

THE EFFECT OF
ENFORCED LOCOMOTOR ACTIVITY ON LIPID CONTENT
IN ALLATECTOMIZED MALES OF *LOCUSTA*
MIGRATORIA MIGRATORIOIDES

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INTRODUCTION

Odhiambo (1966*b*) observed that allatectomized adult males of *Schistocerca gregaria* were persistently inactive, and that activity could be re-established by the implantation of corpora allata. It was suggested that the corpus allatum hormone stimulates locomotor activity, perhaps by a direct effect upon the central nervous system. Since lipid is the main energy store in locusts (Weis-Fogh, 1952), the enormous hypertrophy of the fat body in the allatectomized males could be a consequence of their lethargic condition (Odhiambo, 1966*b*). It is of interest to examine this possibility further and to see what effect enforced locomotor activity has on the lipid content of allatectomized males. This examination has been undertaken using males of *Locusta migratoria migratorioides*, and the results are reported here.

MATERIALS AND METHODS

Only adult insects were used in the experiments. The locusts were reared under crowded conditions in aluminium cages of 60 l. capacity in an insectary maintained at 30° C. A 40 W. electric light bulb (operated by a time switch) provided 12 hr. light per day in each cage, and also warmed the centre of the cage up to 45° C. Fresh grass, dry bran, and water were provided daily. Small groups of insects were kept in celluloid cages of 12 l. capacity grouped around 100 W. light bulbs.

Daily food consumption was estimated from the weight of faeces produced which bears a close relationship to actual amounts of food eaten (Cheu, 1952; Davey, 1954; Norris, 1961). The faeces were dried at 100° C. overnight before cooling and weighing. Live locusts were weighed individually in a tared specimen tube.

The procedure for allatectomy has been described (Strong, 1963).

Enforced locomotor activity was induced by rotating the insects in a polythene cylinder (10 cm. diameter × 20 cm. long) driven by an electric motor. The speed of the treadmill was adjusted so that the insects had to walk quickly to avoid being tumbled. Exercise periods lasted for 1 hr. in the morning and 1 hr. in the afternoon. Since the insects could not feed whilst walking, the control groups were deprived of food during these periods.

At the end of the experiment each locust was weighed, anaesthetized with carbon dioxide, and pinned to a wax block. The accessory sex glands and the gut were

removed and weighed; only the accessory glands were replaced in the carcass, which was then dried at 60° C. for 5 days. The guts were removed, since they contain different amounts of food independently of the age of the locust (Cheu, 1952). Odhiambo (1966a) overcome this problem by starving *S. gregaria* for 24 hr. before sacrifice. Unfortunately, this does not ensure complete emptying of the crop in *L. m. migratorioides*; starvation for more than 24 hr. is obviously undesirable.

Lipid content of the dried bodies was determined by Soxhlet extraction with chloroform for 5 hr. The extracted bodies were dried at 60° C. overnight before the final weighing. Fat content is expressed as percentage of the dry weight.

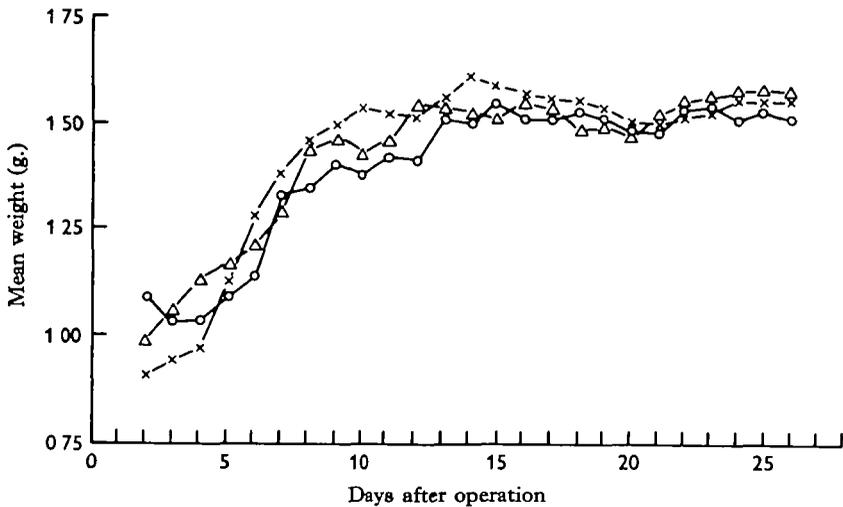


Fig. 1. Growth curves for sham-operated (x—x), allatectomized-control (O—O), and allatectomized-exercised (Δ—Δ) male locusts. Each point represents the mean for 10, 15, and 10 individuals respectively, until day 20 when one sham-operated and two allatectomized-control males died. The standard errors are small and have been omitted for clarity.

RESULTS

Twenty-five 1-day-old male locusts were allatectomized, and ten were sham-operated. The insects were allowed a day for recovery. Ten allatectomized males were selected for exercising, the remaining fifteen providing allatectomized-controls. Each of the three groups was kept in a 12 l. cage. Every day the insects were weighed, the faeces were collected, and the allatectomized-exercised locusts were forced to walk for 2 hr. The curves for daily weight change and faeces production are shown in Figs. 1 and 2 respectively. During the experiment, two allatectomized-control and one sham-operated locust died.

All locusts gained weight steadily during the first week or so, reaching a maximum about the 12th day and maintaining fairly constant weight until the end of the experiment. There were no significant differences in weight between the different groups on any day. Faeces production increased considerably until about the 8th day before falling to a low level. The rate of production was similar in all groups until day 14 when the allatectomized-exercised locusts began to produce slightly more faeces than

the other two groups. This information cannot be treated statistically, since faeces are not collected from individual locusts.

About 10 days after the operation the sham-operated males were becoming yellow, and began to show sexual behaviour. Although the allatectomized insects remained greyish brown until the end of the experiment, both groups began to show sexual

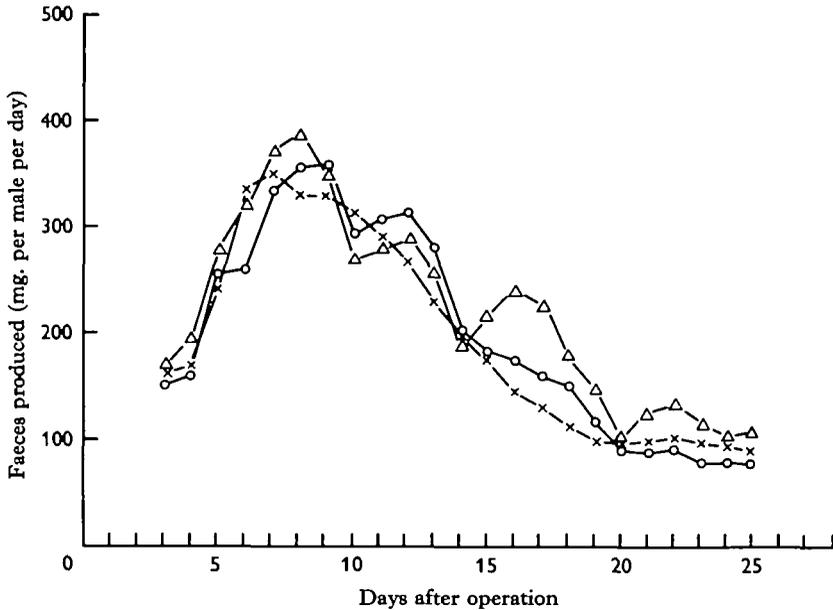


Fig. 2. Dry weights of faeces expelled daily by groups of sham-operated (x—x), allatectomized-control (O—O), and allatectomized-exercised (Δ—Δ) male locusts.

Table 1. *The means and standard errors of the dry weight (mg.), accessory sex gland weight (mg.), water content (% wet weight), and lipid content (% dry weight) in sham-operated, allatectomized-control, and allatectomized-exercised male locusts*

Treatment	Dry weight*	Accessory sex gland weight	Water content*	Lipid content*
Sham-operated (9)	525 ± 42	55.5 ± 2.28	62.0 ± 0.96	22.9 ± 2.18
Allatectomized-control (13)	622 ± 19	17.7 ± 0.56	53.4 ± 0.58	43.8 ± 1.27
Allatectomized-exercised (10)	564 ± 27	20.8 ± 2.85	58.3 ± 0.86	36.4 ± 1.87

* The gut is not included in these measurements. The figures in parentheses show the number of insects in each group.

behaviour within 3-4 days of its appearance amongst the sham-operated males. No females were present, but the males mounted and attempted to copulate with each other. There was considerable sexual activity in all groups for the remainder of the experiment. If locomotor activity in either of the groups of allatectomized males was lower than in the sham-operated group, this was not obvious.

The locusts were sacrificed after 26 days and treated as described in the materials and methods section; the results are shown in Table 1.

In both groups of allatectomized males the accessory sex glands were undeveloped and much smaller than in the sham-operated locusts ($P = < 0.001$). The small difference between accessory sex glands in the allatectomized-exercised and allatectomized-control locusts is not significant. Dry weight is greater in the allatectomized-control males than in the other groups ($P = 0.05-0.02$), but the difference in dry weight between the sham-operated and allatectomized-exercised males is not significant. The sham-operated locusts contain more water than the allatectomized-control ($P = < 0.001$) and allatectomized-exercised males ($P = < 0.01$). The difference in water content between the batches of allatectomized males is also significant ($P = < 0.001$).

The sham-operated locusts have less fat than the allatectomized-exercised locusts ($P = < 0.001$), which have a lower fat content than the allatectomized-control locusts ($P = < 0.001$). Removal of the gut can be criticized, since differential lipid loss might occur in this way. The guts were subjected to 5 hr. of Soxhlet extraction after removal of their contents. The mean fat content of the guts of the sham-operated locusts was 10%, whereas that of both groups of allatectomized locusts was 11%—the difference is not significant. The absolute amount of fat lost by discarding the gut is about 4 mg. per locust.

DISCUSSION

Growth in the adult male *S. gregaria* is characterized by three phases: rapid growth, attainment of maximum weight, and slow decline in weight (Odhiambo, 1966c). A similar pattern is seen in *L. m. migratorioides*, but the decline is not marked. Phipps (1950) did not record a fall in weight after reaching a maximum in males of *L. m. migratorioides*, although his observations ceased on the 20th day of adult life. Removal of the corpora allata from young males of *S. gregaria* has little obvious effect upon growth apart from a tendency to delay the period of decline in weight (Odhiambo, 1966c). In the present work allatectomy does not appear to modify growth in males of *L. m. migratorioides*. However, it can be seen from Table 1 that the operation alters the composition of the locust. Allatectomy causes an increase in dry weight, but this increase is not observed in total weight since it is accompanied by a fall in water content.

Feeding activity in males of *S. gregaria* increases as the young locust grows but diminishes after maximum weight is reached, and falls to a low level for the remainder of adult life (Norris, 1961; Odhiambo, 1966c). The same pattern of feeding activity is observed in males of *L. m. migratorioides* (Cheu, 1952; Strong, 1967). The reduction in food consumption during later adult life suggests that gametogenesis, accessory sex gland activity, and sexual behaviour make only small demands on metabolism. This is in marked contrast to the mature female locust in which demands for yolk precursors are high and in which ovarian development is accompanied by greatly increased feeding activity (Strong, 1967). Allatectomy has no apparent effect upon food consumption in males of *L. m. migratorioides*, as in *S. gregaria* (Odhiambo, 1966c). In the female *L. m. migratorioides*, allatectomy is followed by a reduced rate of yolk synthesis which is reflected in a drastic reduction in feeding activity (Strong, 1967). Food consumption in the allatectomized-exercised males is slightly higher than in the other groups after day 14. It is necessary to collect faeces from individual locusts in order to test the significance of this observation. Collection of faeces from

individuals is a difficult problem: any attempt to isolate locusts introduces alterations in feeding activity and maturation (Norris, 1961). It would be very interesting if enforced activity does stimulate feeding in allatectomized male locusts. Perhaps it is difficult to mobilize stored lipid in the absence of the corpus allatum hormone and, therefore, the energy for increased activity is provided by increased food consumption. Pfeiffer (1945) suggested that one function of the corpus allatum hormone in *Melanoplus differentialis* is to facilitate mobilization of the lipid reserves.

Allatectomy causes a considerable hypertrophy of the fat body in allatectomized males of *L. m. migratorioides*, as in *S. gregaria* (Odhiambo, 1966*a*). If allatectomized males of *L. m. migratorioides* are forced to exercise, hypertrophy of the fat body is limited. This observation supports the hypothesis that lipid accumulation in allatectomized locusts might be due to lethargy (Odhiambo, 1966*b*). However, it is difficult to explain lipid accumulation in allatectomized males of *L. m. migratorioides* in this way. In the first place, locomotor activity in *S. gregaria* was measured because allatectomized males were *obviously* inactive after the operation (Odhiambo, 1965, 1966*b*). In the present investigation allatectomized males of *L. m. migratorioides* were extremely active. This discrepancy can be explained. Allatectomy does not abolish sexual behaviour in males of *L. m. migratorioides*: this has been reported by Cantacuzène (1967), and was recorded in the present work. However, allatectomized males of *S. gregaria* show no sexual behaviour (Loher, 1960; Pener, 1965; Odhiambo, 1966*c*; Cantacuzène, 1967). Since the greater part of adult life of male locusts in captivity is directed towards sexual activity, any operation which reduces the latter must have a considerable effect upon locomotor activity. The lethargic condition observed in allatectomized males of *S. gregaria* is almost certainly due to the absence of sexual behaviour. It was recorded that the allatectomized locusts in this work showed no appreciable difference in locomotor activity from the sham-operated males. The added stress of forced walking for 2 hr. daily for over 3 weeks must have raised the level of activity in the allatectomized-exercised males by a substantial amount. Yet, these locusts contain 14% more fat than the sham-operated insects, and only 7% less than the non-exercised allatectomized males. This result shows that enforced activity can prevent a certain amount of fat accumulation in allatectomized insects, but it is very doubtful whether lipid accumulation in these insects is due to inactivity. This argument cannot be extended to *S. gregaria*, since the mode of action of the corpus allatum hormone is different in the two species of locusts.

SUMMARY

1. Allatectomy has no apparent effects upon feeding activity in males of *L. m. migratorioides*. If allatectomized locusts are forced to take vigorous exercise, food consumption is increased slightly.
2. Allatectomized males exhibit active sexual behaviour, although they do not develop a mature coloration.
3. The accumulation of lipid in allatectomized males can be limited by forcing the insects to take vigorous exercise. The possibility that hypertrophy of the fat body is due to lethargy in allatectomized male locusts is discussed but considered to be unlikely.

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REFERENCES

- CANTACUZÈNE, A. M. (1967). Effets comparés de l'allatectomie sur l'activité des glandes annexes mâles et le comportement sexuel de deux Acridiens: *Schistocerca gregaria* et *Locusta migratoria* (souches *migratorioides* et 'Kazalinsk'). *C. r. hebd. Séanc. Acad. Sci., Paris* **265**, 224-7.
- CHEU, S. P. (1952). Changes in the fat and protein content of the African migratory locust, *Locusta migratoria migratorioides* (R. & F.). *Bull. ent. Res.* **43**, 101-9.
- DAVEY, P. M. (1954). Quantities of food eaten by the desert locust, *Schistocerca gregaria* (Forsk.) in relation to growth. *Bull. ent. Res.* **45**, 539-51.
- LOHER, W. (1960). The chemical acceleration of the maturation process and its hormonal control in the male of the desert locust. *Proc. R. Soc. B* **153**, 380-97.
- NORRIS, M. J. (1961). Group effects on feeding in adult males of the desert locust, *Schistocerca gregaria* (Forsk.) in relation to sexual maturation. *Bull. ent. Res.* **51**, 731-53.
- ODHIAMBO, T. R. (1965). Metabolic effects of the corpus allatum hormone in the desert locust, *Schistocerca gregaria*. *Nature, Lond.* **207**, 1314-15.
- ODHIAMBO, T. R. (1966a). The metabolic effects of the corpus allatum hormone in the male desert locust. I. Lipid metabolism. *J. exp. Biol.* **45**, 45-50.
- ODHIAMBO, T. R. (1966b). The metabolic effects of the corpus allatum hormone in the male desert locust. II. Spontaneous locomotor activity. *J. exp. Biol.* **45**, 51-63.
- ODHIAMBO, T. R. (1966c). Growth and hormonal control of sexual maturation in the male desert locust (*Schistocerca gregaria* Forskål). *Trans. R. ent. Soc. Lond.* **118**, 393-412.
- PENER, M. P. (1965). On the influence of corpora allata on maturation and sexual behaviour of *Schistocerca gregaria*. *Proc. zool. Soc. Lond.* **147**, 119-36.
- PFEIFFER, I. W. (1945). Effect of the corpora allata on the metabolism of adult grasshoppers. *J. exp. Zool.* **99**, 183-233.
- PHIPPS, J. (1950). The maturation of the ovaries and the relation between weight and maturity in *Locusta migratoria migratorioides* (R. & F.). *Bull. ent. Res.* **40**, 539-57.
- STRONG, L. (1963). A simple apparatus for use in removing corpora allata from locusts. *Bull. ent. Res.* **54**, 19-21.
- STRONG, L. (1967). Feeding activity, sexual maturation, hormones, and water balance in the female African migratory locust. *J. Insect Physiol.* **13**, 495-507.
- WEIS-FOGH, T. (1952). Fat combustion and metabolic rate of flying locusts (*Schistocerca gregaria* Forskål). *Phil. Trans. R. Soc. B* **237**, 1-36.