

'PROTEST' SOUNDS OF A GRASSHOPPER: PREDATOR-DETERRENT SIGNAL?*

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INTRODUCTION

Some animals emit sounds when grasped or handled. Referred to as alarm, protest, distress or disturbance signals—the sounds themselves, the behavior accompanying their emission and the mechanisms responsible for their production have been described, analyzed and discussed (Haskell 1974). But only recently have experimental data become available in support of the oft-stated hypothesis that these sounds may startle a predator into releasing a noisy morsel (Bauer 1976; Smith and Langley 1978; Masters 1979; Buckler et al 1981).

The grasshopper *Pareupreocnemis syriaca* Giglio Tos (Acrididae) when grasped, immediately begins to chirp (the biology and acoustic behavior of this grasshopper will be described separately). Though there are individual differences in intensity and quality of the sounds, males have a greater tendency to squeak while females tend to click. Emission of the sounds is easily observed to correspond to movements of the mouthparts; if the labrum is lifted, the mandibles can be seen rubbing against one another to the rhythm of the chirps. Immobilization of the mouthparts prevents sound emission.

It had been observed in our laboratory that on casual feeding of this grasshopper to representatives of several lizard families (Lacertidae, Scincidae, Gekkonidae) the grasshopper was captured, then promptly released. A male grasshopper introduced into the cage of the lizard *Lacerta danfordi* was caught head-first and held in the mouth of the lizard for several seconds, after which the lizard slowly opened its mouth and the grasshopper fell free. Several additional grasshoppers of this species were offered to two *Eublepharis macularius*, a gecko from Pakistan present in the vivarium at the

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time. They grabbed, then released the insects. Additional observations were then made with a microphone in the cage transmitting sounds to earphones worn by the investigator. A skink, *Mabuva vittata* caught and then released a sound-producing *P. syriaca* male; three geckos, *P. h. guttatus* each caught and promptly released sound-producing males of *P. syriaca*. These rejected grasshoppers were removed and immediately replaced by mute grasshopper nymphs of *L. m. migratorioides*, equivalent in size to the rejected *P. syriaca* males; the nymphs were caught and immediately consumed, one by each gecko. These preliminary observations raised the question: were the sounds emitted by the grasshoppers a factor in their release? The following experiments were designed to answer this question.

MATERIALS AND METHODS

Grasshoppers: Adult males of *P. syriaca* were field caught in the hills of Jerusalem a few days prior to experiments and were maintained in 60 l laboratory cages providing fresh plants, light and heat. As males were lifted from the cage for assignment to an experiment, the thorax was squeezed gently. Of 48 males squeezed, only three failed to produce sound. Half the sound-producing males were then silenced by releasing a drop of melted paraffin onto the closed mandibles; when it hardened, these males could no longer emit sound, though they hardly differed in appearance from untreated males.

Fourth instar nymphs of *Locusta migratoria migratorioides* R & F maintained in the gregarious state in stock cages in the laboratory, served as additional controls. Their size, dark color and small wing buds provided a phenotypically reasonable facsimile of the brachypterous adult male of *P. syriaca*. These nymphs did not produce sound when handled.

Predators: *Ptyodactylus hasselquistii guttatus* von Heyden was selected as the predator for the series of experiments. The candidacy of this gecko was supported by the following credentials: *P. h. guttatus*, a poikilotherm like *P. syriaca*, is at least partially sympatric with it and shares its biotope; it is an opportunistic insectivore; like *P. syriaca*, it emerges from its retreat in rock ledges and crevices in warm weather and has been known to feed during daylight (Werner 1965; Perry & Werner 1981); juveniles could handle a grasshopper

the size of the *P. syriaca* male, while adults could handle even the large female; the frequency spectrum of the sounds of *P. syriaca* falls within the hearing range of *P. h. guttatus* (Werner 1976); and finally, a laboratory stock of this gecko was available. Though wild-caught, the geckos had been kept in captivity in the vivarium for months to years. Though the memory span of this gecko species is not known, it may well be that the long laboratory incarceration had dimmed recollections of possible previous encounters with this grasshopper and its ruse.

Experimental procedure: A series of three grasshoppers was introduced simultaneously into the cage of a gecko whose habitual diet of fly maggots had been removed at least a day previous: an untreated *P. syriaca* male, a silenced *P. syriaca* male and a fourth instar nymph of *L. m. migratorioides*. The insects were introduced at noon, prior to the peak activity hours of the gecko (Frankenberg 1979), and observations were made every half hour from noon to 5:00 PM and from 8:00 AM to noon. The first item eaten was assigned the number 1; the second item, 2; and the third, 3. If two grasshoppers disappeared between any two readings, both were assigned the same number. In the few instances in which all three grasshoppers were alive and apparently unharmed at the end of 24 hours, it was assumed that the gecko was not hungry; the experiment was not included in tallying the results. After an interval of several days, the gecko was used again. Silenced *P. syriaca* were checked at the end of the experiment to ascertain that they were indeed still unable to produce sound.

RESULTS AND CONCLUSIONS

In the cages of the 26 geckos tested, no untreated *P. syriaca* was ever the first to disappear and 69% were never eaten at all. The silenced *P. syriaca* was eaten first in 46% and the *L. m. migratorioides* nymphs in 78% of the experiments (Table I and Fig. 1). A G-test (Sokal and Rohlf 1969) was carried out to test for independence between the three choices of prey and the order of predation. It was found significant ($G = 49.9$; $df = 6$, $p < 0.001$). A sign test (Siegel 1956) between each of the three combinations of paired insects for all the 26 instances in which a grasshopper was eaten showed that silenced *P. syriaca* were eaten before untreated ones in 18 experiments ($p \leq 0.002$), *L. m. migratorioides* were eaten before

Table I: Order of predation* by the gecko *P. h. guttulatus*, on a choice of grasshoppers.

| serial number gecko | normal <i>P. syriaca</i> male | silenced <i>P. syriaca</i> male | 4th instar nymph, <i>L.m.m.</i> |
|------------------------|-------------------------------------|---------------------------------------|---------------------------------------|
| 1 | 0 | 1 | 1 |
| 2 | 0 | 1 | 1 |
| 3 | 0 | 1 | 1 |
| 4 | 3 | 1 | 2 |
| 5 | 3 | 2 | 1 |
| 6 | 2 | 0 | 1 |
| 7 | 0 | 1 | 0 |
| 8 | 0 | 1 | 1 |
| 9 | 2 | 3 | 1 |
| 10 | 3 | 1 | 2 |
| 11 | 0 | 2 | 1 |
| 12 | 2 | 3 | 1 |
| 13 | 0 | 0 | 1 |
| 14 | 0 | 1 | 0 |
| 15 | 3 | 1 | 1 |
| 16 | 0 | 2 | 1 |
| 17 | 0 | 0 | 1 |
| 18 | 0 | 1 | 0 |
| 19 | 3 | 1 | 2 |
| 20 | 0 | 0 | 1 |
| 21 | 0 | 2 | 1 |
| 22 | 0 | 1 | 1 |
| 23 | 0 | 2 | 1 |
| 24 | 0 | 0 | 1 |
| 25 | 0 | 2 | 1 |
| 26 | 0 | 0 | 1 |

*The numbers 1, 2, and 3 represent order of predation; 0 indicates that the grasshopper was alive at the end of the 24 hr test period. The same number for more than 1 grasshopper indicates that they were consumed between the same two observation periods.

the untreated *P. syriaca* in 23 experiments ($p \leq 0.001$) and before silenced ones in 14 experiments ($p = \text{n.s.}$). It is therefore concluded that the protest sounds produced by *P. syriaca* apparently reduce predation on it by *P. h. guttatus*.

DISCUSSION

To a hungry caged gecko offered a choice between fly maggots and grasshoppers, the latter are invariably preferred. However, it is

apparent from the present results that the appetite for grasshoppers may be tempered by their behavior. In the present case, mandibular sounds emitted by *P. syriaca* appeared to interfere with predation by this gecko.

Because of its confinement in the cage of the gecko during experiments, a grasshopper which had chirped its way to freedom was prevented from escaping its predator as it might in the wild. *P. syriaca*, though it cannot fly, is an excellent jumper and under natural field conditions would probably have jumped far and hidden itself well before the predator had recovered from its encounter.

The sound itself has a wide frequency spectrum such as that characterizing alarm calls of birds (Marler 1957; Morton 1977). The utility of sounds such as these might include conspecific warning, since these grasshoppers occur in loose aggregates. However, holding a chirping male in close proximity to conspecifics, or playing the recorded sound back into a cage of *P. syriaca* failed to produce any discernible reaction.

It was observed that these grasshoppers are often seized headfirst. It is suggested that the hollow bones of birds, or the large buccal cavity of lizards may act as a resonating chamber, enhancing the intensity of the insect's sounds or vibrations.

For the few grasshopper species known to produce mandibular sounds spontaneously or in encounters with conspecifics, an intraspecific communicative function has been suggested: (*Paratylotropidia brunneri*, Alexander 1960; *Oedaleonotus fuscipes*, Varley 1939; *Calliptamus italicus*, Faber 1949) but no experiments have been reported in support of this hypothesis. Henry (1942) reports that *Mesambria dubia* emits a shrill creak when seized and investigation may reveal that this sound, like the protest sound of *P. syriaca* studied here, may play a predator-deterrent role.

Whether a remnant of an intraspecific communicative cue or a language of predator deterrence, a signal such as that presented here has quite probably been playing a part in the evolutionary history of the struggle for survival in this species.

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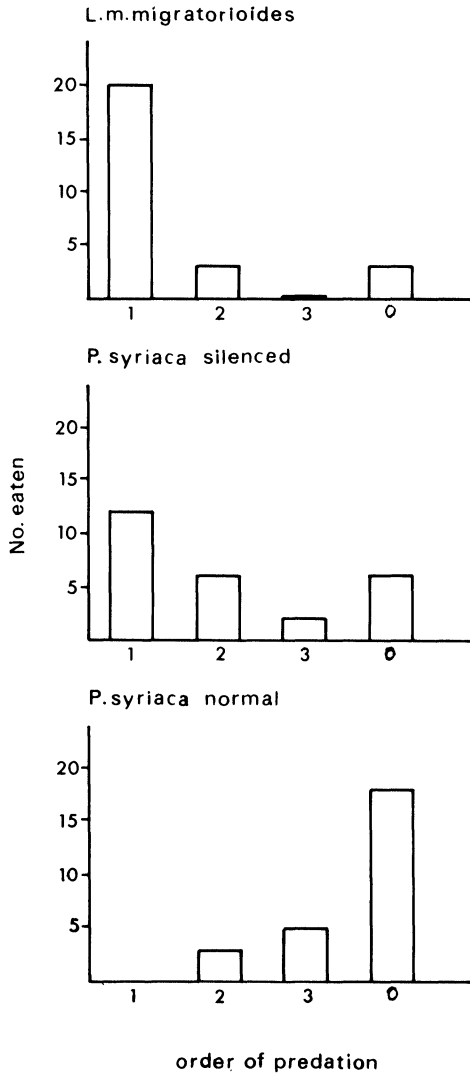


Fig. 1. Order of predation on sound producing and silenced *P. syriaca* males and mute nymphs of *L. m. migratorioloides*.

Legend: The numbers 1, 2, and 3 in the abscissa represent order of predation; 0 indicates that the grasshoppers were alive at the end of the 24-hr. test period.

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SUMMARY

Mandibular sounds produced by the grasshopper *Pareuprepocnemis syriaca* Giglio Tos, when seized, appear to reduce predation on it by a probable natural predator, *Ptyodactylus hasselquistii guttatus* von Heyden, an insectivorous gecko. Sound-producing grasshoppers which had been silenced by treatment in the laboratory, untreated sound-producing grasshoppers, and silent *Locusta migratoria migratorioides* nymphs were introduced simultaneously to the geckos. Survival of normal, sound-producing *P. syriaca* far surpassed that of both controls.

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