



Original Article

# How molting locusts avoid cannibalism

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Group living has various benefits, but it also carries costs, such as risk of cannibalism. Molting is a vulnerable period of being cannibalized in juvenile arthropods, but how gregarious arthropods avoid this threat is poorly understood. Here, we examined how actively migrating gregarious nymphs of desert locust, *Schistocerca gregaria*, avoid cannibalism during molting, in the Sahara Desert of Mauritania. In the field, gregarious nymphs cyclically march and feed on grass during the day. Our field observations found that marching behavior helped separating pre-molting and cannibalistic non-molting nymphs. Cannibalistic non-molting nymphs marched away from roost plants, leaving sedentary pre-molting nymphs behind, creating cannibal-free spaces. Some non-molting nymphs reached a pre-molting state after daytime marching, thus both pre- and non-molting nymphs roosted on same plants at night. However, pre-molting nymphs moved away from conspecifics prior to molting. Starvation experiments confirmed that food-satiation decreased cannibalistic necrophagy. Physiological surveys of diel feeding and molting patterns revealed that nymphs molted at times when conspecifics were food-satiated rather than hungry. Hence, our results indicate that behavioral and physiological traits of gregarious locusts could function to spatiotemporally separate molting locusts from cannibalistic conspecifics, thus reducing molting-associated cannibalism. This is the first report of migration-dependent molting synchrony as a mechanism reducing costs of aggregation in gregarious arthropods.

**Key words:** aggregation, cannibalism, desert locust, marching, migration, molt, trade-offs.

## INTRODUCTION

Virtually all traits of organisms are under trade-offs with some other traits (Roff 2002; Flatt and Heyland 2011; Fabian and Flatt 2012; Mauro and Ghalambor 2020). An extensive literature explores the trade-offs in group-living strategies ranging from temporary clumping to full eusociality (Krause and Ruxton 2002). Aggregation in animals can provide numerous benefits including overcoming plant or prey defense, proximity to mates, lowered risk of predation through combined defense or predator-dilution, etc. (Vulinec 1990; Parrish and Edelstein-Keshet 1999; Treves 2000; Sword et al. 2005). However, group living also carries costs, such as greater disease risk, conspicuousness to predators, subordination of individual reproduction, and increased cannibalism (Fox 1975;

Whitman et al. 1994; Richardson et al. 2010; Santana et al. 2012; Landry and Li 2019).

Cannibalism has not always been well defined in previous papers (Richardson et al. 2012). Two types of cannibalism should be differentiated: 1) “cannibalistic predation” (killing and eating both intact and wounded conspecifics), 2) “cannibalistic necrophagy” (feeding on dead conspecifics) (Maák et al. 2020). In this study, we use cannibalism to refer to the first, most commonly accepted definition and then use cannibalistic necrophagy when specifically speaking of feeding on dead conspecifics. Cannibalism can be a greater threat to group-living species than to solitary species, because: 1) dense aggregations often deplete local food resources, inducing hunger, which favors cannibalism; 2) aggregation increases local population density and encounter rates and, hence, opportunity for cannibalism; and 3) large or social populations often include various

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developmental stages exposing younger, smaller individuals to risk of cannibalism by larger, stronger individuals (Elgar and Crespi 1992). Although possessing or evolving mechanisms to reduce excessive cannibalism has been proposed as a prerequisite for the evolution of gregariousness or sociality (Hopper et al. 1996; Kim 2001; Sainte-Marie and Lafrance 2002), little is known about how gregarious animals mitigate the risk of cannibalism while maintaining the benefits of group living.

In arthropods, molting is a regular developmental event for growth and these events are particularly vulnerable to cannibalism because molting individuals are relatively soft-bodied, immobile, and defenseless (Elgar and Crespi 1992; Whitman et al. 1994). Although appropriate strategies to avoid molting-associated cannibalism are essential to maintain group living in arthropods, little information is available on how gregarious arthropods avoid cannibalism during molting. Locusts, some of the grasshopper species that exhibit density-dependent phase polyphenism (Pener and Simpson 2009; Simpson and Sword 2009), are suitable model animals, because they practice cannibalism, both in the laboratory and the field under certain conditions, and they are group-living (Faure 1932; Duarte 1938; Ellis and Ashall 1957; Whitman et al. 1994; van Huis et al. 2008; Hansen et al. 2011). Here, we explore how the desert locust, *Schistocerca gregaria*, resolves the risk of molting-associated cannibalism in the field.

Density-dependent phase polyphenism for desert locust result in two extreme phenotypes or phases (solitary vs. gregarious) that differ in physiology, morphology, behavior, and life history (Cullen et al. 2017; Ayali 2019). Solitary locust are relatively sedentary and avoid each other, whereas gregarious locusts aggregate and move long distances in dense groups; flightless nymphs “march” in bands, and flying adult locusts “swarm” (Ellis and Ashall 1957; Uvarov 1977). Gregarious nymphs of desert locusts have been used as model animals to address how gregarious animals avoid cannibalism. Previously, marching has been hypothesized to be the main mechanism to avoid cannibalism via an “escape-pursuit” behavior, whereby crowded individuals are continuously escaping and moving forward in order to avoid being eaten by conspecifics approaching from behind, while at the same time pursuing other individuals in front, attempting to eat them (Bazazi et al. 2008; Romanczuk et al. 2009, 2012; Hansen et al. 2011; Simpson 2022). However, this escape-pursuit hypothesis has only been studied in laboratory conditions and cannot be applied for all life stages of gregarious nymphs. Particularly, it cannot apply to molting individuals because molting nymphs are stationary. If locust marching is driven by cannibalism, then it seems that non-molting nymphs should stay and eat their molting and immobile conspecifics. This fact implies that another mechanism to avoid cannibalism could be involved in molting nymphs. During preliminary field surveys of gregarious *S. gregaria* in Mauritania, we noticed high cannibalism rates on molting nymphs in cages, but not in the field (see also: Haroon Khan 1945; van Huis et al. 2008), suggesting that something happens in the field to reduce such cannibalism.

In the present study, we aimed to test three hypotheses based on previous information and our preliminary observations: 1) a marching separation hypothesis, 2) a moving away hypothesis, and 3) an asynchronization of hunger level and molting patterns hypothesis. First, nymphs are known to typically reduce activities, stop feeding, and begin to empty their guts the day before molting, and do not feed or march until their cuticle hardens, several hours after molting (Husain et al. 1949; Uvarov 1966; Hughes 1980; Rackauskas et al. 2006). These behaviors also suppose that

pre-molting nymphs are not cannibalistic. However, as hunger increase marching activity (Dkhili et al. 2019), marching may separate hungry marchers from stationary molting nymphs. Accordingly, we hypothesized that marching spatially separates molting and potentially cannibalistic non-molting locusts, thereby virtually eliminating daytime cannibalization on molting nymphs.

Second, it was previously observed that gregarious nymphs roost at night on relatively large plants creating high densities (Ellis and Ashall 1957; Maeno and Ould Babah Ebbe 2018; Maeno et al. 2021a). This supposed that another mechanism instead of marching could be also involved to avoid molting-associated cannibalism within a limited space at night. To study this, we first explored if the rate of cannibalism increases on night-molting nymphs. Then we hypothesized that pre-molting nymphs move away from cannibalistic conspecifics within roosting plants during night.

Third, it is also reasonable to predict that natural selection could drive the diel molting timing to minimize risk of cannibalism. We checked with a small experiment if hunger levels influence cannibalistic necrophagy and we verified the hunger levels of non-molting nymphs at different times of the day. Then, we assessed our third hypothesis stating that locusts would molt at times of the day when conspecifics are not hungry.

We tested these three hypotheses by surveying migratory bands of late instar nymphs of the desert locust in the field. Here, we show how gregarious locusts pre-empt nearly all molting-associated cannibalism

## MATERIALS AND METHODS

### Study area

We conducted field studies in the northwest African country of Mauritania, a gregarization zone of desert locust (Ould Babah 1997; Babah Ebbe 2010; Piou et al. 2017). Our study sites (19°10' N, 13°41' W in 2015 and 19°24' N, 14°36' W in 2016) were near Akjoujt. The area is a vast flat and arid plain with a variety of habitats, including sparse desert brushlands, grasslands, dunes, and playas. The most common large (0.5–5.0 m tall) plants, *Acacia tortilis* (Fabaceae), *Maerua crassifolia* (Capparaceae), *Boscia senegalensis* (Capparaceae), and *Calotropis procera* (Asclepiadaceae), are distributed patchily and serve as locust nocturnal-roosting plants (Maeno and Ould Babah Ebbe 2018).

### Climate

Our study was conducted during fall (November) of 2015 and 2016, when day (0700–1900 h) and night (1910–0650 h) temperatures averaged 29.8 and 23.7 °C, respectively. Lowest and highest temperatures during our study were 14.3 and 38.7 °C. The largest 24-h range was 15.0–34.5 °C. Survey periods were two months after the end of the rainy season when grasses were beginning to dry.

### Study organism

We studied fall populations of the desert locust, *Schistocerca gregaria* Forskål (Maeno et al. 2021a). All populations were in the gregarious phase and consisted mainly of aggregating and marching bands of last-instar (fifth instar) nymphs, often containing recently molted adults.

We conducted experiments in the field in order to observe natural responses of free-living locusts in an ecological setting. Two experiments used field cages. In order to minimize disrupting

the natural behaviors of locusts we used red lights during night studies.

### Does daily marching separate molting from non-molting nymphs?

We hypothesized that daily marching separated molting from non-molting nymphs and thus reduced risk of cannibalism. Specifically, we predicted that in the morning and afternoon, non-molting individuals would march away from plants, whereas pre-molting individuals would remain in those plants and subsequently molt.

We tested this hypothesis by following in an ecological setting a single band of ~3000 primarily fifth-instar nymphs, while monitoring the percentage of pre-molting individuals in three subgroups: 1) nymphs roosting or sheltering in plants before descent and marching, 2) individuals that left their plant and subsequently marched for >1 h, and 3) nymphs that remained in their roost- or sheltering plant for  $\geq 1$  h in the morning or afternoon after most of the band had marched away. In each case, we randomly determined the molting status of 10 females and 10 males, by visual and tactile inspection and foregut dissection. Pre-molt nymphs can be distinguished many hours before molting because they empty their guts and their exterior cuticles become soft, loose, and discolored as the old cuticle digests away and separates from the underlying new cuticle (Nijhout 1994). We surveyed from noon 18 November 2016 to afternoon the next day, and a temperature range of 24.9–38.7 °C. We used a Fisher's Exact Test with Bonferroni's Correction to test for differences in percentage of pre-molting locusts in subgroups on day 1 and day 2, respectively.

### Does the rate of cannibalism increase on night-molting nymphs?

Although most nymphs molt during the day, some molt at night. Night molting might be dangerous, because nocturnal roosts typically contain large numbers of densely packed non-molting locusts (often with many individuals touching one another), who might cannibalize molting kin. We quantified rates of cannibalism on molting locusts at four separate nocturnal roosting aggregations during Nov 2016. We selected individual *B. senegalensis* bushes containing ~3000, 2000, 2000, and 1000 densely-packed third- to fifth-instar nymphs and a few adults. Each night we used red lights to visually inspect bushes for 15 min each hour from 1900 to 0700 h, recording every case of molting-associated cannibalism found. During the study, night air temperatures ranged from 16.9 to 31.4 °C. Results from the four bushes were combined.

### Do pre-molting individuals move away from non-molting individuals at night?

Because the above study indicated that cannibalism was rare in dense nocturnal aggregations, we hypothesized that pre-molting individuals moved away from conspecifics prior to molting. We measured the number of conspecifics within 10 cm of molting ( $n = 129$ ) versus non-molting individuals ( $n = 20$ ) on branches of a  $4 \times 2 \times 2$  m *B. senegalensis* containing ~2000 individuals. Focal nymphs were chosen to be mainly found on thick trunks and branches and so that the surrounding nymphs that were counted around the focal individual were not counted twice. We employed a Mann–Whitney *U* test to analyze the difference in the numbers of locusts within 10 cm of molting versus non-molting individuals.

### Does hunger level influence cannibalistic necrophagy?

To determine if hunger influences cannibalism, we conducted experiments in semi-natural conditions looking at the rate of cannibalistic necrophagy. We collected 200 foraging last instar nymphs of both sexes from the field, transported them to the CNLA semi-field station, and fed them with fresh lettuce and cabbage ad libitum. The next day, food was withheld from 0600 to 1600 h, whereupon half the nymphs were randomly assigned to a Starved Treatment. In the field, nymphs actively feed around 1600 h without seeking shade and before ascending into night-roosting plants (Maeno et al. 2021a). Hence, at 1600 h, the Fed Treatment individuals were given fresh lettuce leaves for 30 min, mimicking this feeding normal activity. Starved and Fed locusts were marked with different colored paint spots. Then, 20 individuals (5 per sex and treatment) were combined in 40-L cages placed in the afternoon sun (around 1630 h). After a 10-min acclimation period, five recently molted nymphs euthanized at  $-20$  °C and then thawed to ambient temperature were gently introduced into the container. The arena was filmed from above for 20 min, to document individual feeding behaviors (till around 1700 h). Each nymph was individually checked and nymphs that bit a carcass continuously for more than 30 s were regarded as exhibiting cannibalistic necrophagy. The experiment was replicated four times with different individuals and analyzed by Chi-square. The interval from the end of lettuce feeding to the end of the trials was ~30 min.

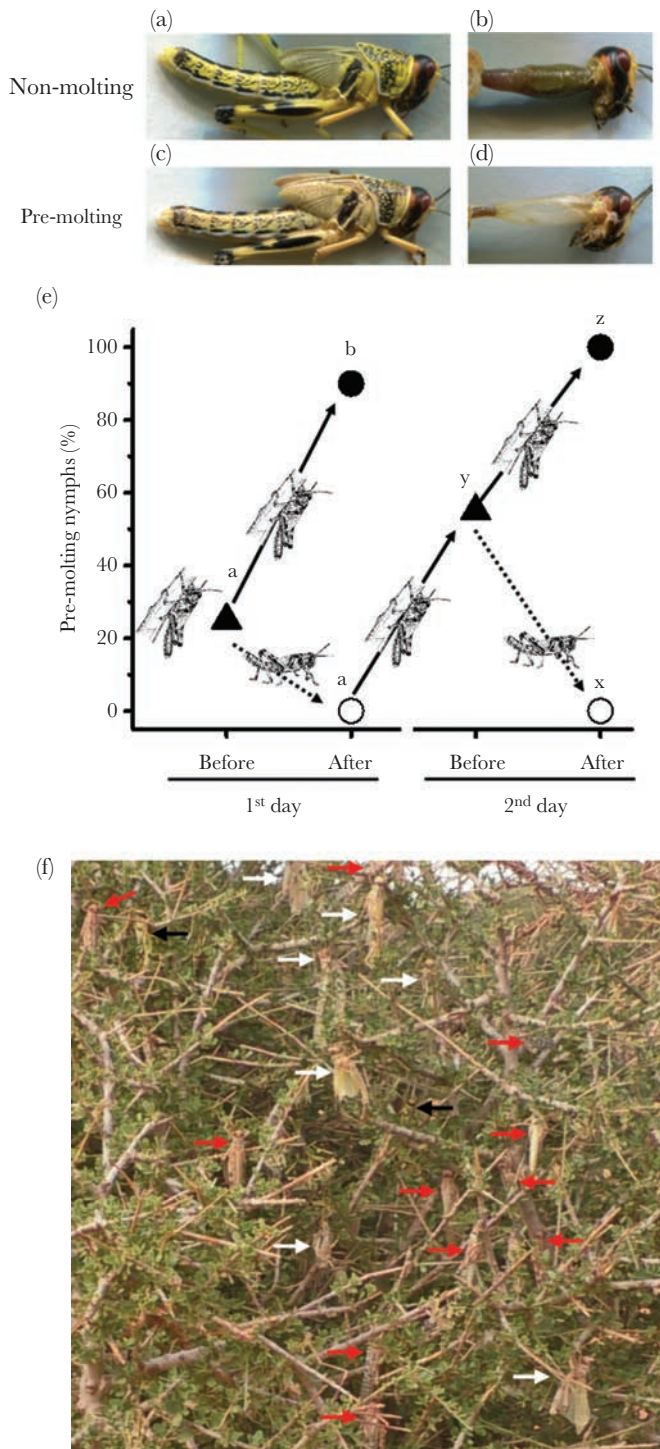
### Daily hunger patterns

We examined diel hunger patterns in wild locusts, using foregut contents as a proxy for hunger level. We hypothesized that during early night-roosting, non-molting nymphs would be satiated (with full foreguts) because locusts typically feed before roosting (Maeno et al. 2021a). We assessed hunger/satiation levels in non-molting, fifth instar, field-collected locusts of both sexes by dissecting their foreguts within 20 min of collection. We assigned an individual as “hungry” if the foregut contained little or no plant material, as per Maeno et al. 2021a (scores 0 and 1 were regarded as hungry). We dissected only hard-bodied individuals to avoid pre- or post-molting locusts, which have empty foreguts. The study was conducted from 18 to 29 November 2015. Gut and weather data for different days were pooled and averaged for each hour.

### Daily molting patterns

We hypothesized that locusts molted at times when conspecifics were food-satiated. To test this, we collected last instar nymphs of both sexes from a single night-roosting plant in the field, transported them to the CNLA semi-field station, and fed them fresh lettuce and cabbage ad libitum for 2 days. We recorded hourly molting rates among 210 insects placed in a  $40 \times 40 \times 40$ -cm wire screen cage in the semi-field conditions. The cage contained branches that could be support of roosting/sheltering/molting and fresh lettuce and cabbage ad libitum. For 7 days in November 2015, we recorded the number of molts/hour, visually or by video camera. Newly molted insects were removed every hour. We also recorded hourly shaded air temperature and humidity at 50 cm above the ground, sunlit soil surface temperature, and any daytime cannibalism on molting individuals.





**Figure 1**

External views (a,c) and dissected guts (b,d) of last instar *Schistocerca gregaria* nymphs, either non-molting (a,b) or pre-molting (c,d). Note that in pre-molting individuals the cuticle is thin and discolored and the large gut is empty. (e) Influence of migratory marching versus stationary roosting on the percentage of pre-molting versus non-molting gregarious *S. gregaria* nymphs in a single band in nature. Symbols indicate percentages of pre-molting individuals for: ▲ nymphs of small migratory band roosting on a plant before marching, ○ nymphs in the migratory band 1 h after marching from the roosting plant, ● nymphs of the stationary roosted group 1 h after other marching migratory members left the roosting plant. → Roosting;

## Statistical analysis

All statistical analyses were conducted using the software package R, version 4.0.1 (R Development Core T. 2020) and JMP (SAS Institute, Cary, NC, USA).

## RESULTS

### Does daily marching separate molting from non-molting nymphs?

When we followed a band of ~3000 last-instar nymphs during two days, pre-molting nymphs behaved differently from non-molting nymphs (Figure 1a–d). On Day 1, 25% of sampled nymphs in a midday sheltering group were pre-molt and 75% were non-molt individuals (Figure 1e). At about 1530 h, this sedentary band split, with most individuals marching away, leaving a smaller fraction in the bush (Figure 1e). The marching group travelled ~200 m that afternoon and subsequently ascended several trees for the night. At dusk, 90% of nymphs sampled from those remaining on the original bush were pre-molt or molting, versus 0% of nymphs sampled from the marching group.

At 0900 h the next morning (Day 2), 55% of nymphs sampled from the group that had marched the previous afternoon had become pre-molting (Figure 1e). As in Day 1, this group subsequently split in the morning, with about half marching away and half remaining in or under the roost-plant. At midday, none of the migrating nymphs sampled were pre-molting, whereas all the individuals sampled from those remaining in the roost-plants were either pre-molting or actively molting (Figure 1e). Hence, relatively synchronous molting occurred after migratory bands left roosting or sheltering sites (Figure 1f). These results show that pre-molting nymphs behave differently from non-molting nymphs: pre-molting nymphs are sedentary, whereas non-molting nymphs march. These results demonstrate a behavioral adaptation of individual locusts to avoid being cannibalized despite the constant threat from conspecifics in crowded group settings

### Does the rate of cannibalism increase on night-molting nymphs?

Cannibalism of night-molting nymphs was rare: only 0.005% (5 of 1088 observed night-molts) were cannibalized (Figure 2a). In two cases, last instar nymphs cannibalized fourth-instar nymphs and in one case a molting last instar nymphs was cannibalized. In the other two cases, molting nymphs were found already partially consumed, presumably by conspecifics, because we observed no predators in those bushes at any time. In this experiment, ~85% of nocturnal molting occurred before midnight (as confirmed in Figure 3). We observed no cannibalism on the ~8000 non-molting locusts in the four nocturnal-roosting aggregations. Hence, overall, we recorded only five nocturnal cannibalizations/~9000 locusts = ~ 0.0006% per night, suggesting that nocturnal cannibalism in the field is rare.

→ marching. Observations were made on 18 November (first day) and 19 November (second day) 2016. Different letters indicate significant differences at  $P < 0.016$  between values (Fisher's exact test after Bonferroni's correction). Statistical analyses were conducted among the three groups on the first day (a,b) and second day (x, y and z), respectively. Sample sizes were 20 (10 females, 10 males) each. (f) Synchronous molting after migratory band left the roosting site. Arrows indicate molting individuals (white,  $n = 7$ ), fresh adults (red,  $n = 11$ ), and nymphs (black,  $n = 2$ ).

**Figure 2**

(a) A molting nymph of *Schistocerca gregaria* being cannibalized by a fourth-instar nymph. (b) A molting nymph. (c) Night-roosting on tree.

### Do pre-molting individuals move away from non-molting individuals at night?

At night, gregarious nymphs aggregated in large numbers on roosting plants, sometimes, even touching one another (Figure 2b). Within these densely packed roosting bushes, pre-molting individuals moved away from conspecifics before nocturnal molting, often moving to the ends of branches or to the less-populated side of the bush (Figure 2c). As a result, significantly fewer locusts ( $\bar{x} = 0.5 \pm 0.1$  SE,  $n = 129$ ) were within 10 cm of molting individuals than within 10 cm of non-molting individuals ( $\bar{x} = 33.4 \pm 3.3$ ,  $n = 20$ ) (Mann–Whitney  $U$ -test,  $P < 0.001$ ) suggesting that night-molting nymphs actively reduce disturbance or cannibalism by moving away from potential cannibals.

### Does hunger level influence cannibalistic necrophagy?

When both fed and starved nymphs were exposed to euthanized molting nymphs, significantly more starved nymphs ( $\bar{x} \pm \text{SE} = 8.0 \pm 0.7$ ,  $n = 4$ ) cannibalized than did fed nymphs ( $\bar{x} = 1.75 \pm 0.85$ ,  $n = 4$ ), indicating that satiation reduces, and hunger increases, cannibalism rates (Chi-square test; d.f. = 1,  $\chi^2 = 26.5$ ,  $P < 0.001$ ). Overall, 80% of starved nymphs displayed cannibalistic

necrophagy versus 17.5% of fed nymphs, confirming that food-satiation decreases cannibalism.

### Daily hunger patterns vs. daily molting patterns

Over each 24-h period, population molting activity was inversely related to population hunger level indicating that locusts tend to molt at times that non-molting locusts were the least hungry (Figure 3a). As shown by their empty foreguts, locusts were most hungry during the latter half of nocturnal roosting between midnight and their first morning feeding at around 0900 h. This period showed the lowest rates of molting. Most molting occurred between 1100 and 1800 h during hottest period, with a much smaller peak at 2100 to 2200 h (Figure 3a,b). These molting times corresponded with high-satiation periods for non-molting individuals. Hence, most molting occurred when the foreguts of non-molting locusts were relatively full. Hunger levels in non-molting nymphs rose after midnight, but few nymphs molted during this coldest part of the night (Figure 3a,b). Roosting locusts tended to be sedentary at this time. Non-molting locusts were most hungry immediately before and around the dawn period, but there was no molting at this time, and thus little opportunity for cannibalism. Indeed, we observed no molting between 0400 and 0900 h. Molting-associated cannibalism did not occur in the cage during this experiment.

## DISCUSSION

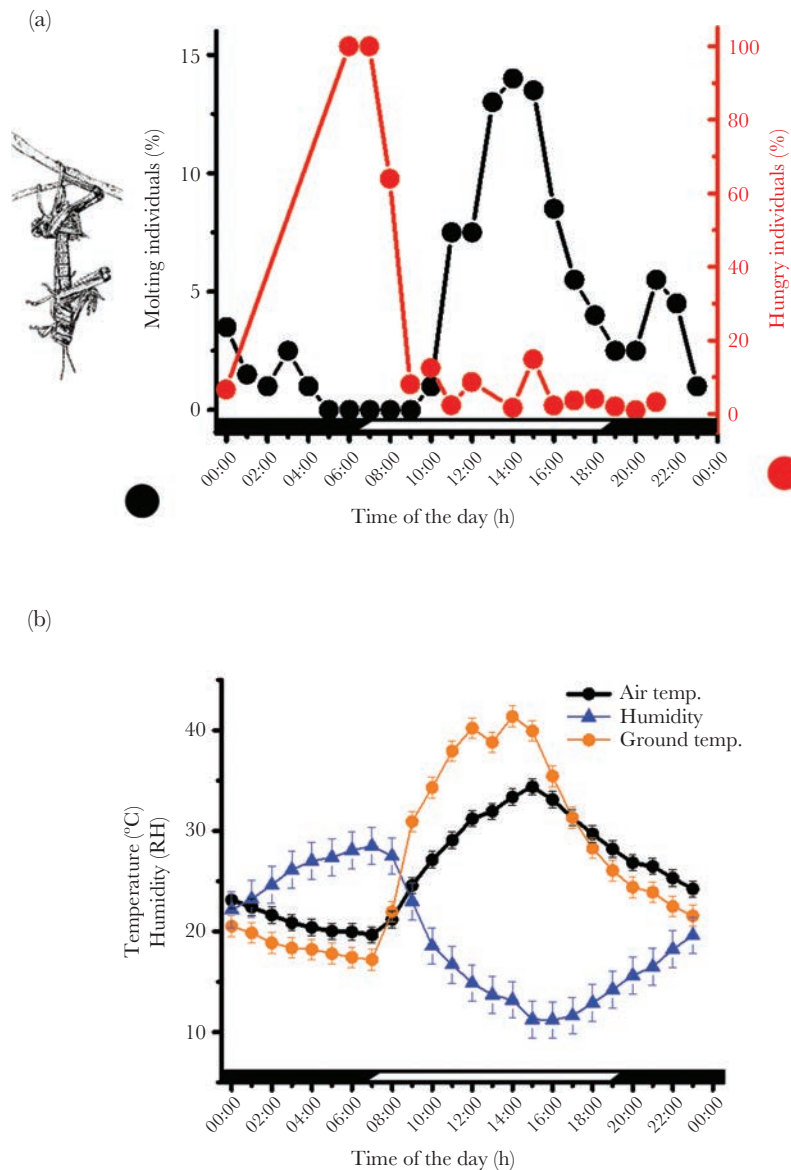
### How do gregarious nymphs avoid cannibalism during molting?

Our study suggests that individual behaviors of gregarious desert locusts lead to avoid being cannibalized in a group-living context. Diverse factors combine to eliminate virtually all molting-associated cannibalism in dense aggregations of free-living gregarious locusts supporting our three hypotheses. 1) Marching separation hypothesis: During the daytime, cannibalism is prevented because molting and non-molting insects occupy different microhabitats. 2) Moving away hypothesis: During the night, cannibalism is reduced because night-molting nymphs move away from conspecifics before molting. 3) Asynchronization of hunger level and molting patterns hypothesis: At dawn, there is no molting-associated cannibalism, because there is no molting at that period, and hungry non-molting nymphs are busy descending to the ground to bask, march, and feed on low-growing plants. Finally, there is no cannibalism within dense aggregations composed of pre-molting locusts, because pre- and post-molting individuals do not feed. In the following, we discuss, in turn, each of these mechanisms as emergent phenomena of these individual behaviors and finish with the evolutionary implications of our findings.

### Marching help a cannibal conspecifics-free situation during the day

Migration has evolved in many taxa for finding new resource, mating partners and reproductive sites (Dingle 2014). Gregarious nymphs of *S. gregaria* have an obligatory march and leave foraging sites before all plants are consumed (Maeno et al. 2021a). Thus, migration allows large numbers of them to access sufficient quantities of food constantly, compensating for energy and water loss (Maeno et al. 2021a). The most important finding of the present





**Figure 3**

(a) Diel molting (●) and hunger patterns (●) of gregarious nymphs of *Schistocerca gregaria*. (b) Diel fluctuations in mean air temperature and ground surface temperature in sunlight, and humidity from 22 to 29 November 2015 in Mauritania. Data for 4 days of diel hunger patterns ( $n = 1577$ ) and for 7 days of molting patterns ( $n = 210$ ) were combined. Error bars represent SE. Dark bar along the horizontal axis in represents night.

study was that marching separated defenseless molting nymphs from potential cannibalistic conspecifics during daytime due to different individual behavioral activities. Pre-molting nymphs stopped marching and remained in roosting plants, while non-molting individuals actively marched and left the former behind. The splitting of a band during the molting period was also observed in previous studies (Ellis and Ashall 1957). Nymphs typically reduce activities, stop feeding, and begin to empty their guts, the day before molting, and do not feed or march until their cuticle hardens, several hours after molting (Husain et al. 1949; Uvarov 1966; Hughes 1980; Rackauskas et al. 2006), so this immobility of pre-molting individuals may facilitate making distance between them, and cannibalism could rarely occur among groups of pre-molting individuals. As a result, molting gregarious nymphs can avoid cannibalism. In fact, cannibalism rarely occurred in the field.

High cannibal rates observed in the laboratory can be explained by absence of this behavioral separation (van Huis et al. 2008). Therefore, it can be considered that different individual mobility associated with molting help to cause a cannibal conspecifics-free situation during migration. Guttal et al. (2012) mentioned that Simpson et al. (2006) recorded that Mormon crickets enter a period of quiescence prior to molting that functions to separate individuals from the band. This observation also implies that marching reduces the risk of cannibalism during molting in Mormon crickets as well.

Living in group composed with conspecifics with different developmental stages tend to cause cannibalism (Crump 1984; Hopper et al. 1996). Previous studies reported molting or metamorphosis synchrony as a means to avoid cannibalism in Crustacea (Ferrero et al. 2002; Sainte-Marie and Lafrance 2002), spiders (Kim 2001),

and anurans (Bragg 1952; Arnold and Wassersug 1978). These nondispersive animals synchronize their physiological state by living with same clutch and use environmental factors as a trigger to synchronize molting. In contrast, migratory gregarious desert locusts cannot use this strategy, because large bands are sometimes composed of different aged nymphs from various clutches (Ellis and Ashall 1957). We found that behavioral segregation allows desert locusts to achieve local synchronous molting on each roosting plant from within a larger population exhibiting asynchronous molting. Previous study observed that small groups composed of pre-molting individuals tend to synchronously molt within individual bushes (Ellis and Ashall 1957), and this situation can be explained by marching separation.

Hence, synchronous, dense molting is achieved at an ecologically relevant scale: single bushes. Dense aggregations of synchronous molting locusts probably gain anti-predator and anti-cannibalism benefits similar to the selfish herd- and predator swamping-benefits shown for other aggregating animals (Vulinec 1990; Sword et al. 2005). Recently, we reported that only gravid desert locust females aggregated and synchronously laid eggs at night and temporally used the oviposition sites (Maeno et al. 2021b). This oviposition system could synchronize the hatching timing leading to a formation of band members composed of similar aged individuals even from different clutches.

Importantly, our results show that morning molting is delayed until after virtually all non-molting insects have descended to the ground and marched away. Likewise, afternoon molting in midday sheltering plants generally occurs after non-molting locusts have left such plants and begun afternoon marching. Hence, during the day, molting and non-molting locusts are separated in space. The behavior of non-molting hoppers marching probably evolved for other reasons than the cannibalism avoidance with the molting conspecifics, in part because it cannot be directly linked to the non-molting individual's fitness. However, locust marching serves as a newly recognized ecological function of separating molting nymphs from potential cannibals. Indeed, in a single day, a marching band can move over a km away from their pre-dawn roost-plants (Ellis and Ashall 1957). Furthermore, increased hunger increases marching activity (Ariel & Ayali 2015; Dkhili et al. 2019), whereas molting locusts are stationary. This results in the interesting feed-back loop that a greater physiological urge to cannibalize (i.e., greater hunger) causes greater spatial separation between potential cannibals and molting preys, thus reducing cannibalism. Of course, other marching locust bands may pass near or under the daytime molting bushes, and shelter under or in such bushes at midday. However, at midday, during this time of year, marching locusts seldom climb into the higher regions of such bushes, where molting occurs.

Haroon Khan (1945) observed that freshly emerged adults of *S. gregaria* were cannibalized by nymphs where vegetation of the area was dried and days were very hot, while he did not observe it where vegetation was green and days were mostly cloudy. Although Haroon Khan (1945) concluded that hot weather and absence of fresh food were the factors causing cannibalism, these situations can be also explained by occurrence of marching and plant abundance. In the first case, hot ground might inhibit migratory marching and shortage of food caused local aggregation concentrating cannibalistic conspecifics and pre-molting individuals at limited site (Ellis and Ashall 1957; Roffey and Popov 1968), so cannibalism may occur. On the other hand, marching apparently occurred in the second case, so migration functioned and green vegetation avoid local crowding. In the present study, migration occurred before

arising temperature and vegetation was abundant. These results suggested that environmental conditions of habitat could influence on occurrence of molting cannibalism through migration.

We note that in different seasons, geographic locations, conditions, populations, and especially during extreme weather, desert locusts sometimes behave differently. For example, various authors have reported atypical behavioral patterns in gregarious *S. gregaria*, including no descent from nocturnal roosts, no marching, nocturnal marching, 24-h feeding, and in some cases, empty guts, severe starvation and death, or feeding on newly hatched nymphs (Haroon Khan 1945; Ashall and Ellis 1962; Uvarov 1977). These unusual events could potentially cause accidental cannibalism.

## Cannibalism avoidance strategy at night

As mentioned above, the daily marching of non-molting nymphs may have evolved from other forces than avoidance of cannibalism. However, the night behavior of avoiding potential cannibals has a direct link to individual's fitness and can be seen as a result of natural selection.

How arthropods in general avoid molting-associated cannibalism is relatively understudied. Nonetheless, there are examples of behaviors of arthropods that evolved to avoid cannibalism. Some species construct temporary molting-shelters (Mossadegh 1978; Kudo 1994), seek refuges, change living habitats, or otherwise move away from kin prior to molting (Ryer et al. 1997; Lucas et al. 2000). Immatures of many species are solitary and sequestered and thus escape cannibalism (e.g., wood-boring larvae). However, competitive- and nutritional-cannibalism does occur even in generally solitary, sequestered larvae, such as some gall dwellers and other plant-boring insects (Breden and Chippendale 1989). Female Crustacea are often mate-guarded or otherwise protected by males during molting (Subramoniam 2017), female land crabs can remain sealed in male burrows up to a month during ecdysis. Some tenebrionid and dermestid larvae refuse to molt when surrounded by conspecifics (Ozawa et al. 2015), and wax moth larvae, *Galleria mellonella*, delay molting when a safe space cannot be found (Woolever and Pipa 1970).

We found that night-roosting pre-molting nymphs of desert locusts on plants typically moved away from the dense aggregations that formed mainly in the centers of the roosting plants, and move toward the peripheries of roost plants, which would reduce encounters with potential cannibals (Whitman and Orsak 1985). Once molting started, the individuals were not able to walk anymore, thus decision on where to molt is important to increase molting success rate. We did not observe molting-associated cannibalism even in a cage under semi-field conditions. We collected locusts from a single night-roosting plants, so their developmental states could be relatively synchronized. In this study, we provided enough amount of food and enough roosting space, so these factors could prevent molting-associated cannibalism.

## Natural selection for diel feeding and molting patterns

Satiation generally reduces cannibalism in many animals (Ellis and Ashall 1957; Fox 1975; Elgar and Crespi 1992; Whitman et al. 1994; Simpson et al. 2006; Hansen et al. 2011). This fact imply that natural selection could drive diel molting timing against feeding patterns. We found a temporal asynchrony of the initiation of two circadian behaviors: molting versus feeding; when non-molting nymphs were the hungriest, there was no molting, while most molting

occurred when they were satiated. Our starvation experiments confirmed that starved locusts display cannibalistic necrophagy on euthanized molting individuals. At night, all locusts occupied the same habitat: bushes and trees, and often in extremely high densities. Hence, there should be ample opportunity for nocturnal cannibalism. However, as Figure 3 shows, marching locusts typically fed and fill their foreguts before ascending nocturnal roost plants, and therefore were unable to feed during the first part of night-roosting, when they were most restless and therefore most likely to contact potential “prey.” Thus, nymphs that molted in the early night were relatively safe because well-fed locusts seldom cannibalized. During the pre-dawn hours, locust foreguts were empty and they presumably were hungry. But at this time there was little molting and thus little opportunity for molting-associated cannibalism. All locust behaviors are reduced during cool nights, including movement, molting, and feeding (Ellis and Ashall 1957; Chappell and Whitman 1990; Maeno et al. 2021a), which together pre-empt cannibalism. Likewise, at dawn, when non-molting nymphs were the hungriest as suggested by their empty foreguts, there was no molting, and hence no molting-associated cannibalism. Cannibalism risk potentially could be the driving factor shaping the diel molting patterns for gregarious locusts. Although the present study focused on gregarious locusts, it would also be interesting to know for solitary ones that have little risk of cannibalism due to low population density.

### Marching and cannibalism in Orthoptera

We have seen above that night behavior of separation for molting and diel molting timing may have evolved to avoid cannibalism by conspecifics. However, we noted that the marching during the day could have evolved for some other reasons. The “Cannibalism Pursuit-Escape Hypothesis” proposes that marching in some aggregating Orthoptera is driven by an “escape-pursuit behavior” (Simpson et al. 2006; Bazazi et al. 2008, 2010, 2011; Romanczuk et al. 2009, 2012; Hansen et al. 2011; Guttal et al. 2012). According to this hypothesis, individuals are continuously escaping and moving forward in order to avoid being eaten by conspecifics approaching from behind, while at the same time pursuing other animals in front, attempting to eat them. This “Cannibalism Pursuit-Escape Hypothesis” assumes that gregarious Orthoptera suffer from a constant risk of cannibalism and should avoid physical contact among each other and therefore keep moving or at least space themselves. In reality, however, non-cannibalistic interactions among locust nymphs are exceedingly common (Ariel et al. 2014; Ariel and Ayali 2015). Indeed, gregarious nymphs frequently stop marching and aggregate at high densities (often touching one another) during morning and pre-dusk stationary basking, midday sheltering, postprandial resting and night-roosting with no cannibalism of healthy non-molting kin (Ellis and Ashall 1957; Ariel and Ayali 2015; Maeno and Ould Babah Ebbe 2018; Dkhili et al. 2019; Maeno et al. 2021a; Piou et al. 2022). In our studies of *S. gregaria* in the field during 11 years, we never observed cannibalism during marching or on healthy non-molting individuals. During 5 years of field studies on grasshopper, *Rhammatocerus schistocercoides*, Michel Lecoq noted densities up to 30,000/m<sup>2</sup>, but never witnessed cannibalism on healthy, active individuals (Lecoq and Foucart 1999, pers. comm.). Likewise, during 20 year of field work on multiple locust species at high densities (Hunter and Spurgin 1999; Hunter et al. 2008), David Hunter has never observed cannibalism on active nymphs (pers. comm.). For most grasshopper species, cannibalism appears to be restricted to injured, sick, dead,

or molting/hatching individuals (Haroon Khan 1945; Ashall and Ellis, 1962; Ariel et al. 2014; Ariel and Ayali 2015). Uvarov (1928) claimed that, “only wounded or dead hoppers are thus attacked.” Taken together, these observations suggest that gregarious desert locusts do not risk cannibalism and do not try to escape from conspecifics at all times. These results also imply that the “Cannibalism Pursuit-Escape Hypothesis” is not appropriate for all locust species (Buhl et al. 2012; Ariel et al. 2014; Ariel and Ayali 2015; Dkhili et al. 2019). Specifically, avoiding cannibalism during molting cannot be explained by the previous hypothesis, because molting locusts cannot march. If cannibalism was beneficial, natural selection would act on individual cannibals to stay next to potential food targets, i.e., would-be cannibals would want to stay with their molting conspecifics and not to separate themselves from them. Therefore, marching behavior alone cannot explain strategies avoiding cannibalism in gregarious locusts.

### CONCLUSION

The cannibalism-avoiding strategies we documented in the field were not observed in the laboratory, because laboratory cages prevented the marching-separation of pre- and non-molting nymphs that would normally occur in the field. As such, our study is yet another reminder that laboratory investigations (and modeling simulations) may not reflect nature’s reality. Importantly, our results argue against cannibalism as a proximal driving cause of marching in locusts. We have never observed cannibalism on healthy, active non-molting locusts in the field, and as this study implies, even cannibalism on defenseless molting locusts is extremely low.

In conclusion, organisms are composed of multitudinous interactive traits, each of which is presumably under multiple selective forces. Virtually all traits (including behaviors and “strategies”) carry benefits and costs. How organisms balance these trade-offs to create a functioning complex-integrated, environmentally adapted organism is a fundamental question in evolution and has presumably driven organismal adaptation and diversity, including behavioral and life-history diversity (Roff 2002). By examining the well-known trade-off between group living and cannibalism our study suggests that natural selection has shaped various life-history traits at individual level for gregarious locusts to reduce cost of cannibalism on molting individuals while maintaining the benefits of group living. These behavioral knowledges can be also applied to improve locust control techniques.

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## AUTHOR CONTRIBUTIONS

K.O.M. conceived the hypothesis, designed the methodology, and collected data. C.P. and K.O.M. analyzed data. K.O.M., D.W.W., and C.P. wrote the first draft of the manuscript and all authors edited and approved the manuscript. S.O.E. identified plant species. S.O.E., S.O.M., M.E.H.J., and M.A.O.B.E., organized the field survey.

## CONFLICT OF INTEREST

The authors have no conflicts of interest to report.

## DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data provided by Maeno et al (2023) and are available in figshare:<https://figshare.com/s/8411f8265aab3a15496d>

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