Upsurges of desert locust populations in Mauritania: Body coloration, behavior and morphological characteristics

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(Received 10 June 2010; Accepted 11 August 2010)

Abstract

A short excursion was made to the western part of Mauritania to investigate increasing populations of the desert locust, *Schistocerca gregaria*, in October 2009. The size of locust populations observed ranged from <1 to >20 individuals per 25 m². Adults from low- and high-density populations were similar in morphometric ratios of F/C and E/F (F, hind femur length; C, maximum head width; E, fore wing length) and the ratios were similar to those reported for solitary forms. However, locusts from high-density populations were mostly yellow, while those from low-density populations were brown or whitish. The former were observed ovipositing in groups. These observations, together with the fact that some of the females from high-density populations had ovarian eggs significantly larger than those found in females from low-density populations, suggested that gregarization might have occurred after adult emergence. Aggregations of nymphs were observed at many sites, and nymphs with black patterns typically observed in transient and gregarious populations were found together with those with solitary body coloration, i.e. green or brown. A prompt action of locust control by National Locust Control Center was likely to have contributed to prevent further upsurges in the locust populations in the following seasons.

Key words: Body color; desert locust; egg size; maternal effects; outbreaks

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INTRODUCTION

The desert locust, *Schistocerca gregaria* Forskål, is one of the most destructive pests in the world. The area infested by this locust can cover as much as 25% of the land surface on the earth (Steedman, 1988). During the last outbreak in 2003–2004, eight million people in the Sahel suffered from it and the losses from locust infestation amounted to 80–100% of the expected yields (Brader et al., 2006). While much information is available about locust populations at and after outbreaks in locusts (Uvarov, 1966; Wilps, 1997; Lecoq, 2005; Tanaka and Zhu, 2005; Huis et al., 2007; Yamagishi and Tanaka, 2009), it is rather difficult to observe how solitary populations turn into gregarious ones in the field mainly because prediction of a locust outbreak is not easy. In 2009, upsurges of desert locust

populations started in Mauritania, and we made a short excursion to the western part of Mauritania to investigate the levels of population density and morphological and physiological changes in the locusts.

The upsurge of locust populations was first noticed by a survey team of National Locust Control Center (NLCC) at the beginning of August 2009 when adults were observed occurring sparsely over a wide range of areas particularly in the southeastern part of Mauritania (Monthly Bulletins at www.claa.mr). This situation first looked usual but was changed after a good rainy season in those areas in September 2009. The rainfall apparently triggered the development of favorable ecological conditions for locusts, which was followed by fast propagation and aggregation of desert locusts.

S. gregaria shows phase polyphenism and vari-

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DOI: 10.1303/aez.2010.641

ous morphological, physiological and behavioral traits vary depending upon the population density (Uvarov, 1966, 1977; Pener, 1991; Pener and Simpson, 2009). For example, solitary hatchlings are green and gregarious ones are black. Later stadium nymphs also show conspicuous differences in body color depending upon the population density and other environmental factors (Faure, 1932; Stower, 1959; Hunter-Jones, 1962). Adult body dimensions also differ between phases (Dirsh, 1951, 1953), and laboratory studies (Hunter-Jones, 1958; Maeno and Tanaka, 2009b) suggest that both nymphal and parental crowding conditions play important roles in determining morphometric ratios.

In the present study, adult locusts were sampled at different sites in Mauritania where locusts were relatively abundant or rare, and their phase status was determined based on classical morphometric ratios of F/C and E/F (F, hind femur length; C, maximum head width; E, fore wing length). These ratios are often used to separate locusts in different phases (Dirsh, 1953; Stower, 1959; Stower et al., 1960; Uvarov, 1966; Maeno et al., 2004; Maeno and Tanaka, 2009b). Another trait recorded was the number of stripes on the compound eyes of adults. Nymphs of this species add one stripe at every ecdysis, and the total number of stripes is predominantly five in gregarious adults and six in solitary adults (Roonwal, 1947; Hunter-Jones, 1958; Injeyan and Tobe, 1981; Maeno and Tanaka, 2008a). Therefore, it is possible to infer the population density during the nymphal stage by counting the number of stripes on the adult compound eyes. We also measured lengths of ovarian eggs in some of the female specimens. Egg size is considerably flexible and larger in those produced by gregarious (crowd-reared) locusts than in those laid by solitary (isolated-reared) ones (e.g. Maeno and Tanaka, 2008b, 2009a). It is influenced by the crowding conditions to which the female parents have been exposed as adults (Hunter-Jones, 1958; Maeno and Tanaka, 2008b). Therefore, this trait may be used as an indicator of the population density experienced by the female locusts shortly before they are collected in the field (Tanaka and Maeno, 2010). Attention was also paid to locust body color and behavior in relation to their habitat and population density. The present paper describes the results of these observations and discusses the phase status of the field populations ob-

served.

MATERIALS AND METHODS

Survey sites. Mauritania, in West Africa, covers an area of 1.1 million km² and represents an important area in which gregarization takes place within the recession zone of the desert locust (Babah, 1997). An excursion was made from 16 to 22 October 2009. Table 1 summarizes a list of survey sites in Mauritania where the population densities were estimated and/or locust samples were collected. The exact locations were recorded with a

Fig. 1. Maps showing collection sites in Mauritania. A, enlarged map of the square area in map B.

Table 1. The population densities and body coloration in *S. gregaria* adults at 10 collection sites in Mauritania in 2009

Study sites	Location	Date	Population density ^a	Adult body coloration ^b
1	18.43°N 14.40°W	16 October	high	yellow
2	18.44°N 14.39°W	16 October	low	white/brown
3	18.52°N 14.22°W	17 October	high	yellow
4	18.52°N 14.21°W	17 October	low	yellow
5	18.50°N 14.27°W	18 October	high	yellow
6	18.58°N 14.12°W	18 October	high	yellow
7	19.45°N 14.24°W	18 October	low	white/brown
8	18.04°N 15.56°W	21 October	low	white/brown
9	18.17°N 16.00°W	21 October	high	yellow
10	17.59°N 15.57°W	22 October	low	white/brown

^a Population density was roughly estimated as low and high when it was <1 adult and >10 adults per 25 m², respectively.

^b Body color indicates white/brown or yellow in more than half of individuals.

GPS device (GH-615, Global Sat, Taiwan). These sites were chosen either based on information from other stuff of NLCC or by checking flying adults from a moving vehicle. Locusts were caught with an insect net or by hands. At site 5, locusts were sprayed a week before we visited, and locust remains were collected.

Estimation of population density. The population density was roughly estimated at each of 10 collection sites to determine if the number of adults exceeded 1, 10, 20 or 30 per 25 m² (5×5 m) in an area (ca. 0.5–1 ha) where locusts were collected. In the present study, the populations with a density <1 per 25 m² will be called low-density populations for convenience, whereas those with a density >10 per 25 m² will be called high-density populations. Adult body coloration was also noted. The brown spots and patterns on the body and wings do not change conspicuously throughout the adult stage in *S. gregaria*. However, the background body color is pink, whitish, brown or yellow depending upon the age and population density experienced (Norris, 1954; Uvarov, 1966). It is pink shortly after adult emergence and turns yellow as gregarious locusts mature sexually (Pener, 1991). Adults were divided into three groups based on the intensity of yellowing on the face and abdomen: brown, whitish adults with no yellow flush or spot, yellow adults with a whitish area on the lower half of the face and on the abdomen except for the last few yellow segments, and bright yellow adults without any whitish area or with a whitish area only in the first few tergites of the abdomen.

Body coloration of first stadium nymphs. First stadium nymphs identified by their body size and morphology (Uvarov, 1966) were sampled with an insect net at four sites and killed by heat in plastic bags which were placed on the ground or the hot roof of a car during the day. They were then divided into five groups based on the darkness of the body color according to the method of Maeno and Tanaka (2007). Body coloration was also recorded for nymphs at other stadia. The penultimate and last nymphal stadia were identified by the size and position of the wing pads: the wing pads move to the dorsal surface at the penultimate stadium and their size increase at the last stadium, as described for other species (Uvarov, 1966).

Morphometric measurements. Hind femur length (F), maximum head width (C) and fore wing

length (E) of adults were measured with a digital calipers (SC-15S, Mitsutoyo Co., Japan) to determine the classical morphometric ratios of F/C and E/F (Dirsh, 1951, 1953).

Determination of ovarian egg lengths. Some female adults had eggs in the ovaries when dissected 1–4 days after being collected. The ovaries were dissected out to measure egg lengths. Five chorionated oocytes or eggs were randomly chosen from the ovaries of each female and lengths were measured with a digital calipers to the nearest 0.1 mm.

RESULTS

Population density

Among 10 sites examined, locust density was >10 adults per 25 m² at five sites (high-density populations), whereas it was <1 adult at the other sites (low-density populations) (Table 1). The densest population observed was found at site 1 where >20 adults were found per 25 m². Adults in the low-density populations were apparently in the solitarious phase (Fig. 2A), as will be described below. They were hard to capture, because they tended to fly easily when they were approached.

Ovipositing behavior and adult body coloration

Site 1 was visited at 16:00 and 19:30 on 16 October. At 16:00 several thousand of yellowish adults were found over several ha and most of them were mainly walking or sitting still in sunshine. Most females were mounted by a male, but no individuals were found ovipositing. Plants such as *Tribulus alatus* (Zygophyllaceae) and *Heliotropium ramosissimum* (Boraginaceae) occurred sparsely and some adults were observed feeding on the former. Body color was bright yellow in most males and some females (Fig. 2B). A half of females were light yellow or whitish. At 19:00 several thousand of adults were still found at the same site and many females were ovipositing in groups of 5–20 pairs. Ovipositing females were also observed during the day at other sites. Site 9 was visited in the morning (10:00–12:00, 21 October) when it was sunny and hot (34°C; 20% relative humidity). Many locusts were actively ovipositing in groups of 5–15 pairs (Fig. 2C, D). Most females were also mounted by males. Single males were trying to mount females, but no males were observed attack-

Fig. 2. Photographs of *S. gregaria*. A, a female adult; B, an adult pair; C, group oviposition at site 9; D, ovipositing females at site 1; E, aggregation of 1st stadium nymphs on *T. alatus*; F, a nymph with black patterns with a white background color; G, a nymph with black patterns with a yellow background color; H, a nymph with black patterns with a green background color; I, a green last stadium nymph on *Z. waterlotii*; J, a brown last stadium nymph; K, nymphs with black patterns with a white background color on *C. conglomeratus*; L, a nymph trapped in an antlion conical pit.

Fig. 3. E/F (fore wing length/hind femur length) ratios plotted against F/C (hind femur length/maximum head width) ratios for female (A) and male *S. gregaria* adults (B) collected in low-density ($\circ$) and high-density populations ($\bullet$) in Mauritania.

ing paired locusts during a 30-min observation period ($n > 20$). In one case, a male passed paired locusts as if he had not noticed the presence of the female, the situation being similar to what has been reported in the laboratory (Seidelmann and Ferenz, 2002; Ferenz and Seidelmann, 2003).

Body color and morphometric ratios of adults

Locusts from low-density populations were mostly whitish or brownish and those from high-density populations were yellow (Table 1). The incidence of yellow individuals was different among high-density populations and between sexes. For example, the proportions of white, yellow and bright yellow adults were 13.3%, 50.0% and 36.7% in females ($n=30$) and 3.4%, 6.9% and 89.7% in males ($n=29$) at site 6. The corresponding figures were 42.9%, 42.9% and 14.2% in females and 0%, 2.9% and 97.1% in males at site 9 ($n=35$ each).

The ranges of the distribution for the morphometric ratios in the low- and high-density populations overlapped each other (Fig. 3), and no significant difference was found in either F/C or E/F ratio between the two groups in each sex (Table 2; $p > 0.05$; Mann-Whitney's U -test). The two groups of adults were almost identical in all body dimensions measured except for total body lengths in females in which a significant but slight difference was detected (Table 2). These results indicated that the two groups of adults showed a marked difference in body coloration but their morphometric traits were virtually identical. Table 3 summarizes the body dimensions and morphometric ratios for adults with five (six eye-stripes) and six nymphal stadia (seven eye-stripes) separately. In either sex, adults with five nymphal stadia had significantly smaller body dimensions, smaller F/C ratios and

larger E/F ratios than those with six nymphal stadia.

The number of eye stripes

The collected adults had six or seven stripes on each compound eye, and the proportion of individuals with seven eye-stripes was significantly larger in females than in males irrespective of the population density (Table 2). The total proportion of individuals with seven eye-stripes was larger in low-density populations than in high-density populations in females and the reverse was true in males. However, the differences between the low and high populations were statistically insignificant in either case (χ^2 test; $p < 0.05$).

Lengths of ovarian eggs

Only a few females derived from low-density populations had mature ovaries and mean egg length was 7.1 mm (SD=0.3 mm; $n=55$). More females were found with eggs among those collected in high-density populations (sites 1, 3, 6 and 9), but this was simply because more individuals were collected in those populations. The mean length of eggs from these females was significantly larger than that from females collected in low-density populations (mean $\pm$ SD = 7.5 ± 0.3 mm; $n=245$; t -test; $p < 0.001$; $df=299$; Fig. 4).

Aggregation and body coloration of nymphs

Aggregations of early stadium nymphs were observed at several sites including sites 1, 3, 4 and 10. The size of aggregation was not estimated. One aggregation was found on *T. alatus* sparsely inhabiting over an area of approximately 2×10 m (site 1 at 17:00 pm) where most individuals were 1st stadium nymphs. When the same site was visited at

Table 2. Body dimensions (mean $\pm$ SD, mm), proportion of adults with seven eye-stripes, and morphometric ratios (mean $\pm$ SD) of field-collected *S. gregaria* adults at various sites in Mauritania in October 2009

	Site no.	C	F	E	Total body length	% of adults with 7 eye-stripes	F/C	E/F	<i>n</i>
Low-density	Females								
	2	7.7 $\pm$ 0.2	31.0 $\pm$ 1.3	62.0 $\pm$ 2.4	77.0 $\pm$ 2.8	66.7	4.05 $\pm$ 0.10	2.01 $\pm$ 0.05	15
	4	7.8 $\pm$ 0.2	31.3 $\pm$ 1.1	62.9 $\pm$ 1.4	77.9 $\pm$ 2.2	100.0	4.04 $\pm$ 0.13	2.02 $\pm$ 0.07	10
	7	7.8 $\pm$ 0.4	32.4 $\pm$ 1.4	65.2 $\pm$ 3.4	80.8 $\pm$ 2.1	100.0	4.15 $\pm$ 0.07	2.01 $\pm$ 0.03	3
	8	8.2 $\pm$ 0.4	32.7 $\pm$ 0.2	66.8 $\pm$ 0.8	82.6 $\pm$ 0.9	100.0	3.96 $\pm$ 0.14	2.04 $\pm$ 0.01	2
	Total	7.7 $\pm$ 0.3	31.3 $\pm$ 1.3	63.1 $\pm$ 2.8	78.1 $\pm$ 2.9*	83.3	4.05 $\pm$ 0.11	2.02 $\pm$ 0.05	30
	Males								
	2	6.5 $\pm$ 0.2	26.1 $\pm$ 1.3	53.1 $\pm$ 2.3	65.2 $\pm$ 2.3	17.6	3.99 $\pm$ 0.10	2.03 $\pm$ 0.06	17
	4	6.5 $\pm$ 0.8	25.9 $\pm$ 0.2	52.6 $\pm$ 1.1	63.9 $\pm$ 2.3	25.0	3.98 $\pm$ 0.02	2.03 $\pm$ 0.06	4
	8	6.6 $\pm$ 0.2	25.8 $\pm$ 1.5	51.4 $\pm$ 2.4	64.6 $\pm$ 3.1	0.0	3.90 $\pm$ 0.15	2.00 $\pm$ 0.08	3
	10	6.7	26.3	53.7	65.9	0.0	3.93	2.04	1
	Total	6.5 $\pm$ 0.2	26.0 $\pm$ 1.2	52.8 $\pm$ 2.0	64.9 $\pm$ 2.3	16.0	3.97 $\pm$ 0.10	2.02 $\pm$ 0.06	25
High-density	Females								
	1	7.7 $\pm$ 0.3	30.8 $\pm$ 1.3	62.5 $\pm$ 2.4	76.1 $\pm$ 2.6	68.6	4.03 $\pm$ 0.10 a	2.02 $\pm$ 0.05	35
	3	7.7 $\pm$ 0.2	31.4 $\pm$ 1.1	62.9 $\pm$ 2.1	77.2 $\pm$ 2.4	74.3	4.07 $\pm$ 0.08 ab	2.01 $\pm$ 0.05	35
	5	7.7 $\pm$ 0.2	30.7 $\pm$ 1.2	62.1 $\pm$ 1.7	77.3 $\pm$ 2.1	44.1	4.01 $\pm$ 0.10 a	2.03 $\pm$ 0.05	34
	6	7.7 $\pm$ 0.4	31.4 $\pm$ 1.5	62.7 $\pm$ 2.7	77.3 $\pm$ 3.2	73.3	4.08 $\pm$ 0.10 ab	2.02 $\pm$ 0.05	30
	9	7.7 $\pm$ 0.2	31.3 $\pm$ 1.0	63.2 $\pm$ 2.2	77.4 $\pm$ 2.2	77.1	4.10 $\pm$ 0.10 b	2.02 $\pm$ 0.07	35
	Total	7.7 $\pm$ 0.3	31.1 $\pm$ 1.2	62.7 $\pm$ 2.2	77.1 $\pm$ 2.6	67.5	4.06 $\pm$ 0.10	2.02 $\pm$ 0.06	169
	Males								
	1	6.5 $\pm$ 0.2	25.7 $\pm$ 1.0	51.6 $\pm$ 2.3	63.2 $\pm$ 2.6	25.7	3.98 $\pm$ 0.11 b	2.00 $\pm$ 0.06	35
	3	6.6 $\pm$ 0.3	26.3 $\pm$ 1.3	52.6 $\pm$ 2.1	64.7 $\pm$ 2.5	31.4	3.99 $\pm$ 0.11 b	2.00 $\pm$ 0.05	35
	5	6.6 $\pm$ 0.3	25.7 $\pm$ 1.3	52.0 $\pm$ 2.6	64.9 $\pm$ 3.1	22.9	3.92 $\pm$ 0.09 a	2.03 $\pm$ 0.05	35
	6	6.6 $\pm$ 0.2	26.2 $\pm$ 1.2	52.7 $\pm$ 2.0	64.6 $\pm$ 2.6	30.0	3.97 $\pm$ 0.09 ab	2.01 $\pm$ 0.06	30
	9	6.5 $\pm$ 0.3	26.1 $\pm$ 1.1	52.3 $\pm$ 2.0	64.6 $\pm$ 2.5	20.0	3.99 $\pm$ 0.12 ab	2.01 $\pm$ 0.04	35
	Total	6.6 $\pm$ 0.3	26.0 $\pm$ 1.2	52.2 $\pm$ 2.2	64.4 $\pm$ 2.7	25.9	3.97 $\pm$ 0.11	2.01 $\pm$ 0.05	170

C, maximum head width; F, hind femur length; E, fore wing length. For explanation of sites, see Table 1. Different letters after values indicate significant differences at 5% by a Sheff's test. *, a significant difference between the low- and high-density groups at 5% by a *t*-test.

Table 3. Comparison of body dimensions (mean $\pm$ SD, mm) and morphometric ratios (mean $\pm$ SD) between field-collected *S. gregaria* adults with five and six nymphal stadia, respectively, in Mauritania in October 2009

Number of nymphal stadia	C	F	E	Total body length	F/C	E/F	<i>n</i>
Females							
5	7.5 $\pm$ 0.2	30.1 $\pm$ 1.1	61.2 $\pm$ 1.9	75.6 $\pm$ 2.4	4.02 $\pm$ 0.09	2.03 $\pm$ 0.05	60
6	7.8 $\pm$ 0.3***	31.6 $\pm$ 1.0***	63.4 $\pm$ 2.1***	77.9 $\pm$ 2.4***	4.07 $\pm$ 0.10**	2.01 $\pm$ 0.06**	139
Males							
5	6.5 $\pm$ 0.2	25.6 $\pm$ 0.9	51.8 $\pm$ 2.0	63.9 $\pm$ 2.4	3.95 $\pm$ 0.10	2.02 $\pm$ 0.05	147
6	6.7 $\pm$ 0.2***	27.1 $\pm$ 1.2***	53.6 $\pm$ 2.2***	66.1 $\pm$ 2.6***	4.03 $\pm$ 0.12***	1.98 $\pm$ 0.06***	48

C, maximum head width; F, hind femur length; E, fore wing length. The number of nymphal stadia was determined based on the number of eye-stripes. **, $p < 0.01$; ***, $p < 0.001$ by a *t*-test or Mann-Whitney's *U*-test.

Fig. 4. Mean lengths (+SD, mm) of ovarian eggs dissected out from *S. gregaria* adults collected at various sites in Mauritania. The numbers in parentheses indicate *n*.

19:30 pm, they were actively feeding on *T. alatus* (Fig. 2E). Many individuals were also found on *Schouwia thebaica* (Brassicaceae), but no feeding was observed on this plant. An aggregation at site 3 (ca. 4×10 m) consisted of numerous nymphs at the 1st to 4th nymphal stadia (12:45 pm) on *T. alatus* and *Cyperus conglomeratus* (Cyperaceae). At site 10, nymphs were also observed over an area of 50×200 m (10:30 am). Most medium-sized nymphs including those before or at the penultimate stadium had black patterns with a white, yellow or green background color (Fig. 2F, G, H). Those with a white or yellow background color looked similar to those typically observed in the gregarious phase (Fig. 2K; 5.6 a in Plate III; 3.4 b in Plate IV; Stower, 1959). Several last stadium nymphs were also found at the same site but they were at least 20 m away from the aggregations of early stadium nymphs. Some looked like typical solitary nymphs: they were green without black patterns (1.1 a and 2.2 a in Plate IV; Stower, 1959). Others were brownish with black patterns on the thorax, abdomen and legs. One nymph was found on *Zygophyllum waterlotii* (Zygophyllaceae), a non-host plant, but its green body color matched the color of the plant underneath (Fig. 2I). Another nymph was also found on vegetation containing some wilted brown seeds and stems of *C. conglomeratus*. Its brownish body color with black patterns looked very cryptic against the habitat background (Fig. 2J).

Many medium-sized nymphs in the aggregations had black patterns with a whitish background (Fig. 2F), the coloration being similar to what can be ob-

Fig. 5. The frequencies of 1st stadium *S. gregaria* nymphs in different body color grades (HCGs) in samples collected at various sites in Mauritania. Nymphs were categorized into five color groups (HCGs 1–5) based on the darkness of body color: nymphs in HCG 1 are green as typically observed in solitary forms and those in HCG 5 are almost completely black as observed in gregarious forms. Those in HCGs 2–4 are intermediate in color and increasingly darker. The numbers in parentheses indicate *n*.

served under crowded conditions in the laboratory (Maeno and Tanaka, 2007). They looked fairly cryptic on vegetation with shades (Fig. 2F, K). Their behavior also seemed to be cryptic when approached by an observer: nymphs at or before the penultimate stadium perching on a grass stem moved behind the stem every time when an observer changed his position to see their body.

Figure 5 compares the proportions of 1st stadium nymphs with different body colorations collected at different sites. The majority of nymphs were green without black patterns (HCG 1), as typically observed in solitary hatchlings (1.1 a and 1.1 b in Plate I; Stower, 1959), but 20–35% of nymphs had black patterns on various parts of the body. At sites 1 and 5, completely black nymphs (HCG 5) looking similar to gregarious hatchlings (3.3 d in Plate I; Stower, 1959) were also observed. Although the precise measurements were not performed, black hatchlings apparently looked larger than green ones, conforming to laboratory observations by Maeno and Tanaka (2009b).

Body coloration at low-density populations

At site 2, several green early stadium nymphs were found on vegetation (*T. alatus*) on 16 and 17 October. The temperature close to vegetation was 34.6°C with relative humidity of 16.5% at 20:00 pm and 28.2°C with relative humidity of 18.0% at 09:00 am. All six nymphs found were green and no

brown form was observed. At another site ca. 50 km north of Nouakchott, one adult was found during a 30-min observation period on 19 October. However, three small nymphs presumably at the 1st or 2nd stadium were found on vegetation. Two of them were green without black patterns and the last individual was apparently a newly hatched nymph with completely black body coloration.

Two last stadium nymphs were found after a half-hour searching over an area of $200 \times 1,000$ m by four persons at site 9 where nymphal density was very low (<1 per 25 m^2). They jumped out of vegetation (*Z. waterlotii*) when the bushes were disturbed by a human foot. One individual was green and the other brown with black patterns. The brown nymph, which looked similar in body coloration to the individual observed at site 10 (Fig. 2J), quickly returned to vegetation where it stayed still.

Natural enemies and host plants

Several potential natural enemies of locusts were encountered during the present excursion. They included birds, lizards, spiders and insects. Predatory insects such as tiger beetles, antlions and ants were common, but larvae of antlion were the only insects observed catching locust nymphs during the entire period of excursion (Fig. 2L). Numerous conical pits made by antlion larvae were found at various sites, suggesting that these insects may be effective natural enemies of locusts. The fringe-toed lizard, *Acanthodactylus dumerili* (Squamata: Lacertidae), was common at site 10 where many holes of their nests were found. They were mostly 20–35 cm long, but no feeding behavior was observed during 10:00 am to 13:00 pm.

Although the ground coverage by plants is low in the desert, more than 1,400 species of plants have been described in Mauritania (Barry and Celles, 1991a, b). Various potential host plants for locusts were observed at various sites. They included *T. alatus*, *Fagonia oliveri* (Zygophyllaceae), *H. ramosissimum*, *Boerhavia repens* (Nyctaginaceae), *Farsetia stylosa* (Brassicaceae) and *Citrullus colocynthis* (Cucurbitaceae). Among them *T. alatus* was the most abundant. *Hyoscyamus muticus* (Solanaceae), which is a favorite locust food (Sword et al., 2000; Despland and Simpson, 2005), was searched, but could not be found during the present excursion.

DISCUSSION

Desert locusts are common in Mauritania. During the present survey, nymphs and/or adults were found almost everywhere if host plants such as *T. alatus* and *H. ramosissimum* occurred. This was partly because locust populations were relatively large at some locations visited, but solitary locusts could be found on vegetation easily even in those areas where the locust population density was low and no gregarizing locusts were found. The population densities of adult locusts observed ranged from <1 to <30 per 25 m^2 , and even the latter (0.8 per m^2) was much lower than that reported for gregarious last stadium nymphs (e.g. 40–1,000 individuals per m^2 ; Uvarov, 1977).

Inference of the history of crowding from adult morphometric ratio and body coloration

Stower (1959) is the first who made inference of the history of crowding in desert locust populations based on adult morphometric ratios and nymphal body coloration. The present study showed that *S. gregaria* adults collected at various sites in Mauritania were similar in body dimensions irrespective of the population density. The F/C ratio was 4.06 and 3.97 on average in females and males, respectively, and these values are similar to those reported for typical solitary adults in other populations (Dirsh, 1953; Stower et al., 1960). The high proportions of adults with seven eye-stripes (Table 2) formed due to extra molting may also suggest that the collected adults would have grown at a low population density, because extra molting usually is not induced under crowded conditions (Uvarov, 1966; Maeno and Tanaka, 2008a). A comparison of morphometric ratios between adults with five nymphal stadia and those with six nymphal stadia suggested that adults with extra molting had ratios more typical of solitary forms (larger F/C ratios and smaller E/F ratios) than those without it, conforming to laboratory observations (Maeno and Tanaka, 2009b).

In the present study, adult body coloration was also recorded. Locusts in high-density populations were generally yellow, whereas those in low-density populations were mostly whitish or brown. Yellowing is a characteristic of gregarious adults in this locust and another locust, *Locusta migratoria* (Pener, 1991). However, it can be induced even in

solitary (isolated-reared) adults by exposure to a crowd of locusts in the laboratory (Pener, 1976, 1991; Pener and Simpson, 2009; De Loof et al., 2010). Therefore, it is likely that all adults collected during the present excursion were in the solitary phase morphometrically, but gregarization probably occurred in some populations after adult emergence, causing them to turn yellow at sexual maturity. At one site (site 4) most adults were yellow in spite of the low population density. They might have moved to this site in small numbers after they gregarized as adults at another site. Unfortunately, ovarian egg size is unknown for the collected female adults, because none of them had mature oocytes in the ovary.

The significance of the yellow body coloration in locusts is unknown. Yellowing has been regarded as a male-specific trait in laboratory-reared *S. gregaria* (De Loof et al., 2010), but it occurs in both sexes in wild desert locusts (Fig. 2B, D), although whether the same pigment(s) is involved in the two sexes or not, is not certain. Considerably bright yellow color was observed in some females particularly in the upper part of the body. Because ovipositing females are probably most vulnerable to predators, the yellow color might have some protective function against the latter. Some females may have a whitish area on the lower side of the first few tergites, but it is not obvious while they are ovipositing, exposing only the bright yellow color on the upper part of the body. Likewise, mounting males would also be vulnerable. If the bright yellow color has an aposematic function, their bright yellow color on the whole body might protect not only themselves but also the female ovipositing underneath from predators. In the desert, yellow adults look quite conspicuous, yet there was no sign indicating predation by birds or other vertebrates during the entire period of the present study. Although large birds such as kestrels, vultures and hawks are known to follow large swarms of locusts and consume many locusts (Ellis and Ashall, 1957; Popov, 1959), whether they also serve as potent predators on transient populations is unknown. Desert locusts are primary consumers, exploiting particular food resources (trees and shrubs) that domestic livestock avoid (Sánchez-Zapata et al., 2007). A toxic plant, *H. muticus*, is limited to small areas (Babah Ebbe, 2008) and was not found during the present study.

However, other locust host plants such as *T. alatus* and *H. ramosissimum* are common and they are known to contain various alkaloids (Sharawy and Alshammari, 2009). Therefore, adult locusts feeding on such plants might not be preferred food items by predators. If this is the case, there is a possibility that yellowing in adults in the transient and gregarious phase might serve as an aposematic function. Such function should work more effectively when the population density is higher. This hypothesis should be tested in the future.

Juvenile hormone (JH), which controls sexual maturation in locusts, is required to induce yellowing in crowded locusts, but another factor appears to be involved in this phenomenon, because JH can stimulate locusts to mature sexually but fails to elicit yellowing under isolated conditions (Pener, 1991; Pener and Simpson, 2009). In *L. migratoria*, implantation of corpora cardiaca (CC) taken from crowded locusts accelerated the expression of yellowing in crowded locusts, suggesting that CC may contain an important factor inducing yellowing (Hasegawa and Tanaka, 1996). In *S. gregaria*, the presence of a yellow-color inducing factor in the brain-CC is also suggested (De Loof et al., 2010), but the chemical identity is unknown in either locust.

Prediction of future hatchling characteristics from ovarian egg size

Gregarization influences other developmental traits such as egg size in locusts (Uvarov, 1966). In *S. gregaria*, gregarious adults produce larger eggs than solitary adults. In the present study, females from low-density populations had smaller eggs than did those from high-density populations in spite of the fact that they were morphologically equivalent to solitary forms. This seemingly paradoxical phenomenon may be explained by their flexible response to crowding conditions: actively reproducing isolated-reared (solitary) female adults start producing larger eggs upon exposure to crowded conditions (Maeno and Tanaka, 2008b, 2010). Therefore, it is possible that upsurges in locust populations brought solitary adults together so that crowding stimulated them to produce larger eggs than those produced in low-density populations. Pheromonal and visual factors are known to be involved in recruiting solitary locusts into gregarized groups, facilitating the

spread of gregarious characters across a reproductively active solitary population in this species (Ould Ely et al., 2006).

Increased egg sizes are closely associated with production of dark-colored hatchlings in *S. gregaria* (Papillon, 1960; Albrecht, 1962; Tanaka and Maeno, 2008, 2010). Whether eggs laid by female adults in high-density populations gave rise to such hatchlings or not was not directly confirmed in the present study. It is highly possible that they did so. In fact, some dark-colored 1st stadium nymphs had started appearing among gregarizing nymphs at various sites during the present excursion. The locust populations in Mauritania did not increase appreciably during the first half of 2010. This was partly because the winter season probably decelerated their reproductive activity. It is sometimes difficult to explain why partially increased populations do not undergo outbreaks under apparently favorable conditions (Wilps, 1997). However, the action by NLCC for preventive control should be a factor contributing to the failure of locusts to build up their populations efficiently.

In response to upsurges in locust populations in September 2009, the NLCC teams undertook several measures to prevent an outbreak. The number of survey teams, each consisting of five members, was increased from five to 22 and 14 spraying units of control were used. The whole areas of infestation were covered by these and other logistic teams and backup facilities were activated at the head quarter of the Centre National de Lutte Antiacridienne (CNLA) in Nouakchott to facilitate logistic supply (fuel and pesticides). A total of 13,907 ha was sprayed with an insecticide (Duesban 240) within 315 spray operations during a period from October to December. Biological control using *Metharizium acridum* was also carried out during this period to prevent locust damage in certain areas where high concerns for the environment and human health were felt.

In a low-density population (at site 7), one of the nymphs observed looked like a gregarious hatchling with intensive black patterns. The occurrence of such individual may be expected even in solitary populations, because egg pods laid by solitary females sometimes contain a mixture of green and black hatchlings (Papillon, 1960; Tanaka and Maeno, 2008), especially in the first reproductive cycle (Maeno and Tanaka, 2008b). A similar situa-

tion occurs for egg pods laid by gregarious females. In either case, green hatchlings are consistently smaller than black hatchlings (Tanaka and Maeno, 2008).

Some observations concerning nymphal body coloration

S. gregaria nymphs display two types of body-color polyphenism (Pener, 1991; Pener and Simpson, 2009). One type is called the phase polyphenism in which body coloration varies continuously depending upon the population density. Nymphs growing at a high density develop intensive black patterns with an off-white-light rose, or yellow background body color in early and late hopper stadia, respectively. The other type is called the green-brown polyphenism. It is widely accepted that this polyphenism is controlled by humidity in *S. gregaria*: the green form is induced by high humidity and the brown form by low humidity (Pener, 1991; Pener and Simpson, 2009). Hunter-Jones (1962) reported that nymphs grown at relative humidity of 55–70% were predominantly green, whereas those at 30–55% were red-brown. In the present study, most early stadium nymphs found in low-density populations were green. However, the relative humidity recorded near green nymphs on vegetation was considerably low (<20%), and mean relative humidity in October is 49% with a range from 11 to 77% in Nouakchott (NLCC, unpublished data). Therefore, it seems difficult to explain the common occurrence of green nymphs in the desert by humidity. While other factors such as temperature and food quality have been suggested to influence the background color of nymphs (Stower, 1959; Hunter-Jones, 1962), systematically designed experiments are yet to be carried out to determine how the green-brown polyphenism is controlled.

ACKNOWLEDGMENTS

This study was funded in part by a Kakenhi Grant of Japan (No. 19380039) to Tanaka and the Japan Society for the Promotion for Science for a research fellowship for PD (No. 20-2008) to Maeno. Thanks are also due to the Centre National de Lutte Antiacridienne staff for logistical support in the field.

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