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Contents

Contributors	v
Regulatory Mechanisms in Insect Feeding L. BARTON BROWNE	1
The Cytophysiology of Insect Blood A. CLIVE CROSSLEY	117
Development and Physiology of the Oöcyte-Nurse Cell Syncytium WILLIAM H. TELFER	223
Major Patterns of Gene Activity During Development in Holometabolous Insects JOHN A. THOMSON	321
Subject Index	399
Cumulative List of Authors	429
Cumulative List of Chapter Titles	431

Regulatory Mechanisms in Insect Feeding

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1	Introduction	1
2	Regulatory changes in components of feeding behaviour	2
2.1	General comments on the design and interpretation of experiments	3
2.2	Regulation of locomotor pre-ingestion behaviour	5
2.3	Regulation of nonlocomotor pre-ingestion behaviour	21
2.4	Regulation of ingestion	42
3	Long-term regulation of intake	88
3.1	Constancy of intake	88
3.2	Effect of deprivation on subsequent <i>ad lib.</i> feeding	89
3.3	Effect of dilution of the food on intake	91
3.4	Temporal patterning of ingestion	98
4	Some factors other than feeding and deprivation which affect feeding behaviour	102
5	Concluding remarks	104
	Acknowledgements	105
	References	105

1 Introduction

There is abundant evidence that insects possess mechanisms which enable them to regulate their intake of food and water with a considerable degree of precision (Dethier, 1969; Gelperin, 1971a). The literature relevant to the understanding of the regulation of feeding by insects is too large to be dealt with fully in one review and I have therefore selected only two aspects for detailed discussion.

The total feeding behaviour of most insects is made up of a number of components, and the first topic I will discuss is how the performance of these may vary according to the insect's state of deprivation. The second part of the review consists of a discussion of the long-term regulation of feeding, especially in relation to some of the previously discussed behavioural variations in the components of feeding. Since the emphasis is on the role in the regulation of feeding of behavioural changes resulting from

feeding and deprivation, much of the review is concerned with the regulation of intake of materials taken repeatedly by the insect and which are usually required for the maintenance of life, rather than with special foods required for particular purposes such as reproduction. These two topics were selected for emphasis because it seems clear that the basis for regulation of the intake of food and water over a period by most, and perhaps all insects, is that food-deprived individuals behave differently from recently fed ones. Moreover, considerable information is available about the physiological bases of some of these behavioural differences.

A number of factors other than feeding and deprivation are known to influence the feeding behaviour of insects and, although I have placed the detailed discussion of these beyond the scope of this review, I have included a brief section on some of these influences. In this, I have included enough of the more important references to allow entry into the literature relating to these aspects.

2 Regulatory changes in components of feeding behaviour

The number of behavioural components involved in the total feeding behaviour of an insect depends upon its temporal and spatial relationships with its food. An insect which feeds intermittently and ranges widely from its food between bouts of feeding would probably have, as components of feeding behaviour, "random" locomotor activity, orientated movements towards food or food sources in response to visual or olfactory stimuli, a variety of responses concerned with the initiation of feeding when the food is reached, responses which are responsible for the maintenance and then the cessation of feeding and, finally, locomotor activity again which takes it away from the food source. An insect which feeds intermittently but remains in contact with its food shares the components concerned with initiation, maintenance and termination of feeding, but not those related to locomotor behaviour in the period between feeding episodes. An insect which feeds more or less continuously lacks all components except those concerned with the maintenance of feeding. The bases for the regulation of intake by an insect might be differences, according to its state of deprivation, in any or all of the components of its total feeding behaviour, with insects showing a greater number of components having greater possibilities for exhibiting regulatory behaviour than ones with behaviour patterns with fewer components.

In this section, I shall discuss examples of behavioural regulation in the components of feeding. The discussion is divided into four parts: the first consisting of a general discussion of several kinds of experiments commonly used in the investigation of these regulatory processes; the second deals

with the regulation of locomotor pre-ingestion behaviour; the third with that of nonlocomotor pre-ingestion behaviour; and the fourth with the regulation of ingestion. The division of pre-ingestion behaviour into locomotor and nonlocomotor is somewhat arbitrary, since even when an insect is in contact with its food it usually makes some movement before beginning to ingest. In the first category, I shall discuss the regulation of movement whether clearly orientated or not, which involves considerable displacement of the whole insect. Any kinetic component of the behaviour assigned to the second category usually involves the movement of only part of the body or the displacement of the whole body only over a short distance.

2.1 GENERAL COMMENTS ON THE DESIGN AND INTERPRETATION OF EXPERIMENTS

Investigations into the regulation of the components of feeding behaviour and of its physiological bases have involved the use of a relatively small number of general types of experiments. Several of those which have commonly been used have a number of inherent problems relating to the interpretation of the results.

Investigations of the effect of feeding and deprivation on components of feeding behaviour have involved either a comparison of the behaviour of deprived insects with that of insects immediately after feeding, or the monitoring of behaviour during a period of deprivation, or both. Difficulties in interpretation occur when the only evidence for behavioural changes has been obtained from experiments in which behaviour has been monitored throughout a period of deprivation. The problems arise because insects increase in age during the period of the study and may, therefore, change their physiological characteristics in ways which are unrelated to deprivation. It is important, therefore, that experimental designs should be such that the effects of deprivation are clearly distinguishable from those of ageing. This is most easily achieved by having available for comparison recently fed insects which are otherwise strictly comparable to the ones undergoing deprivation. Another satisfactory but somewhat more complex method is to subject cohorts of insects of different ages to deprivation. If then the behaviour of the cohorts is similar, it can fairly be stated that the behavioural changes are due to effects of deprivation.

Investigations into the physiological mechanisms underlying behavioural changes with feeding and deprivation are usually concerned with determining which of the many internal factors, that vary according to the state of deprivation, might play a role in bringing about the behavioural differences. The experiments performed fall into two basic categories. The first is that in which the aim is to obtain, and to determine the behavioural character-

istics of, insects which are in a satiated condition with respect to one parameter, but deprived with respect to all others, or vice versa. This may be achieved either by altering artificially one parameter while keeping others constant (e.g. by injection), or by preventing one parameter from changing during a period of deprivation, or following ingestion. Two kinds of clear-cut results have been obtained from experiments in this general category, it having been found that the insect displays behavioural characteristics which accord either with the state of the one parameter being manipulated or of the remaining parameters. Results of the first type are usually taken as evidence that the factor under investigation is involved in the particular facet of behavioural regulation being studied, and those of the second as evidence for its noninvolvement. The first of these conclusions is soundly based and it remains only to caution against believing that the factor under examination is necessarily the only one involved. Conclusions of the second kind concerning noninvolvement require rather more comment in that the strict interpretation of the negative result is only that this factor in question is not *alone* responsible for the behavioural regulation. It is possible, at least in theory, that the regulatory system might be such that no single factor has any detectable effect on behaviour, when caused to vary independently of other factors with which it normally changes in concert. If this were so, the successive manipulation of single parameters would not reveal the controlling mechanism.

In the second type of experiment commonly used, nerves suspected of carrying input from receptors monitoring various parameters, which change according to the state of deprivation of the insect, are sectioned. Implicit in the design of these experiments is the often unstated belief that the inputs are maximal when the insect is fully fed, and that these are inhibitory to the performance of the component of feeding behaviour being investigated. Again, two types of fairly clear-cut results have been obtained. In some instances it has been found that the particular operation has no detectable effect on behaviour, whereas in others the operation results in the insect behaving, in some respects at least, as if deprived even though it is fully fed, with the result that its ability to regulate its feeding is diminished. The lack of effect of an operation is usually interpreted as meaning that input normally travelling via the nerve which was sectioned plays no important part in the regulation of the behaviour being investigated. There is, of course, the additional possibility that input via this nerve is only one of several sources of inhibition and that no significant loss of control occurs when the central nervous system (CNS) is deprived of any one of them. The finding that nerve section does cause a fed insect to behave as if deprived certainly indicates that input via that nerve is involved in, and indeed is essential for, the regulation of the particular component of

behaviour under investigation. The possibility cannot be excluded, however, that other inputs might play a part but that they are able to express their effect only if the input normally carried via the sectioned nerve is reaching the CNS. In these circumstances loss of control might result from the sectioning of any one of a number of nerves.

Recognition of the limitations of the kinds of experiments frequently performed necessitates re-examination, and in some instances re-interpretation, of some of the results which have been obtained.

2.2 REGULATION OF LOCOMOTOR PRE-INGESTION BEHAVIOUR

It is well known that the locomotor behaviour of a number of insects changes according to their state of deprivation in ways which enhance the deprived insect's chances of making contact with food. Changes have been demonstrated in the general level of "spontaneous" apparently randomly directed locomotor activity, in behaviour involving usually orientated movement in response to stimuli provided by the food itself, and in orientated behavioural responses to physical factors of the environment. Data relating to these three behavioural categories are discussed separately.

2.2.1 *Level of locomotor activity*

The effects of feeding and deprivation on apparently random locomotor activity have now been examined in a number of species, and it has generally been found that deprived insects are more active than fed ones. It should be realized, however, that, under almost any set of conditions, the level of locomotor activity displayed by an insect has two components, spontaneous activity and reactivity (or responsiveness) to features of its environment, and that the importance of each will vary according to the type of experimental situation. Findings discussed in sections 2.2.2 and 2.2.3 show that the readiness of insects to make orientated movements in response to various kinds of stimulation changes according to the state of deprivation; and it seems certain therefore that the reactivity of insects to stimulation which results in their engaging in nonorientated movement would also change. It is probable, therefore, that changes in observed activity with feeding and deprivation would usually be reflecting changes in both spontaneous activity and reactivity. It would, however, seem unwise to assume *a priori* that the physiological mechanism controlling each would be identical, particularly in view of the finding by Connolly (1967) that there was no correlation between the two parameters in three strains of *Drosophila melanogaster* selected for differences in spontaneous activity and in reactivity to inanimate features of the environment. For this reason, reference is made whenever possible to the probable roles played by the

two components of the activity in the particular experimental situations in which the measurements were made.

The effects of feeding and deprivation on the locomotor activity of the blowfly *Phormia regina* were extensively studied by Barton Browne and Evans (1960), and by Green (1964a, 1964b) and attempts were made to elucidate the underlying physiological mechanisms. The results of Green are the more readily interpretable in terms of spontaneous activity in that he scored the activity of single flies in a rocking actograph. Under these conditions, there was no stimulation from other individuals and it is likely that the level of effective stimulation from the inanimate environment would have been fairly low because the insects remained in the actograph chambers throughout the period of deprivation, and therefore would probably have become, to some extent, habituated to their surroundings. In addition, according to Green, the flies did not perceive the tilting action of the actograph. The experiments of Barton Browne and Evans (1961) are, superficially at least, less readily interpretable since these workers determined the rates at which groups of flies dispersed along a line of boxes, connected by funnels, in response to light stimulus. It was shown, however, that the relationship between the rate of dispersal of fed flies and that of deprived flies obtained with the light stimulus was similar to that in darkness, Barton Browne and Evans having chosen to conduct their experiments using the light stimulus rather than in darkness only because of the higher rate of dispersal obtained and the consequently lower variability. It seems therefore that the relative rates under the directed stimulus can be taken as a measure of locomotor activity. It is not certain, however, to what extent reactivity to the presence of other individuals played a role, but since both sexes were present interactions between males and females may have played some part in determining the rate of dispersal. The relationships between the amount of locomotor activity and the state of deprivation obtained by Barton Browne and Evans are generally similar to those obtained by Green and it seems valid, therefore, to discuss the two sets of results together, largely in terms of effects of feeding and deprivation on spontaneous activity.

Both Barton Browne and Evans (1960) and Green (1964a) showed that the activity of flies which had recently been fed to repletion on any of a variety of sugar solutions was very low compared with that of flies which had been deprived of food for 24 h. Barton Browne and Evans (1960) found that the ingestion of glucose, mannose or fucose reduced the activity of flies and Green (1964b) showed that the rate at which their activity increased again after feeding was inversely related to the concentration of sucrose solution consumed. Green showed, further, that feeding and deprivation affected the proportion of the time the flies engaged in

locomotor activity rather than the speed of walking, which was the main method of progression in his actograph chambers.

The attempts by Barton Browne and Evans (1960) and by Green (1964b) to elucidate the underlying mechanisms in *P. regina* were not completely successful, but their experiments eliminated, more or less satisfactorily, a number of possibilities and gave some indications as to what the underlying mechanisms might be. Barton Browne and Evans concluded that no significant regulatory role was played by an inability of the flies to move because of increased weight after feeding, by the metabolic state of the fly, by the total concentration of sugar in the haemolymph, or by the haemolymph potassium level. Green concluded, further, that no part was played by input concerning the state of distension of the abdomen, crop, or posterior portion of the crop duct, by input from the receptors of the labellar lobes which would have been stimulated during regurgitation, or by possible limitation in the amount of oxygen reaching the thoracic musculature because of the collapsed state of the abdominal air sacs after feeding.

The elimination of two of the above factors depended, however, upon evidence from experiments in which one parameter was held essentially constant at a level more or less typical of satiated flies, a type of experiment about which some general remarks were made earlier. The conclusion that the concentration of carbohydrates in the haemolymph was not involved was based on the finding by Barton Browne and Evans (1960) that flies are active despite the presence in the haemolymph of high concentrations of the non-metabolizable sugar fucose, and that of Green (1964b) concerning the noninvolvement of the state of distension of the crop or of the abdomen, was drawn from his finding that fed flies with subsequently ligated crop ducts became active within a short time. These results should be reinterpreted as showing, strictly, only that neither a high fucose concentration in the haemolymph nor the possession of a full crop *alone* causes a reduction of locomotor activity. The elimination of the other factors appears acceptable without such qualification.

Two positive results, in the sense that treatments other than actual ingestion reduced the activity of starved flies, were obtained. Barton Browne and Evans (1960) found that injection of less than 3 μ l of water or 2.0 M glucose into the haemolymph markedly reduced the activity of the flies as measured one hour later, the injection of glucose being rather more effective. On the basis of this result they suggested that changes in the composition of haemolymph due to the absorption of material from the mid-gut was an important factor in bringing about the post-feeding reduction in activity. Green (1964b) joined flies parabiotically and found that the activity of the starved "motile" fly was reduced when the fly

riding inverted on its back was fed. Green interpreted this result as indicating that hormonal material released into the haemolymph of the fed fly was responsible for the reduced activity in its parabiotic partner. The result would, however, seem to be explicable equally well in terms of changes of composition of the shared haemolymph supply.

Finally, I will make brief reference to the conclusion reached by Barton Browne and Evans (1960) that the mechanism controlling locomotor activity after a fly has ingested sugar solution is different from that controlling tarsal taste threshold to sugar (see section 2.3) after a sugar meal. They based their argument on the lack of correspondence between the curves relating threshold to crop volume and activity to crop volume in flies previously fed 2.0 M mannose or 2.0 M glucose. This comparison, although valid, is somewhat circumstantial in that the two sets of data were obtained at different times and for different purposes and perhaps more convincing evidence can be drawn from the observation that activity but not tarsal threshold is influenced by alteration of the composition of the haemolymph. The result obtained on a single fly by Green (1964b) that recurrent nerve section did not influence the activity pattern may be further evidence that the mechanisms are distinct but, as pointed out below (section 2.3), the exact effects of recurrent nerve section on tarsal taste threshold are somewhat uncertain.

It is apparent that the investigations so far have gone only part way towards elucidating the mechanism by which feeding inhibits subsequent locomotor activity in *P. regina*. The available evidence, however, is consistent with the view that the level of locomotor activity is related to changes in the composition of the haemolymph. Not only is there evidence for this from injection and parabiosis experiment, but also from the data of Green (1964b) which show that locomotor activity remains depressed only so long as sugar solution is being released from the crop, and hence is passing from the mid-gut to the haemolymph. The inverse relationship between crop emptying rate and locomotor activity in flies fed 0.5 M sucrose is quite striking. A comparison of Green's (1964a) results relating locomotor activity to the concentration of imbibed sucrose solution with those of Gelperin (1966a), who established that a dilute solution emptied from the crop more rapidly than a concentrated one, lends further support to this view. On the basis of the available evidence, one can say no more than that this hypothesis that activity is related to the composition of the haemolymph seems the most likely one, if it is assumed that one factor dominates the causal mechanism. It may yet be shown, however, that such is not the case and that the control mechanism is more complex than previously believed.

The effect of feeding and deprivation on the levels of various kinds of

locomotor activity exhibited by the adults or larvae of several species of locusts have been investigated. One study, concerning the orientated movements of larvae in response to grass odour, will be discussed in detail in section 2.2.2, but will be referred to briefly in this. The remainder, which were investigations of the effects of deprivation on several somewhat different kinds of nondirected locomotor activity, are discussed here.

Blaney and Chapman (1970) allowed single 5th instar larvae of *Locusta migratoria ad lib.* access to palatable food and found that the insects took their food in the form of discrete meals separated by considerable periods, during which no feeding occurred. Observations during this inter-meal period showed that the proportion of the time for which the insects were moving declined progressively after the completion of one meal until just before the beginning of the next. Bernays and Chapman (1974a) have provided evidence that hormonal material released from the storage lobes of the corpus cardiacum (CC) as a result of distension of the fore-gut is at least partially responsible for the reduction in activity following feeding. They demonstrated that the injection into the haemolymph of homogenates of the CC storage lobes caused a reduction in the proportion of the time for which larvae were active and, further, that a comparable reduction in locomotor activity occurred when the fore-gut was artificially distended by filling it with agar, the determination of activity in these experiments being carried out under similar conditions to those used by Blaney and Chapman (Bernays and Chapman, personal communication). It is well known that feeding in locusts causes the release of neurosecretory material from the storage lobes of the CC. Mordue (1969) demonstrated the release of material with diuretic activity and Bernays and Chapman (1972a) and Bernays and Mordue (1973) showed that material released from the CC was responsible for the closure of the apical pore of chemoreceptors on the palps. It is not certain whether the hormonal material responsible for the reduction in activity is identical with that responsible for either or both of the other known effects. It can be said, however, that the time course of changes after feeding in locomotor activity and in the proportion of chemoreceptors with closed apical pores are rather different. The lowest level of locomotor activity is reached some time after feeding (Blaney and Chapman, 1970), whereas the proportion of closed pores is at a maximum within a short time after feeding ceases. This difference cannot, however, be taken as proof that different hormones are responsible, since one effect concerns the CNS, whereas the other is probably entirely peripheral. It is reasonable to expect that central nervous responses to hormones might be less immediate than the responses of receptors.

More recent experiments by Bernays and Chapman (personal communication) indicate that yet another factor might play a part in causing the re-

duction in activity which follows feeding. They found that the activity levels of larvae of *L. migratoria* when measured 1½-2 h after the injection of a variety of solutions, which caused an increase in the osmotic pressure of the haemolymph, was generally less than that of either water-injected insects or stabbed controls.

The activity measurements made by Blaney and Chapman (1970) and Bernays and Chapman (1974a) were carried out under conditions purposely designed to reduce to a minimum the reactivity component, and therefore probably give a good indication of the levels of spontaneous activity. The only complication would appear to be the possibility that the observed activity might include orientated movement to visual and olfactory stimuli provided by the food present in the cages.

Ellis (1951) made a detailed study of the effects of food deprivation on the marching behaviour of 5th instar larvae of the African migratory locust, *Locusta migratoria*. Marching is a social form of locomotor activity engaged in by groups of locust larvae, which depends for its maintenance on interactions between individuals (Ellis and Hoyle, 1954). Any measurement of marching activity would, therefore, have in it strong elements of reactivity, even though it would undoubtedly contain some elements of spontaneous activity.

Ellis (1951) performed a number of experiments in which she determined the effects of feeding and deprivation on the percentage of the time spent marching and on the speed of marching. Because marching is a social activity requiring a build up of excitation by mutual stimulation (Ellis and Hoyle, 1954), neither fed nor deprived larvae began marching immediately after the beginning of a trial. The time taken for the insects to reach a given level of marching activity was found, however, to decrease markedly with increasing period of previous deprivation up to about 4 h. The rate at which the larvae marched increased rather more rapidly with deprivation reaching a maximum after 3 h.

Hoyle (1954) demonstrated that the potassium ion concentration in the haemolymph of fed locusts was significantly higher than in the haemolymph of ones which had been deprived of food, and showed that this reduced the resting membrane potential of the leg muscle fibres. Further, he demonstrated that fed insects jumped somewhat shorter distances than deprived ones. On the basis of these results, Ellis and Hoyle (1954) sought to explain Ellis' (1951) previous results in terms of a direct effect of the post-feeding increase in potassium concentration in the haemolymph on the response of muscles to motor output from the CNS. In an experiment designed to test this hypothesis, they showed that the proportion of time spent marching by larvae which had fed on filter paper soaked with sucrose solution and either 2.0 M or 3.0 M potassium chloride was at least as

low as that by grass-fed locusts. Others which had consumed filter paper soaked with only sugar solution began marching just as rapidly as insects which had been deprived of all food. Unfortunately, the potassium ion concentration of the haemolymph of the variously fed groups was not determined. It is not known, therefore, whether the concentrations reached after the locust had fed on these high concentrations of potassium chloride were in any way comparable with those normally reached by insects feeding on plant materials, which contain much lower concentrations of potassium. Although the guts of the larvae fed on potassium-laden filter paper were less full than that of those fed grass, their intake was apparently quite substantial and would have resulted in their consuming relatively large amounts of potassium.

Other workers have attempted to determine whether the concentration of potassium in the haemolymph plays an important role in explaining the relationships they observed between the state of deprivation of larvae of locusts and some kind of locomotor activity other than marching. Their findings, as well as those of Bernays and Chapman (1974a) which implicate hormones and of Bernays and Chapman (personal communication) which implicate haemolymph osmotic pressure in the regulation of post-feeding locomotor activity, suggest that the potassium concentration of the haemolymph may not be solely, if at all, responsible for the deprivation-dependent changes in the tendency of larvae of *L. migratoria* to march.

As argued above, the results of Blaney and Chapman (1970) and Bernays and Chapman (1974a) would relate largely to spontaneous activity and it seems reasonable to assume that spontaneous activity also plays some role in determining the percentage of time for which locust larvae engage in marching. The findings of Bernays and Chapman (1974a) that the filling of the fore-gut with agar, a procedure which could not have directly influenced the haemolymph potassium ion concentration, and the injection of CC homogenate both caused reductions in activity comparable with those following feeding on grass (Bernays and Chapman, 1974a), show that the potassium ion concentration of the haemolymph is certainly not the sole explanation of the post-feeding reduction in spontaneous locomotor activity and indicate that its role is at most a minor one. It is unlikely, therefore, that the haemolymph potassium concentration plays an important part in determining the level of any spontaneous activity component of marching.

Moorhouse (1969), in an investigation which will be discussed more fully later, showed that haemolymph potassium concentration was certainly not alone, if at all, responsible for deprivation-dependent changes in the responsiveness of larvae of *Schistocerca gregaria* to the odour of grass. The relationship of these results to the hypothesis of Ellis and Holye (1954)

that the potassium concentration of the haemolymph determines marching activity is not certain, but two features suggest that some common mechanisms might be involved in these two aspects of locomotor behaviour. The first is that both involve the reactivity or responsiveness of larvae to stimuli, in marching to stimulation from other locusts, and in upwind movement to an odour-bearing stream of moving air. The second is that the insects, during their period of unresponsiveness to either kind of stimulation, assume a characteristic post-prandial resting position. It seems reasonable, therefore, to take the results of Moorhouse as an indication that the potassium concentration of the haemolymph may not be playing a central role in determining the level of the reactivity component of marching.

On the basis of these results, it would seem that the relationship between the state of deprivation of locust larvae and the proportion of their time that they spend marching cannot be explained adequately by direct effects of the potassium ion concentration in the haemolymph on either the spontaneous activity or the reactivity component of marching behaviour. In addition, I believe that more general considerations also tend to argue against the possibility that changes in the potassium level of the haemolymph are solely responsible for the deprivation-dependent behavioural changes observed by Ellis (1951), since it seems very unlikely that an effect so nonspecific and lacking in integrative possibilities as that of potassium concentration on the response of muscle could control anything so complex as the temporal patterning of locomotor behaviour. It is likely, however, that the changes in the haemolymph potassium concentration would influence the speed of marching through its effect on jumping distance.

Chapman (1958, 1959) found that adults of the red locust, *Nomadacris septemfasciata*, which, on the evidence of their gut contents, had fed recently, were less likely to take flight than those which had not done so. In field and laboratory experiments, he examined the possibility that this relationship might be explicable in terms of changes in the haemolymph potassium concentration, and found that the potassium concentration was remarkably independent of feeding and deprivation. He concluded, therefore, that the relationship observed in the field between gut contents and the tendency to fly in *N. septemfasciata* was not explicable in terms of changes in the potassium concentration in the haemolymph.

Data are available about the relationships between food deprivation and locomotor activities in several insects other than the blowfly and locusts but generally no information is available about the physiological bases for the effects.

Bursell (1957) and Brady (1972a) have shown that the tsetse fly, *Glossina morsitans*, becomes progressively more active over a number of