PROCEEDINGS OF A SYMPOSIUM,
ATHENS,
22-26 APRIL 1963
JOINTLY ORGANIZED
BY THE
IAEA AND FAO

Radiation and
Radioisotopes
Applied to
Insects of
Agricultural
Importance

INTERNATIONAL ATOMIC ENERGY AGENCY, VIENNA, 1963
RADIATION AND RADIOISOTOPES APPLIED
TO INSECTS OF AGRICULTURAL IMPORTANCE
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OF AGRICULTURAL IMPORTANCE

PROCEEDINGS OF THE SYMPOSIUM ON THE
USE AND APPLICATION OF RADIOISOTOPES AND RADIATION
IN THE CONTROL OF PLANT AND ANIMAL INSECT PESTS
JOINTLY ORGANIZED BY THE
INTERNATIONAL ATOMIC ENERGY AGENCY
AND THE FOOD AND AGRICULTURE ORGANIZATION
OF THE UNITED NATIONS
AND HELD IN ATHENS, 22 - 26 APRIL 1963

INTERNATIONAL ATOMIC ENERGY AGENCY
VIENNA, 1963
Since the pioneer work on the application of radiisotopes to cattle, many countries have gained a considerable amount of interest in entomology and the use of these species in better food production. An obvious way of interest in the subject is the participation of 100 participants from various countries, together with the use of radiisotopes in the study of migration and life history of such subjects as animals. The emphasis is placed on the role of radiisotopes in the control of insects and the protection of livestock and crops.

The emphasis on protection and its importance in the preparation of the proceedings is acknowledged. Appreciation is expressed to the sponsoring institutions and its generous support.
FOREWORD

Since the pioneer work of the United States Department of Agriculture in the application of radiation and radioisotopes in the control of insect pests to cattle, many countries and organizations have pursued the advantages which might be gained in this field. Two years ago the IAEA organized the first international symposium in Bombay to study this problem, since when a considerable amount of basic research on the application of nuclear science in entomology and insect pest control has been undertaken. The potential gain of these studies, which would be in the form of an increased output of better food, is obvious to all Governments; hence the extensive international interest in the subject of this present Symposium, which was attended by 100 participants from 26 countries and 5 international organizations.

The proceedings consist of 37 papers presented by experts from 10 countries, together with a record of the discussions, and cover the use of radioisotopes in the study of the ecology of insects, such as their dispersal, migration and life-cycle. The application of radioisotopes to insecticides covers such subjects as labelling, application, uptake, translocation, metabolism, mode of action, and the determination of residues in plants and animals. The present position on the effects of radiation on insects is dealt with, including mutation, sterilization and the use of the sterile-male technique for the control and eradication of insect pests, and the need is emphasized for integration of chemical, biological, radiation and other methods of insect control.

The emphasis of this Symposium has been mainly on aspects of crop protection and it is hoped that the next symposium will also deal with aspects of livestock protection.

The sponsoring organizations wish to express their gratitude to the Government of Greece for its invitation to hold the Symposium in Athens, for its active assistance in the preparation and organization of the meeting, and for its generous hospitality to both participants and secretariat.

Appreciation is also due to Dr. E. Horber, of the Swiss Federal Experimental Station for Agriculture, Zürich-Oerlikon, who kindly assisted in the preparation of the Introduction to these proceedings and in the scientific editing of the discussion records.
EDITORIAL NOTE

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similar techniques, might profitably be in
Isotopes have con physiology and insecti
and fungicide studies tion of insects by in amounts of labelled re may be appreciated a
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The increase of residues is reflect were used to follow if residues in plants and concentration and the plants.

Insect metabolism of isotope techniques studies on carbamate
INTRODUCTION

The contributions of the atomic sciences to entomological research are broad and continue to amaze and attract scientists interested in agricultural, silvicultural, industrial and medical entomology. Entomological research is an appropriate showcase to demonstrate the ever-widening range of the versatility of the atom's inherent possibilities.

A great deal of atomic energy research is dedicated to basic problems concerned not so much with immediate practical benefits, but with the development of techniques or materials which may be applied subsequently. Such exploratory studies have in many cases advanced to the stage of field tests. Break-throughs in one sector have to be considered against the increasing flow of background information in most other sectors which, through accretion, solidify the foundations for more striking progress in the future. This is the accepted procedure even for the more conventional and long-established branches of science.

From the papers presented and discussed at the Symposium at Athens it is evident, however, that the different fields of entomological research have shared unequally in the benefits of atomic energy.

Insect ecology depended on tracer application to study food exchange in social insects such as bees, wasps, ants and termites. Isotopes were also used to assess insect plant relationships quantitatively or to study the distribution of insecticides in a forest ecosystem. To trace the migration of aphids, grasshoppers, thrips, the Colorado potato beetle and soil insects, or the dispersal of the adult olive fly and the Mediterranean fruit fly, these insects were tagged with radioisotopes. The behaviour and biology of cotton insects, the Spn pest and malaria-carrying mosquitoes were observed with similar techniques. Yet in this field of application atomic energy research might profitably be intensified.

Isotopes have contributed to a high degree to the fast progress in insect physiology and insecticide research. The techniques of labelled insecticide and fungicide studies have been elaborated in order to study the contamination of insects by insecticide solutions or to calibrate dosage of minute amounts of labelled residual insecticides on test surfaces. Radioautography may be appreciated as a delicate tool of high resolution power to trace the radioisotopically tagged insecticides down to the cellular level if applied properly and evaluated conscientiously.

The increased emphasis given to insecticide and fungicide toxicology and residues is reflected in the widespread use of labelled compounds. They were used to follow the fate of insecticides and fungicides to determine the residues in plants and animals, to characterize surface deposits, areas of concentration and the diffusion and degradation of systemic insecticides in plants.

Insect metabolism, as well as insecticide toxicology, has felt the impact of isotope techniques, as shown by the key role played by radiotracers in studies on carbamate insecticides, other systemic and residual insecticides,
as well as on the metabolism and utilization of sterols in the house fly, tyro-
sine metabolism in the blowfly and tegumentary pigmentation in Orthoptera.

Irradiation of insects has received wide attention in all aspects, from
the fundamentals of genetics, through the different approaches of exploratory
development to technology and successful application to limited areas or to
country-wide insect-pest eradication programmes. Radiation studies on
specific effects have been carried out on male and female germ cells in
Diptera, Hymenoptera, Coleoptera and Hemiptera in order to measure vari-
ations in response and sensitivity to radiation at different stages of oogenesis
and spermatogenesis. The principles and applications of the irradiated-male
technique were demonstrated on a wide variety of insects and other
arthropods. Among the Diptera studied are a horn fly, the Mediterranean
fruit fly, the melon fly, the Mexican fruit fly, the olive fly, the oriental
fruit fly, several species of mosquito, the screw-worm and the stable fly.
In Coleoptera, data are now available on the boll weevil, the Colorado potato
beetle, the cowpea weevil, the grain-borer, the Mexican bean beetle, the
rice weevil, the rust-red flour beetle, the tomato lady beetle and a white
grub. Among the Lepidoptera were considered the European corn-borer,
the gypsy moth, the pink bollworm and among other arthropods the Lone
Star tick and a scorpion. Great efforts are directed towards the control of
the olive fly. Mass-rearing techniques need to be elaborated before it will
be possible to release sufficient numbers of irradiated males.

Insect pests of stored commodities are a very important problem,
especially in sub-tropical and tropical countries; this was reflected in the
number of contributions in that area of research. Putting into practice the
irradiation of foodstuffs, e.g. the irradiation of grain to render it insect-
free, depends not only on acquiring the necessary basic radiobiological
knowledge and on advances in irradiation technology, but also on health
and safety considerations.

The harrowing question of whether arthropods are able to build up re-
stance to radiation as they do to insecticides remains to be answered.

An attempt has been made by the sponsoring organizations to assemble
representative experts at regular intervals to review progress in the field.
The papers selected for the Athens Symposium varied greatly in scope, ap-
proach and level of contribution, but this too is representative of the stages
reached in the various aspects of such research.

It has been our aim to reduce the time-lag between the meeting and the
publishing of the Proceedings to a minimum. Only then can the Proceedings
be a valid tool of communication enhancing or catalysing progress instead
of being relegated to a cemetery for forgotten facts or obsolete ideas. The
Symposium reported here should be regarded as a milestone marking a
successful research period and stating out the directions in which more
effort has to be concentrated before measurable progress can be expected.
It can then be assumed that the Athens Symposium of 1963 is serving its
purpose as fully as the previous one held in Bombay in 1960*.

In the house fly, tyrothricin-resistant strains have been developed. Radiation studies on male and female germ cells in different stages of oogenesis and meiosis of the irradiated male and female insects and other house flies, the Mediterranean fruit fly, the olive fly, the oriental fruit fly, and the stable fly. The Colorado potato beetle, the Mexican bean beetle, the lady beetle, and the white and European corn-borer, have been used as basic radiobiological studies, but also on health problems are able to build up research to be answered. Organizations to assemble new progress in the field, extended greatly in scope, are representative of the stages between the meeting and the using the Proceedings analyzing progress instead of or obsolete ideas. The milestone marking directions in which more progress can be expected. The ion of 1963 is serving its role in 1960.

Insect Ecology: Tracer Applications
Some uses of radionuclides

Early work (Au-198-labelling) on bees from a colony. After impedance of the bee was done to study exchange of food within small hives, between individuals. Similar trophalactic studies by Au-198 was likewise the basis of one of the early studies was the study of different species (Formica) and itself was labelled, revealed a way to explore the same route and to experiment abnormal radioactivity. This discovery would seem to fall-out, natural radioactivity rates in ants and bees.

An attempt was made to assess an autoradiogram of Au-198 in the body of the bee.

Quelques emplois des radionucléides

Les premiers travaux concernant des colonies ont été étudiés par l'INRA. Certaines estimations sont de l'ordre de 90 individus. Une analyse approfondie a été réalisée par des individus de même estime à 99 environ. En dehors de ces résultats, c'est l'employ de radionucléides (c'est trophalactique) ont récemment été

Les implications de ces premières études de 90 m et d'espèces différentes peuvent être définies par le fait que les résultats sont en accord avec les études antérieures.
QUELQUES EMPLOIS DES RADIOÉLÉMENTS ET DES RAYONNEMENTS EN ENTOMOLOGIE

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Abstract — Résumé — Anotación — Resumen

SOME USES OF RADIOISOTOPES AND RADIATIONS IN ENTOMOLOGY. The paper revises the applications of radiocounter in entomology that have been developed at our two centres during the last few years.

Early work (Ant³⁸ superlabelling) related to the bee and more particularly to the radioactivity of workers were from a colony. After investigations on the individual dose received in tagging of this kind, the radioactivity of the bee was determined, the lethal dose being estimated at about 90 µr. Ant³³ was also used to study exchange of food within a bee hive. On the other hand, Ec³¹ was used for studies of exchange of food in small hives, between individuals of different functions (male, workers and queens) or different colonies. Similar trophallactic studies have recently been performed on wasps.

Ant³³ was likewise the basic radiocounter used in work on ant's nests. The most interesting finding from one of the early studies was that exchange of food takes place between ants more than 50 m apart and belonging to different species (Formica rufa and Formica polyctena). A later study, in which an ant was not the nest itself was labelled, revealed a division of responsibility within the nest: the tagged ants were found invariably to explore the same run and to have little contact with other individuals of the same colony. In the same experiment, abnormal radioactivity was noted in the ants before labelling, due in particular to (Tr³³ + Nb³¹). This discovery would seem to point to accumulation of radioactive fall-out in ants' nests. At a period of low fall-out, natural radioactivity attributed to K³⁹ was observed and was used for purposes of potassium determination in ants and bees.

An attempt was made to label acidophilus with Bi³¹ and the findings are described in the paper.

Lastly, an autoradiographic study has been made of the distribution of certain radiocounters (Ps¹³¹ and Ge³¹) in the body of the bee.

QUELQUES EMPLOIS DES RADIOÉLÉMENTS ET DES RAYONNEMENTS EN ENTOMOLOGIE. Le mémoire passe en revue les applications des radiocences en entomologie qui ont été mises au point au CEN et à l'INRA durant ces dernières années.

Les premiers travaux concernaient l'abeille, plus particulièrement la dispersion des butineuses en provenance d'une colonie. L'étude a été réalisée par des marquages à Ant³³. Suite à ces considérations sur la dose reçue par l'individu de sels marquées, la radioactivité de l'abeille a été déterminée et la dose établie à 90 µr environ. Ant³³ a également servi à étudier les échanges de nourriture entre l'intérieur d'une ruche. Par contre, c'est Nb³¹ qui fut utilisé pour des études d'échanges de nourriture à l'intérieur de ruches entre individus de fonctions différentes (mâles, ouvrières, reines) ou de colonies différentes. Des études analogues de trophallaxies ont été faîtes sur ces groupes.

Ant³³ a été également le radiocounter de base de travail sur les fourmières. Le résultat le plus fréquent d'une première étude a été découvrir d'échanges de nourriture entre fourmières différentes de plus de 50 m et d'espèces différentes (Formica rufa et Formica polyctena). Dans une deuxième étude, par marquage d'un chemin de fourmis et aux de la fourmière elle-même, on a mis en évidence une division des responsabilités à l'intérieur de la fourmière, les fourmis marquées prospectant toujours qui même chemin et n'ayant que peu d'échanges avec les autres individus de la même colonie. Dans cette même expérimentation, on a constaté avant tout marquage une radioactivité anormale des fourmis, due notamment à K³⁹ (Tr³³ + Nb³¹). Cette découverte aurait tendance à montrer un amasage des émissions radioactives dans les fourmières. En période
de faibles activités, une radioactivité naturelle attribuée au 40K avait été constatée et avait servi à faire un dosage du potassium dans les fourmis et dans les abeilles.

Un examen de marquage d’acétates à 14C a été fait et les résultats obtenus sont décrits dans la mémoire.

Enfin, une étude de la répartition de certains radioéléments (18F, 32P) dans le corps de l’abeille au moyen de la méthode autoradiographique a été effectuée.

**Exemples des applications de radioéléments et de radiations en entomologie.**

On peut ouvrir des méthodes de radiobiochimie à l’abeille et à d’autres espèces de fourmis.

**La première observation** au laboratoire, c’est la répartition de certains radioéléments dans le corps de l’abeille.

**La deuxième observation** est la répartition de certains radioéléments dans le corps de l’abeille.

**La troisième observation** est la répartition de certains radioéléments dans le corps de l’abeille.

**La quatrième observation** est la répartition de certains radioéléments dans le corps de l’abeille.

**La cinquième observation** est la répartition de certains radioéléments dans le corps de l’abeille.

**La sixième observation** est la répartition de certains radioéléments dans le corps de l’abeille.
Le présent article passe en revue les applications des radioéléments dans l'écologie et la biologie des insectes, développées dans nos deux centres ou avec leur collaboration, durant ces dernières années.

1. ÉTUDE SUR LES ABEILLES

1. Étude du secteur de butinage [1, 2, 3]

La première étude réalisée a été celle du rayon d'action et de la dispersion des abeilles butineuses en provenance d'une ruche. Cette étude, commencée dès 1958, a été effectuée grâce à un marquage total de l'ensemble de la population de la colonie, soit environ 40 000 individus. Différentes considérations de caractéristiques radioactives, de nocivité et de facilité d'assimilation nous ont fait choisir comme tracqueur, incorporé à la nourriture, le $^{198}$Au (période: 2,7 j), émetteur entre autre d'un gamma de 0,411 MeV.

L'activité d'environ 1 µc par individu a été choisie en fonction de la période biologique de $^{198}$Au (2 à 3 j) et des hétérogénéités de marquage d'une abeille à l'autre. Ainsi une quarantaine de millicuries de $^{198}$Au, permet-il de faire le marquage d'une colonie entière dont chaque individu peut être repéré pendant 4 à 5 jours après début du marquage.

Les échanges de nourriture entre insectes aident, au bout d'un temps variable, mais toujours inférieur à 48 h, la quasi totalité des abeilles possède une activité suffisante pour permettre la détection dans la nature. Dans le secteur de butinage, la détection s'effectue à l'aide d'un détecteur portatif à scintillation (cristal NaI(Tl) 1$/10^3$), chaque insecte étant préalablement agréé à l'aide d'un filet à papillon à mailles fines. Ce procédé permet l'examen d'insectes posés dans des endroits inaccessibles à la seule détectrice, branchés hautes des arbres par exemple, et donne loisir d'examiner attentivement les cas douteux.

Le terrain expérimental toujours le même comportait un rucher de trente colonies parmi lesquelles était choisie celle marquée, huit autres ruches se trouvant dans un rayon d'environ 1 km.

En 1958, 17 butineuses marquées furent retrouvées sur 1027 examinées; en 1960, le pourcentage fut de 81 butineuses marquées sur 2442 ouvrières attrapées. On constate que dans les conditions de l'expérience, aucune butineuse ne dépasse sensiblement 1 km de distance, le gros de la troupe se trouvant à l'intérieur d'un cercle de 600 m de diamètre (figure 1 et tableau I). D'autre part, l'hétérogénéité de la distribution dans l'espace des butineuses marquées est très frappante. Ainsi, nous avons pu trouver un champ de crêpes où la proportion d'abeilles marquées était de 33%. Un certain nombre de facteurs conditionnant le choix des secteurs de butinage a pu ainsi être mis en évidence tel que l'effet répulsif du relief et celui des grandes étendues stériles.

En 1959, un marquage similaire fut tenté, mais avec des conditions météorologiques mauvaises, abondantes chutes de pluie et température assez basse. Malgré une forte miellée de robiniers et bien que le sirop de sucre ait été absorbé plus rapidement que dans les autres cas, les pourcentages de butineuses marquées furent loin d'être aussi importants et ne
dépassèrent pas 70%, l'activité individuelle étant d'ailleurs plus faible. Une seule abeille active put être retrouvée sur le secteur de butinage.

2. Résistance au rayonnement gamma de l'abeille ouvrière [4]

Lors de tels marquages, nous nous sommes inquiétés de connaître les doses reçues par abeille et l'influence que pourraient avoir de telles doses sur le comportement des individus. Un calcul approximatif, considérant que l'émission β de 1 MeV de $^{198}$Au est dissipé dans un individu, montre que la dose maximum reçue par une abeille marquée par 1 µc de $^{198}$Au est de 800 r.

Nous avons donc soumis des ouvrières à $^{1}$ action croissante du rayonnement du $^{60}$Co (450 c de $^{60}$Co fournissant une dose d'environ 100 000 r/h sur un volume de 500 cm$^3$).

Les abeilles ainsi irradiées furent comparées à deux cages de témoins. Aucun effet décelable n'apparait en-dessous de 18 000 r, au moins

* Les chiffres renvoient au tableau 1.
d'ailleurs plus faible. Une étude du secteur de butinage.

Le ouvrage [4]

Les enquêtes de connaître pouvaient avoir de telles calculs approximatifs, cons-
dissipé dans un individu, marqué par 1 µC de 14C

En croissance du rayonmen-
e l'environ 100 000 r/h sur

bes à deux cages de tâ-
e de 18 000 r, au moins

---

**TABLEAU 1**

<table>
<thead>
<tr>
<th>Prélèvements</th>
<th>Plantes visitées</th>
<th>Abeilles capturées</th>
<th>Abeilles marquées</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Clée (Cistus albidus)</td>
<td>125</td>
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<tr>
<td>2</td>
<td>Crepis sp.</td>
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<tr>
<td>2'</td>
<td>Mélilot (Melilot officinalis)</td>
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</tr>
<tr>
<td>3</td>
<td>Sainfoin (Avena sativa)</td>
<td>212</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>Clée * Thym (Thymus sp.)</td>
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<td></td>
</tr>
<tr>
<td>4</td>
<td>Moutarde (Sinapis arvensis)</td>
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<td>Clée</td>
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<tr>
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<tr>
<td>24</td>
<td>Sainfoin</td>
<td>111</td>
<td>0</td>
</tr>
</tbody>
</table>

*Voir figure 1.*
au cours des huit premiers jours, soit à des doses bien supérieures à celles reçues lors d’expériences par tracés radioactifs. Entre 18 000 et 70 000 r, les dommages subis semblent dépendre des conditions physiologiques des individus, les abeilles les plus âgées semblant plus sensibles au rayonnement.

La dose létale (mort de la moitié des individus) semble être atteinte vers 90 000 r, 200 000 r étant la première dose qui entraîne la mort immédiate de tous les insectes.

3. Échange de nourriture à l’intérieur d’une ruche [5, 6]

A l’intérieur d’une ruche expérimentale d’observation formée d’un cadre unique et ayant des parois transparentes, une certaine quantité de 32P a été fournie à cinq à huit butineuses. La paroi de cette ruche étant munie d’un quadrillage de repère, une prospection a été continuellement faite après le nourrissage. L’examen a été fait à l’aide d’un détecteur à scintillation, sans collimateur, l’expérience ayant montré que la mesure était peu affectée par le rayonnement des zones voisines.

Contrairement à ce qu’on aurait pu attendre, les échanges de nourriture ne se font pas à partir du nourrisseur vers le centre de la grappe d’abeilles, mais il apparaît de manière certaine que les ouvrières, après avoir rempli leur jabot de miel radioactif, se dirigent rapidement vers le centre de la grappe, point privilégié à partir duquel s’effectue par la suite la pré\-\-que totalité des échanges et la diffusion de la nourriture à travers l’ensemble de la population. Ce point correspond au centre thermique de la ruche où pendant la période d’hivernage se tient généralement la reine. Il fut également constaté que, contrairement à ce qu’on obtenait en période active en été, le nombre d’individus ayant ingurgité de la nourriture active était faible, soit 15 à 20% des individus. Il est vrai que la radioactivité avait été initialement fournie à un nombre très restreint d’ouvrières.

Sur ces bases, Milé SALLERON [6] a étudié les échanges de nourriture entre individus de castes (reines, butineuses, mâles, etc.) ou de colonies différentes. Le travail a été effectué en ruchettes expérimentales, adossées l’une à l’autre et munies de trous permettant l’échange de nourriture sans autoriser le passage d’un insecte d’une ruchette à l’autre. Dans ce cas, les abeilles n’ayant pas accès à l’extérieur, le tracer employé fut le 32P, émetteur β pur, sous forme de phosphate monosodique. Il fut incorporé à une nourriture solide à base de miel et de sucre préférrable pour l’entretien des abeilles élevées en cages. Les comptages furent effectués soit sur des insectes morts soit sur des insectes vivants à l’aide d’un compteur G-M cloche de 1,5 mg/cm² de paroi. Trois questions furent étudiées à l’aide de cette technique:

1° Échange entre ouvrières

De par les études faites, il n’est pas apparu évident, contrairement à l’opinion déjà émise, que des ouvrières préfèrent échanger de la nourriture avec des ouvrières de la même colonie plutôt qu’avec des étrangères en provenance de ruche différente. Si cette tendance existe, elle est faible. Il semble que les échanges s’effectuent plus volontiers avec les abeilles soeurs pendant les deux premiers jours, soit avec des âgées, mais aussi avec des étrangères à partir de la troisième semaine. La chose est probablement due à la vie d’une ruche qui consiste à échanger des abeilles plus âgées et plus sensibles au rayonnement.

2° Échange entre castes

Ce travail a mis en évidence l’importance des échanges entre castes. De plus, ces échanges ont été faits entre les ouvrières, les mâles, et les reines. Les mâles, bien que plus âgés que les ouvrières, ont été moins sensibles au rayonnement. Les reines, quant à elles, ont été les plus sensibles.

3° Échange entre colonies

L’existence d’un échange entre colonies a été constatée. Les abeilles de la colonie expérimentale ont été nourries avec du 32P et ont été étudiées par rapport à la colonie de contrôle. Les résultats ont montré que les abeilles de la colonie expérimentale avaient ingurgité une quantité de 32P comparable à celle des abeilles de la colonie de contrôle.

4. Répartitions de ce rayonnement

Par la méthode des colonies d’hivernage, les abeilles de la grappe d’hivernage ont été nourries avec du 32P. Les comptages ont été effectués sur des insectes morts et vivants. Les résultats ont montré que la radioactivité s’étendait à travers l’ensemble de la population.

II. ÉTUDE SUR LES ÉCHANGES

Les résultats obtenus ont été utilisés pour étudier les échanges entre colonies. Les abeilles d’une colonie expérimentale ont été nourries avec du 32P et les échanges avec les abeilles d’une colonie de contrôle ont été suivis. Les résultats ont montré que les abeilles de la colonie expérimentale avaient ingurgité une quantité de 32P comparable à celle des abeilles de la colonie de contrôle. Les échanges ont été effectués entre les deux colonies de manière régulière et constant. Les abeilles de la colonie expérimentale ont ingurgité une quantité de 32P comparable à celle des abeilles de la colonie de contrôle. Les échanges ont été effectués entre les deux colonies de manière régulière et constant.
QUELQUES EMPLOIS EN ENTOMOLOGIE

sœurs pendant les deux premiers jours, pour s'inverser ensuite et se faire plutôt avec les étrangers. Peut-être les nourrices moins généreuses avec elles au début les ont-elles obligées à demander davantage?

2° Echange entre mâles et ouvrières

Ce travail a montré sans ambiguïté que les mâles sont capables dans une certaine mesure de se nourrir seuls mais qu'en présence d'ouvrières, ils préfèrent se faire nourrir par ces dernières. D'autre part, il y a transfert de radioactivité des mâles vers les ouvrières, ce transfert pouvant être dû dans certains cas à l'absorption par les ouvrières des régurgitations des mâles déposées sur le substrat, dans d'autres cas à un échange direct de nourriture, échange qui a d'ailleurs pu être directement observé.

3° Echange entre reines et ouvrières

L'existence d'un transfert de radioactivité des reines aux ouvrières paraît maintenant une chose certaine. D'autre part, ces échanges ne sont le fait que d'un très petit nombre d'abeilles spécialisées même au sein de colonies expérimentales restreintes composées d'une vingtaine d'ouvrières.

4. Répartitions de certains radioéléments dans le corps de l'abeille.

Par la méthode autoradiographique, on s'est proposé de localiser les radioéléments dans le corps de l'abeille. Un certain temps après ingurgitation du traceur, les abeilles sont placées à -35° et incluses dans une solution de gelose. L'insecte est ensuite coupé en totalité au moyen d'une scie circulaire très fine; sur la coupe ainsi obtenue on place le film dont l'exposition a lieu à -35°.

Cette technique a été utilisée pour le 32P sous forme de phosphate monosodique et pour le 35S sous forme de 35SO₄²⁻, introduits tous deux dans de la nourriture solide.

Le rayonnement trop énergique du 32P ne permet pas l'obtention de bons clichés comme par exemple celui de la figure 2 qui montre la localisation du 35S.

II. ÉTUDE SUR LES FOURMIS

Les résultats obtenus à l'aide des radioéléments dans l'étude des abeilles nous ont incités à l'utiliser pour d'autres insectes sociaux et notamment pour les fourmis.

1. Transmission d'isotopes radioactifs entre deux fourmilières d'espèces différentes [7].

Chauvin étudiant depuis six ans de nombreuses fourmilières d'un certain bois, le terrain nous apparut propice à l'étude de la transmission de nourriture entre fourmilière à l'aide de traceurs radioactifs.
Une grosse fourmi en versant sur elle 50 mg épaisse. Si l'on considère indulgents si l'activité initiale vers une activité de 0, par le moins sensible du portatif à scintillation fixe, muni d'un cristal.

Le lendemain matin les différentes pistes par variables, l'activité des grande que celle des extérieur, le temps mais restent particulière radioactivité de l'activité totale.

Le résultat le plus couvert d'une certaine mine, Formica rufa, situa. Nous avons pu en traversant les pistes de ensuite la population de pas la possibilité pour se faire housspiller d'un polycetna par les rufa qu'leurs colonies des matières attaquées dans la nat cordent à admettre que taquerait rufa. Peut-être tétraux de construction nous sommes dans l'un nous considérons pour aussi que les rufa fréquentent les mêmes pucerons, jusqu'ici, mettre e pins de polycetna et nou nous pensons donc qu'il tiles radioactives au les ouvrières de rufa, nourriture entre des milientes voisines.

2. Echanges de nourr

Durant l'été dernier la nourriture non plus a nage à environ 50 m du Les comptages c: jours montré une très lèvements effectués si...
Une grosse fourmilierre de *Formica polyctena* fut marquée, un soir, en versant sur elle 50 mc de $^{18}$Au mélangées à 50 cm$^3$ d'une solution sucrée épaisse. Si l'on considère cette colonie comme peuplée d'un million d'individus et si l'activité initiale se répartit entre toutes les fourmis, nous arrivons à une activité de 0,05 μc par insecte très largement décelable même par le moins sensible des détecteurs dont nous disposions: un détecteur portatif à scintillation et un ensemble de comptage à scintillation à poste fixe, muni d'un cristal creux 1"3/4 × 2".

Le lendemain matin, le comptage de prélèvements de fourmis sur les différentes pistes partant de la fourmilierre marquée donnent des résultats variables, l'activité des individus du milieu des pistes étant toujours plus grande que celle des extrémités. Ces inégalités s'atténuent d'ailleurs avec le temps mais restent cependant notables. On constate sur une fourmi particulièrement radioactive que l'activité est interne, l'abdomen portant 88,9% de l'activité totale.

Le résultat le plus intéressant obtenu lors de ces essais a été la découverte d'une certaine activité dans trois fourmilières d'une espèce voisine, *Formica rufa*, situées à une dizaine de mètres du nid des polyctena. Nous avons pu exclure l'hypothèse que les *rufa* se contaminent en traversant les pistes de *polyctena* car ces pistes elles-mêmes sont inactives, ensuite la population de *polyctena* qui s'y déplace est si dense qu'on ne voit pas la possibilité pour une fourmi d'une autre espèce de la traverser sans se faire housser de l'importance. Reste alors des attaques possibles des *polyctena* par les *rufa* qui pourraient les dévorer et emporterait ainsi dans leurs colonies des matières radioactives. Mais nous n'avons pu constater ces attaques dans la nature et d'autre part, les auteurs généralement s'accordent à admettre que c'est *polyctena*, l'espèce la plus agressive, qui attaquerait *rufa*. Peut-être aussi les *rufa* pourraient-elles emporter des matériaux de construction souillés des excréments radioactifs de *polyctena*; nous sommes dans l'incapacité d'influer cette dernière hypothèse que nous considérons pourtant comme assez improbable. On pourrait penser aussi que les *rufa* fréquenteraient les mêmes pins que *polyctena* et chercherait les mêmes pucerons pour en obtenir du miel, mais nous n'avons pu, jusqu'ici, mettre en évidence des pistes de *rufa* se dirigeant vers les pins de *polyctena* et nous n'avons jamais vu de *rufa* sur le tronc de ces pins; nous pensions donc qu'il faut rejeter l'hypothèse d'une régurgitation de matières radioactives auprès des pucerons qui seraient ensuite absorbées par les ouvrières de *rufa*. Il semble donc assez probable qu'il y ait échange de nourriture entre des fourmis d'espèce différente appartenant à des fourmilières voisines.

2. Échanges de nourritures entre individus de la même fourmilierre [8]

Durant l'été dernier, un nouveau marquage a été réalisé en plaçant la nourriture non plus sur la fourmilierre, mais au milieu d'une piste de butinage à environ 50 m du nid.

Les comptages effectués sur des prélèvements de 50 fourmis ont toujours montré une très nette supériorité du taux de comptage pour les prélèvements effectués sur la piste initialement marquée (voir fig. 3) et les
Les prélèvements bruit de fond (ensu G–M à circulation 
La radioactivité à une teneur d’environ 
Une étude au dans l’abeille préal.

4. Les fourmis

Cependant le statos avant tout liberté et ambiance ceci sur toutes les dans les fourmis e une fourmilière dé ce phénomène.

Un prélèvement d’un spectromètre trois pics :
- un pic à 780 keV ;
- un pic aux alentours ;
- un léger pic ver.

Échanges de nourriture restent très faibles entre ouvrières travaillant sur des pièces différentes. On observe cependant une augmentation générale des taux de comptage d’un jour à l’autre et la transmission de nourriture est lente, mais certaine, et intéresser l’ensemble de la population de la fourmilière.

Il semble donc possible de supposer l’existence à l’intérieur de la fourmilière de groupes de travail ayant relativement peu de contact pendant les périodes de butinages. Le fait que cette couverture soit moins forte entre les chemins voisins peut tenir au fait que les groupes de travail butinant dans des secteurs voisins occupent dans la fourmilière un emplacement généralement voisin, soit être due à ce qu’un certain nombre de butineuses peuvent changer de lieu de travail en le faisant toutefois dans des limites relativement étroites.

3. Teneur en potassium des fourmis et des abeilles

Lors des expériences précédemment décrites, nous avons constaté que le bruit de fond relevé au scintillomètre portatif sur les fourmilières était légèrement supérieur de l’ordre de 1 chop/s au bruit de fond ambiant.
Des prélèvements effectués ont été analysés et comptés au détecteur à bas bruit de fond (ensemble Philips à couronne d'anticoincidence, détecteur G-M à circulation de bruit de fond 0,8 cpm environ).

La radioactivité trouvée a été attribuée au $^{40}$K. Elle correspondrait à une teneur d'environ 1% en poids de potassium dans la fourmi.

Une étude analogue chez l'abeille conduit à une teneur de 1,5% en poids dans l'abeille préalablement desséchée.

4. Les fourmis indicateurs possibles de retombées radioactives [9].

Cependant lors d'une dernière expérience, fin juillet 1962, nous constatons que tout marquage une différence de bruit de fond entre fourmilibre et ambiance de 25 choix/s très visible avec le détecteur portatif et ceci sur toutes les fourmilikres sans exception. La radioactivité se trouve dans les fourmis et non dans les matériaux constitutifs de la colonie, car une fourmilibre désertée depuis un mois est la seule à ne pas présenter ce phénomène.

Un prélèvement de 880 g de fourmis est suivi d'un examen à l'aide d'un spectromètre gamma 80 canaux. Le spectre obtenu (fig. 4) présente trois pics:
- un pic à 780 keV ± 20 keV attribuable à la filiation $^{95}$Zr ($^{90}$Zr) (période: 85 j);
- un pic aux alentours de 140 keV attribuable au $^{144}$Ce (période: 33 j);
- un léger pic vers 500 keV attribuable au $^{109}$Ru (période: 40 j).

Figure 4
Spectre d'un prélèvement de fourmis en juillet 1962.
880 g de fourmis. Stockage 15 min. Bruit de fond déduit.
Une évaluation de l'activité due au $^{90}(\text{Zr} + \text{Nb})$ donnait $3.5 \times 10^{-9}$ c/kg de fourmis.

Le mécanisme par lequel les fourmis fixent les retombées parait en liaison directe avec leur habitude de prélever les excréments sucrés des pucerons des arbres, ou miellat. Les multiples gouttelettes gluantes ainsi exposées à l'air doivent capter une très grande quantité de poussières atmosphériques et, par conséquent, celle des retombées. D'ailleurs, les gouttelettes de miellat qui tombent sur les feuilles sont recollées aussi par les abeilles, et l'on sait depuis longtemps que le miellat d'abeilles est bien plus riche en poussières que les miels floraux (où les nectaires sont bien abrités en général, ou même au fond de cavités étroites). Il est possible aussi et même probable que la résine des conifères fixe aussi ces poussières, et que les fourmis en entraînent quelque peu au cours de leurs innombrables marches et contremarches, sur les troncs. D'autre part, le fait que les fourmillières abandonnées ne montrent pas d'activité supérieure au bruit de fond, même quand l'abandon est très récent (c'était le cas dans notre premier prélèvement) prouve que les fourmis ne déferquent pas à l'intérieur de la fourmilière: on le pensait depuis longtemps, mais nous croyons que, pour la première fois, la démonstration en est apportée dans la nature.

Quant à l'importance des fourmis comme détecteurs des retombées, elle reste à évaluer, par rapport aux méthodes traditionnelles de comptage du bruit de fond sur échantillons de végétaux prélevés au hasard. Nous pensons qu'il serait nécessaire pour évaluer la sensibilité de la méthode par les fourmis, de suivre comparativement l'histoire d'une retombée dans la fourmilière, par comparaison avec les méthodes classiques.

III. ÉTUDES SUR LES ACRIDIENS MIGRATEURS

A la suite d'un problème posé par M. Descamps du Centre de défense des cultures, nous avons regardé la possibilité de marquage radioactif d'un grand nombre d'acridiens jusqu'à 500 000, pendant une période suffisamment longue de deux à trois mois, pour faire une étude d'un secteur de grégarisation au Niger.

Le problème posé conduisait à prendre un radioélément de période radioactive et biologique suffisante. Les essais en laboratoire ont été effectués avec de $^{137}$Cs sous forme d'une solution de chloroidrate d'ammonium dispersée sur de jeunes feuilles de blé servant de nourriture aux lots d'insectes étudiés. Chaque lot était constitué de 100 insectes d'âge différent d'un lot à l'autre (fig. 1).

Les résultats obtenus peuvent être divisés en éléments favorables et défavorables à un marquage de grande envergure.

1. Éléments favorables

Période apparente satisfaisante: La période apparente est de l'ordre de six jours indépendamment de l'âge des insectes; cependant la dispersion des résultats sont part, suivant les "nature, il se pourra pour être le pourcent ager soit encore Comportement la période étudiée Dispersion terrestres non marqués Individus non de l'activité reste Pas de dimi

* Études effectuées en collaboration avec M. Descamps, Centre de défense des cultures.
Les tombées paraissent être des moments sucrés des pluies glaires ainsi que des poussières atmosphériques. Les gouttelettes aussi par les arbres, les abattis, etc. sont bien sûr à exclure. Il est possible que ce soit aussi ces poussières qui disparaissent de leurs intérieurs en quelques jours. D'autre part, le comportement de la période supérieure à 9 jours était le cas dans les expériences précédentes, mais nous croyons que ces tombées se réalisent dans la nature. Enfin, des retombées, des showers, de comptage du 

Centre de défense nucléaire radioactif de la région. Une période suffisante pour la réalisation du témoins de l'intensité de la dispersion de période supérieure à 9 jours a été établie. Il est important que la période de l'ammonium nitrate ait été réalisée aux lots d'insectes de différentes tailles d'âge différent

des résultats semble plus élevée pour les insectes les plus jeunes. D'autre part, suivant les experts, le métabolisme étant moins important dans la nature, il se pourrait que dans un marquage dans la nature, la période apparente soit encore plus importante (fig. 6).

Comportement satisfaisant des acrildens marqués: Il n'y eut pendant la période étudiée, ni mortalité ni changement de comportement notable.
Dispersion raisonnable de l'activité absorbée: Il y eut peu de sauterelles non marquées et aucune ayant absorbé 10 fois plus que la moyenne.
Individus non contaminant en dehors des excrêments: Plus de la moitié de l'activité reste localisée dans la tête.
Pas de diminution de l'activité au passage à l'état adulte.
2. Eléments défavorables

Rendement du marquage faible: A peine 10% du traceur mis en œuvre semble avoir été absorbé par les insectes. Ceci est dû en partie à la mauvaise utilisation du traceur sur le blé. Ceci peut être, pense-t-on, fortement pallié par l'emploi de son, qui absorbe mieux le liquide traceur, comme nourriture marquée.

L'activité totale utilisée est élevée: Avec les détecteurs actuellement à notre disposition et le rendement de marquage précédent, il faudrait utiliser une trentaine de curies de $^{192}$Ir pour le marquage de 500 000 individus, ce qui semble excessif. Encore faut-il noter qu'avec une telle activité, au bout de deux mois un insecte ne serait décelable qu'au contact même de l'appareil (au lieu de 50 cm réclamés par le demandeur).

Pour ces raisons entre autres, le marquage au Niger n'a pas eu lieu.

IV. ÉTUDES SUR LES GUÊPES*

Une étude assez semblable à celle entreprise avec les abeilles et concernant les échanges trophallactiques a été effectuée sur les guêpes *Parasolidae.*

* Études effectuées en collaboration avec M. Montagner, Faculté des sciences de Nancy.
vespula vulgaris, germanica et Dolichovespula media. Une dizaine d'indi-
vividus ayant été nourris avec de l'or radioactif ont été re-introduits dans
le guêpier et nous ont servi à étudier la vitesse de transmission de la nour-
riture marquée dans le nid. Ces vitesses sont en général très grandes.

Ces études ont permis de dégager les principaux aspects des relations
interindividuelles au cours des échanges alimentaires et d'éclaircir les rap-
ports entre couvain et adultes.

1. Échanges entre ouvrières

Cette étude a été effectuée dans des cages à 3 compartiments, dont
celui du milieu contenait seul la nourriture marquée; il était séparé des
deux autres par une cloison perforée en plexiglas. Nous avons essentiel-
lement montré que les ouvrières du compartiment central apprivoisent
beaucoup mieux leurs sucrer que les étrangères. Ainsi, nous avons établi,
pour deux séries d'expériences, que les pourcentages d'activité des ouv-
rières sans nourriture, rapportée à celle des nourricières du comparti-
ment central, étaient, après 24 heures, de 45,1 et 43% pour les sucrer et de
19,4 et 22% pour les étrangères. D'autres expériences effectuées dans
le même sens ont toujours confirmé ces résultats. Mais cette discrimi-
nation nutritionnelle disparaît avec le temps et n'est plus nettement décelable
après 2 jours de vie commune.

2. Alimentation des mâles — leurs rapports avec les autres membres de la
société

Les capacités de «self-alimentation» des mâles dépendent non seulement
de leur âge, mais aussi du degré d'évolution du nid. Ainsi, les jeunes
sont parfaitement capables de bien s'alimenter tout seuls, mais les adultes
semblent refuser la prise de nourriture à une époque qui coïncide avec l'appa-
rition des fondatrices adultes ou la décroissance de l'activité sociale. Il
semble donc qu'il se produise un arrêt dans l'alimentation des mâles, au
moment des fécondations.

En outre, ils sont peu alimentés par les ouvrières. Nous avons mon-
tré que, dans le nid, ils se nourrissent essentiellement en provoquant les
régurgitations des larves. Il semble donc que dans le nid les individus
mâles vivent par parasites sur ces régurgitations larvaires, qu'ils savent ob-
tenir facilement.

3. Les relations alimentaires entre les ouvrières et le couvain

Les ouvrières nourrissent les larves en fonction de leur taille et de
l'intégrité de leurs cellules. Lorsque des larves d'ouvrières et de fondo-
trices sont élevées en compétition, ces dernières sont toujours approvi-
sionnées de façon plus abondante. Ajoutées à d'autres résultats cette con-
statation nous incline à plus en plus à penser que la quantité de nourri-
ture donnée aux larves doit jouer un rôle essentiel dans leur différenciation
en deux castes femelles.
V. ÉTUDE DE RÉPARTITION D'UN FONGICIDE

Bien que ce travail sorte du cadre imposé par le titre de cet article, nous en dirons quelques mots car il s’inscrit dans le programme de ce colloque.

Dans les plantations de bananiers, des huiles minérales sont utilisées en tant que fongicide sous forme de diffusion lente de quelques centimètres cubes en un point déterminé de la plante. L’emploi d’une huile fongicide marquée au tritium a permis d’en étudier la distribution à l’intérieur du bananier, la vitesse d’écoulement dans différents tissus, et de comparer l’efficacité de différents modes d’injection.

La simple dissolution d’un élément marqué dans une huile n’a pas été utilisée car le métabolisme de l’élément dissous peut être très différent de celui de l’huile elle-même. La solution adoptée a donc été la fixation de tritium sur les doubles liaisons du squalène pour obtenir une huile comparable aux huiles minérales.

Figure 7

Autoradiographie d’une hampe de bananier marqué au squalène traité.

* Études effectuées en collaboration avec Mme Cuillot et Laville, Institut de recherches fruitières d’Outre-Mer [10].

Après une étude proposée, une planification et date de l’injection.

Périodiquement différentes régions et racine. Cette méthode est courante et s’emploie également simultanément à forte activité spé radiographie après les résultats longtemps à l’end et les feuilles et les d’être éliminées pa

W. KLOFT: doing ourselves sin also found that ho workers. We first they were not gene tracers and fur am able to regurgitate radioactive drone drones can excrete excrement is taken quickly. By using to exclude this sou

At the sugges...
Après une étude en laboratoire démontrant la validité de la méthode proposée, une plantation de 30 bananiers, située à la Guadeloupe, a été traitée à raison de 50 mc de squalène tritié par arbre. On a fait varier les conditions d'injection (activité spécifique de l'huile, emplacement, durée et date de l'injection) et le traitement des arbres.

Périodiquement, des échantillons ont été prélevés sur les arbres dans différentes régions (limbes et nervures des feuilles, pseudotrônca, bulbe et racine). Ces échantillons ont été brûlés, l'eau de combustion récupérée et comptée par scintillation liquide. L'activité de l'eau de la terre aissiante a également été mesurée. 

Simultanément, en laboratoire, de jeunes pousses ont été marquées à forte activité spécifique (250 mc/cm²) et les diffusions étudiées par auto-radiographie après congélation des échantillons dans l'azote liquide (fig. 7).

Les résultats obtenus montrent notamment que l'huile séjournait assez longtemps à l'endroit d'injection, puis se déplaçait préférentiellement vers les feuilles et les fruits, et qu'une faible fraction traversait le bulbe avant d'être éliminée par les racines.

**Références**


**Discussion**

W. Kloft: Your paper deals with work similar to what we have been doing ourselves since 1956, and it is very interesting to hear that you have also found that honey-bee drones are able to regurgitate crop food to workers. We first published our findings on this subject in 1958, but since they were not generally accepted, we repeated the study last year, using tracers and film analysis, and we found quite definitely that the drones are able to regurgitate. One great source of error lies in the distribution of radioactive drone excrement in the honey-bee community; as you know, drones can excrete their food two hours after intake and their radioactive excrement is taken up by the workers and spread through the colony very quickly. By using a special experimental set-up, however, we were able to exclude this source of error.

At the suggestion of Mr. Lecomte, the results of the experiments we carried out last year will be submitted to the journal Annales de l'abeille with a view to publication.
J. Lecomte: I was most interested to learn that you had continued your work on this particular problem. The fact that similar phenomena have been observed in a different laboratory confirms our findings.

M. Feron: I was very interested in what the authors of this paper had to say on food exchange in social insects, and I think the same methods could also be applied to non-social insects. In the case of Diptera, the process of food exchange by frequent regurgitations is well known and the part it plays in the spread of pathogenic germs may be of importance both to man and animals and to the insects themselves. Perhaps this labelling method could provide useful information regarding such phenomena.

J. Lecomte: That is true. However, the tracer study should then be coupled with other observations such as film analysis, designed to verify the absorption of regurgitated material and to eliminate the possibility of contamination from other sources.

R. Caullendor: In investigating the mechanism by which ants fix radioactive fall-out, did you measure the radioactive spectrum of the honeydew of aphids?

J. Lecomte: No, but this has been done in Freiburg in Germany, using the honeydew taken up by bees from aphids.

R. Caullendor: What species of Acrididae did you use in your experiments?

J. Lecomte: The Locusta migratoria.

W. Kloft: We too have done field experiments on food distribution in ant colonies, especially in Formica polyctena and related species, and we obtained similar results with a spread of activity up to 200 m. However, in our field experiments on natural colonies of Formica polyctena with interspersed nests of Formica rufa, the Formica rufa did not take part in the exchange. I know this does not conflict with your own results, because we have done a lot of laboratory experiments which prove that there is good exchange between different species of the genus Formica. The explanation is to be found in the complex conditions existing in the field: relations between nests are influenced by the saturation of single nests, isolation, the distances involved, etc.

J. Lecomte: We were indeed surprised at the exchange of food between different colonies of ants, but the determination of species was carried out in your own laboratories and I do not think we can question the results.

W. Kloft: I did the sample analysis myself and the results are undoubtedly correct. Regarding your interpretation of the way in which ants have concentrated radioactive fall-out, I should like to say that I have done a lot of work on trophobiosis and have demonstrated that ants usually take food directly from the anus of aphids. Only in rare cases do they take honeydew from leaves, whereas the honey-bees have no direct relations with the aphids and always take the honeydew from leaves. I think, therefore, that in the case of predacious ant species the concentration of this fall-out may be due to the ingestion of leaf-eating insects.

J. Lecomte: To reach some definite conclusions on this point, one would have to study in the same area and at the same time not only the radioactivity of the ants and bees but also that of the aphids, caterpillars, leaves, etc. Our supposed contamination from leaves probably observed in ants.

G. T. Scailly: I fully accept the possibility that the uptake of radioactive materials is carried out in its starting in the leaves and not the bees. We have no difference between plants.

J. Lecomte: Our observations indicate that the radioactive tritium in uptake of Autobee and Radiobee stand that there is a different insect activity. Perhaps this fact is due to the difference in the resins. Our observations clearly show that resin is a plant-specific factor.

J. Halbe: I have seen that the uptake of radioactive materials is carried out in its starting in the leaves and not the bees. We have no difference between plants.
etc. Our supposition is perhaps not correct, but we felt that honeydew taken from leaves probably plays an important role. The radioactivity spectrum of the honeydew collected by the honey-bee is very similar to what we observed in ants.

G. T. SCARASCIA: Have you any experimental evidence regarding the possibility that the resin of conifers may fix radioactive fall-out? Work carried out in Italy by the Agricultural Chemistry Station (Ministry of Agriculture) and by the National Commission for Nuclear Energy has shown no difference between the fall-out radioactivity of pines and that of other plants.

J. LECOMTE: We have no experimental evidence on the role of the resins. Our observations were limited to honeydew only, in view of the fact that resin is not collected by ants or bees.

J. HALBERSTADT: I noted in the paper that there is a difference in uptake of Au¹⁹⁸ and Ir¹⁹² by bees, ants and grasshoppers. I also understand that there is a big difference in the location of these isotopes in different insects after uptake. Could you give an explanation of these differences? Perhaps it is because gold is used in the form of a colloidal solution while iridium is used as a suspension and is therefore taken up poorly.

J. LECOMTE: The form in which the radioisotope is administered will certainly have some effect on the fixation rate and the biological half-life. We did not try to find out where the gold and the iridium are localized, but it appears that gold is mainly found in the walls of the digestive tract. We were interested in gold because of its ease of use, and we obtained good results with the colloidal form without appreciable difficulty. It was not necessary for us to try to improve the rate of fixation. As regards iridium, we have so far done only preliminary experiments. We have not gone very far in this field yet, and possibly by varying the method of administration we could improve the rate of fixation and the biological half-life, but this has not been studied as yet.
TRACER EXPERIMENT

Aspects of social insects, such as changes, which can be studied at a rapid rate of exchange in the behavior of ants, which must be taken towards trophallactic exchange, especially Formica polyctena, in the preventive biological study of food exchange within one species. Another question is whether the same species, by labelling different nests in the colony, and in different years. The regulating effect on the saturation of any nest through tracer experiments that the role of the whole wood ant is discussed.

Using labelled food, which is small, capable of direct feeding or workers are most effective. Greater aggressiveness of the flavuscolets were labelled with white, while other groups were formic acid and calculating the biologic tracer remained longer. The result can be explained by individual members of the subfamily. The greater effect of "group-effect" in social insects, is special problems of this kind are dealt with.

EMPLOI DES RADIOISOTOPES DES TERMITES. Un aspect par abeilles et les termites est marqué. Des études compa qu'elles varie considérablement dans les expériences faites ici a été relevée cher les insectes nuisibles aux forêts. conditionnée par la température de savoir s'il y a également
TRACER EXPERIMENTS ON FOOD EXCHANGE IN ANTS AND TERMITES

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Abstract — Résumé — Anotacmia — Resumen

TRACER EXPERIMENTS ON FOOD EXCHANGE IN ANTS AND TERMITES. One of the most important aspects of social insects, such as ants, honey-bees and termites, is their tendency to trophallactic food exchanges, which can be studied well by the use of labelled food. In comparative studies we found the most rapid rate of exchange in honey-bees, but extreme differences were observed among the different subfamilies of ants, which must be taken into consideration in case of tractor field-experiments. The greatest tendency towards trophallactic exchanges was found in the subfamily Camponotinae. Ants of the genus Formica, especially Formica polyctena Foet., and related polygynous and monogynous species known to be important factors in the preventive biological control of forest insect pests, were intensively analysed. It was found that the rate of food exchange within one nest is conditioned by temperature, time, number of individuals and saturation. Another question is whether food exchanges also take place between the different nests of ant-colonies of the same species. By labelling single nests with radioactive food we were able to find intensive food exchanges between different nests in the colony, up to distances of 200 m. We obtained similar results in three different colonies and in different years. The existence of such long-range food exchanges is very important for the estimation of the regulating effect of insect pests of useful Formica species, since these exchanges prevent the quick saturation of any nest through local mass-inflation of insects in their feeding area. It was shown by the tractor experiments that the collected food flows in most of the surrounding nests of the ant-colony: thus colonies of these useful wood-ants act as a complex system with high ecological effectiveness.

Using labelled food, we studied in termites (Kalotermes flavicollis Fair.) which stages and castes are capable of direct feeding or are receptors of trophallactically or procedurally given trophallactic food. Pseudoworkers are more effective. We also attempted to use tracers methods to elucidate the greater longevity and greater aggressiveness of termites when in groups than as single individuals. Pseudoworkers of Kalotermes flavicollis were labelled with tritium. After feeding, some of these labelled termites were caged individually, while other groups were formed which also included unlabelled individuals. By measuring the effective half-life and calculating the biological half-life, which primarily depends on the rate of excretion, we found that the tracer remained longer in groups — when the group is viewed as one unit — than in isolated individuals. The result can be explained by the measured trophallactic exchanges of food and the repeated circulation among individual members comprising a group. Similar results were obtained with two ant-species from different subfamilies. The greater economy in the use of food and other substances may be a contributing factor to the "group-effect" in social insects.

Special problems of comparable measuring techniques for living single individuals and insect groups are dealt with.

EMPLOI DES RADIOINDICATEURS DANS L'ÉTUDE DE LA TROPHAUXÉS CHEZ LES FOURMES ET LES TERMITES. Un aspect particulièrement important de la vie des insectes sociaux comme les fourmis, les abeilles et les termites est la transmise à la trophallaxis, qu'il est facile d'étudier au moyen de nourriture marquée. Des études comparatives ont montré que la trophallaxis est la plus rapide chez les abeilles, mais qu'elle varie considérablement d'une sous-famille de fourmis à l'autre, facteur qui doit être pris en considération dans les expériences faites sur le terrain à l'aide de radioindicateurs. La plus forte tendance à la trophallaxis a été notée chez les individus de la sous-famille Camponotinae. Les auteurs ont étudié tout particulièrement les fourmis de genre Formica, en particulier la Formica polyctena Foet (fourmi rouge) et les espèces polygynes et pluriouennes apparentées, qui représentent un facteur biologique important dans la lutte contre les insectes nuisibles aux forêts. Les auteurs ont observé que la trophallaxis à l'extérieur d'une fourmilière est conditionnée par la température, l'humidité, le nombre d'individus et la saturation. Un autre problème est de savoir s'il y a également trophallaxis entre différentes fourmilières de colonies appartenant à la même
spécies. En introduisant de la nourriture marquée dans diverses fourmilières, les auteurs ont pu détecter des échanges transferts entre des fourmilières séparées par des distances allant jusqu’à 200 m. Ils ont observé des réactions semblables pour des colonies différentes, au cours de plusieurs années. Cette trophalaxie a grandement accru l’importance de l’analyse de la nourriture dans la compréhension de l’organisation de la fourmilière. Les auteurs ont observé des communications entre les colonies des mêmes espèces marquées, après le développement de la nourriture. Les colonies qui recouvrent ces paramètres constitueront un exemple de la manière dont les colonies marquées peuvent être utilisées dans des essais sur le plan écologique.

A l’aide de nourriture marquée, les auteurs ont étudié quelques formes et castes de larves (Kairomone flaviolcris Fabr.) introduites par voie bactérienne ou écrite dans la trophalaxie. Les larves les plus intéressantes ont été choisies par les auteurs eux-mêmes. Les larves sont un excellent outil d’étude, à l’aide des larves individuelles, le nombre de spécimens est plus élevé et la compétitivité plus forte dans les colonies où les larves sont isolées. Les larves marquées ont été utilisées pour étudier des caractéristiques biologiques et environnementales. Les larves ont été placées dans des cages indépendantes, dans le but d’étudier leur évolution. Les larves ont été nourries dans des cages indépendantes, dans le but d’étudier leur évolution. Les larves ont été nourries dans des cages indépendantes, dans le but d’étudier leur évolution. Les larves ont été nourries dans des cages indépendantes, dans le but d’étudier leur évolution. 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EMPIDO DE INDICADORES RADIOACTIVOS PARA ESTUDIAR LA TROFAXISMA EN LAS HORMIGAS Y LOS TERMITAS. En los insectos sociales —hormigas, abejas y termitas— se da suma importancia la tendencia a la trofaxisma, que puede manifestarse bien mediante alimentos marcados. Los autores de la memoria han podido comprobar en estudios comparativos que la trofaxisma es más rápida en las abejas, pero han observado diferencias considerables entre las diversas subfamilias de hormigas, lo que debe tener en cuenta cuando se efectúen experimentos con indicadores. La subfamilia Camponoterinae es la que tiene una tendencia más marcada a la trofaxisma. Los autores estimularon hormigas del Género Formica, en particular la Formica polyctena Forel, y otras especies polígénicas afines que desempeñan un importante papel en la lucha biológicos preventiva contra las plagas de insectos forestales. La trofaxisma dentro de un nido está condicionada por la temperatura, el tiempo, el número de individuos y la cantidad. Un problema es el de saber si existe también trofaxisma entre diferentes nidos de colonias de hormigas de la misma especie. Introduciendo en algunos nidos alimentos marcados, los autores observaron un considerable intercambio de alimentos entre los nidos de la colonia hasta 200 metros de distancia. Lograron resultados análogos en otras colonias diferentes y en otros distritos. La trofaxisma a grandes distancias es un factor muy importante para evaluar la acción destructiva que ejercen las especies Guías de Formica sobre los insectos nocivos, ya que impide la rápida saturación de los nidos por una infestación local masiva de insectos en la zona de mercado. Los experimentos con indicadores mostraron que los alimentos acumulados pasan a la mayoría de los nidos vecinos de las colonias de hormigas. Por tanto, las colonias de la Formica sufrían acciones como un sistema complejo de gran eficacia ecológica.

Con ayuda de alimentos marcados, los autores escindieron en los termitas (Kalotermes flavicollis Fabr.) qué formas intervienden en la trofaxisma local o anal. Los resultados son los más afortunados. Utilizando indicadores radioactivos, los autores trataron de descubrir por qué razón los termitas en grupo son más agresivos y tienen mayor longevidad que los termitas solitarios. Los señoresobres fueron marcados con U-14. Después de alimentarlos, algunos de estos termitas marcados fueron encontrados en casos por separado, y el mismo tiempo se formaron otros grupos que componíanse de termitas no marcados. Midiendo el período eficaz de inactivación, se puede determinar el tiempo de efecto, los autores observaron que el indicador permanecía más tiempo en los termitas en grupo —considerando el grupo como una unidad— que en los individuos aislados. Este resultado puede explicarse por la trofaxisma y una circulación frecuente entre los individuos del grupo. Se observaron resultados análogos con dos especies de hormigas de dos subfamilias distintas. La mayor económica en el empleo de alimentos y otras substancias puede escribirse al «efecto de grupo» en los insectos sociales.

En la memoria se examinan algunos problemas especiales de las técnicas de medición comparables para grupos de insectos e insectos aislados.

INTRODUCTION

The exchange of food and other substances between individuals of the colony is one of the most important integrative mechanisms among social insects. Especially among the highly organized social insects forming insectes- states, the labile equilibrium between one or a few reproductions and a very large number of non-reproductive possessing a more or less latent sexual potentiality (worker ants and honey-bees) or potentiality for development into reproductive (termite larvae) is maintained primarily through such mutual exchanges. Social food exchanges are among the preconditions of division of labour, of brood-rearing in the optimal ecological conditions of the nest,
and of any other development into higher forms of social life among insects. They may be also a means of communication between individuals. The study of these exchanges is not only of great scientific interest but also of practical interest, since many of the social insects have great economic importance in agriculture and forestry. The use of radioactive isotopes as tracers offers excellent possibilities for the basic study of these processes. In 1952, NIXON and RIBBANDS [1] introduced the tracer method into the study of food transmission within the honey-bee community; we followed in our laboratory with a series of papers from 1956 on concerning ants [2-15, 37-38], termites [4, 9, 16, 17, 18] and honey-bees [4, 9, 19]. The present paper outlines the results of our tracer studies with special reference to unpublished experiments on ants and termites.

A. FOOD EXCHANGE IN ANTS

1. Methods

In the experiments, $^{14}$C and $^{15}$N were used as tracers. They were administered to the ants in honey-water, saccharose solutions or pure water [20] at specific activities of 1 mc/ml up to 1 mc/ml, depending on the specific experimental purposes. The liquid food was offered on small glass dishes or the ants were individually supplied through glass pipettes, and the greatest possible care was taken to prevent external contamination. If necessary we decontaminated the radioactively fed ants that were to act as food donors by a special method, bathing them first in watery solutions of the inactive compound (sodium phosphate or sodium iodide) and then in pure water. They were dried quickly by letting them run about on layers of soft absorbent cellulose, which were changed several times. Measurements were carried out with G-M end-window counting tubes (window thickness 1.2-1.4 mm/cm²) or with a scintillation counter, both in conjunction with electronic scalers and if necessary with automatic sample-changers.* Live ants were enclosed for counting in small measuring cages consisting of a ring of glass covered by a thin membrane. The diameter of these rings was adapted to the size of the ant-species and ensured the same geometrical arrangement in comparative studies.

2. Food exchange among worker ants

The most intensive studies were carried out with ants of the genus Formica, especially the Formica rufa group (F. rufa L., F. polyctena Forst., F. pratensis Retz. (syn. F. nigricans Em.), F. cordieri Bondr.). If one freshly fed worker is placed as donor within a group of hungry individuals, the donor supports through direct feeding (regurgitation of crop-content) the major part of the food ingested up to 8-8% [2, 3, 7]. Between 7°C and 35°C the percentage of transmitted crop activity is the same, but the time required depends on the temperature [12]. The primary recipients of food act as secondary donors as a multilateral food flow of one crop. With high crop-content only up to crop-content only up [crop → midgut → re. is influenced by time group. Under condit food distribution for all individuals, up to exchange starts at 5 and then falls until temperature is ident. The greater the group of radioactivity. By also the activity rate is very heterogeneous show extremely low rations, the distribution following a Gauss 'ho

* Made by Priemke & Hoepfner, Bingen
life among insects, the study of food exchanges is also of practical economic importance especially in soil processes. In 1952, we started into the study of transport processes in our laborato-
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secondarily donors and so on, and the food exchanges continue to produce a multilatitudinal food chain. In this way up to 80 % can take part of the content of one crop. With honey-bee workers we found such distributions from one crop-content only up to 50 individuals, since the individual food consumption crop-content only up to 50 individuals, since the individual food consumption (crop → midgut → resorption) is higher than in ants. The distribution rate is influenced by time, temperature and the number of individuals within the group. Under conditions of constant temperature, the temporal course of food distribution follows an exponential function, so that after some time all individuals, up to a maximum of about 80, have been reached. Food exchange starts at 5-7°C, reaches its highest frequency between 25 and 30°C and then falls until the limit of 45-50°C is attained [12]. This optimal temperature is identical with the temperature in the centre of the nest-hill. The greater the group the more individuals can take part in the distribution of radioactivity. By measuring not only the number of radioactive ants but also the activity rate of each individual, we find that at first the distribution is very heterogeneous: some individuals have very high activities while others show extremely low activities. Through often repeated secondary regurgita-

tions, the distribution reaches after some time a statistical equalization, following a Gauss "normal distribution" (Fig. 1) [4, 6, 7]. Over a longer period of time, it is found that the "normal distribution" does not persist but gives way to a single-peak distribution with preference for progressively smaller exchange units. In this way each individual of the group or colony is assured of an adequate food supply. An increase in the number of donors results in a corresponding increase in the speed of distribution. We have not yet done such detailed experiments in honey-bee groups, but we can state that the individual food exchanges through regurgitation from proboscis to proboscis take place more quickly among bees than among ants.

In comparative tracer studies with more than 20 species of ant we found extreme differences between the four subfamilies available in our region and also between biological different species within the same subfamily. The
highest tendency to trophallactic exchanges was found in the subfamily Camponotinae (genera Camponotus, Formica, Lasius), although there is one species of this subfamily that has been shown in our laboratory to act only as receptor of labelled food \([7, 13]\); this is *Polyergus rufescens* Latr., the Amazon ant, which keeps in its nest workers of other species \( (G. Serviformica) \) as slaves responsible for food supply and distribution. While the workers of the Amazon ant are still able to ingest some food directly, other social-parasitic species have lost the capacity to do this, as has been proved by tracer techniques \([7]\). In tracer experiments with colonies of *Epipyrma gosswaldi* Meis. living on a social-parasitic basis with colonies of the genus *Leptothorax*, it was possible to demonstrate a significant preference on the part of the parasitic ants for food supply through donors of the host ant \( (L. unifasciatus \) in our case). This result points the way towards one possible explanation for the process of selective evolution from normal independent ant species through social parasites of varying degrees up to the end-type, the workerless ant. Workers of the subfamily *Monericinae* have only very weak food exchanges among themselves; the individuals seem to be self-supporting. One species of *Dolichoderinae* that was studied showed relatively good food exchanges. Great differences were found among *Myrmicinae*; this agrees with the results of Wilson & Eischer \([21]\), who carried out tracer studies with five American species. A high trophallactic tendency among workers seems, according to our experiments, to be correlated with trophobiotic habits. The demonstrated differences must be taken into consideration in field tracer experiments with ants. In the light of our experience we recommend that some distribution experiments should first be carried out among worker groups before starting with species not yet studied.

3. Food distribution among different castes and stages

Old queens, young queens before and after mating and males of *F. polycotona* feed directly on radioactive honey-water in amounts similar to those for workers. We also proved the capacity of females to distribute food by regurgitation in the following experimental combinations: \( \frac{9^*}{9^*} \); \( \frac{9^*}{9^*} \); \( \frac{9^*}{9^*} \); \( \frac{9^*}{9^*} \); \( \frac{9^*}{9^*} \); \( \frac{9^*}{9^*} \); \( \frac{9^*}{9^*} \). In all cases the experiments were positive, the rate of distribution of \( \frac{9^*}{9^*} \) being similar to that of workers, while that of males was smaller. The most notable observation was the capacity of *Lasius* and especially with *Camponotus ligniperda* \( \frac{9^*}{9^*} \) \([40]\). These males remain for about nine months in the imaginal stage in their mother’s nest and not only distribute food to other \( \frac{9^*}{9^*} \) and \( \frac{9^*}{9^*} \) but even transfer radioactivity to larvae. This trophallactic tendency is less marked when the over-wintering and the subsequent mating phases are reached. Using tracer methods, we obtained similar results with the drones of honey-bees which are undoubtedly also able to regurgitate and distribute crop food \([4, 9, 19]\). A source of error are radioactive excrements which are fed and distributed through workers. Mated queens of *Apis mellifica* distribute radioactive crop substances among workers. In further experiments that we carried out with newly founded colonies of *Lasius niger* L., the queen showed a decreasing tendency after the first imaginal and the queen acted larvae of the species during the overwintering conditions is maintained normally receive for small amounts of lat. In agreement with relatively large \( \frac{9^*}{9^*} \) of radioactive crop food \( \frac{9^*}{9^*} \), it was found that these substances are assimilated through the crop and takes 24-48 h. d.

In special crop food and transfer were isolated for 48 through repeated regurgitation food solution hungry workers. By the point at which the tivity. After some time these glands open into secretion and swallowed a kind of reservoir for is regurgitated, espe specially as a special food for to have caste-determined. After external foraging these special food is for the often very we.

4. Field experiment colonies

As shown in the tracer methods, the t especially Formica sp ecially polygynous an in the biological previ ous important question is what kinds of ant colonies of the polygynous is apparent from the that close relations a daughter-nests. Later
decreasing tendency to supply larvae with radioactive food through herself after the first imaginal workers (pygmies) had hatched: The pygmy workers and the queen acted mutually as both donors and receptors of food. The larvae of the species Camponotus ligniperda L. and C. herculeanus L. have during the overwintering phase a growth diapause which under laboratory conditions is maintained even at relatively high temperatures. They do not normally receive food but at higher temperatures they were supplied with small amounts of labelled food [14].

In agreement with WILSON & EISNER [21], we often found that queens in relatively large groups or colonies showed no preference for the supply of radioactive crop food introduced through foraging ants. By the application of P52, it was found that the reason was transfer of glandular substances. These substances cannot be labelled until the ingested radiophosphorus is assimilated throughout the body. This process begins 1-2 h after feeding and takes 24-48 h, depending on the temperature [4,7].

In special experiments we were able to distinguish between primary crop food and transfer of glandular secretions [15]. Radioactively fed workers were isolated for 48 hr, after which they were allowed to empty their crop through repeated regurgitations. Then they were fed several times with inactive food solution which they were permitted to regurgitate to feed further hungry workers. By measuring these receptors we were able to determine the point at which the crop was completely cleared of the primary crop activity. After some time, especially in Spring, the crops of such workers acquired secondary radioactivity due to secretion of pharyngeal glands. Since these glands open into the pharynx and have no reservoirs of their own, their secretions are swallowed and may be stored in the crop, which thus acts as a kind of reservoir for the pharyngeal glands. This secondary crop content is regurgitated, especially during the early springtime, more or less pure as a special food for queens and for rearing the sexual brood. It seems to have caste-determining or differentiating effects on the female larvae [38]. After external foraging begins, the external food is mixed with gland secretions through repeated regurgitations and thus becomes more or less ameliorated before reaching brood or queens. Thus we have an explanation for the often very weak transfer of radioactivity to queen ants in colonies.

4. Field experiments on food exchange among different nests of Formica colonies

As shown in the previous sections we have intensively analysed, using tracer methods, the trophallactic exchanges of ants of the genus Formica, especially Formica polyctena Foerst. and related species. These ants, especially polygynous and polycalous species, are known to be important factors in the biological prevention and control of forest insect pests [22]. An important question is whether food exchanges also take place between the different nests of ant colonies of the same species. It is known that natural colonies of the polygynous F. polyctena develop by forming daughter nests. It is apparent from the occasional exchanges of brood, workers and queens that close relations at first continue to exist between mother-nests and daughter-nests. Later the nests seem to be more or less independent except
for periodical migrations between nests which are at present under investigation. Our special problem was to find out whether exchanges of food take place under normal conditions, i.e., in visible migrations and exchanges of population. The tracer method was first used for problems of this kind by KANNOWSKI [23] who employed labelled food to determine whether each of the numerous nest-mounds of the subterranean ant Lasius minutus Emery in a swamp was an independent unit or not. He found that usually four or five neighbouring mounds seemed to form a colony with close feeding relations. Similar studies were carried out by MORTREUIL and BRADER [24] in African pineapple plantations in order to elucidate the dimensions of ant nests, their underground relations and their associations with harmful coccids. As was pointed out during the discussion of Mortreuil and Brader's paper at the Bombay Symposium (1960) [25], we have carried out this type of ecological tracer study for several years with interesting results. Beginning in 1959 and continuing through 1961/62 we labelled single nests of Formica polycyctica in one natural and two artificially founded colonies [22].

The tracer (P³² and/or I³¹) was given in honey-water solutions. To prevent external contamination we offered the food in small special glass or plastic vessels which were introduced into the nest-mounds; this prevented the contamination of other insects. During the first experiments we gave only small activities, e.g., in a natural colony, 1 mc I³¹ dissolved in 10 ml honey-water. The activity was introduced in a single food-vessel into the south-west sector of nest-mound A (31.5.1959, 11 a.m.). After 48 h we took several samples of 20 ♀♀ each out of all 5 nests, which were counted in the laboratory with a scintillation counter. Secondary radioactivity was found in ants from nests C and D (Fig.2); though weak, it was significantly different from the background activity and from the activity of ants from untreated nests in the same area. Surprisingly, we detected no transfer of radioactive food into nest B and the very near newly founded daughter-colony a. We suggest that a single food vessel was insufficient for labelling the whole population of the nest. Meanwhile, CHAUVIN, COURTOIS and LECOMTE, who independently from us did similar work with Formica [26, 27], showed in their case migration within ant-into 8-10 vessels within neest-mound.

Further experience artificial food migrations of chaff daughter-nest (No. 5 founded nest No. 59/3 in 4 ml honey-water) taken from 39/1, 59/70 m away from the tube and scintillation in Table I, which is obtained with two different activity was positive was about 20% of conditioned in this case exchange.

AMONC NEST

Fig. 2

Distribution of radioactive food among nests of a natural colony of Formica polycyctica Forst.
- primary labelled nest, labelled with 1 mc I³¹
- nest showing secondary radioactivity after 48 h
- nest inactive after 48 h

The next experiment of F. polycyctica showed migrations up to 200 m, [I³¹] in 30 ml honey-water of 100 ♀♀ each and that the scintillation counts significant secondary levels.
showed in their second paper similar sectorial preferences of food transmission within ant-nests. In all later experiments we divided the tracer into 6-10 vessels which were well distributed over the primary labelled nest-mound.

Further experiments were done in artificially founded colonies [22]. One artificially founded nest (No. 59/1) showed two months after foundation migrations of changing intensity over a distance of 75 m to a secondary daughter-nest (No. 59/3a) which had been established through the artificially founded nest No. 59/3. Nest 59/1 was labelled with 0.12 mc P°° + 0.2 mc I°°° in 4 ml honey-water (5, 8, 1959). After 96 h samples of 25 % each were taken from 59/1, 59/3a and two other old-established nests (No. 104, No. 3) 70 m away from the primary-labelled 59/1. They were counted with G-M tube and scintillation counter in the laboratory. The results can be seen in Table I, which gives the counts per minute, including statistical error, obtained with two different counting methods. The transmission of radioactivity was positive only to nest 59/3a, in which the level of radioactivity was about twice that of the counts in 59/1. The transmission may have been conditioned in this case by mixing of the nest population as well as by food exchange.

### Table I

<table>
<thead>
<tr>
<th>Sample</th>
<th>G-M Tube (counts/min)</th>
<th>Scintillation Counter (counts/min)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Background chamber</td>
<td>18.2 ± 1.8</td>
<td>133.7 ± 2.5</td>
</tr>
<tr>
<td>25 % from nest 60/1</td>
<td>18.5 ± 1.9</td>
<td>136.9 ± 8</td>
</tr>
<tr>
<td>25 % from nest 60/3</td>
<td>18.4 ± 1.8</td>
<td>210 ± 8</td>
</tr>
<tr>
<td>25 % from nest 60/39</td>
<td>100 ± 7</td>
<td>163 ± 8</td>
</tr>
<tr>
<td>25 % from nest 104</td>
<td>89 ± 6.3</td>
<td>174 ± 5.8</td>
</tr>
<tr>
<td>25 % from nest 5</td>
<td>18.9 ± 1.7</td>
<td>199 ± 7</td>
</tr>
</tbody>
</table>

The next experiment, carried out with an artificially enlarged colony of *F. polyctena*, showed long-range transmissions of radioactivity over distances up to 200 m. The primary-labelled nest No. 7 (Fig. 3) received 10 mc I°°° in 30 ml honey-water (12 June 1959). Countings of samples consisting of 100 % each and taken 72 h after primary labelling were carried out with the scintillation counter in the laboratory. Seven of 13 nests carried significant secondary labelling. Visible connection, through migration of
workers in both directions, existed only between No. 7 and No. 9, including the small unnumbered daughter nest.

During the same summer season we started a twice-repeated experiment in an artificially founded colony of *F. polyctena* in an area containing single nests of a natural population of *F. rufa*. Radioactivity was transmitted during June into most surrounding nests up to a distance of 70 m in a direct line, except for one nest of *F. rufa* which was at the shortest distance (30 m) from the primary-labelled nest of *F. polyctena* (the tracer dosage was the same as in the experiment described earlier). In the surroundings of the primary-labelled nest were three newly founded (two months old) artificial daughter nests. These did not partake of the radioactive food. But when we repeated the experiment under the same conditions three months later (4 September 1959) we found radioactivity in the daughter nests too. Especially this last result is very important since it shows that new daughter colonies, founded with ants of the same species but strange origin, will be integrated in the colony-system in the course of a few months. The experiment also confirms an observation published in 1940 [39] that ants of artificially founded daughter nests established in the mother nest's area migrate back, since they have too close social relations. Daughter nests of the same species but strange origin need some months to develop such relations and become well-established in the meantime.

The results of these field tracer experiments are of great importance in evaluating the regulating effect of useful *Formica* species on insect pests [28], since it can be observed by local mass infestations, as shown by nests of the ant colony as a complex preda connection it should have with a radioactive source; were taken as living was not very high, *F. polyctena* under these conditions.

We do not know how ant nests operate, reactions may play a two workers of the same species can be observed, but in natural conditions, combination of extens.

In some further transmission experiments, there was carried out at the beginning of the wintering phase the fat-bodies of a part of the colony have been suggested [39].

These "fat" and "inert" compound is reduced and they do not seem to be filled up for the winter.

For the last two of current mains, 1.5 m, used and equipped with the G-M tube with d-electronically in two months later (30 m).

10 min is also fitted for the winter.

The experiments showed that the situation in the case of solid...
FOOD EXCHANGE IN ANTS AND TERMITES

pests [28], since these exchanges prevent the quick saturation of any nest by local mass infestation by insects in its predating area. The food-collected flows, as shown by the tracer experiments, into most of the surrounding nests of the ant colony. Thus colonies of these useful wood-ants are acting as a complex predating system with high ecological effectiveness. In this connection it should be mentioned that we also have tested the distribution of radioactive caterpillars (activated by feeding on radioactive leaves), which were taken as living prey. Though the specific activity of the caterpillars was not very high, we observed good transmission within small colonies of *P. polyctena* under laboratory conditions.

We do not know exactly how the exchanges of radioactivity among different nests operate. Mixing of populations through migrations in both directions may play a part, as well as food transmission through regurgitation between workers of different nests meeting outside the nests. Both events can be observed, but may be different from case to case under the complex natural conditions. They should be analysed by labelling the ants with a combination of externally visible colours and radioactive food.

In some further experiments we tried to determine whether the food transmission operates better among artificially founded nests of the same origin than among nests of different origin. Since these experiments were carried out at the beginning of the overwintering phase we found only weak transmissions of radioactivity between nests (1-15 October 1962). However, these experiments yielded another very interesting result: during the overwintering phase the population stores food reserves in the hypertrophied fat-bodies of a part of the population [12, 20], especially of young workers, as has been suggested [20].

These "fat" individuals with swollen gasters are in the depth of the nests. During overwintering their behaviour pattern changes; their metabolism is reduced and they do not accept radioactive food [12]. Though they are already in the deep parts of the nests, they show a significant preference for supply with radioactive food offered at the nest surface. The storing individuals seem to be filled up as well as possible during this period of preparation for the winter.

For the last two years we have been using a portable counter independent of current mains. The apparatus was developed in conjunction with an engineering bureau * for our special purposes. The apparatus is fully transistorized and equipped with Ni-Fe batteries and a 220-V AC generator. It supplies the G-M tube with direct current up to 1800 V and the counter (which works electronically in two decades and mechanically in three) with 220-V alternating current (see Fig. 4). A start-stop device with time-intervals of 1 to 10 min is also fitted.

B. FOOD EXCHANGE IN TERMITES

Since termites are hemimetabolic insects, all stages - apart from the egg - are mobile and have well-developed mouth-parts, though specialized in the case of soldiers. For that reason it is more difficult to obtain an

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* Radioned (Firma Erich Jaeger), Würzburg
insight into the food relations among the members of a termite-colony than with social Hymenoptera. However, the tracer method offers excellent possibilities of studying these problems in termites. We began work of this type in 1958 in our laboratory with the drywood termite Kalotermes flavicollis Fabr. [4, 16, 9, 17, 18]. This species is very suitable as a laboratory termite for testing the termite-resistance of materials [29, 30, 17, 18].

It first had to be determined which stages were capable of direct uptake of foodstuffs. The termites were carefully separated into the different stages. We offered them as food filter paper soaked with $^{32}$P solution (specific activity 1 mc/ml). To avoid contamination, the termites were forced to eat through a small hole (diameter corresponding to the head width of the stage studied) in a plastic foil stretched over the radioactive filter-paper. The experiments showed that larvae of the first stage, soldiers and preimagines (short interstage between second nymph and adult), and also alate termites never feed directly. Larvae of the second stage take up only very small amounts. The most active feeders are larvae of the third, fourth and fifth stages and pseudergates. In relation to their size, the two last-mentioned stages eat the largest amount of radioactive paper, thus demonstrating their suitability for test purposes [17]. Nymphs of both stages are also very active feeders, but they need a pre-adaptation time of two days. In a similar way imaginal sexuals, more than three years old, regained the capacity to feed directly after an isolation time of 65-75 h.

Food exchange among individuals of K. flavicollis takes place relatively slowly. Putting radiolabelled termites at 27°C into normal colonies (ratio labelled: unlabelled and after 35 h 100% and young nymphs, while young larvae Mouling individuals event [18]. The takes place both stomach content or gl rectal content with are known also an methods enabled t! C. STUDIES ON COMPARISON OF IN A GROUP

As shown in to trophallactic él creted $^{32}$P [11, 32 transmissions are might be more e measurements of viduals and in individ problem, because as a rea β-particles preci repeated measurer counters [32], until aphids [33]. Howe used as tracers Pseudo-work Formica pratensis, Myrmica scabrinata scribed above (te) water. After the h containers which w radioactivity, eith nest (K. flavicollis labelled) under co (98% r.h.), Durh available.

Both the initia the insects were to geometric and oth background activit the measurements

* Shortly before th similar tracer studies of brevi Walker [41].
FOOD EXCHANGE IN ANTS AND TERMITES

labelled: unlabelled = 1 : 10), we found that after 12 h 40%, after 20 h 70%, and after 35 h 100% of the individuals were radioactive. The older larvae and young nymphs, especially the pseudergates, play the main part as donors, while young larvae, older nymphs, sexuals and soldiers are receptors of food. Moulting individuals do not feed two days before and two days after this event [18]. The exchange of food and other substances between termites takes place both stomaedly (i.e., by mouth-to-mouth feeding of regurgitated crop content or glandular secretions) or proctorally (by feeding of excrated rectal content with a more or less fluid consistency). Such protodermal exchanges are known also among ants of the subfamily Dolichoderinae [31] and tracer methods enabled them to be demonstrated also in larvae of Myrmicinae [7].

C. STUDIES ON THE EXCRETION OF $^{131}$ IN ANTS AND TERMITES: COMPARISON OF SINGLE ISOLATED INDIVIDUALS WITH INDIVIDUALS IN A GROUP

As shown in the previous sections social insects have a high tendency to trophallactic changes of food and other substances, e.g., cuticularly excreted $^{131}$ [11, 32]. We supposed that, as a consequence of such repeated transmissions among individuals, the utilization of substances in groups might be more economic than in single individuals. A comparison of measurements of the biological half-life of a tracer in single isolated individuals and in individuals within a group seemed to be a convenient method for this problem. We studied the biological half-life of a $\gamma$-emitter, $^{131}$, because as a result of changing body distribution and body absorption of $\beta$-particles precise determinations of the real effective half-life through repeated measurements of living insects are nearly impossible with $\beta$-detecting counters [32], unless the insects are very small and have thin cuticles, e.g., aphids [33]. However, all these complications are greatly reduced if $\gamma$-sources are used as tracers and the measurements are made with scintillation counters.

Pseudo-workers of the termite K. flavicollis and workers of the ant Formica pratensis Retz. (sym. Formica nigricans Em.) (Camponotinae) and Myrmica scabrinodis Ny. (Myrmicinae) were fed with $^{131}$ by the methods described above (termites with labelled filter paper, ants with labelled honey-water). After the insects had eaten, the labelled ones were separated and kept in containers which were changed daily to avoid contamination through excreted radioactivity, either singly or in groups with unlabelled individuals of their nest (K. flavicollis: 1 labelled + 4 unlabelled; ants: 1 labelled + 5–15 unlabelled) under constant conditions of temperature (27°C) and air humidity (88% r.h.). During the experimental time fresh inactive food was always available.

Both the initial and the subsequent measurements of the radioactivity of the insects were taken with the help of a scintillation counter under the same geometrical and other physical conditions. Before each measurement the background activity was first measured and subsequently subtracted from the measurements of the radioactivity of the insects. The insects were kept

= Shortly before the opening of the Symposium, a paper by MAHAN received, dealing with similar tracer studies of termite feeding relationships carried out with the drywood termite Cryptotermes

brevis Walker [42].
under the scintillation counter enclosed in a small glass ring. Its diameter was different depending on whether single insects or a group of insects as a single unit were to be measured. It is interesting to note that the sum of the measurements of the individual insects composing a group was found statistically to be the same as the measurement of the radioactivity of the group when viewed as a unit.

The biological half-life (T_{biol}), which primarily depends on rate of excretion, was calculated from measured effective half-life (T_{eff}) and the known physical half-life (T_{phys}) by means of the following relationship:

\[
\frac{1}{T_{eff}} = \frac{1}{T_{phys}} + \frac{1}{T_{biol}}.
\]

The results are given in Table II. More details will follow in special papers [10,34].

**TABLE II**

| Biological half-life (T_{biol}) of 131I in isolated individuals and in groups of termite pseudoworkers and worker ants |
|---|---|---|---|---|
|   | Isolated single individuals | No. of experiments | Statistical constant (C) | Probability |
| K. flavicollis | 554.3 | 580.9 | 21 | 2.22 | 0.05 |
| F. parvus | 19.3 | 48.9 | 24 | 2.15 | 0.05 |
| (syn. F. nigricans) | | | | | |
| M. scabrinodis | 83.0 | 191.2 | 14 | 2.24 | 0.02 |

* Student's t-test (1928)

The summarized results show that the biological half-life is shorter in isolated individuals than in groups. Since the measurements of the single individuals clearly showed the repeated interindividual exchanges of radioactivity among individuals, it became apparent that the prolonged T_{biol} was a consequence of this circulation. The greater economy in the use of food and other substances may be a contributory factor to the "group-effect" by which GRASSE and his group [35, 36] tried to explain the higher longevity and greater vigour of social insects in groups than as single individuals. Nevertheless these results cannot be generalized, since sometimes through storage in certain individuals (the above-mentioned fat ants during over-wintering phase or "honey-pot" ants), the situation may be quite reversed. Tracer experiments carried out with replete workers of Proformica nasuta Nyl. in our laboratory [37] seem to indicate this.
ACKNOWLEDGEMENTS

These studies were supported by grants from the Bundesministerium für Atomkernenergie und Wasserwirtschaft and the Bundesministerium für Ernährung, Landwirtschaft und Forsten of the Federal Republic of Germany, and from the Bayerisches Staatsministerium für Unterricht und Kultur. To these Ministries we wish to express our best thanks. Our gratitude is also due to our collaborators and guests, especially to Mme. J. Albert of Paris, Dr. R. Stumper of Luxembourg and Mr. P. K. Som-Sarma of Dehra Dun, India.

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DISCUSSION

J. LECOMTE: Although your studies on the important question of transmission of food in the form of labelled caterpillars have been confined to the laboratory, do you consider that such exchanges can be as intense as the exchange of sugared foods?

W. KLOFT: Your question is an important one, and we did take this problem into consideration. As I stated, the laboratory experiments with labelled caterpillars were positive throughout, but ought to be repeated under outdoor conditions. These caterpillars were given in the form of living prey. The specific activities of the caterpillars were not very high, but we know from our experiments that the genus *Formica* prefers haemolymph when feeding on insects, and takes up the cell complexes suspended therein—particularly from the fat-body, and of course other tissues also. This more or less liquid precipitate can then be directly distributed in the same way by regurgitation.

D.A. CROSSLEY: I would like to ask Dr. Kloft what percentage of the $^{32}$P in the body would be excreted through the salivary gland and consequent passage through the gut.

W. KLOFT: We carefully measured these percentages. I do not know the exact figures but they will be published by our colleague, H. Neumann. The total amount excreted in this way in the course of one day is about 1–5% of the total body activity remaining after there is no more primary activity in the crop. It is important to bear in mind that this only occurs with individuals during a certain phase of life, and especially with over-wintered young workers from the previous year. Workers which are born this year can do this next year, in April to May. During that time the young workers which have over-wintered feed the young queen-larvae with glandular secretions and in this way substances coming from the fat-body are used for rearing young sexual forms, especially young queens.

D.A. CROSSLEY: May I ask a further question? If you now consider the concentration of radioisotopes in various steps in the food chain, would it not be possible to measure the flow of energy through an ant nest, that is the amount of transfer of stored energy from one phase to another? You should be able, should you not, through this type of distribution, to calculate how much trophallaxis occurs in theory at least?

W. KLOFT: We have not yet made this calculation, though it should be possible, using your special techniques for summation of the ingested activity of one queen larva, for example.

Mme. S. FUZEAU-BRAESCH: May I ask Dr. Kloft something about his experiment on measuring activity in isolated animals and grouped animals? He finds that the biological half-life of isolated animals is less than that of animals in groups, and mentions a group-effect phenomenon in that connection. I would like to ask if this effect—that is, an additional and acts on the within-grouping of several or otherwise.

W. KLOFT: This extent be conditional a complex phenomenon that is only exchange of licking and so on, i.e., pure energy from every individual who exchange them. Hormone secretion, the exchange among each other, a group is a main effect.

As you know, a honey-bee worker cannot live as a lone group. Only through these excretions, all indi, other substances, and other nervous doubts related to the intense increase in the they are kept isolated.

D.A. CROSSLEY: Millipedes. They are eaten, it from eating is working has a size. If the animal is growing, it becomes much shoer.

Mme. S. FUZEAU-BRAESCH: Biological half-life be that is to a phenomenon?

W. KLOFT: Individuals lick each other biological half-life excreted substance and this type of excretion gamma-emitting tritium problems as regards Bombay Symposium. At the in the

* Radioisotopes and
FOOD EXCHANGE IN ANTS AND TERMITES

W. KLOFT: Naturally I am aware that the group-effect must to a large extent be conditioned by sensorial and nervous stimuli. We regard it as a complex phenomenon in which the mutual exchange of food and other substances plays a contributory part, as one single factor. Through the continuous exchange of crop-content with or without glandular secretions by licking and so on, essential substances as well as pure calorie providers, (i.e., pure energy foods) are distributed evenly throughout the group; not every individual has these or is always in a physiological condition to produce them. Radioactive phosphorus was excreted through the cuticula of queens and the excreted P²⁵ was picked up by the workers and distributed among each other. We think this food transfer between individuals within a group is a main cause of their longer expectation of life.

As you know, if we isolate one single individual, a termite, an ant or a honey-bee worker, and give her all the energy substances she needs, she cannot live as long as the same individuals with the same food supply in a group. These things are well described by Grassé and his group in Paris. Through repeated exchanges of such food substances and also glandular excrections, all individuals have about the same equilibrium in foodstuffs and other substances. I know they need the stimuli, including all the olfactory and other nervous stimuli, but I think the longer biological half-life is undoubtedly related to the so-called group-effect.

G. COURTOIS: I should like to add that by using Ir¹⁹² we have also found this increase in the biological half-life in grasshoppers, depending on whether they are kept isolated or in groups.

D.A. CROSSLEY: Dr. Frank Gaully reports a similar increase for millipedes. He can produce the effect with an individual animal by preventing it from eating its own faeces. The particular millipede with which he is working has a strong tendency to eat a good number of its own droppings. If the animal is prevented from doing this, its measured biological half-life becomes much shorter.

Mme. S. FUZEAU-BRAESCH: Could part of the difference in the biological half-life be due to immediate recontamination between individuals, that is to a phenomenon similar to the one mentioned in the millipede?

W. KLOFT: Undoubtedly, we also have external contamination because individuals lick each other externally. We cannot prevent that. I take the biological half-life as a total effect for the whole group. These external excreted substances are always taken up from one individual to the other, and this type of external contamination is undoubtedly included, but using gamma-emitting tracers and measuring with scintillation counters, we had no problems as regards absorption effects. In other cases, as I reported at the Bombay Symposium, we get higher rates of radioactivity, after excretions, on the cuticula. At the beginning of the experiment, using gamma-emitters, we
had no such problems, but I agree with you that we do have some external contamination. The substance, however, is not lost to the community. Individuals take it from one another.

Mme. S. FUZEAU-BRAESCH: I believe I could suggest a useful experiment. This prolonged sensorial effect, which is a real group-effect, concerns a whole group of insects.

To eliminate contamination I suggest that isolated animals should be measured. Some of them could be isolated from a long time, and the others kept in groups before the experiment. Since the group-effect is an effect which is prolonged, any difference in the half-life occurring will be due solely to a "group-effect".

W. KLOFT: Mutual contamination with the radioactive group is of course unavoidable. In fact, the technique is based directly on it. The animals lick each other constantly and— as we have been able to show by the tracer method—they distribute, by regurgitation-feeding, substances excreted by the cuticula. Thus in actual fact a substance already excreted returns again to the intestinal tract of other individuals or, by means of regurgitation, even enters into the metabolism of the original producer.

Nevertheless I agree with you that further differentiation should be made in the experiments, in order to solve these complex problems.

J. HALBERSTADT: In connection with biological half-life problems, and in order to get more exact data, would it not be helpful to run parallel experiments using two isotopes of the same element, $^{52}$Fe and $^{53}$Fe, for instance, or $^{111}$In and $^{112}$In? Would that not give you much more exact information?

W. KLOFT: We have not yet done the experiment with two isotopes of the same element, but our field experiments on ants were done partly with two different tracers, $^{52}$Fe and $^{111}$In, and we had different half-lives for these two, because $^{52}$Fe is very well assimilated in the body while $^{111}$In is less well assimilated. However, I will bear your suggestion in mind.

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USE OF RADIOACTIVITY OF RADIOACTIVE TRACERS IN AGRICULTURE. USING RADIONUCLIDES TO EVALUATE INSECTICIDAL EFFICIENCY AND INSECTICIDAL DILUTION OF RADIONUCLIDES. IN BOTH FIELD AND LABORATORY EXPERIMENTS, THE USE OF RADIOISOTOPES THROUGH FEEDING (RATE OF INGESTION) = (RATE OF EXCRETION) X (BIOLOGICAL HALF-LIFE) PER UNIT TIME. FOOD CONSUMPTION AND INSECTICIDAL EFFICIENCY OF SPECIES POPULATIONS. IN A FIELD OF FOOD CONSUMPTION, THE USE OF RADIOISOTOPES TECHNIQUES TO MEASURE SPECIFIC RATES, THROUGH THE USE OF MULTIPLE SPECIES AMONG THE SITES, TO MEASURE AN AVERAGE BIOLOGICAL HALF LIFE OF CERIUM-137. THIS USE TRADION OF CERIUM-137 IN PREDATORS.
USE OF RADIOACTIVE TRACERS IN THE STUDY
OF INSECT-PLANT RELATIONSHIPS

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Abstract — Résumé — Anotación — Resumen

USE OF RADIOACTIVE TRACERS IN THE STUDY OF INSECT-PLANT RELATIONSHIPS. In early use of radioactive tracers in ecological investigations of pests, dispersion and migration phenomena were studied with radioisotopes as markers for individual insects. A more recent development is the use of radioisotopes to evaluate insect-planta and predator-prey associations through estimates of food utilization. Biological elimination of radioisotopes, a nuisance in dispersion studies, is being utilized as a measure of feeding rates. In both field and laboratory experimentation, insects are allowed to reach steady-state concentrations of radioisotopes through feeding. Then the rate of intake is equal to the rate of elimination of the radioisotope. (rate of ingestion) = (steady-state amount) / (fractional rate of loss). Measurements of elimination rates (biological half-lives) permit the steady-state concentrations to be translated into intake rate functions.

Food consumption studies have been performed for single-insect-species populations and for multispecies populations. In a single-species investigation, radiocaesium in tagged field sites was used to estimate the consumption of willow leaves by populations of the beetle Chrysomela kubal. Direct measurements of food consumption made in the laboratory showed good agreement with field estimates of feeding rates based on the radioisotope techniques. Biological half-lives differed for the larval stages and these had to be considered separately. Radioisotopes provided a means of separating overwintering adults from newly emerged ones, through the more rapid elimination of caesium from overwintering adults. In multiple-species work, the relationship between size of insect and elimination rate was used to derive an average biological half-life for radioacesium elimination from herbivorous insects in a field site tagged with caesium-137. This average rate, used in conjunction with data on plant and insect biometrics and concentrations of radioacesium, permitted an evaluation of plant consumption by an entire insect community. Similarly, the utilization of insects as food by predaceous arthropods was estimated from steady-state concentrations of radioacesium in predators and prey, biometrics, and an average elimination rate.

EMPLOIS DES RADIOMARQUEURS DANS L'ÉTUDE DES RELATIONS INSECTE-PLANTE. Dans les premiers travaux écologiques sur les insectes nuisibles effectués à l'aide de radioisotopes, les chercheurs ont étudié les phénomènes de dispersion et de migration en utilisant les radioisotopes comme marqueurs individuels. Plus récemment, ils en sont venus à étudier les relations insecte-plante et prédateur-prédateur, en procédant à des évaluations de l'utilisation des aliments. L'élimination biologique des radioisotopes, qui constitue un inconvénient dans les études sur la dispersion, est utilisée dans ce cas comme mesure de taux d'alimentation. Dans les expériences en plein champ ou en laboratoire, on attache une importance à la concentration des radioisotopes ingéés par les insectes par rapport à l'équilibre. Le taux d'absorption des radioisotopes est alors égal à leur taux d'élimination (taux d'ingestion) / (quantité à l'équilibre) / (taux de perte fractionnaire). Les mesures des taux d'élimination (période biologique) permettent de traduire les concentrations à l'équilibre en fonction exprimant les taux d'ingestion.

Les auteurs ont procédé à des études sur la consommation d'aliments dans des populations composées d'une seule espèce d'insectes et dans des populations composées de plusieurs espèces. Dans une étude en plein champ sur une seule espèce, ils ont procédé au marquage par le radioacésium afin d'évaluer la consommation de feuilles de saule par des populations de chrysomèles (Chrysomela kubal). Les mesures directes de la consommation d'aliments faites en laboratoire ont bien concordé avec les évaluations des taux d'alimentation faites en plein champ au moyen des méthodes radioisotopiques. Les périodes biologiques ont été différentes pour les stades larvaires, ce qui a permis d'étudier séparément. Les radioisotopes ont permis de distinguer les adultes ayant survécu à l'hiver de ceux qui avaient d'apparaître; en effet, le calcium est éliminé plus rapidement par les larvaires.
En los estudios sobre el índice de eliminación sobre insectos herbívoros en plantas vegetales se han observado diferencias en la tasa de eliminación entre diferentes especies de insectos. Se ha encontrado que la tasa de eliminación disminuye con el aumento de la densidad de población de insectos. Esto se debe a que los insectos tienen un comportamiento de búsqueda y evitación, lo que减少 el índice de eliminación en poblaciones densas.

**INTRODUCCIÓN**

En modernos sistemas de cultivo, como los huevos de insectos, es esencial controlar la población de insectos. Para esto, se utilizan técnicas de radiotécnica para detectar la presencia de insectos y monitorear su población. En este estudio, se evaluó el índice de eliminación de insectos herbívoros en plantas vegetales utilizando técnicas de radiotécnica. Se encontró que la tasa de eliminación disminuye con el aumento de la densidad de población de insectos. Esto se debe a que los insectos tienen un comportamiento de búsqueda y evitación, lo que reduce el índice de eliminación en poblaciones densas.
En los estudios sobre poblaciones formadas por varias especies, la relación entre el tamaño del insecito y el índice de eliminación sirvió para calcular el período medio biológico para la eliminación del radioisótopo por insectos herbívoros en una zona atada con $^{14}C$. Este período medio y los datos sobre las masas biológicas vegetales y insectos y sobre las concentraciones de radioisótopo han permitido calcular el consumo de vegetales por una población enteras de insectos. Del mismo modo, se ha podido calcular el consumo de insectos de los arácnidos depredadores basándose en las concentraciones estacionales de radiocarbono en los depredadores y en las víctimas, las masas biológicas y el índice medio de eliminación.

INTRODUCTION

In modern insect-control practices, an integration of chemical, biological, cultural and other manipulative procedures is increasingly visualized as the ideal means for minimizing the depredations of pest insects and mites. From the purely biological aspects, entomological work on pest insects has always been considered meritorious and ecological phenomena were prominent in the attempts at "biological control" during the past few decades. Recent concepts, however, transcend the older ideas of biological control in that pest insects are regarded as members of more extensive ecological systems. For example, SMITH[1] has listed three principles for an integrated control concept which may be restated briefly as follows: (1) Crops, pest insects, and other biota and environment should be treated as a functional unit - the ecosystem; (2) Control measures should aim to keep pests below economic levels rather than attempt complete eradication; and (3) Disruption of other parts of the ecosystem must be considered in the evaluation of control procedures.

Implicit in such concepts is a consideration of insect-crop relationships as part of a unit system and the evaluation of control measures as a shifting of balances within the system. Such an integrated control procedure is not always necessary and may even be undesirable in some instances. The evaluation of even a very effective chemical control procedure must be made on more than destruction of pest insects, however, and such evaluation falls within the realm of ecology.

Radioisotope techniques provide an effective means of studying insect-plant relationships within an ecosystem context, and the full value of these techniques evidently is yet to be realized. Early uses of radioisotopes in economic entomology involved studies of dispersal and migration phenomena[2]. The unique value of radioactive materials as markers for individual insects has become a universally appreciated technique [3]. In mass tagging experiments, the loss of ingested radioisotope due to biological elimination was noted and deemed to be of nuisance value only. DAVIS and FOSTER [4] seem to be the first ecologists to suggest that biological elimination of radioisotopes be used to measure feeding rates, although this concept is inherent in numerous physiological studies [5]. The new doctrine of health physics also has contributed functional models and terminology. Essentially these methods use elimination rates to estimate accumulation rates, so that the concentration of a radioisotope in an insect (for example) can be used to infer rates of plant consumption or prey consumption by predaceous insects. The elimination rate technique offers a widely applicable and uncomplicated means for trophic analysis.
ELIMINATION RATES AND BIOACCUMULATION

The amount of a radioisotope which is retained in an insect following ingestion of a single dose decreases exponentially, because of biological elimination. Fig. 1 shows the retention of caesium-137 by a female grasshopper (Melanoplus differentialis); the exponential decrease produces a straight line in a semilogarithmic graph. Expressions of such rates of elimination are usually made in terms of the biological half-life. This is defined as the time required for the amount of a radioactive element in the body to decrease to one-half its initial value as the result of biological processes. The data in Fig. 1 suggest a biological half-life of approximately 2.5 d. Since these data were not corrected for radioactive decay, the result is technically an effective half-life; however, the physical half-life of Cs-137 is so long in comparison with the observed half-life (25 yr as against 2.5 d) that radioactive decay can be ignored. In the general case these three rates are related as follows:

$$T_{eff} = \frac{T_b \cdot T_r}{T_b + T_r}$$  \hspace{1cm} (1)

where $T_{eff}$, $T_b$, and $T_r$ are the effective, biological, and radioactive half-lives respectively.

By analogy with radioactive decay, the loss of radioactivity from the insect's body can be described from the relationship:

$$A_t = A_0 \cdot e^{-kt}$$  \hspace{1cm} (2)

where $A_t$ is the radioactivity of the insect at time $t$, $A_0$ is the initial activity, $k$ is the rate constant, and $t$ is time.

The amount of radioactivity absorbed by an insect depends on the rate of intake and the retention of the material in the insect's body. The rate of intake affects the total amount retained. For example, if a plant receives a daily dose of a radioactive material, the daily intake must be equal to the daily dose in order to reach a steady-state condition. If the daily dose is not equal to the rate of intake, the amount of radioactivity retained will be affected. The retention factor is the ratio of the total amount retained to the total dose received. The retention factor is a measure of the efficiency of the insect in retaining a particular radioactive material.

APPLICATION TO INSECTS

Two types of insects will be discussed, the scale insect and the Colorado potato beetle. Each of these has a different half-life for the retention of a radioactive material. The single-species potato beetle is a herbivorous insect that feeds on potatoes. The scale insect is a sap-sucking insect that feeds on the sap of trees. The scale insect has a shorter half-life for the retention of a radioactive material than the Colorado potato beetle.

Feeding rates are also important in determining the amount of radioactivity retained by an insect. For example, if an insect feeds on a leaf with a high concentration of a radioactive material, it will retain more of the material than if it feeds on a leaf with a low concentration. The feeding rate affects the amount of radioactivity absorbed by the insect. The feeding rate is the amount of material that an insect consumes per unit of time. The feeding rate determines the amount of radioactivity retained by an insect. The feeding rate is a measure of the efficiency of the insect in absorbing a particular radioactive material.

Laboratory studies have shown that the retention of a radioactive material depends on the feeding rate of an insect. For example, if an insect feeds at a higher rate, it will retain more of the radioactive material than if it feeds at a lower rate. The retention of a radioactive material is a function of the feeding rate. The retention of a radioactive material is a measure of the efficiency of the insect in absorbing a particular radioactive material.
where \( A_t \) is the radioactivity at any time \( t \), \( A_0 \) is the initial radioactivity of the insect at time \( t = 0 \), and \( k \) is an elimination constant equal to \( 0.593/T_{\text{h}} \) (or \( 0.693/T_{\text{eff}} \) in the general case). For the case illustrated in Fig. 1, \( k \) is \( 0.693/2.5 \) d, or \( 0.277 \) d\(^{-1}\).

The amount of radiisotope eliminated during any given day, in this example, is equal to the radiisotope content of the insect times the elimination constant \( k \). Thus when an insect feeds continually on radioactive plants the daily rate of elimination will increase until daily intake is balanced by daily elimination. At that time the concentration of radiisotope in the insect may be said to have reached a steady state. The relation between intake and elimination in a steady state is:

\[
r = kA_t
\]

(3)

where \( r \) is the rate of feeding (\( \mu \)c/d), \( k \) is the elimination constant (d\(^{-1}\)), and \( A_t \) is the whole-body radioactivity (\( \mu \)c) in steady-state equilibrium. Thus, if the steady-state radioactivity of the insects is measured and the biological half-life for the particular radiisotope is known, the rate of feeding \( r \) can be calculated directly. If the concentration of radiisotope in the food of the insects is known, then \( r \) can be expressed as the amount of food consumed per day. If only a fraction of the radiisotope ingested is assimilated, a correction must be applied. The right-hand side of Eq. (3) may be divided by the fraction assimilated, or the elimination of unassimilated material may be treated as an additional exponential factor. No such correction is necessary for the results discussed in this report since they are based on radiocaesium, which is almost completely assimilated [6].

The approach to the steady-state equilibrium concentration is asymptotic; the time required to reach 50% of the equilibrium value is equal to one biological half-life. Practically, equilibrium is considered to be attained after a time equivalent to five biological half-lives. This would be 97% (31/32) of the final value.

**APPLICATION TO FIELD POPULATIONS**

Two types of field application of these radioactive tracer methods will be discussed, the single-species population and the multiple-species population, since each presents its own set of requirements.

**Single-species population**

Feeding rates were estimated for the third-instar larval stage of *Chrysochla knabi* Brown, feeding upon willow leaves. This beetle species overwinters in the adult stage. Eggs are laid on young willow leaves in early May, in the East Tennessee area. A single generation of beetles develops each year. All three larval stages as well as adults feed exclusively on willow leaves. Development is completed usually by mid-June. The life history of this beetle species has been described by BROWN [7].

Laboratory studies showed that biological half-lives for radiocaesium in this insect increased with age and size during development. Elimination
Retention of Ca\textsuperscript{44} by an individual beetle (Chrysomela nubi)

Third-instar larvae, pupa, and adult stages are shown.

of Ca\textsuperscript{44} occurred at rates corresponding to a 7-h biological half-life for first-instar larvae (mean of 4 individuals), an 8-h T\textsubscript{12} for second-instar larvae (10 individuals), an 8-h T\textsubscript{12} for third-instar larvae (14 individuals), and a 10-h T\textsubscript{12} for newly-emerged adults. Fig. 2 illustrates Ca\textsuperscript{44} retention by one individual. Loss during the third instar, no elimination during the pupal stage, and further loss by the newly emerged adult are shown. These short biological half-lives suggest that a steady-state concentration would be reached in less than two days of feeding. However, the average duration of the larval stages also is short, and only during the third instar (5-d average duration) and the adult stage might a steady-state equilibration be expected.

Beetles containing Ca\textsuperscript{44} were obtained from willows growing on the White Oak Lake bed. White Oak Lake was formerly part of the Oak Ridge National Laboratory's low-level waste disposal system. The lake was drained in 1955, and the plants and animals which invaded the lake basin accumulated various radioisotopes from the sediments [8]. Ca\textsuperscript{44} accumulated by willows (Salix nigra) growing in these sediments is transferred to insects feeding upon these plants. The consumption of leaves was calculated for third-instar larvae, which were more readily collected than were adults. The Ca\textsuperscript{44} content of a sample of 122 third-instar Chrysomela nubil larvae was 72.9 ± 14.6 pc/g dry wt. This value represents the steady-state equilibrium concentration. The elimination constant k, based on a biological half-life of 5 h (t 0.333 d), is estimated as 0.693/0.333 = 2.08 d\textsuperscript{-1}. By substitution in Eq. (3), \( \tau = (2.08)(72.9) = 151 ± 30.4 \text{ pc/g beetle per day} \). The average Ca\textsuperscript{44} concentration in willow leaves was 37.8 ± 2.38 pc/g dry wt., on the basis of leaves from which the beetle larvae were collected. Dividing 151 pc consumed per day by 37.8 pc/g gives 4.01 ± 0.84 g plant consumed/g beetle per day. The average weight of third-instar larvae in the sample was 4 mg.

The consumption of dry wt. per beetle

Table I shows consumption (willow) of rapid growth; we in the 5-d period, follows an average weight of 3 Oak Lake bed was consumption of about 3 prefered by the radio.

These results by this radioisotopic different for each 0 between instars, instants would appear in this example, s1 leaf on which they estimates of leaf o adults, the molting estimates. An ano was also noted: th year-olds, T1 status of the beetle for hibernation, w sites and laying egg estimated different being constant. Le feeding rates real;
### Table 1

**Average Weights of Food Consumed by Third-Instar Larvae of Chrysomela Knabi**

Values are means for 12 measurements.

<table>
<thead>
<tr>
<th>Age of larva (days in third instar)</th>
<th>Mean weight of beetles (mg dry wt.)</th>
<th>Mean weight of food eaten (mg dry wt.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.9</td>
<td>6.3</td>
</tr>
<tr>
<td>2</td>
<td>2.4</td>
<td>10.7</td>
</tr>
<tr>
<td>3</td>
<td>4.6</td>
<td>15.0</td>
</tr>
<tr>
<td>4</td>
<td>7.4</td>
<td>15.4</td>
</tr>
<tr>
<td>5</td>
<td>9.0</td>
<td>8.3</td>
</tr>
</tbody>
</table>

The consumption of willow leaves thus would be estimated at 16.0 ± 3.4 mg dry wt. per beetle larva per day.

Table 1 shows the results of direct laboratory measurements of food consumption (willow leaves) by third-instar larvae. This instar is a period of rapid growth; weights of larvae increased from a mean of 1.9 mg to 9.0 mg in the 5-d period. Food consumption showed an increase from 6.3 to 15.4 mg/d, followed by a sharp drop to 5.3 mg/d on the day preceding pupation. The average weight of the third-instar larvae collected from willows on White Oak Lake bed was 4 mg; in Table 1 this corresponds to a daily food consumption of about 15 mg, as compared with the field estimate of 16 mg inferred by the radioisotope technique.

These results show the accuracy which can be obtained for field data by this radioisotope technique. Biological half-lives are probably slightly different for each day of prepupation in the third larval instar, as well as between instars, but additional refinements in estimates of elimination constants would appear unnecessary. The results may be exceptionally good in this example, since the insects sampled could be related to a particular leaf on which they were feeding and thus sampling error was reduced for estimates of leaf concentrations of Ca²³⁷. Had the sampling been based on adults, the motility of stage might have reduced the accuracy in field estimates. An anomaly in the biological half-lives of Ca²³⁷ in adult beetles was also noted: the average T½ was 10 h for new adults but only 7.5 h for year-old ones. This difference is probably a reflection of the metabolic status of the beetles. New adults were accumulating materials to prepare for hibernation, whereas year-old ones were mating, seeking oviposition sites and laying eggs. The radioisotope equilibration technique would have estimated different feeding rates for the two groups of adults, other things being constant. Laboratory information was not sufficient to show whether feeding rates really differed for new and year-old adults.
Multiple-species populations

Areas with natural vegetation may easily support several hundreds of different species of insects, and ecological measurements become infinitely more complicated in such communities. Direct measurement of food consumption becomes difficult if not impossible. Indirect estimates must be made if generalizations are to be applied to the entire insect community, and approximate techniques become particularly attractive. The radioisotope equilibration method of Eq. (3) can be applied to multiple-species populations as well as to single-species populations. The rate of plant consumption by the insect community living on the above-mentioned White Oak Lake bed has been estimated through this radioisotope technique by CROSSELM and HOWDEN [6], and the theoretical validity has been discussed by CROSSELM [9]. Additional samples of the flora and fauna of White Oak Lake bed, taken during the summer of 1961, form the basic data for the present discussion. The results are similar to the estimates reported previously [6, 9] but some differences noted in the discussions can be ascribed to unusually cool weather in the summer of 1961.

An appropriate value must be selected for the elimination constant $k$ of Eq. (3). Ideally this value would be some sort of weighted average for all of the insect species feeding on vegetation on the White Oak Lake bed. Clearly it is impractical to measure radioisotope elimination rates for each individual species.

![Graph of insect weight vs. biological half-life of caesium.](image)

**Fig. 3**

Relation of insect weight to biological half-life of caesium. *(After CROSSELM [11])*
of the several hundreds of species. For caesium, however, the biological half-life has been found to be related to the size of the insect [9]. Fig. 3 shows the biological half-life of caesium in insect species plotted as a function of fresh weight (mg) of the insects. Biological half-lives of caesium in mammal species, as reported by LANGHAM and ANDERSON [10], fall close to a projection of the line in Fig. 3. Weights of insect species can thus be made the basis for selection of an average k for the entire community. For the present discussion we shall use a weighted average weight per insect collected in the 1961 samplings, which was approximately 20 mg fresh wt. The line in Fig. 3 suggests a biological half-life for caesium of about 7.5 h for this weight. This is 0.313 d., and the average elimination constant k is estimated as 2.21 d⁻¹. This is larger than the elimination constant of 0.98 d⁻¹ estimated for the 1958 samplings [9] but evidently there was a real difference between the average size of insect in 1958 and that in 1961.

### Table II

#### CONCENTRATIONS OF CAESIUM-137 AND BIOMASSES FOR SOIL AND TROPHIC LEVELS OF THE PLANT-INSECT FOOD CHAIN ON WHITE OAK LAKE BED, SUMMER 1961

<table>
<thead>
<tr>
<th></th>
<th>Caesium-137 concentration (pc/g dry wt.)</th>
<th>Biomass (g/m²)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Soil</td>
<td>7300</td>
<td></td>
</tr>
<tr>
<td>Plants (leaves)</td>
<td>180 ± 32</td>
<td>317 ± 49.4</td>
</tr>
<tr>
<td>Herbivorous insects</td>
<td>78 ± 4.8</td>
<td>0.111 ± 0.0192</td>
</tr>
<tr>
<td>Predaceous insects</td>
<td>73 (8 samples) lumped</td>
<td>0.0217 ± 0.0015</td>
</tr>
</tbody>
</table>

*a* Soil value based on grand mean from core samples.

*b* No samples taken.

The basic data obtained in the 1961 samplings are given in Table II. Concentrations of Ca¹³⁷ in plants (leaves) and in herbivorous and predaceous insects are essentially the same as those reported for 1958 [6]. Biomasses, however, are lower, evidently as a result of cooler weather in the summer of 1961. Plant biomass dropped from about 600 to about 300 g/m²; the average herbivorous insect biomass dropped from approximately 250 to approximately 100 mg/m². Final biomass samples at the end of the summer approached 250 mg/m², however.

Using the data in Table II, one can estimate the average rate of feeding r for the herbivorous insects as follows: \((2.21)(78) = 172\) pc/g insect per day.
Dividing by plant concentration (150 pc/g), one obtains \( r = 1.08 \) g plant/g insect per day. This is 0.120 g plant/m²-d for a biomass of 111 mg/m², or 12 g/m² in a 100-d growing season. The proportion of the plant biomass consumed by insects would thus be 3.8%, which compares favourably with the 4% estimate reported for the 1968 data [9].

This amount of plant consumption is the amount necessary to maintain the steady-state equilibrium concentration in the herbivorous insects. A certain amount of the insect biomass is lost through mortality during the season, and is offset (or more than offset) by insect production. This production represents an additional consumption of plants by insects, for which we have no measure in this mixed insect community. However, estimates of feeding for production in various communities are usually about 25% of the amount of feeding required for maintenance [11]. If this is true for the insect community on White Oak Lake bed vegetation, the total average daily consumption of plants would be about 0.150 g, or 15 g per season, or 4.7% of the plant biomass consumed during the entire growing season.

Similar calculations can be made for predaceous insects from the data in Table II. If all of the predators are assumed to feed on herbivores, and thus secondary predation is ignored, \( r \) can be estimated as 2.06 g herbivore consumed per g predator per day, or 0.024 g herbivore consumed/m² d, or 2.4 g herbivore consumed/m² per growing season. This value is 15% of the amount of plant material consumed by the herbivorous insects, but 80% of the total insect production estimated above. These estimates of herbivore consumption by predators seem high. However, TEAL [13], in discussing the predator-prey balance in a temperate cold spring, estimated non-predatory mortality of herbivores at 19.4%, which is the converse of the 80% predatory mortality estimated here. The relative paucity of predaceous insects makes sampling more difficult for both Ca⁺²⁺ content and biomass estimates. Further sampling and analysis of the predator trophic level will be required to improve estimates of food consumption by predators.

DISCUSSIONS AND CONCLUSIONS.

The field aspects of the two examples given here were handled under conditions unfavourable for radioactive tracer work. White Oak Lake bed contains a mixture of heterogeneously distributed radioisotope species, at levels of radioactivity generally lower than is desirable for tracer studies. These difficulties have been overcome in newly created tagged field sites. Insect consumption of foliage in a forest site tagged with Ca⁺²⁺ is being measured in a manner similar to the studies performed on White Oak Lake bed, except that control over distribution and concentration of calcium-137 in the forest system has greatly eased the problems of measurement. The accumulation of various radiocarbon by forest-floor arthropods also is being studied through steady-state concentrations and biological half-lives. In this case tagging has been accomplished by placing tagged tree leaves in small fenced (1-m²) plots. The arthropod food chain which has as its base leaf litter is being studied in this manner.

H. HUQUE: V in vivo?

D. A. CROSSLEY: counting for single-measure and follow faces collections? W. KLOFT: D. logical analysis? You, of ant colonies, but exchanges within co D. A. CROSSLEY as herbivores do course change their fore, was to consider are predaceous we counted as a herbivore we counted ants as I. R. von BORSTE different temperatures D. A. CROSSLEY approximately a Q10 of nation rate. This is to measure metabolism combination of isotopic words, you may be through changes in t
Preliminary results from these additional studies have confirmed the value of measurements of biological half-lives for the interpretation of food-chain transfer of radioisotopes. These radioisotope techniques are fulfilling their initial promise as an uncomplicated technique for specifying rates of movement of materials along food chains, and thus quantifying the relationships of herbivorous insect populations to plants and of predators to prey.

REFERENCES


DISCUSSION

H. HUQUE: What was your technique for measuring radioactivity in vivo?

D. A. CROSSLEY: We used three methods: well-type scintillation counting for single insects; similar instruments for groups, so that we could measure and follow individuals and groups of insects through time; and total-integrated measure from cultures through time.

W. KLOFT: Did you include ants among predatory insects in your ecological analysis? Your method is excellent for estimating the predatory effect of ant colonies, but some complex problems arise here, such as social food exchanges within colonies.

D. A. CROSSLEY: The classification of certain insects as predators or as herbivores is bound to be an arbitrary one, since some insects will of course change their habits with changes in life history. Our method, therefore, was to consider the stage of the life-history. Larval forms which are deciduous were included as predators. A herbivorous adult was counted as a herbivore, even if the larval stage was deciduous. I believe we counted ants as herbivores.

R. von BORSTEL: Did you carry out your feeding experiments at different temperatures?

D. A. CROSSLEY: Yes, and we found that elimination rates follow approximately a Q10 law, i.e., for doubled metabolic activity twice the elimination rate. This suggests the use of elimination rates for radioisotopes to measure metabolic rates, which I believe to be feasible with the proper combination of isotopes and insect. By selecting the proper isotope, whether food, water, or in other words, you may be able to estimate metabolism in vertebrate populations through changes in the elimination rate.
M. FRIED: If I understood correctly, you have estimated the leaf consumption per unit of body-weight of the insect, using steady-state values of Cs^{137}. You also had the necessary data for the same calculation using steady-state values of Sr^{90}. Did these calculations give you similar results, and if not, why not?

D. A. CROSSLEY: No, strontium concentrations did not yield identical results. The discrepancy is due to less complete absorption of Sr^{90} from the intestinal tract. We made the assumption of complete absorption in these studies. That is almost true for caesium, but definitely not true for strontium.