-time control operations have been poorly documented, we are planning to test the efficacy of spraying from the ground at night. In 2013, the Mauritanian National Anti-locust centre (CNLA) have collected adults in bags by hands in the early morning within the natural park.

In addition, although the present study did not show any data about locust density of migratory swarms, their density was apparently high when they migrated along the coast. Migratory swarms avoid the polarization of oceans [60], thus members of swarms could be locally concentrated due to such a natural barrier. Therefore, remote sensing techniques and historical survey data could be used in the future to predict night-roosting areas [27,34,61–63]. As suggested by multi-agent models [19,64], the spatial conditions and accessibility of locusts should be considered to improve preventive control system.

In the future, if we can develop techniques to repel and attract swarms, a combination of these two techniques can concentrate swarms in a limited area. At the present, unfortunately, we have not developed such techniques, but integrating various information such as night-roosting site preference, natural barriers such as water, and meteorological and topographical information can help to inform which areas are suitable for extensive control operations. The present study identified factors potentially influencing locust group size on night-roosting plants such as site, plant type, plant conditions (green/dry), plant relative size, plant abundance and plant community. We should determine major parameters by using appropriate statistical models. It will be necessary to repeat this exercise with data from other countries and seasons in order to broaden our understanding.

Local people and field workers have empirically known that swarms roost on large trees at night, but this has yet to be sufficiently reported in the scientific literature. It is important to share field and local observations, not only to inspire scientists but also to improve control methods.

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