UNIVERSITÉ DES SCIENCES ET TECHNIQUES DE LILLE

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DYNAMIQUE DE POPULATION CHEZ *ISCHNURA E. ELEGANS* (VANDER LINDEN) (INSECTES : ODONATES) AVEC INTÉRÊT PARTICULIER POUR LES CHANGEMENTS MORPHOLOGIQUES DE COLORATION, LE POLYMORPHISME DES FEMELLES ET L'INFLUENCE DE CYCLES PLURIANNUELS SUR LE COMPORTEMENT.

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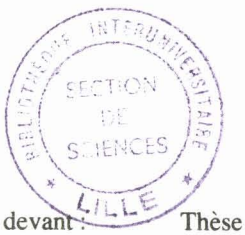

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TABLE DES MATIERES

PREFACE

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LISTE D'ABREVIATIONS

F farnésol

JH hormone juvénile

Lm longueur de vie maximale observée

$\bar{L}$ longévité moyenne

c corrigée

a des spécimens de la population active

LT méthode table de vie

FF méthode de Fisher & Ford

1 méthode de correction 1

2 méthode de correction 2

$\bar{s}$ taux de survie journalier

Sx déviation standard

$S\bar{x}$ marge d'écart ("standard error")

$\bar{x}$ moyenne ("mean")

SOMMAIRE

Ischnura e. elegans est un Zygoptère commun en Europe, dont la saison de vol s'étend de mi-mai à mi-septembre. Cette espèce montre des changements morphologiques de coloration qui coïncident avec des stades de développement de l'adulte : un polymorphisme accusé est constaté chez les femelles (Annexes A 85-A 86).

Lord (1961) a démontré qu'il s'agit d'un polymorphisme génétique et a aussi décrit le tégument des types différents et la façon dont les couleurs sont produites. Une première couche de petits granules juste en dessous de la cuticule, par diffraction de la lumière par effet Tyndall, produit la couleur bleue, par l'interaction d'une matrice plus au moins jaune et une deuxième couche de granules plus larges, composées d'ommochromes, absorbant ou réflechissant la lumière selon les cas. L'andromorphisme féminin est démontré être un désavantage quant aux chances d'accouplement.

Parr (1965,1969) a comparé plusieurs méthodes pour estimer la longévité, le sex-ratio et le nombre d'animaux grâce à des méthodes de marquage et recapture. Le problème réel est l'évaluation des résultats. Il a étudié un grand nombre de populations et certaines ont été suivies pendant plusieurs années. Il a confirmé le schéma des changements de coloration proposé par LORD et les a situés chronologiquement.

Le premier but de la présente étude est d'étudier le pourquoi et le comment de ces changements de coloration et du polymorphisme et comment ces phénomènes sont supposés jouer un rôle dans le comportement des animaux

et même dans la dynamique de population . Les facteurs influençant le comportement, la distribution de la population, la longévité moyenne ($\bar{L}$), le taux de survie journalier ($\bar{s}$) et l'effectif des populations seront analysés. Un autre but est aussi de démontrer les mécanismes physiologiques et le système d'hérédité gouvernant les changements de coloration et le polymorphisme. Une synthèse sera faite des résultats et de la connaissance actuelle pour essayer de placer le comportement d'Ischnura elegans dans un cadre plus général quant à la dynamique de population situé dans un arrière-plan physiologique.

Parmi la série d'habitats étudiés par les autres auteurs existe une lacune : un habitat ouvert et non isolé, lequel a été trouvé à Denderleeuw (Belgique, Flandre orientale, A 83) où une expérience de marquage a été effectuée (A 1 à 34).

Pour pouvoir évaluer les résultats obtenus dans des conditions naturelles par ces diverses expériences, nous avons essayé de garder des adultes d'I.elegans en vie au laboratoire.

Les animaux ont été traités par l'hormone juvénile pour démontrer le mécanisme gouvernant les changements de coloration, la maturation et la longévité.

METHODES

Pour garder des adultes d'Odonates en vie dans le laboratoire, Seidel & Buchholtz (1962) avaient construit tout un système écologique, tandis que Johnson (1965,1966a) utilisait des insectariums de plus petites dimensions. Ces méthodes sont très valables pour permettre en fin de compte

des recherches éthologiques, et d'élevage, mais ne le sont guère pour des recherches physiologiques.
J'ai utilisé des petits récipients en plastique transparent (8x4x4 cm), le fond couvert d'un gros papier absorbant mouillé. Les Odonates aux ailes coupées près du nodus occupent ces cages à deux et sont nourris de Drosophila melanogaster. Ce nourrissement de longue durée (± 1 heure par jour par 20 spécimens) est l'inconvénient pratique de la méthode. Les animaux de laboratoire utilisés sont des I.elegans ténérales (*) du premier ou du deuxième jour.

Pour l'expérience de marquage à Denderleeuw un nouveau système de marquage a été utilisé (un code simple à points et tirets appliqués avec de l'encre non soluble à l'eau). Il s'agissait d'une population d'I.elegans, vivant dans un cratère d'une bombe de la deuxième guerre mondiale, entourré de plusieurs autres étangs : un système ouvert et non isolé(A 83).
Les données de Lord (1961) et Parr (1965, 1969, 1973a, 1973b) Parr & Palmer (1971) et Parr & Parr (1972) sont aussi utilisées. Lord a fait une expérience sur un étang de dimensions non spécifiées à Anglesey near Bangor (GB). Parr a étudié quatre populations, dont deux durant plusieurs années. Trois de ces populations ont été observées pendant toute la saison de vol à Dunham (GB). Sa quatrième expérience est exécutée à Dale, Pembrokeshire (GB). Un de ces habitats était très isolé. Enfin Van Noordwijk(1978) a étudié des populations de plusieurs espèces dans un système de marais et étangs à Welle (Belgique, Flandre orientale) près de l'habitat de Denderleeuw.

(*) Stade ténérale ("teneral stage") : les deux premiers jours après l'éclosion; les ailes ont encore une brillance opaque.

LONGEVITE

La longévité obtenue au laboratoire(table 1) nous permet de trouver une distribution théorique de mortalité par groupe d'âge (distribution F, $\nu_1 = 2$, $\nu_2 = 15$) et la distribution d'âge de la population théorique (A 80-82, table 2). Nous remarquons également qu'il n'y a pas de différence entre la $\bar{L}$ des mâles et des femelles.

Les valeurs obtenues dans la nature tant par la méthode de Fisher & Ford (1947) que par l'utilisation de la table de longévité sont fortement influencées par la durée de l'expérience de marquage. La première fait une estimation du $\bar{s}$ tandis que la deuxième calcule la $\bar{L}$, mais ces résultats sont sous-estimés.

La table de longévité peut être corrigée de deux façons : 1) en prenant la moitié de la période de marquage et en considérant un même nombre de jours de recapture pour chaque jour de marquage, ceci donne à chaque longévité une même probabilité d'être observée. C'est la méthode la moins influencée par des fluctuations de la fréquence des recaptures. 2) En calculant une table de longévité corrigée en réévaluant chaque nombre observé à sa propre valeur. $\left[N_i' = N_i \cdot (n-i)^{-i} \cdot n \right.$

N_i = nombre d'insectes au jour i, n = nombre de jours de recapture.$\left.\right]$

Il est évident que la durée de l'expérience limite la longueur de vie maximale observée (L_m).

De la $\bar{L}$ de mon expérience de laboratoire (table 1) un $\bar{s}$ est dérivé ($\bar{L} = 1/1-\bar{s}$) avec lequel une table de longévité avec $\bar{s}$ constant est construite (table 4). Pour chaque jour une $\bar{L}$ avec les données de la période considérée a été calculée, jusqu'à 50 jours. La comparaison

avec la $\bar{L}$ initialement obtenue nous donne un facteur de correction suivant le nombre de jours de recapture.

En traitant toutes les données numériques de la littérature (table 3, A 36-41) avec ces facteurs, il est constaté que cette $\bar{L}$ corrigée ($\bar{L}c$) est presque identique pour un même type de biotope (table 6). Une même constatation a été faite à partir de données de Corbet (1956) de populations de Pyrrhosoma nymphula (table 7). Les valeurs les plus petites correspondent aux habitats ouverts et non isolés. La valeur la plus élevée correspond à un habitat fermé.

PERIODE DE MATURATION ET DISTRIBUTION D'AGE DE LA POPULATION ACTIVE.

Beaucoup d'espèces d'Odonates montrent des changements morphologiques de coloration (Gambles 1960, Jacobs 1955). La coloration juvénile se développe dans le stade ténéral, les premiers jours après l'éclosion. Après ce stade de gamétogenèse (commencé au dernier stade larvaire) suit le stade juvénile dans lequel le comportement sexuel se développe et on remarque pour I.elegans un changement de coloration. En vieillissant un dernier changement se produit.

Beaucoup d'observations (Pajunen 1962a, Waage 1972, Corbet 1952, Heymer 1964, Parr & Parr 1979, Trottier 1966, Van Noordwijk 1978, Moore 1953, Gambles 1960, Bick & Bick 1961, 1965, Zahner 1960) nous montrent que c'est à partir de la période de maturité que les Odonates regagnent la population active près de l'eau après une période de maturation en zone neutre (*), sans comportement sexuel.

(*) Zone neutre ou hinterland : l'arrière pays où les animaux sont plus dispersés et où il n'y a pas d'interactions sexuelles (A 84)

Une table de longévité corrigée nous donne les fractions près de l'eau de chaque groupe d'âge comme : $\sum n.\bar{s}^{-i}$ ($\sum n$ = nombre de survivants, $\bar{s}$ = taux de survie, i = temps en jours). Une série de valeurs est obtenue qui montre un maximum bien défini. (table 5, A 43-54). Cette période peut être considérée comme sous-estimée par la nature de la méthode de la table de longévité. En estimant la population (le maximum obtenu le jour de la maturation ou une valeur plus élevée) et en le multipliant avec $\bar{s}^{i}$, il est possible d'obtenir une série qui montre que le nombre d'animaux, qui ne sont plus jamais recapturés près de l'eau après le marquage, est la somme des spécimens qui sont morts le jour du marquage, plus ceux qui ne sont revenus qu'après la fin de l'expérience, plus ceux qui sont morts pendant l'expérience mais inaperçus et éloignés de l'eau.

INFLUENCE DE L'HORMONE JUVENILE (JH) SUR LES CHANGEMENTS DE COLORATION ET LA $\bar{L}$.

Des adultes d' I.elegans, tenus en conditions de laboratoire, ont été traités par la JH et le farnésol (de Calbiochem) (A 55-79). La méthode d'injection des doses avec l'éthanol comme solvant a été abandonnée parce que le mortalité était trop élevée. Des imprégnations de la cuticule du thorax ont ensuite été essayées dans des solutions à base d'éthanol et d'huile de paraffine.

RESULTATS

LONGEVITE

Le fait le plus remarquable est que la $\bar{L}$ masculine et féminine au laboratoire sont identiques (table 1). Les $\bar{L}c$ sont pour la plupart proches de la $\bar{L}$ théorique et la longévité maximale est proche de 50 jours comme le laisse supposer notre distribution théorique d'âge. (tables 2 et 6).

PERIODE DE MATURATION, CHANGEMENTS DE COLORATION ET DISTRIBUTION DE LA POPULATION.

On constate que l'âge de maturation est plus élevé pour les femelles (table 14, A 43-54, Fig. 1 et 2) ce qui est probablement dû au fait que la spermatogenèse est plus rapide que l'oogenèse (Smith 1916, Pajunen 1962a). A aucun moment l'ensemble de la population n'est proche de l'eau. On remarque aussi que dans la population fermée, l'échange avec le hinterland (*) est très limité. L'étude est menée avec mes propres données, avec celles de Parr (1969) et celles de Corbet (1952) sur Pyrrhosoma nymphula. Dans chaque cas l'âge de maturation femelle est le plus élevé et les fractions mâles de la population proche de l'eau sont les plus élevées.

DISTRIBUTION DE LA POPULATION ET SEX-RATIO EN FONCTION DE LA DENSITE DE POPULATION.

La durée des changements de coloration en laboratoire (tables 15 et 19) permet de calculer le nombre relatif d'immatures et de

(*) ou zone neutre (A 86)

matures d'une population en se servant de la table de longévité théorique de mon expérience (table 8). Ces valeurs théoriques peuvent être pris comme des valeurs sans interaction intraspécifique, donc à densité hypothétique zéro. Avec les données des populations de Parr (1973), considérées en fonction de la densité de population (Fig. 3) on constate que les fractions immatures diminuent quand la population devient plus dense. Les femelles réagissent plus fortement au stimulus de densité que les mâles. Il en résulte que la fraction de mâles matures devient la plus importante avec une densité de population augmentante et que le sex-ratio est déterminé dans la population active par la densité de population. C'est ainsi un moyen de mesurer cette densité. Ceci était déjà indiqué par le fait que le sex-ratio (*) basé sur le total des captures et recaptures est plus en faveur des mâles que celui basé sur le nombre d'individus et celui-ci plus que celui basé sur une estimation de l'effectif de la population. (A 35) Les relations entre la densité de population et fractions à l'eau sont linéaires (Fig. 3), ainsi que la relation du sex-ratio en fonction de la densité de population (table 9, $a_o = 0.51$, $a_1 = 0.03$, $r^2 = 0.97$, $n = 4$). La population de l'habitat fermé donne des chiffres aberrants car l'échange entre les zones n'est pas libre. Ceci signifie aussi que le temps passé en zone neutre est déterminé par la densité de la population.

Que la $\bar{L}c$ différente des mâles et femelles est due à leur comportement peut être démontré une fois de plus en divisant la $\bar{L}$ masculine par la

(*) Sex-ratio comme la fraction des mâles de la population donc comme fraction de 1.

$\bar{L}$ féminine et en mettant les résultats en fonction du sex-ratio (comme mesure de la densité de population). Il en résulte pour les habitats ouverts et isolés une fonction linéaire qui rend acceptable notre point théorique (sex-ratio = 0,5; $\frac{\bar{L}\sigma'}{\bar{L}\varphi} = 1$) (A 42).

GENETIQUE DE POLYMORPHISME FEMELLE.

I.elegans a trois phénotypes femelles : un andromorphe et deux hétéromorphes (A 85-86). Johnson (1964a, 1966b) a démontré pour quatre zygoptères, dont deux du genre Ischnura, qu'il s'agissait d'une hérédité mono-allèlique autosomale avec une expression liée au sexe. La répartition des trois génotypes est théoriquement 25 % d'homozygotes andromorphiques, 25 % d'homozygotes hétéromorphiques et 50 % d'hétérozygotes (1-2-1)(Fig. 4). Lord (1961) et Parr & Palmer (1971) ont démontré que la préférence sexuelle des mâles va vers les femelles hétéromorphiques. Ceci laisse supposer une distribution différentielle non seulement entre les sexes, les matures et immatures, mais aussi entre les différents formes. Aucun auteur n'a constaté un comportement différent entre les deux hétéromorphes.

En regardant les fractions correspondantes des immatures et matures de deux populations, on constate que, dans celle à basse densité, la similarité des fractions est frappante, dans celle à haute densité la différence l'est aussi : elle est due à la fraction des andromorphes (tables 10 et 11).

Les données des trois populations de Parr & Palmer (1971) et la répartition théorique du type d'hérédité de mon hypothèse (1-2-1) à densité zéro et sans interaction, nous donnent des relations linéaires en fonction de la densité pour les fractions des andromorphes et la fraction des deux hétéromorphes ensemble. La différence entre les deux hétéromorphes n'est exprimée qu'à maturité (table 12).

FREQUENCE DE COPULATION ET LA DENSITE DE POPULATION COMME REGULATEUR DE LA POPULATION.

Evidemment les fréquences de copulation des mâles et femelles sont égales au sex-ratio 0,5 et nulles au sex-ratio 1.
En ajoutant les fréquences de copulation trouvées par Lord (1961) et Parr & Palmer (1971) et en les considérant en fonction du sex-ratio (les immatures que Parr avait omis sont ajoutés) une relation linéaire est obtenue (a_o= 0.90, a_1= 10.78, r^2= 1.00, n = 4 pour les mâles et a_o = - 29.33, a_1 = 68.37, r^2 = 0.90, n = 4 pour les femelles). La fréquence de copulation augmente avec une densité de population grandissante (plus démonstratif dans le cas des femelles, parce qu'en même temps leur nombre dans la population active diminue) jusqu'à un maximum, après lequel cette fréquence diminue suivant une fonction parabolique chez les mâles (a_o = 77.99, a_1 = 166.23, a_2 = 88.25, n = 4) et une fonction de puissance chez les femelles (a = 0.29, b = - 10.47, r^2 = 1.00, n = 3) (table 13, Fig. 5).

En regardant les deux populations pour lesquelles il y a des données étalées sur deux années différentes non consécutives, j'ai constaté que ces populations connaissent un cycle de six ans (Fig. 5).

INFLUENCE DE LA DENSITE DE POPULATION SUR LA PERIODE DE MATURATION.

Les périodes de maturation obtenues pour les populations de Parr (1969) et la population que j'ai étudiée en relation avec le sex-ratio montrent que la période de maturation décroit linéairement en fonction de la densité de population. (table 14 , mâles $a_o = 43.95$, $a_1 = -45.00$, $r^2 = 0.93$, $n = 4$; femelles $a_o = 67.50$, $a_1 = -75.00$, $r^2 = 1.00$, $n = 3$).

INFLUENCE DE LA JH SUR LA PERIODE DE MATURATION ET LA PERIODE DES CHANGEMENTS DE COLORATION.

Les périodes des changements de coloration ainsi que la longévité sont raccourcies de plus en plus avec des doses croissantes de la JH (d'une façon linéaire) (Tables 15 à 19). Le premier changement de coloration coïncide avec la période de maturation; le deuxième dû au vieillissement est probablement provoqué par une déshydratation (constatée par prélèvement de l'hémolymphe (*)).

EVOLUTION DE $\bar{L}$ DURANT LA SAISON DE VOL.

En corrigeant les $\bar{L}$ données par Parr (1969), j'ai constaté que $\bar{L}$ est la plus élevée au début de la saison, diminue ensuite et réaugmente légèrement à la fin de la saison (A 39 à 41, Fig. 6 et 7). L'évolution de la $\bar{L}$ des femelles montre même deux pics de densité de la population (les femelles sont plus influencées par la densité).

(*) La tête et le tube digestif sont enlevés, le thorax compressé et l'hémolymphe prélevé avec une capillaire dite de microhématocrite.

$\bar{L}c$ (1) < $\bar{L}$ réelle (2) < $\bar{L}c$ + période passé en zone neutre. (3)

La valeur (1) est sous-estimée. La valeur (3) est surestimée à cause de l'échange continuel entre les deux zones.

La valeur (1) des femelles montre dans la pluspart des cas une valeur inférieure, la tendance inverse est constatée pour la valeur (3) (table 20). Ceci montre que les différences entre les sexes de la $\bar{L}$ mesurée à l'eau sont des fautes expérimentales dues au comportement différent des sexes.

DISCUSSION.

$\bar{L}$ A L'EAU : UN RESULTAT DU COMPORTEMENT

La $\bar{L}$ près de l'eau est en effet la somme de la période pendant laquelle les animaux restent dans la population active plus la période pendant laquelle il se produit des échanges entre la zone neutre et la zone active (A 84). $\bar{L}c$ est une limite minimale. $\bar{L}c$ plus le temps durant lequel ils vivent éloignés de l'eau, est la limite maximale de la $\bar{L}$ réelle. La technique de Corbet (1952) ajoutant à la $\bar{L}$ le temps de maturation est également une limite maximale. $\bar{L}c$ peut être considérée comme la $\bar{L}$ active, qui semble être constante, dépendante du type d'habitat, mais indépendante de la densité de la population. Dans des populations très denses la $\bar{L}$ active approche la $\bar{L}$ réelle, bien que la période dans la zone neutre se prolonge et que les visites à l'eau se raccourcissent, mais les échanges entre les deux zones devient très fréquent.

INFLUENCE DU TYPE D'HABITAT.

Un habitat non isolé avec beaucoup de possibilités d'émigration donne des valeurs de $\bar{L}c$ sous-estimées. Un habitat clos donne des valeurs de $\bar{L}c$ beaucoup plus proches de la $\bar{L}$ réelle car les animaux peuvent être observés pendant la plus grande partie de leur vie.

EVOLUTION DE $\bar{L}c$ DURANT LA SAISON DE VOL.

Une $\bar{L}c$ élevée au début de la saison est due au fait que tous les individus sont jeunes et que les animaux restent près de l'eau car la densité de la population est basse. A densité maximale de population, $\bar{L}c$ est minimale, comme le temps passé en zone active. A la fin de la saison $\bar{L}c$ est intermédiaire, due à une densité de population peu élevée et à l'absence d'animaux jeunes.

PERIODE DE MATURATION.

Mon expérience de laboratoire a permis d'obtenir des valeurs de la période de maturation dans une population dense. La littérature ne donne que des valeurs du même type et très peu de valeurs pour des populations moins denses. Les chercheurs préfèrent des petites populations à haute densité et se limitent involontairement à une petite partie du cycle de la population.
Toutes les données confirment que la période de maturation femelle est plus longue que celle des mâles, Smith (1916) et Pajunen (1962a) l'attribuent au fait que l'oogenèse prend plus de temps que la spermatogenèse.

DISTRIBUTION DE LA POPULATION.

Le comportement agressif et territorial et la distribution spatio-temporelle de la population sont gouvernés par la densité de la population. Ces facteurs peuvent limiter une population aussi fortement que le manque de nourriture ou que la prédation.
A faible densité de population, il n'y a que peu d'interactions et d'agressivité. Beaucoup d'immatures restent près de l'eau et le sex-ratio est près de 0,5.
Si la densité augmente, l'agressivité se développe (Johnson 1962, Crumpton 1975, Pajunen 1964), le sex-ratio est en faveur des mâles et une certaine territorialité est observée.(Kormondy 1959, 1961, Pajunen 1964, 1966a, St.-Quentin 1964, Heymer 1964, 1968a). Les interactions sont plus nombreuses et la période proche de l'eau plus courte (Kaiser 1974).

A plus forte densité de population les territoires deviennent moins adaptés (Pajunen 1966b) et un certain nombre de mâles non-territoriaux, chassant même des femelles dans l'ensemble de l'habitat, y-compris celles in copula, réduisant ainsi le succès reproductif (Pajunen 1966b). Les jeunes animaux, les mâles âgés et les femelles ne sont trouvés près de l'eau qu'en petites quantités. Chez les femelles l'andromorphisme devient un avantage.

Cet avantage des femelles andromorphiques devient de plus en plus important dans des populations à densité extrème, évitant l'élimination des andromorphes par sélection naturelle. Un désavantage devient un avantage à plus forte densité de population.

Dans les populations à extrême densité l'agressivité disparaît (Pajunen 1962b, Buchholtz 1951, Zahner 1960, Crumpton 1975, Klötzli 1971) car la compétition pour un partenaire n'existe plus : il n'y a presque plus de femelles près de l'eau. Agressivité et territorialité constituent une stratégie d'adaptation continue à des différentes circonstances de densité.

La densité de la population est le facteur déterminant le temps passé en zone neutre; le nombre de spécimens présents en zone neutre et donc le sex-ratio en bord d'eau. Le vrai sex-ratio est 0,5, les autres valeurs mesurés en zone active ne résultent que du comportement de l'animal.

Ces valeurs en faveur des mâles chez les Zygoptères et en faveur des femelles chez les Anisoptères sont facilement acceptées d'autant plus que des valeurs similaires sont trouvées chez les larves.

Ce phénomène a été expliqué par la plupart des auteurs par une mortalité différente : il semble que ce ne soit pas le cas étant donné que ce sex-ratio est maintenant démontré être le résultat du comportement.

En acceptant une distribution similaire pour les stades larvaires et adultes, le mécanisme devient plus simple et évident : dans le courant du stade larvaire les sexes commencent à se comporter différemment. La distribution change et le sex-ratio s'éloigne de 0,5 : les mâles occupent les endroits les plus avantageux de l'habitat, profitant d'une meilleure nourriture et ayant un développement plus rapide. Ceci provoque l'éclosion plus rapide chez les mâles. Cette hypothèse est soutenue par plusieurs observations publiées. (Lawton et al. 1980, Ingram 1976, Lawton 1970, Johannson 1978, Blois 1985). Il est vraiment dommage que si peu d'auteurs aient fait attention au comportement différent des sexes et au comportement évoluant selon l'âge des larves.

Ma conviction que le comportement est continu à travers la vie et non interrompu par la métamorphose est soutenue par le fait que certains auteurs ont observé aussi un certain degré d'agressivité et de territorialité chez les larves (Corbet 1952, 1962, Needham 1930, Heymer 1968b, 1970, Rowe 1980, Macan 1970).

MECANISMES PHYSIOLOGIQUES

La JH est connue comme stimulant du vol, de la migration et du métabolisme (Rankin & Riddiford 1978); de même un rôle de contrôle a été accordé aux corps allates à la période de maturation de Dictyoptères (Engelmann 1960).

INFLUENCE DE LA JH SUR LA PERIODE DE MATURATION.

Staal (1961) a observé une longévité plus longue chez Locusta migratoria (Orthoptera) privé des corps allates, tandis que Loher (1960) a remarqué déjà l'influence de la densité de la population et la concentration de la JH sur le changement de coloration. Norris (1964) trouvait que des mâles matures font accélérer la maturation des autres mâles, tandis que un grand nombre de juvéniles inhibe la maturation par l'intermédiaire de phéromones.
Ces observations correspondent avec l'effet raccourcissant que la JH a sur la durée des périodes de changement de coloration et sur la $\bar{L}$, mais m'aident aussi à expliquer beaucoup mieux l'évolution de $\bar{L}c$ durant la saison de vol : au debut de la saison la majorité des animaux est juvénile ce qui inhibe la maturation. Au moment où la densité de la population augmente, la fraction des mâles matures devient plus importante, stimule la maturation et raccourcit la vie.

Le fait que la coloration soit tellement importante pour le choix du partenaire et que cette coloration soit un facteur de reconnaissance du stade de développement sexuel me font croire que le stimulus qui intervient dans ce mécanisme de synchronisation de la maturation est un stimulus visuel chez I. elegans.

CHANGEMENT DE COLORATION AU NIVEAU CELLULAIRE.

Les couches de granules d'ommochromes en dessous du cuticule ont été décrits par plusieurs auteurs (Lord 1961, O'Farell 1968, Veron 1973, Charles & Robinson 1981). Chez I. elegans la couche de petites granules à effet Tyndall est liée aux mâles et aux femelles andromorphiques homozygotes et hétéromorphiques hétérozygotes.

Il est aussi remarquable que la différence entre les deux génotypes hétéromorphiques ne s'exprime qu'au stade mature.

La façon dont agit la JH au niveau de la maturation et du développement du comportement sexuel n'est pas connue, mais comme la JH stimule le métabolisme et l'activité, un métabolisme élevé donne une haute concentration de tryptophane toxique (un produit catabolique de protéines), un précurseur d'ommochromes (Bückmann et al. 1966).
La couleur jaune de la matrice est très probablement due à des précurseurs d'ommochromes.
Il est aussi connu qu'une concentration basse de la JH provoque une déshydratation, que j'ai trouvée chez I.elegans également (Alltman 1956, Raabe 1959). Cette réduction du contenu d'eau est considérée comme le

mécanisme causant le changement de coloration coïncidant avec le vieillissement. Un déficit en eau provoque une faible excrétion de tryptophane, dont la concentration augmente ainsi que les autres précurseurs d'ommochrome. La contraction des tissus renforce aussi l'effet Tyndall.

CONCLUSION.

L'interaction intraspécifique doit être considérée comme beaucoup plus importante que l'interaction entre espèces différentes d'Odonates et c'est la densité de la population qui, par l'intermédiaire de plusieurs mécanismes physiologiques, est un des facteurs les plus importants dans la dynamique de population. La JH joue ici un rôle important. L'agressivité et la territorialité sont les moyens par lesquels les animaux s'adaptent à la densité de population résultant en une distribution de population et des chances de copulation plus au moins grandes.

Ces mécanismes donnent un cycle pluriannuel de la population.

Les formes de couleur d'I.elegans forment une stratégie d'adaptation aux différentes densités et sont les stimuli qui influencent les processus physiologiques qui gouvernent le développement du comportement sexuel.

La synchronisation larvaire (Schaller 1972, Yagi 1976) est suivie par une synchronisation de maturation pour obtenir le plus grand nombre d'adultes matures en même temps, tandis que les individus

dans les autres phases de développement sont chassés de la zone active par l'agressivité des mâles matures. Il a été montré qu'une haute densité de population accélère les phénomènes physiologiques et la vie entière. Ceci est également un mécanisme d'adaptation à des différentes densités de population, lesquelles seraient encore plus élevées si la $\bar{L}$ n'était pas raccourci par l'effet de densité.

La meilleure stratégie pour préserver une espèce est l'expansion. A fin de produire un maximum de spécimens, les effets négatifs de la densité de population (comme le manque de nourriture et les chances de copulation moins favorables) doivent être neutralisés. La dispersion de la population (avec la possibilité de coloniser d'autres habitats) et le raccourcissement de la vie sont les moyens uitlisés.

POPULATION DYNAMICS OF ISCHNURA E. ELEGANS (VANDER LINDEN) (INSECTA: ODONATA) WITH SPECIAL REFERENCE TO MORPHOLOGICAL COLOUR CHANGES, FEMALE POLYMORPHISM, MULTIANNUAL CYCLES AND THEIR INFLUENCE ON BEHAVIOUR.

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Keywords: Odonata, Population dynamics, Juvenile hormone, Morphological colour changes, Genetical polymorphism, Longevity, Maturation, Population distribution, Crowding, Visual stimuli, sex ratio.

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ABSTRACT

Laboratory and field experiments in adult I. elegans provide correction techniques for the estimation of population parameters based only on capture-recapture data. Thus it is demonstrated that male and female longevities are identical and that their sex ratio is 0.5. (Male fraction) Longevity, measured at the water, erroneously appears to differ between sexes, and sex ratio is also biased. This bias is a function of population density, which causes a different distribution in males and females, matures and immatures, andro- and heteromorphic females, and is regulated by aggressive, territorial and mating behaviour of individuals. The female maturation period exceeds that of the male. Female polymorphism is an adaptation to population density, high density favouring andromorphs. This polymorphism is determined by single allellic autosomal inheritance with a sex-linked expression.

In crowded populations, intense visual interactions between individuals occur. These cause their juvenile hormone titer to rise, which shortens maturation time, the period of morphological colour changes, and life span. This mechanism counteracts crowding, and synchronises maturation and development of sexual behaviour.

In the course of their life, individuals go through a

number of colour changes. The development of teneral colours coincides with spermato- and oogenesis. The morphological colour change at sexual maturity is due to the neutralisation of toxic waste products of the protein metabolism. The ageing colours are partly due to dehydration.

INTRODUCTION.

The zygopteran Ischnura elegans, (Vander Linden) widely distributed in Europe, has a long flight season, extending between mid-May and mid-September. It has been intensively studied by different authors in the field and in the laboratory.

I. elegans shows a morphological colour change during its life span, further complicated by the fact that females display different colour morphs. The colour changes in I. elegans are called morphological if they coincide with developmental stages and are irreversible. Reversible colour changes induced by temperature or humidity are called physiological. Morphological colour changes are observed in many Odonate species, e.g. in Crocothemis erythraea, C. sanguinolenta, C. divisa, Trapezostigma b. basilare, Pantala sp. (Gambles 1960), and Plathemis lydia (Jacobs 1955). Polymorphism is very common in Ischnura spp. and has been described by Tillyard (1905) in I. heterosticta, by Grieve (1937) in I. verticalis, by Killington (1924) and Longfield (1936, 1949) in I. elegans, by Johnson (1966b) in I. demorsa, and by Johnson (1964a) in I. damula.

In what follows, we define as tenerals all specimens with a typical vitreous sheen on the wings (first and second day after eclosion).
Immatures are all animals not showing sexual behaviour. The

immature stage is further divided into a teneral and a juvenile stage.

Matures are all animals showing sexual behaviour and the term adults is used as a synonym for imagines.

During the teneral stage the definitive juvenile colours appear. Omura (1955) found that spermatogenesis is fully developed in tenerals and that there is no difference between tenerals and mature specimens in Pseudothemis zonata. Smith (1916) even states that spermatogenesis starts in larvae. Spermatogenesis thus coincides with the development of the juvenile colours in adults. The maturing colour change of the juvenile stage is related to development of sexual behaviour.

In Leucorrhinia dubia and L. rubicunda, Pajunen (1962a) found undeveloped gonads in larvae and tenerals until the age of 4 to 5 days. The maturing colour change started later. Buchholtz (1951) and Zahner (1960) observed copulation 3 days after eclosion, and in warm weather even on the first day. This shows that the ability to mate exists as soon as the teneral stage ends and the juvenile stage begins, even before the onset of sexual behaviour.

Lord (1961), in a short capture- recapture experiment at Anglesey (U.K.), and by keeping specimens in a large out-door cage, demonstrated that I. elegans shows a genetic polymorphism in females and a morphological colour change, but proposed no inheritance mechanism.

Males change from green (juvenile), through turquoise (mature), to blue (old). Female colour changes and

polymorphism are shown in Fig. 4. The violacea form has a violet thorax, rufuscens is orange-fawn or somewhat red and has no or light brown humeral stripes, infuscans-obsoleta has light or dark brown humeral stripes and is fawn in colour. Infuscans is greenish to greenish-brown. All forms except rufuscens and infuscans-obsoleta have black humeral stripes.

A85
A86

Lord (loc. cit.) gave an extensive description of the integument of the different I. elegans morphs. The colours are formed by the interaction of small granules directly under the cuticle, which scatter light by a Tyndall effect and produce a blue colour (Mason 1923), combined from a more or less yellow or dark yellow matrix and underlying larger ommochrome granules, absorbing and in some cases reflecting light. Female andromorphism was shown to be disadvantageous to reproduction.

Different methods exist to study populations of imaginal Odonata, providing estimates of mean longevity, sex ratio and population number. All these methods are more or less valuable, but the real problem consists in gauging the results and their interpretations.

Parr (1969) studied several populations in the United Kingdom at Pembrokeshire and Dunham and made a follow-up study of some of these over several years. Different estimating techniques to calculate mean longevity ($\bar{L}$), daily survival rate ($\bar{s}$), and population number were

compared. This threw some light upon the many problems of estimating $\overline{L}$. Lords scheme of colour changes was confirmed and was put on a time scale.

My first aim was to study the how and why of ischnuran colour changes and polymorphism. As these phenomena are supposed to play a role in the behaviour and population dynamics of the species, factors influencing behaviour, population distribution and the measurement of $\overline{L}$, $\overline{s}$ and sex ratio were analysed. Another purpose was to disclose the physiological mechanisms ruling colour changes as well as the inheritance scheme itself. A final aim was to synthesise my findings with preexisting knowledge as to integrate behaviour and the ischnuran colour system into a general population dynamics and physiological framework.

Other authors have studied populations within a nearly complete range of habitats, but they always selected isolated populations. In contrast, my capture-recapture
A83 experiment was set up at Denderleeuw (Belgium) on a non-isolated population.

Live I. elegans specimens were kept in laboratory
A61-62 conditions to obtain $\overline{L}$, $\overline{s}$ and a time scale for the colour
A78-79 changes, as a basis for comparison with field data.

Finally, specimens were treated with juvenile hormone to study the physiological mechanisms governing colour changes, maturation and longevity.

MATERIALS AND METHODS.

MAINTAINING A LABORATORY STOCK OF LIVE ODONATA FOR PHYSIOLOGICAL STUDIES.

PREVIOUS METHODS.

Methods for keeping Odonata alive in laboratory conditions were described by Johnson (1965, 1966a) and by Seidel & Buchholtz (1962).

Johnson (1965) first used terraria 60 cm long, 35 cm wide and 55 cm high, blackened with aluminium paper to make the cage vision-proof and to inhibit escape behaviour. The top was covered with a screen-coated wooden frame and the bottom with moistened absorbent paper. Each cage contained 16 specimens, that were fed Drosophila sp..

Later, Johnson (1966a) used breeding cages with fine mesh screening, covered by plate glass. As the animals are sensitive to low humidity, a fingerbowl with water-soaked sand was added.

Seidel & Buchholtz (1962) used an artificial biotope: a room 4.55 m x 3.30 m in size, 2.70 m high, with a pond of 3.00 m x 2.30 m, flowing water, waterplants and artificial sunlight.

Although these methods work well for breeding and ethological experiments, they are expensive, use much space and are impractical for physiological work.

DESCRIPTION OF A NEW METHOD FOR MAINTAINING A STOCK OF LIVE ODONATA.

A simple, yet satisfactory method using cages without cover was developed. The bottom of each cage was covered with thick wettened filter paper, and the size was adapted to the dimensions of the species used. For I. elegans, for example, a plastic box of 8 x 4 x 4 cm per 2 specimens gave excellent results. In our experiment, transparent plastic boxes were used, placed one against another in a block, allowing visual contact between the animals.

In Zygoptera, wings were cut at the nodus. Enough of the wings was left to provide a grip for handling specimens for feeding and other treatments. Because in Anisoptera the centre of gravity lies higher than in Zygoptera, individuals with part of the wings removed, lose balance, cannot get up again, and die. Instead of cutting them, a light plastic plate was therefore glued across the four wings, fixing them in a horizontal position. This effectively kept the animals quiet and in upright position.

A drawback of this technique is the time-consuming nature of individual feeding, which requires daily individual handling of all specimens. Live Drosophila melanogaster were used as food; they were presented to the Odonata with a forceps and were readily accepted.

Individual I. elegans consume an average of 4 Drosophila per day. Lord (1961) recorded a consumption of 8 prey items per day in large outdoor cages. However, specimens without wings obviously use less energy than flying insects.

Feeding was accompanied by hoarding. The Odonata were fed once or twice a day and accepted up to 4 Drosophila specimens at a time. In I. elegans several prey items were chewed into a single meatball, kept under the mandibles, and slowly ingested afterwards. The anisopteran Sympetrum sanguineum hoarded up to eight Drosophila at a time, but kept the meatball inside its mouthparts instead of beneath them. Regularly, Odonata were observed in natural conditions with such a meatball too, but it remains uncertain whether this was composed of a single or of several prey items. An individual refusing food almost invariably died the next day.

Freshly emerged I. elegans were captured in the morning hours at the Gates reservoir (Welle, Eastern Flanders, Belgium), a habitat described by Dumont (1968, 1971), and transported to the laboratory in a chest with fine mesh screening. Two-day old tenerals, completely coloured, but still with opaque wings, were also included.

CAPTURE-RECAPTURE EXPERIMENTS.

Parr (1965) reviewed methods to estimate population number, $\bar{s}$ and $\bar{L}$, such as Jackson's first and second method (1948), Fisher & Ford's method (1947), Bailey's triple-catch method (1951), and Jolly's method (1965), and compared their respective results. The life table method, Fisher & Ford's, Joly's and Manly & Parr's method (1968) were simultaneously used and compared by Parr (1973a, 1973b, 1976) and by Parr & Parr (1979).

The method most commonly applied to estimate population numbers is that of Fisher & Ford. It can also be used to obtain $\bar{s}$ and $\bar{L}$, but the life table method is of course the simplest way to compute $\bar{L}$ (the mean of all periods between first and last capture).

A capture recapture experiment was run in August 1973 on a population of I. elegans on one of the bomb holes of World
A83 War II in the area at Denderleeuw described by Dumont
A4-34 (1971).

The population studied is situated on H_4, a circular bomb crater with a shore length of 49 m. In the vicinity, 4 other bomb craters and 2 rectangular fish ponds occur. The pond studied had the largest population of I. elegans at that time. It is topologically very open and has a free exchange with the other ponds. The vegetation around the pond is regularly cut. A small region with high grass at 30 m from the pond, where many females were found, was included.
A1-3 For marking, the individual method of Hinnekint (1974) was

used, applying numbers in a point-dash fashion on the wings with waterproof ink.

Lord (1961) studied a population of I. elegans at Anglesey (U.K.), an open, isolated system, at a pond with indeterminate dimensions and provided $\bar{L}$ based on life table ($\bar{L}_{LT}$) and $\bar{L}$ calculated with the Fisher & Ford technique ($\bar{L}_{FF}$) for two short consecutive periods. She also observed female mating frequencies in the different morphs.

Parr (1965) studied a population at an open, isolated habitat at Pembrokeshire (U.K.) during a short period and 3 populations at different ponds at Dunham (U.K.) during a complete flight season. Dunham ponds I and II are open isolated systems but pond III is isolated and closed as it is sheltered in a deep hollow and surrounded by mature oak trees. Populations I and III were also studied for a shorter period a few years later. (Parr 1969, 1973a, 1973b, Parr & Palmer 1971, Parr & Parr 1972).

Parr's work provides $\bar{L}_{FF}$, $\bar{L}_{LT}$, pond dimensions, total season population numbers mating frequencies and numbers of matures, immatures and different female morphs.

Van Noordwijk (1978) marked I. elegans and several other zygopteran dragonflies in a marsh-and-pond system at
A83 Welle (Belgium) to collect information on interspecific interactions. Such a habitat is of course an open, non-isolated system. He captured randomly, and included a large

part of the hinterland.

MEAN LONGEVITY IN LABORATORY CONDITIONS.

A61-62 $\bar{L}$ of 91 specimens of both sexes is given in table 1.

A78-79 There was no significant difference $\left[t = |-0.90| < 1.66 \text{ (t for df=89 at 5\% level)} \right]$ between $\bar{L}$ of males and of females. Both sexes may therefore be pooled. A mathematical expression describing the frequencies of the survivals was

A80-82 determined by trial and error. Normal, logarithmic normal, Poisson and χ^2 distributions were rejected. A χ^2 distribution with $\nu = 2$ provided a rough approximation, but an F distribution (i.e. a fraction with nominator and denominator χ^2 distributed) with $\nu_1 = 2$ and $\nu_2 = 15$ gave the best fit.

(χ^2 -test for goodness of fit: $\chi^2 = 15.45 < 22.4$, df=13 at 5% level).

This distribution was accepted as a theoretical base and used to calculate daily mortality, daily total number of survivors in a population, their age distribution, $\bar{s}$ and $\bar{L}$ per considered period. (Table 2).

CORRECTION OF THE LIFE TABLE DATA AND OF $\bar{L}$.

For an unbiased comparison between laboratory and field conditions, a similar method to compute $\bar{L}$ should be used. I chose as a base the time between first and last capture. All literature figures (table 3) are arithmetic means of the observed survival times, without corrections.

They underestimate $\bar{L}$ because

-the first capture is rarely during the teneral phase and the last capture is rarely at the very end of an animal's life.

-the probability of recording a short life span is larger than that of observing a longer life span.

This last point provides a way to correct field data. A capture-recapture experiment of, say, 15 days contains 1 day of only captures, and 14 days of captures and recaptures. Specimens of the first capture day can be caught during 14 days, but specimens caught on day two can only be observed for 13 days, and so on. The chance of recapturing an animal after 1 day is 14 times higher than after 14 days.

There are two ways to avoid this. The first one is to give all survival times an equal chance to be observed by using, in the example of a 15 day experiment, only the first 7 days for marking, and for each marking day 7 recapture days. This leads to 7 observation days for each of the 7 survival times, but reduces the observation period to half.

A second method is to reevaluate the observations themselves. Ni individuals (one individual should only be taken into account once, even if it is recaptured several times) taken at the i^{th} day of an n day experiment with the first day (captures only) as day 0, are reevaluated as $Ni.(n-i)^{-1}.n.$

This expression includes all observations of the experiment, but is influenced by the rareness of aged specimens. It can only be used when the experimental period exceeds or at least approaches the maximum longevity (Lm) of the species studied. The maximum survival period observed definitely influences $\overline{L}$. In the example of 15 days, no animal can be seen for longer than 7 days in the first method and 14 days in the second one. A table can be constructed to correct for this. Table 2 yields a theoretical $\overline{L}$ of 9.6302 days (Sx=9.2075, Sx=0.9269) for Lm=50 days.

This theoretical $\overline{L}$ is somewhat below the value observed in the laboratory (at Lm=50, the upper limit of $\overline{L}$ is not yet reached), but these figures fall within each others error range.

Not knowing the exact age of a specimen in the field, a constant $\overline{s}$ based on the theoretical value of $\overline{L}$ is derived from the expression $\overline{L}= 1/1-\overline{s}$, as $\overline{s}$=0.89616, and is used to construct table 4, giving a correction factor for the life table data. Attention should be paid to use the proper factor for the number of recapture days, not for the whole experimental period. Corrected $\overline{L}$ based on each of the data-correcting methods for life table data ($\overline{L}_{LTc}$) will be referred to respectively as $\overline{L}_{LTc1}$ and $\overline{L}_{LTc2}$.

CORRECTION OF $\bar{L}$ CALCULATED AFTER FISHER & FORD.

The Fisher & Ford method provides $\bar{L}$ from an estimated $\bar{s}$. However, the shorter the period of observation, the lesser the chance a marked individual will be caught again. The observation period will therefore influence the measured $\bar{s}$. Thus table 4 was used for correcting $\bar{L}_{FF}$ as well and will be referred to as $\bar{L}_{FF_c}$.

A38 For female $\bar{L}$ in Parr's 1965 13-days study (table 3), a correction factor for only 8 recapture days was used to reevaluate $\bar{L}_{FF}$. Indeed, on the first two and on the last day he captured hardly any females, while on the third day no observations were made.

A36-37 Female $\bar{L}$ in the second experiment of Lord (1961) is probably underestimated. The experiment is discontinuous and based on too few specimens. Parr's figures for the Dunham ponds are averages of $\bar{L}$ for overlapping periods. To

A39-41 adjust these, $\bar{L}$ was corrected for each period, and the average calculated.

MATURATION PERIOD AND AGE DISTRIBUTION IN AN ACTIVE POPULATION.

A84 Evidence that teneral specimens leave the active population and the water, and live in a neutral zone, without sexual behaviour is given by Pajunen (1962a) in Leucorrhina rubicunda and L. dubia, Waage (1972) in C. maculata, Corbet (1952) in Pyrrhosoma nymphula, Heymer (1964) in Oxygastra curtisi, Parr & Parr (1979) in

Ceriagrion tenellum, Trottier (1966) in Anax junius, Van Noordwijk (1978) in Coenagrion puella and C. pulchellum (here many mature female specimens also lived away from the water), Moore (1953) in Brachytron pratense, Aeschna cyanea, Anax imperator, Orthetrum cancellatum, Libellula quadrimaculata, L. depressa and Sympetrum striolatum, Gambles (1960) in Lestes virgatus, Bick & Bick (1961, 1965), Zahner (1960) and many others. It is thus a widespread behaviour in Odonata. Only rarely (Parr 1973b) do tenerals and immatures not leave the water.

A measure of presence at the water in different age groups can be extracted from the corrected life table, showing equal chances to observe each survival period. Table 5 shows an example based on a fixed $\bar{s}$. Column 1 gives the survival periods, column 2 the surviving individuals for each period, column 3 the total survivors on the i^{th} day, column 4 the total survivals revised by raising the corresponding $\bar{s}$ to the power -i. For example one specimen living for 4 days corresponds to $1.s^{-4}$ specimens on the first day. This expansion shows a maximum, representing the maximum active population fraction at the water, and is entered on top of column 6. In column 6 the maximum active population decreases each day by multiplying it with $\bar{s}$ to give the theoretical attendance at the water of each age group. The difference between columns 6 and 3 is shown in column 7 as the number of animals away from the water. A maximum in column 7 indicates a maximum in column 5. Column

5 gives the fraction of the population at the water based on column 4 and on the total survivors of column 3. Emergence peaks do not interfere, because figures of first and last captures of many days are pooled. The accuracy of this method can be checked by verifying that the difference of the top figures of columns 3 and 6 (115) approximately equals the maximum number of animals away from water (day 1: 337-238=99) plus the number of animals surviving after 13 days (11). If this is not so, the maximum active population size has been erroneously estimated. In such
A43-54 cases, several larger top values for column 6 were tried until a reasonable match was obtained.

ACTION OF JUVENILE HORMONE (JH) ON COLOUR CHANGE PERIODS AND $\bar{L}$.

A55-79 Teneral I. elegans males kept under laboratory conditions were treated with JH (Calbiochem) and farnesol
A63 diluted in ethanol. Injecting JH solutions caused a very high death rate, probably due to the ethanol solvent. However, it was found adequate to apply the hormone solution on one side of the thorax to impregnate the cuticle, although a few specimens surviving an injection with the ethanol solution reacted more strongly to the same dose of JH than impregnated ones. In tests with 250 µg of
A74 farnesol, the dose was split into 3 subdoses applied on 3 consecutive days.

This same experiment was repeated using JH and farnesol solutions in paraffin oil for cuticular

impregnation. The experiment was mainly run on males because female polymorphism complicates the evaluation of colours changes. In females, only changing $\bar{L}$ was studied.

RESULTS.

$\bar{L}$ IN FIELD AND LABORATORY CONDITIONS.

Table 1 shows $\bar{L}$ obtained in laboratory conditions. Most remarkable is the identical male and female $\bar{L}$ whereas field data usually show a lower female $\bar{L}$ (Table 3). These field data also show a large and unlikely spreading, caused by the methods used or by the behaviour of the animals. Table 6 presents $\bar{L}_{LTc1}$ (experiments of table 3, where enough data were available), $\bar{L}_{LTc2}$ (the larger Dunham experiments) and $\bar{L}_{FFc}$. Most figures are now close to those measured in the laboratory, and to theoretical $\bar{L}$.

APPLICATION OF THE GAUGING TECHNIQUES FOR $\bar{L}$ TO PYRRHOSOMA NYMPHULA.

The same procedure as before was followed for Pyrrhosoma nymphula (Table 7), and figures matching each other closely were obtained after correction, while uncorrected figures for different experiments were widely divergent. Strictly speaking, it is not known whether the same correction table can be used, as $\bar{L}$ in laboratory conditions is unknown for P. nymphula. The approximation

seems quite reasonable, however. In the case of I. elegans and P. nymphula, my correction of Lord's $\overline{L}_{LTc}$ may still be an underestimate as I used survival periods between captures instead of the survival period between the first and the last capture.

MAXIMUM LONGEVITY.

Lm observed in field conditions in I. elegans is 45 days (table 3). In laboratory conditions, it was 42 days (this study) and in semi-natural conditions, it was 41 days (Lord 1961). This matches the age distribution of table 4 well: 50% elimination after 6.2 days, 75% after 12.7 days, and only 1% survival after 42 days. That there is some possibility that some I. elegans can survive for about 50 days is shown by Parr (1973b): he found an andromorph female which survived for 45 days, to which at least 5 days should be added for its teneral and violacea stages.

SURVIVAL RATE.

Table 2 shows that in laboratory conditions $\overline{s}$ is 0.8907 on day 1. It goes up to 0.9037 on day 10, 0.9190 on day 25, and ends at 0.9362 on day 50. On comparing tables 2 and 4, it is seen to be a good approximation to accept a fixed survival rate.

MATURATION PERIOD, COLOUR CHANGES AND POPULATION DISTRIBUTION.

Figure 1 shows that at eclosion all animals are at the water. Their number drops immediately thereafter (0.56),
A43 but most of the population (0.80) is back at day 10, while older animals leave the water again. Maturation time here is 10 days in male I. elegans. This example illustrates that the supposed mass-mortality between day 0 and 1 is in fact the sum of real mortality on that day, plus the animals that escaped notice due to the shortness of the experiment, and those that died on other days, away from the pond. The same $\bar{L}$ is obtained and the lack of immatures in the active population is explained, bringing field data into agreement with laboratory data, where $\bar{s}$ is only a little lower at the beginning and a little higher at the end of life. The very high mortality between days 0 and 1 was explained by Parr (1973b) as natural mortality in I. elegans, whereas, in Enallagma cyathigerum, he considered the marking itself as the source of mortality (Parr 1976).
A44 In females, the number initially drops even more (0.37) than in males, and climbs to 0.47 at day 12 (Fig. 1).

The same method can also be applied to other species,
A45-46 e.g. to Corbet's (1952) life table of Pyrrhosoma nymphula (corrected with method 2: $N'=Ni.(n-i)^{-1}.n$). Most males (0.91) are at the water on day 12; in females, only a fraction (0.61) reaches the water on day 14 (Fig. 2). Knowing that the maturation period away from the water is

underestimated by the nature of the life table technique, these figures match remarkably well the maturation period of approximately 15 days observed by Corbet (1952) as the interval between an eclosion peak and a peak of new animal arivals at the pond.

In both species, we see that more males are observed at the water at maturity while in females only a small fraction is seen and the presence at the water of every age group is inferior to the corresponding age group in males. In both species, male maturation is of shorter duration than for females. However, when applying this calculation

A47-52

to the Dunham populations of I. elegans from Parr (1969), I found that the fraction of the populations at the water are, by the nature of the technique, directly influenced by $\bar{s}$ and indirectly by the recapture intensity. In the populations at ponds I and III, the fractions of immature specimens match reality (Table 8) and are absolutely reliable. In the pond II population with low recapture intensity, this is not the case. $\bar{L}$ is underestimated, and the fractions are only of relative value. The low recapture rate of pond II is caused by the fact that an island in the pond renders recapture difficult. Pond III is a special case, where large fractions of tenerals stay at the water (0.73 in males and 0.58 in females) and all animals return to the water after 17 days.

Data about the 1966 populations of Coenagrion puella

A53-54 and Enallagma cyathigerum (Parr 1969 and Parr & Palmer 1971) give male maturation times of, respectively, 26 and 22 days at the Dunham pond III.

MORPHOLOGICAL COLOUR CHANGES.

Male I. elegans change colour from green, through turquoise, to blue. In laboratory conditions, the first
A61-62 colour change occurs after 14.13 days (Sx=5.66, $S\bar{x}$=1.41, n=16) and the second after 19.62 days (Sx=6.51, $S\bar{x}$=1.81, n=13). From capture-recapture data, Parr (1973a) and Van Noordwijk (1978) derived values of 7.38 days and 20.44 days for both periods. Obviously, there is good agreement for the second period, but the first one is underestimated by the capture-recapture technique because few immatures are present at the water and tenerals are only rarely marked. Similarly, the underestimation of $\bar{L}$ is due to the behaviour of the immature stages.

We now know how many specimens of each age group are in the neutral zone. Similarly, it is possible to divide the population into mature and immature specimens. Table 2 indicates that for a male immature period of 14 days, 0.386 immatures and 0.114 matures are the theoretical population fractions. Similar theoretical figures for females are unknown. Parr (1973a) gives the figures in table 8 for the Dunham experiments. They match well with values found with the life table technique in populations with sufficient recapture frequency.

My laboratory experiment can also serve as a basis to calculate ideal immature and mature population fractions at population density zero, since the relationship between the theoretical life table and maturation time is exactly known. I accept this relation as being constant in all density conditions, as suggested by the linearity of the regressions obtained. (In natural conditions, at the hypothetical density zero, no intraspecific interaction can occur. In the laboratory, such interaction causing different distribution patterns is, of course, not possible and population density zero can be accepted if only distribution patterns are studied.)

SEX RATIO AND POPULATION DENSITY.

That the sex ratio observed in nature is influenced by behaviour is shown by the population at Denderleeuw in 1973 (this study), which had a sex ratio of 0.74 (based on captures), 0.71 (based on the number of individuals), and
A35 0.66 (based on population number estimates with the Fisher & Ford method).

The most reliable estimate of population density is the total season population (Sheppard 1951) per meter of shoreline. Figures used for the Dunham ponds were published by Parr (1973a), together with the sizes of the ponds. As no estimate is given for pond I females, I took only male density into account. As males are the largest fraction at the pond and as aggression is a rather typical male

behaviour, this seems a logical choice. I derived the following densities: pond I: 6.4, pond II: 4.1 and pond III: 1.7 males per m. Considering male and female immature and mature fractions as a function of population density and including theoretical male values at hypothetical density zero, a linear relationship is obtained (Fig. 3) (r^2 =1.00 in both cases with n=3). Figure 3 shows that immatures are progressively banned from active populations at increasing densities, where mature males form the majority.

The data of pond III are omitted from the regression. They lie closely together, as the topological features are hindering Odonata in leaving the active population.

The linear relationship for immature and mature females again provides a theoretical value for both fractions at density zero: immatures 0.428 and matures 0.082, and these figures are entered into table 8. Based on table 2, a maturation time in females of 17.55 days is found, confirming the longer female maturation period.

Even though I have only 2 data points, I accept that in females the relationship is linear, in analogy with the males and because of the correlation of sex ratio with population density (Table 9). The latter calculation was done on Parr's 3 Dunham populations and a theoretical 0.5 sex ratio at density zero. (a_0 =0.51, a_1 =0.03, r^2 =0.97, n=4).

TIME AWAY FROM THE WATER AS IMMATURES.

In table 8, we can use the proportion between the fractions of immatures observed in nature and the theoretical immature fraction to estimate the average time spent away from water (using table 4 to see how long the total immature fraction had been away to be reduced to its actual level by mortality). A linear relationship with population density using data from ponds I and II and, as a theoretical point, no time away at density zero is found. (a_0 =-0.13, a_1 =0.66, r^2 =0.98, n=3 in males and in females a_0 =-0.26, a_1 =1.31, r^2 =0.98, n=3). For the special case of pond III, time spent away from water is too long, as could be expected.

DIFFERENT ACTIVITY OF MALES AND FEMALES.

Parr (1973b) suggested different $\bar{s}$ in males and females, but male $\bar{L}_c$ divided by female $\bar{L}_c$ produces a ratio indicative of a different activity in both sexes. $\bar{L}_c$ is here taken as the mean of the values given by the two correcting methods (Table 6). Data on populations in unusual conditions are omitted (Dunham pond III, the non-isolated bomb hole at Denderleeuw, and the marsh-and-pond system of Van Noordwijk 1978). At a sex ratio 0.5, a similar behaviour pattern and the same $\bar{L}_c$ are expected for both sexes. By including these theoretical figures, a
A42 linear relationship is found between $\bar{L}c\sigma^{\prime}$ /$\bar{L}c\varphi$ and sex

ratio, as a measure of population density. (a_0 =0.39, a_1 =1.14, r^2 =0.89, n=6). Sex-linked behaviour and measured $\bar{L}$ are thus both influenced by population density. In almost all populations, we find that female $\bar{L}_c$ is lower than male $\bar{L}_c$. However, analysis of the corrected life table shows that in the Dunham pond III, female $\bar{L}_c$ is higher, because older males are forced to leave the population under the aggression of younger males, while older females can stay in the active population longer. At the Denderleeuw bomb hole, a high female $\bar{L}_c$ resulted from the recapture of many marked females in long grass, about 30 m from the pond, in the early morning hours.

INHERITANCE OF FEMALE POLYMORPHISM.

Johnson (1964a, 1966b) studied the inheritance of (female) polymorphism in I. damula and I. demorsa. Both species have dimorphic females that can be andromorphic or heteromorphic. Males have only one phenotype. He found a single allelic autosomal inheritance and a sex-linked expression. Andromorphic females are homozygous recessive and heteromorphic females are homozygous dominant or heterozygous. A similar genetic control is proposed by Johnson (1964b) in Enallagma civile and E. praevarum.

In I. elegans, 3 female phenotypes exist, which is compatible with the above mentioned inheritance system, with rufuscens and infuscans-obsoleta as homozygous

heteromorphic (both without black humeral stripes), infuscans as heterozygous heteromorphic, and the andromorph as a homozygous andromorph (the latter 2 morphs having similar immature stages and all having black humeral stripes). Parr (1969) rejected this mode of inheritance, but I will maintain this hypothesis (Fig. 4). If males and females, and immatures and matures have a different distribution pattern, why not the different morphs as well? Lord (1961) and Parr & Palmer (1971) found no difference in mating behaviour of both types of heteromorphs, but a significant difference was found between andromorphs and heteromorphs, andromorphic females being disadvantaged. Obviously, males do not readily recognize andromorphs as females. A different behaviour of males towards female morphs has also been described by Johnson (1975, 1964b), who noticed that phenotype frequencies change during development to maturity. He ascribed this fact to selection. However, this phenomenon is simply due to a different behaviour. In table 10, frequencies of female phenotypes from the dense (sex ratio = 0.67) Pembrokeshire population (Parr 1965) are separated into mature and immature stages. The homozygous heteromorph form is underrepresented at maturity and the andromorphs are overrepresented. In the less dense Anglesey population of Lord (1961) (sex ratio=0.52 to 0.59), this effect is nearly negligible (Table 11).

Based on this hypothesis, a frequency of 0.25 homozygous heteromorphs, 0.50 heterozygous heteromorphs and 0.25

homozygous andromorphs should be found. This theoretical frequency at density zero, and that of the Dunham ponds (Parr 1969) provide a linear regression for andromorphs and heteromorphs (r^2 =0.97 in both cases, n=4) but no such relationship is found upon separating both types of heteromorphs (table 12). This shows that the differential distribution of andro- and heteromorphs under the influence of population density is a fact. No difference is found between the 2 heteromorphs, confirming what was found by an analysis of mating frequencies by Lord (1961) and by Parr & Palmer (1971). My hypothesis about the inheritance of the female polymorphism is thus acceptable.

MATING FREQUENCY AND POPULATION DENSITY AS A POPULATION REGULATOR.

I showed that sex ratio is directly determined by population density, therefore sex ratio can be used as a measure of population density where sufficient data are not available.

Mating frequency and sex ratio at the Dunham ponds (Parr & Palmer, 1971) are represented in table 13.
In females, the number of mating males versus total female number was taken to include as many juvenile females as possible in the frequency data. These mating juveniles should not be omitted (as Parr & Palmer did) because they compete with mature females.

These corrected mating frequencies are represented in figure 5, together with a theoretical point at sex ratio 1.0, and, of course, zero as mating frequency, because only males are present in the population.

At a sex ratio of 0.5, an equal mating frequency should be found. The 3 low density points in males give a linear relationship (a_0 =0.90, a_1 =10.78, r^2 =1.00, n=4), with, at sex ratio 0,50, a mating frequency of 4.49. If this extrapolation is included with female figures, a linear regression can again be derived (a_0 =-29.33, a_1 =68.37, r^2 =0.90, n=4) with a mating frequency at sex ratio 0.50 of 4.80.

In males at high density, we get a parabolic curve (a_0 =77.99, a_1 =166.23, a_2 =88.25, n=4) whereas in females a power curve occurs (a=0.29, b=-10.47, r^2 =1.00, n=3, pond III omitted).

We also note that the mating frequency in females is invariably higher than that in males, caused by a male-biased sex ratio at the water. Mating frequency in both sexes increases linearly to an optimum population density (at sex ratio 0.676). In denser populations, male mating frequency falls parabolically to zero at sex ratio 1.00. Females pushed out of the population at rising densities are becoming so rare that couples are often disturbed by other males, and females are chased by several males at a time, especially non-territorial ones which occur in large numbers in dense populations (Pajunen 1962b, 1966a). This

may explain why the female curve drops in a power fashion.

Pond III shows in 1970 an abberantly high mating frequency as females at the pond cannot move away into the neutral zone. (This mating frequency gives an acceptable point for the linear regression at low density).

The phenomenon described acts as a population regulator: in low density populations, a large fraction of females is in the active population and has a chance to copulate; the population expands (Fig. 5).
When the optimum density is reached, the population continues to grow. The next year, however, a density occurs which is unfavorable and the population decreases, thus closing the cycle. In England, we see a 6-year cycle, beginning with a population at sex ratio 0.5 (the Anglesey population) climbing up to a sex ratio of 0.75 (Dunham pond III 1970 and, also, Denderleeuw 1973, this study). This is sustained by the 2 Dunham ponds for which data for two different non-consecutive years are available.

The mating frequency in I. elegans is rather low compared with other species (Parr & Palmer 1971), perhaps because many couples leave the water (Van Noordwijk 1978). Couples leaving the water were also observed in Leucorrhinia sp. (Pajunen 1963).

INFLUENCE OF CROWDING ON MATURATION PERIOD.

The maturation time obtained by analysing life tables of the Dunham and the Denderleeuw populations of I. elegans are presented as a function of sex ratio (a measure of crowding) in table 14. In males this relationship is found to be linear (a_0 =43.95, a_1 =-45.00, r^2 =0.93, n=4). In females, much more influenced by population density, pond III had to be eliminated (a normal exchange with the hinterland being prevented) to obtain a good linear fit. (a_0 =67.50, a_1 =-75.00, r^2 =1.00, n=3).

INFLUENCE OF JH ON MATURATION TIME AND LIFE SPAN.

Results of the experiment treating male I. elegans specimens in laboratory conditions with JH or farnesol are given in tables 15, 16, 17, and 18.
With untreated specimens as a reference, significant linear relationships were obtained between the colour change associated with maturation, the ageing colour change, and $\bar{L}$ in males. $\bar{L}$ and maturation time become shorter with increasing JH titer.

Administering 250 µg farnesol, split up in 3 subdoses applied on 3 consecutive days showed a shortening of the colour change period fitting the obtained regression, but a much lower death rate than with a single dose.

The ageing colour change is probably due to dehydration. A progressive dehydration was observed

while measuring the quantity of hemolymph obtained for analysis. A turquoise specimen yielded about half the amount of hemolymph of a teneral one, while old, blue pruinescent animals contained only one fifth of the teneral amount.

The results obtained by treatment of females are shown in table 19. Life span was essentially changed in the same way as in males under the influence of JH.

EVOLUTION OF L DURING THE FLIGHT SEASON.

A39-41 $\bar{L}_{FFc}$ for the Dunham populations of Parr (1969) shows a seasonal trend: $\bar{L}_{FFc}$ is very high at the beginning of the season, lowest in late July and early August and again rises towards the end of the season, but not sufficiently to reach spring values again.

Unfortunately, the $\bar{L}_{FFc}$ at Dunham pond II suffers from a low recapture rate. This leaves us with only 2 ponds showing related circumstances and sufficient data: Dunham ponds I and III (Table 20). If we look at the values of $\bar{L}_{FFc}$, it is clear that high density at pond I causes low $\bar{L}_{FFc}$. To improve the picture, time away from the water is added (this will, in fact, overshoot reality because there is continuous exchange between the active population and the hinterland) to have a maximum $\bar{L}$. Again crowding is a negative factor and, in all ponds, maximum $\bar{L}$ appears to be higher in females than in males. As true $\bar{L}$ is intermediate

between $\bar{L}_{FFc}$ and the sum of $\bar{L}_{FFc}$ plus the time away from the water, and, as in the first case, female $\bar{L}_{FFc}$ is mostly inferior but in the second case superior to male $\bar{L}_{FFc}$, we may conclude that they are in fact equal, as found in my laboratory experiment. A closer look at the calculated regressions not only shows that female $\bar{L}_{FFc}$ is higher than male $\bar{L}_{FFc}$ at density zero but also that female $\bar{L}_{FFc}$ is shortened more by increasing density. This, however, is an illusion caused by a different attendance at the water. In populations with a real $\bar{L}$ exceeding the $\bar{L}$ found in laboratory conditions, time away from the water at low density is underestimated by using our theoretical life table. The magnitude of the error increases proportionally to $|\text{real } \bar{L}\text{-laboratory } \bar{L}|$.

In males, there is no sign of effects of population peaks (fig. 6). Females react much more strongly to the density stimulus and show 2 peaks, with $\bar{L}_{FFc}$ reaching a minimum (fig. 7) in the pond II population.

DISCUSSION.

MEASURED $\bar{L}$ AT THE WATER: A RESULT OF BEHAVIOUR.

$\bar{L}$ measured at the water, in the active population, is in fact only the mean period individuals can be observed at the pond, it is the period specimens stay at the water plus the period that specimens exchange regularly with those in the hinterland. $\bar{L}c$, computed with either method will

invariably be an underestimate. Real $\bar{L}$ is intermediate between $\bar{L}c$ and $\bar{L}c$ plus the average time spent away from water by the immature fraction. The two values should not be added as the equilibrium between the neutral zone and the active population is a dynamic one. We may conclude that the high field $\bar{L}c$ values at the beginning of the season are realistic, but the lower ones are underestimates. Another way of setting an upper limit to $\bar{L}$ was developed by Corbet (1952), who added maturation time and $\bar{L}_{FF}$ or $\bar{L}_{LT}$. This, however is an overestimate due to the exchange between the active and neutral zone. It was called adult mean longevity. Looking at table 6 of $\bar{L}_c$ values, we see that this "active $\bar{L}$" ($\bar{L}a$) is a constant for a species in one type of habitat, not depending on population density or selective predation. Types of habitat can be open, closed, isolated, or not isolated.
The denser the population, the more real $\bar{L}$ is close to $\bar{L}a$, the longer is the time away from the water, the shorter are the visits to the water, but the more frequent is the exchange between the two zones.
$\bar{L}$ measured and corrected with either method is determined by life span, population distribution and maturation period and indirectly by JH titer and crowding.

INFLUENCE OF THE TOPOLOGICAL FEATURES OF THE HABITAT.

Low $\bar{L}$ at the bomb hole at Denderleeuw is due to the fact that the habitat is open and surrounded by other

ponds. Garrison (1978) also suggests that non-isolated ponds provide opportunities to emigrate causing an underestimated $\bar{L}$ in Enallagma cyathigerum (In addition, his marking period was short: only 10 days).

The male $\bar{L}_{FFc}$ (female $\bar{L}$ is more easily influenced) at the bomb hole corresponds to the male $\bar{L}c$ of the marsh-and-pond system studied by Van Noordwijk (1978). This illustrates the great importance of the topological features of the habitat. Thus, the extreme high $\bar{L}c$ at Dunham pond III can be explained by the fact that very few specimens can leave the habitat, situated in a deep shelter, where they are captured during their entire life span. However, low population density is also a factor. The fact that Dunham pond III had to be excluded in the relationship between immature and mature population fractions and population density, and could be included if sex ratio as a function of population density are concerned, shows that the topological features are important in preventing immatures from leaving the pond.

EVOLUTION OF $\bar{L}c$ DURING THE FLIGHT SEASON.

High $\bar{L}c$ at the start of the flight season is caused by the fact that all specimens in the population are young and, because of their low density, stay in the active population. In all other periods the population consists of specimens of all ages. At peak density, $\bar{L}c$ is lowest: more young and old specimens leave the water, and the time spent

at the water is at a minimum. At the end of the season the population density decreases, less specimens leave the water, but only few young specimens are left, with an intermediate $\overline{L}c$ as a result.

MATURATION PERIOD.

The maturing colour change period gave me the maturation period in the dense population, created by my laboratory experiment. Similar data about maturation time have been published on several species: 11 days in Brachytemis leucosticta (Adetunji & Parr 1974), 12-15 days in Nesciothemis nigeriensis (Parr & Parr 1974), 11 days in male and 14 days in female Acisoma panorpoides inflatum and 10 days in Palpopleura lucia lucia (Hassan 1977), 11 days in Calopteryx maculata (Waage 1972), 10 days in Calopteryx haemorrhoidalis (Heymer 1972), 14 days in Agria moesta (Borror 1934), 14 days in Leucorrhinia dubia (Prenn 1930, Steiner 1948), 5-12 days in male and 13-16 days in female Anax imperator (Corbet 1957), 10 days in Orthetrum coerulescens and O. bruneum (Heymer 1969), 15 days in Platycnemis acutipennis and Lestes barbarus (Aguesse 1961) and 14.5 days in Erythemis simplicicollis (McVey 1981). The literature provides only few longer maturation times: Corbet (1956) and Gross (1930): 16-30 days in Lestes sponsa, Loibl (1958): 2-3 weeks in L. sponsa, Jacobs (1955): 8-14 days in male and 13-24 days in female Plathemis lydia. I believe this is due to the

fact that almost every investigator is inclined to select a small but fairly dense population to study, thus subconsciously tailoring his results to a particular portion of the population cycle. Data published for both sexes invariably confirm the fact that female exceeds male maturation period, supposedly because oogenesis takes more time than spermatogenesis (Smith 1916, Pajunen 1962a).

POPULATION DISTRIBUTION.

Aggressive and territorial behaviour and specific spatio-temporal population distribution are regulated by population density. Such factors may limit population sizes as effectively as availability of food or predation. At low population density, the interaction of individuals is minimal and so is aggressivity. A large part of immatures remains at the water where the sex ratio is near 0.5.

At rising density, aggressiveness develops (Johnson 1962 in Hetaerina americana, Crumpton 1975 in Xanthocnemis zealandica, Pajunen 1964 in Leucorrhinia caudalis), sex ratio becomes male biased and territorial behaviour appears (Kormondy 1959, 1961; Pajunen 1964, 1966a; St.-Quentin 1964; Heymer 1964, 1968a). Increased interactions and a shortened stay at the water were also observed by Kaiser (1974) in Aeschna cyanea.

If density increases even further, territories become so small as to be unsuitable (Pajunen 1966b in

Calopteryx sp.) and a number of males act non-territorially, chasing females all over the habitat instead of inside a territory. Non-territorial males disturb ovipositing females and thereby negatively influence reproductive success. (Pajunen 1966b, in Calopteryx virgo). Immature specimens, females and older individuals, spend almost no time at the water and andromorphic females gain an advantage.

The denser a population, the more andromorphs are at an advantage, escaping the attention of males. Thus, a disadvantage in mating frequency in sparse populations becomes an advantage in dense populations. If there were no such alternating circumstances, the andromorphic genotype would have disappeared by natural selection.

In extreme dense populations, the fraction of mature males is very large. Now aggressivity drops (Pajunen 1962b in Leucorrhinia sp., Buchholtz 1951 and Zahner 1960 in Calopteryx sp., Crumpton, 1975 in Austrolestes colensonis, Klotzli 1971 in C. virgo) because there are hardly any females in the active population and competition for mates is relieved. Aggressivity and territorial behaviour thus appear to be a continuous adaptation to changing population densities. Moore (1952, 1953, 1962 and 1964) and Kaiser (1973) see aggressive behaviour as an attempt to keep a constant density at a pond, in continuous exchange with the hinterland.

It is my strong conviction that the fact that some species develop territorial behaviour and others do not is mainly due to the fact that the former ones are often found in relatively dense populations, while the latter ones are almost always seen in relatively sparse populations.

Aggressive behaviour was recognized as a distributive factor by Schmidt (1964) and Kaiser(1974). It is seldom interspecific, as demonstrated by Moore (1962) in Pyrrhosoma nymphula and Ceriagrion tenellum.

Density is the determining factor for the amount of time spent in the neutral zone, for the number of specimens away from the water, and therefore for the sex ratio. In the same way, the population density also influences $\bar{L}$ and the difference between male and female $\bar{L}$. In fact real sex ratio is 0.5 and independant of the type of habitat. Other values are only the result of behaviour. This also applies to Fisher & Ford population underestimates, especially in females.

The fact that a male-biased sex ratio has long been accepted as a reality was corroborated by a similar larval sex ratio in Zygoptera, while in Anisoptera an excess of females is common (Waage 1980, Testard 1975 and Lawton 1972, Parr & Palmer 1971, Van

Noordwijk 1978). Sex ratios determined on large numbers of larvae (>1000) range between 0.499 and 0.544. The larger the samples, the more of the population is observed, and as there is no hinterland, the limit for larval sex ratio is 0.5. A 0.5 sex ratio was found by Pickup et al. (1984) in young Lestes larvae. Later in the larval growth season, the population was male biased, but in the final period a female excess was found. This phenomenon was explained by differential mortality. If a similar distribution in larval and adult populations is accepted, this is easy to explain: as larvae develop, they begin to behave differently sexwise. Distribution will be influenced, and measured sex ratio will diverge from 0.5, males occupying the most favorable positions in the habitat. Lawton et al. (1980) demonstrated that development in larvae of I. elegans is directly proportional to prey density. This means male larvae will develop quicker and eclode earlier. Such an earlier eclosion period was observed in Lestes (Ingram 1976) and age-dependent distribution was described by Lawton (1970) and Johannson (1978), while Blois (1985) observed age-dependent distribution in larvae.

We should, of course, be careful not to generalize this conclusion prematurely, as population density plays a role and a density which is high for some species is not for others. However, it is clear

that behaviour determines sex ratio in adults and in larvae. Even at eclosion (different eclosion period, perhaps a different choice of substratum) and thus in exuviae, one may find a behavioural influence on sex ratio.

More attention should be given to this part in future studies. My contention that behaviour is continuous throughout life, without a fundamental interruption caused by metamorphosis, is strengthened by the fact that, to some extent, aggressive behaviour is found in larvae (Corbet 1952, Needham 1930, Heymer 1968b and 1970, Rowe 1980, Macan 1977), and so is a certain form of territoriality (Corbet 1962). Interspecific competition is avoided in larvae (Johannson 1978) as well as in adults (Van Noordwijk 1978).

Adult aggressive and territorial behaviour and different distribution of sexes, mature and immature have one goal to create optimum reproductive conditions. Therefore, when elbow-room becomes scarce, immatures and older specimens are driven out of the active population. Behaviour was described by Moore (1954) as a basic mechanism to keep an active population at optimum density. On the other hand, specimens which have just matured acquire the best chances to mate (Pajunen 1962a).

A long maturation period implies that only the best adapted animals survive and finally mate. This form of natural selection must be of great importance. Indeed, the major part of a population is eliminated before reaching maturity.

The emigration of immatures and older specimens from the water can lead to dispersal and colonisation of new habitats. Immatures play the most important role having a longer life expectancy and the largest numbers. This whole mechanism has mass migration as an extreme. A sequence of phenomena is required to allow a mass migration to take place. First, larval development (Schaller 1972, Yagi 1976) must be synchronized, but a synchronized eclosion (Corbet 1952, 1957 and Trottier 1966, 1973) and a synchronized maidenflight (Corbet 1957 and Trottier 1966) are also necessary. This synchronized maiden-flight may take huge proportions if population density is high enough. Tenerals, juveniles, but also older specimens with a tendency to leave the active population under density pressure will tend to join the swarm. As a result, mass migration is most likely to occur one or two years after optimal population density and optimal mating frequency were reached.

Most species seem to regulate their population density as described here in I. elegans, i.e. by excluding or not excluding females of the active population and

reducing or increasing mating frequency. However, in some species with mass migration, this phenomenon serves to eliminate the surplus number of specimens.

PHYSIOLOGICAL MECHANISMS INVOLVED.

Changes in behaviour, like emigration and immigration, are partly mediated by certain hormones. It is well documented that a low juvenile hormone titer before metamorphosis is a necessity to metamorphosis, but also to oogenesis in the last larval instar and in the teneral phase of adults. Moulting hormone (20-OH ecdysone) is essential for the moulting process itself and, at least in Diptera, also for vitellogenesis (De Loof et al. 1984 and Briers & Huybrechts 1984). In recent years, steroids like progesterone, testosterone etc., once believed to occur in Deuterostomes only, have been demonstrated in insects (De Clerck et al. 1984). By means of immunological techniques, many peptides resembling 'typical' vertebrate neuropeptides, have also been found. However, no functions have yet been assigned to these candidate hormones.

Effects of JH on behaviour have been described by Rankin & Riddiford (1978), who observed a stimulating effect of low JH titer on flight and migration in Oncopeltus fasciatus (Heteroptera). A declining JH titer was found at increasing population density,

shortening the larval stage and increasing spermatogenesis in Mamestra and Spodoptera (Lepidoptera) (Yagi 1976). Finally, the precopulatory or maturation periods found in Nauphoeta cinera (Roth & Barth 1964), Leucophaea maderea and Byrsotria fumigata (Dictyoptera), (Barth 1962), have been claimed to be controlled by the corpora allata (Engelman 1960).

INFLUENCE OF JH ON MATURATION TIME AND LIFE SPAN.

In adult Odonata, population density probably influences JH secretion by some unknown stimuli. Norris (1964) found that mature males had an accelerating effect on male and female maturation and that crowded immature males inhibited male maturation. This is a synchronizing mechanism that maximizes the number of mature males in the population at one given time. High activity (in Odonata also a higher degree of aggressive behaviour) is associated with rapid maturation. In locusts, pheromones are involved in this phenomenon. Loher (1960) observed L. migratoria to turn yellow under the influence of the corpora allata in dense populations, but not in less dense populations. He also observed JH to control maturation and colour change in Schistocerca gregaria, and, also, Staal (1961) recorded a longer $\bar{L}$ in Locusta migratoria specimens without corpora allata.

The findings of Loher and Norris are in agreement with the shortening effect of JH action on colour change periods, maturation period and life span in I. elegans and the findings of Norris can help to understand the evolution of $\bar{L}c$ during the flight season: at the beginning of the season, juveniles inhibit maturation but with rising density the large fraction of mature males speed up maturation. Formerly, Parr & Parr (1972) tried to explain differences of $\bar{L}$ in several habitats by different predation rates. Loher (1960) explained changes in maturation time as a direct action of the corpora allata. Norris (1964) gave the stronger attraction between mature specimens of both sexes as an indirect cause. In Odonata, colours influence partner choice, but mating frequency is also influenced by population density. This leads us to believe that the stimulus in Norris' theory is visual in Odonata, in which individuals can be seen to return to the active population as soon as their colour is acceptable.

COLOUR CHANGE AT THE CELLULAR LEVEL.

The cellular arangement of the integument as described by Lord (1961) was confirmed (O'Farell 1968, Veron 1973, Charles & Robinson 1981). Ommochromes seem

to be randomly distributed in Odonata (Becker 1941, 1942 and Butenandt 1957). Vuillaume (1969) gives a review of their characteristics.

In I. elegans, the Tyndall light scattering layer is linked to the male, homozygous andromorph and heterozygous heteromorph female. The difference between the two heteromorph genotypes only expresses itself after maturation. Whether JH titer has any role in this genetic expression is not yet known. Formation of ommochrome is a way to eliminate the toxic tryptophane liberated by protein breakdown (Buckmann et al. 1966). More tryptophane is available at a high metabolic rate in active periods.

The mechanism of action of JH is still unknown as far as maturation and induction of sexual behaviour are concerned, but it is well known that JH seems to stimulate metabolism and possibly gives high activity, aggressivity, and increased interaction, all stressed by crowding. The effect of crowding on ommochrome formation has been reviewed by Vuillaume (1969). Colour changes are thus an inevitable part of metabolism, and a mirror of internal changes.

Lord (1961) found that ommochromes are protein bound (as also observed by Fox & Vevers 1960) and presented evidence that the large, light absorbing granules are of ommine nature, and the smaller light

scattering ones xanthommatine.

The yellow colour of the matrix could be an ommochrome precursor. As Altman (1956) and Raabe (1959) ascribed reduced water content of the body and haemolymph to a reduced JH titer (or to the neurosecretion stored in the corpora allata) this is likely to be the mechanism behind the ageing colour change. The reduced water content can easily trigger higher titers of ommochrome precursors and stimulate the formation of more granules. It also contracts the tissue and reinforces the Tyndall effect of the upper layer. Finally, the low water content may cause an excess of uric acid or leucopterin, breakdown products of proteins, which are deposited in the integument, as is the fact in Lepidoptera (Hopkins 1891) and can cause pruinescence. This appears even more reasonable as ommochromes, pterines and uric acid are situated on the same genetic chain (Danneel & Escherich-Zimmerman 1957).

CONCLUSION.

Interspecific interaction in Odonata is largely avoided by separated flight seasons, separate spacing, or different behaviour (Van Noordwijk 1978) and is not recognized as a major organizing force in insect communities (Shorrock *et al.* 1984).

Through a variety of physiological mechanisms, population density governs the intraspecific behaviour. It can be considered as one of the main factors involved in population dynamics. *Corpora allata* products provide the chemicals behind the mechanisms. Aggressive behaviour is their main expression resulting in the distribution pattern of the population and more or less favorable mating frequencies. Another mechanism that possibly interferes is lowered fertility at rising densities, as observed by Grechanyi (1984) in *Drosophila melanogaster*.

These complex mechanisms result in a multiannual population cycle. A related regulatory phenomenon was hypothesized by Dumont & Hinnekint (1973) in *Libellula quadrimaculata*. They noticed a 10 year population cycle resulting in mass migration at density peaks.

The colour morphs of *I. elegans* females provide an important adaptive strategy at all possible levels of

population density. Another illustration of its adaptability, in relation to salinity of the larval environment, was described by Dumont & Dumont (1969).

The morphological colour forms are important visual characters by which an animal can identify the sexual status of its congeners. They directly influence, as visual stimuli, the rate of physiological processes involved in the development of sexual behaviour.

The larval synchronization is followed by a synchronization in adult maturing to create as many mature animals as possible at the same time at the water, while other developmental phases are chased away by aggressive pressure from mature males. Crowding is shown to speed up the whole life history and most, if not all, physiological phenomena. This is also a mechanism of adaptation to different population densities. If life was not shortened, density would, in fact, be much higher.

The best strategy to preserve a species is expansion. To produce as many specimens as possible, crowding, with as negative factors shortage of food and unfavorable mating chances, must be avoided. This is done by distributing the population (with the possibility to colonise new habitats) and by shortening life span.

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Sex	$\bar{L}$	Sx	$S\bar{x}$	n
Males	11.53	10.87	1.66	43
Females	9.92	5.84	0.84	48
Males + Females	10.63	8.58	0.90	91

Table 1. $\bar{L}$ of I. elegans in laboratory conditions.

Days	Days.Sx^{-1}	Survivals	Deaths	$\bar{s}$	$\bar{L}$
0	0	100.0000	-	-	-
1	0.1166	89.0740	10.9260	0.8907	-
2	0.2331	79.4990	9.5750	0.8925	-
3	0.3497	71.0496	8.4494	0.8937	- -
4	0.4662	63.6173	7.4323	0.8954	2.3500
5	0.5827	57.0540	6.5633	0.8968	2.7469
6	0.6993	51.2429	5.8111	0.8981	3.1347
7	0.8159	46.0935	5.1494	0.8995	3.5039
8	0.9324	41.5265	4.5670	0.9009	3.8551
9	1.0490	37.4523	4.0742	0.9019	4.1902
10	1.1655	33.8460	3.6063	0.9037	4.5069
11	1.2821	30.6176	3.2284	0.9046	4.8090
12	1.3986	27.7362	2.8814	0.9059	5.0958
13	1.5152	25.1562	2.5800	0.9070	5.3682
14	**1.6317**	**22.8466**	**2.3096**	**0.9082**	**5.6266**
15	**1.7483**	**20.7728**	**2.0738**	**0.9092**	**5.8720**
16	**1.8648**	**18.9113**	**1.8615**	**0.9104**	**6.1045**
17	1.9814	17.2352	1.6761	0.9114	6.3251
18	2.0979	15.7267	1.5085	0.9125	6.5341
19	2.2145	14.3550	1.3717	0.9128	6.7338
20	2.3310	13.1364	1.2186	0.9151	6.9199
21	2.4476	12.0246	1.1118	0.9154	7.0978
22	2.5641	11.0191	1.0055	0.9164	7.2662
23	**2.6807**	**10.1071**	**0.9120**	**0.9172**	**7.4258**
24	2.7972	9.2804	0.8267	0.9182	7.5769
25	2.9138	8.5288	0.7516	0.9190	7.7200
26	3.0303	7.8451	0.6837	0.9198	7.8556
27	3.1469	7.2241	0.6210	0.9208	7.9838
28	3.2634	6.6579	0.5662	0.9216	8.1052
29	3.3800	6.1411	0.5168	0.9224	8.2203
30	3.4965	5.6636	0.4775	0.9222	8.3305
31	3.6131	5.2384	0.4252	0.9249	8.4322
32	3.7296	4.8443	0.3941	0.9248	8.5298
33	3.8462	4.4831	0.3612	0.9254	8.6224
34	3.9627	4.1525	0.3306	0.9263	8.7099
35	4.0793	3.8489	0.3036	0.9269	8.7929
36	4.1958	3.5705	0.2784	0.9277	8.8715
37	4.3123	3.3148	0.2557	0.9284	8.9458
38	4.4289	3.0793	0.2355	0.9290	9.0164
39	4.5455	2.8627	0.2166	0.9297	9.0833
40	4.6620	2.6633	0.1994	0.9303	9.1466
41	4.7786	2.4794	0.1839	0.9310	9.2067
42	4.8951	2.3099	0.1841	0.9316	9.2685
43	5.0117	2.1532	0.1567	0.9322	9.3225
44	5.1282	2.0086	0.1446	0.9328	9.3737
45	5.2448	1.8748	0.1338	0.9334	9.4222
46	5.3613	1.7512	0.1236	0.9341	9.4683
47	5.4779	1.6365	0.1147	0.9345	9.5120
48	5.5944	1.5304	0.1061	0.9352	9.5535
49	5.7110	1.4320	0.0984	0.9357	9.5928
50	5.8275	1.3407	0.0913	0.9362	9.6302

Table 2 : Chi-square distribution of mortality frequencies of I.elegans in laboratory conditions (ν_1=2, ν_2=15)

Sex	$\bar{L}_{FF}$	$\bar{L}_{LT}$	Lm	Marking period in days	Habitat and Reference
Males	5.5	-	9	12	Anglesey 1
Females	5.3	-	8		LORD 1961
Males	6.2	-	15	17	Anglesey 2
Females	4.3	-	8		LORD 1961
Males	5.4	3.1	11	13	Penbrookshire
Females	3.5	2.4	7		PARR 1965
Males	9.9	5.6(9.7)	39	119	Dunham pond I (1965)
Females	7.6	- (8.7)	42	92	PARR 1969
Males	7.8	3.3(8.2)	33	120	Dunham pond II (1965)
Females	7.5	- (7.6)	33	119	PARR 1969
Males	15.2	11.0(13.7)	39	72	Dunham pond III (1966)
Females	18.0	- (16.1)	45	72	PARR 1969
Males	4.5 (1)	-	-	3 months	Welle
Females	3.7 (1)	-	-		VAN NOORDWIJK 1978
Males	3.9	4.0	16	24	Denderleeuw
Females	5.0	4.4	17		HINNEKINT (this study)

Table 3 : I. elegans : $\bar{L}$ as given by different authors.

(1) Regression method. Figures between parentheses for the Dunham ponds are calculated from raw recapture data (PARR 1969), omitting animals which were never recaptured.

Days	Survivals	Deaths	$\bar{L}$	$s\bar{x}$	Correction factor
0	100.0000	-	-	-	-
1	89.6160	10.3840	-	-	-
2	80.3103	9.3057	-	-	-
3	71.9709	8.3394	-	-	-
4	64.4974	7.4735	2.3634	0.1894	4.0747
5	57.8000	6.6974	2.7819	0.2186	3.4617
6	**51.7980**	**6.0020**	**3.1826**	**0.2458**	**3.0259**
7	**46.4193**	**5.3787**	**3.5658**	**0.2717**	**2.7007**
8	**41.5991**	**4.8202**	**3.9318**	**0.2966**	**2.4493**
9	**37.2795**	**4.3196**	**4.2808**	**0.3208**	**2.2496**
10	33.4084	3.8711	4.6133	0.3442	2.0875
11	29.9393	3.4691	4.9295	0.3671	1.9536
12	26.8304	3.1089	5.2300	0.3894	1.8413
13	24.0443	2.7861	5.5150	0.4113	1.7462
14	21.5475	2.4968	**5.7850**	**0.4325**	**1.6647**
15	**19.3100**	**2.2375**	**6.0405**	**0.4534**	**1.5943**
16	**17.3048**	**2.0052**	**6.2820**	**0.4737**	**1.5330**
17	**15.5079**	**1.7969**	**6.5100**	**0.4935**	**1.4793**
18	**13.8976**	**1.6103**	**6.7249**	**0.5127**	**1.4320**
19	**12.4544**	**1.4432**	**6.9272**	**0.5315**	**1.3902**
20	**11.1611**	**1.2933**	**7.1175**	**0.5497**	**1.3530**
21	**10.0021**	**1.1590**	**7.2963**	**0.5674**	**1.3199**
22	**8.9635**	**1.0386**	**7.4641**	**0.5845**	**1.2902**
23	**8.0327**	**0.9308**	**7.6213**	**0.6011**	**1.2636**
24	**7.1986**	**0.8341**	**7.7685**	**0.6171**	**1.2396**
25	**6.4511**	**0.7475**	**7.9062**	**0.6326**	**1.2181**
26	**5.7812**	**0.6699**	**8.0348**	**0.6475**	**1.1986**
27	**5.1809**	**0.6003**	**8.1549**	**0.6619**	**1.1809**
28	**4.6429**	**0.5380**	**8.2669**	**0.6757**	**1.1649**
29	**4.1608**	**0.4821**	**8.3712**	**0.6889**	**1.1503**
30	**3.7287**	**0.4321**	**8.4682**	**0.7016**	**1.1372**
31	**3.3416**	**0.3871**	**8.5585**	**0.7138**	**1.1252**
32	**2.9946**	**0.3470**	**8.6423**	**0.7254**	**1.1143**
33	**2.6836**	**0.3110**	**8.7202**	**0.7365**	**1.1044**
34	**2.4049**	**0.2787**	**8.7924**	**0.7471**	**1.0953**
35	**2.1552**	**0.2497**	**8.8592**	**0.7572**	**1.0870**
36	**1.9314**	**0.2238**	**8.9212**	**0.7669**	**1.0795**
37	**1.7309**	**0.2005**	**8.9785**	**0.7760**	**1.0726**
38	**1.5511**	**0.1798**	**9.0315**	**0.7847**	**1.0663**
39	**1.3901**	**0.1610**	**9.0804**	**0.7929**	**1.0605**
40	**1.2457**	**0.1444**	**9.1256**	**0.8007**	**1.0553**
41	**1.1163**	**0.1294**	**9.1673**	**0.8081**	**1.0505**
42	**1.0004**	**0.1159**	**9.2058**	**0.8151**	**1.0461**
43	**0.8965**	**0.1039**	**9.2412**	**0.8217**	**1.0421**
44	**0.8034**	**0.0931**	**9.2738**	**0.8279**	**1.0384**
45	**0.7200**	**0.0834**	**9.3038**	**0.8337**	**1.0351**
46	**0.6452**	**0.0748**	**9.3315**	**0.8393**	**1.0320**
47	**0.5782**	**0.0670**	**9.3568**	**0.8445**	**1.0292**
48	**0.5182**	**0.0600**	**9.3801**	**0.8494**	**1.0267**
49	**0.4644**	**0.0538**	**9.3823**	**0.8498**	**1.0264**
50	**0.4162**	**0.0482**	**9.4020**	**0.8542**	**1.0243**

Table 4 : Age distribution for I. elegans in laboratory conditions based on a fixed $\bar{s}$ = 0.89616 and correction factors for $\bar{L}$.

(1)	(2)	(3)	(4)	(5)	(6)	(7)
Survival in days	Survivals for each period	$\sum$ survivals from bottom to top	survivals.$\bar{s}^{-i}$	Fraction of population at the water	Maximum active population.$\bar{s}^{i}$	(3)-(6)
0	327	565	565	1.00	450	115
1	63	238	318	0.56	337	- 99
2	50	175	312	0.55	252	- 77
3	27	125	297	0.53	189	- 64
4	18	98	311	0.55	142	- 44
5	18	80	339	0.60	106	- 26
6	15	62	351	0.62	79	- 17
7	9	47	355	0.63	60	- 13
8	9	38	383	0.68	45	- 7
9	4	29	390	0.69	33	- 4
10	8	25	450	0.80	25	0
11	6	17	408	0.72	19	- 2
12	9	11	352	0.62	14	- 3
13	2	2	-	-	11	- 9
13 +	4				11	

Table 5 : I. elegans (males) : Computation of maturation time and fractions of the total population at the water. (Denderleeuw, bomb hole, 1973).

Sex	$\bar{L}_{FFc}$	$\bar{L}_{LTc}$	$\bar{L}_{c}$ (Mean of the 2 methods)	Reference
Males	10.7	8.9	9.8	LORD, 1961
Females	10.4	9.8	10.1	
Males	9.5	9.7	9.6	LORD, 1961
Females	6.6	11.5	9.1	
Males	9.9	9.2	9.6	PARR, 1965
Females	8.6	7.9	8.3	
Males	11.0	10.4	10.7	PARR, Pond I
Females	8.8	8.7	8.8	1969
Males	9.0	8.7	8.9	PARR, Pond II
Females	9.0	8.0	8.5	
Males	16.3	15.6	16.0	PARR, Pond III
Females	19.0	18.2	18.6	
Males	4.4	6.9	5.6	HINNEKINT (this
Females	6.3	7.6	7.0	study)

Table 6 : $\bar{L}_{c}$ of I. elegans.

Sex	$\bar{L}_{FF}$	$\bar{L}_{LT}$	Lm	$\bar{L}_{FFc}$	$\bar{L}_{LTc}$	$\bar{L}_{c}$	Marking period in days	Reference
Males	4.0	-	10	7.8	7.8	7.8	12	
Females	4.0	-	9	7.8	8.0	7.9		LORD 1961
Males	6.7	7.0	31	7.3	9.6	8.5	36	
Females		5.5	19		7.0	7.2		CORBET 1952

Table 7 : P. nymphula : Maximum longevity, corrected and raw $\bar{L}$.

	Immature males		Mature males		Immature Females		Mature Females	
	n	Fraction	n	Fraction	n	Fraction	n	Fraction
Theoretical distribution		0.386		0.114		0.428		0.082
POND I	131	0.238	228	0.415	92	0.167	99	0.180
POND II	448	0.300	439	0.294	389	0.261	217	0.145
POND III	84	0.263	80	0.250	81	0.253	75	0.234

Immatures at the water as a fraction of the theoretical immature fraction

	Population density	Males	Time away from the water in days	Females	Time away from the water in days
POND I	6.4	0.62	4.3	0.39	8.6
POND II	4.1	0.78	2.2	0.61	4.4
POND III	1.7	0.68	3.4	0.59	4.7
Theoretical	0	1.00	0	1.00	0

Table 8 : Fraction of immature and mature males and females of different habitats and immature fractions versus own theoretical immature fraction and time away from the water during immature stage. (Based on the Dunham experiments of PARR 1973).

Population density	Sex ratio based on captures	Habitat and reference
6.4	0.70	Dunham pond I, PARR 1969
4.1	0.62	Dunham pond II, PARR 1969
1.7	0.58	Dunham pond III, PARR 1969
0	0.50	Theoretical

Table 9 : Sex ratio in relation to the population density

Immature stages			Juvenile stage (tenerals omitted)		Mature stages			
	n	Fraction				n	
Green	25	0.284	0.352	0.676	0.927 — 0.567	93	Andromorph
violacea	23	0.261	0.324		0.360	59	infuscans
rufuscens	23	0.261	0.324		0.073	12	infuscans-obsoleta
Teneral	17	0.194					

Table 10 : Morphs of female I. elegans as fractions of the female population at Pembrokeshire. (Based on data of PARR 1965).

Immature stages	n		Mature stages	n	
violacea	36	0.632	0.578 — 0.385	178	Andromorph
			0.578 — 0.193	89	infuscans
rufuscens	21	0.388	0.422	195	infuscans-obsoleta

Table 11 : Morphs of female I. elegans as a fraction of the female population at Anglesey (Based on LORD 1961).

Dunham ponds	Andromorph		Heteromorph			infuscans and infuscans-obsoleta	Population Density
	n		n		n		
I	59	0.347	111	0.653	47	0.276	6.4
					64	0.377	
II	120	0.328	246	0.672	122	0.333	4.1
					124	0.339	
III	62	0.272	166	0.728	64	0.281	1.7
					102	0.447	
Theoretical		0.250		0.750		0.250	0.0
						0.500	

Andromorphs : $a_o = 0.2502$, $a_1 = 0.0161$, $r^2 = 0.97$

Heteromorphs : $a_o = 0.7498$, $a_1 = 0.0161$, $r^2 = 0.97$

$y = a_o + a_1 x$ (y = population fraction, x = population density)

Table 12 : Frequencies of female morphs as fractions of the total female populations Dunham ponds. Population density = male total season density per m bank. (Based on PARR 1969).

Habitat	Year	Sex	n	Matings	Mating frequency in %	Sex ratio based on captures
Dunham I	1965	Male	505	21	4.2	0.699
		Female	170	(15) 21	(8.8) 12.4	
	1970	Male	783	50	6.4	0.676
		Female	284	(43) 50	(15.1) 17.6	
Dunham II	1965	Male	806	47	5.8	0.623
		Female	366	(45) 47	(12.3) 12.8	
Dunham III	1966	Male	349	19	5.4	0.583
		Female	228	(18) 19	(7.9) 8.3	
	1970	Male	420	14	3.3	0.748
		Female	70	(13) 14	(18.6) 20.0	
Anglesey	1959	Female	519	52	10.0	0.545
Theoretical		Male }	-	0	0	1.000
		Female }				

Table 13: I. elegans : mating frequencies.

n and matings found in PARR & PALMER (1971)for the Dunham Ponds and in LORD (1961)for the Anglesey habitat.

Age at which maximum fraction are at the water		Sex ratio based on captures	Habitat
Males	Females		
13	15	0.70	Dunham pond I
17	21	0.62	Dunham pond II
17	17	0.58	Dunham pond III
10	12	0.74	Denderleeuw

Table 14 : I. elegans : Age at which maximum fractions are at the water computed with a life table.

Administered JH in µg	Green → Turquoise $\bar{x}$	Sx	$S\bar{x}$	n	Turquoise → Blue $\bar{x}$	Sx	$S\bar{x}$	n	$\bar{L}$ $\bar{x}$	Sx	$S\bar{x}$	n
70	8.23	2.52	0.70	13	14.75	4.00	1.16	12	8.43	8.33	1.41	35
100	5.67	2.42	0.99	6	8.50	2.08	1.04	4	6.30	3.77	1.19	10
140	7.33	2.31	1.33	3	10.00	0.00	0.00	2	5.06	7.53	1.77	18
200	2.50	0.71	0.50	2	-	-	-	-	1.90	0.91	0.20	20
210	-	-	-	-	-	-	-	-	2.31	0.75	0.21	13
280	-	-	-	-	-	-	-	-	3.00	1.41	1.00	2
Reference	14.13	5.66	1.41	16	19.62	6.51	1.81	13	11.53	10.87	1.66	43

Table 15 : Influence of JH diluted in ethanol on adult I. elegans males.

First colour change as a function of treatment : $a_o = 12.93$, $a_1 = -0.05$, $r^2 = 0.87$, $n = 5$

Second colour change as a function of treatment : $a_o = 19.25$, $a_1 = -0.08$, $r^2 = 0.83$, $n = 4$

$\bar{L}$ as a function of treatment : $a_o = 10.44$, $a_1 = -0.03$, $r^2 = 0.86$, $n = 7$

Administered farnesol in µg	Green → Turquoise $\bar{x}$	Sx	$S\bar{x}$	n	Turquoise → Blue $\bar{x}$	Sx	$S\bar{x}$	n	$\bar{L}$ $\bar{x}$	Sx	$S\bar{x}$	n
35	12.00	1.15	0.44	7	15.83	3.82	1.56	6	9.94	8.05	2.01	16
70	4.60	0.89	0.40	5	4.60	0.89	0.40	5	5.40	8.17	2.11	15
140	2	-	-	1	3	-	-	1	1.25	0.50	0.25	4

Table 16 : Influence of farnesol diluted in ethanol on adult I. elegans males.

First colour change as a function of treatment : $a_o = 13.80$, $a_1 = -0.09$, $r^2 = 0.89$, $n = 4$

Second colour change as a function of treatment : $a_o = 18.42$, $a_1 = -0.13$, $r^2 = 0.83$, $n = 4$

$\bar{L}$ as a function of treatment : $a_o = 11.72$, $a_1 = -0.08$, $r^2 = 0.97$, $n = 4$

(Reference included in regressions)

Administered JH in µg	Green → Turquoise $\bar{x}$	Sx	$S\bar{x}$	n	Turquoise → Blue $\bar{x}$	Sx	$S\bar{x}$	n	$\bar{L}$ $\bar{x}$	Sx	$S\bar{x}$	n
83	7.94	1.73	0.43	16	11.78	4.24	1.41	9	6.04	5.12	0.75	47
167	3.40	0.89	0.40	5	-	-	-	-	3.00	0.83	0.17	24

Table 17 : Influence of JH diluted in paraffin oil on adult I. elegans males.

First colour change as a function of treatment : $a_o = 13.84$, $a_1 = -0.06$, $r^2 = 0.99$, $n = 3$

Second colour change as a function of treatment : $a_o = 19.62$, $a_1 = -0.09$, $n = 2$

$\bar{L}$ as a function of treatment : $a_o = 11.11$, $a_1 = -0.05$, $r^2 = 0.97$, $n = 3$

(Reference included in the regressions)

Administered farnesol in µg	Green → Turquoise $\bar{x}$	Sx	$S\bar{x}$	n	Turquoise → Blue $\bar{x}$	Sx	$S\bar{x}$	n	$\bar{L}$ $\bar{x}$	Sx	$S\bar{x}$	n
83	8.17	3.93	1.13	12	15.85	2.48	0.94	7	6.59	5.73	0.75	59
167	6.83	3.25	1.33	6	14	-	-	1	3.59	2.37	0.28	69
250 *	4.75	1.26	0.63	4	5	-	-	1	4.50	1.15	0.29	16

Table 18 : Influence of farnesol diluted in paraffin oil on adult I.elegans males.

First colour change as a function of treatment : $a_o = 12.89$, $a_1 = -0.04$, $r^2 = 0.89$, $n = 4$

Second colour change as a function of treatment : $a_o = 20.47$, $a_1 = -0.05$, $r^2 = 0.90$, $n = 4$

$\bar{L}$ as a function of treatment : $a_o = 10.16$, $a_1 = -0.03$, $r^2 = 0.77$, $n = 4$ (not significant)

$\bar{L}$ as a function of treatment (without 250 µg treatment) : $a_o = 11.20$, $a_1 = -0.05$, $r^2 = 0.98$, $n = 3$

* Administered in 3 doses spread over 3 days

Administered	$\bar{L}$			
JH in µg	$\bar{x}$	Sx	$S\bar{x}$	n
83	4.29	2.17	0.33	42
140	3.57	0.85	0.23	14
Reference	9.92	5.84	0.84	48

Table 19 : Influence of JH diluted in paraffin oil on adult I. elegans females. $\bar{L}$ as a function of treatment : $a_o = 9.42$, $a_1 = -0.05$, $r^2 = 0.91$, $n = 3$

	Average time away from the water $\bar{L}$ Maximum $\bar{L}$		Population density
	Males	Females	
Pond I	10.7	8.8	6.4
	4.3	8.6	
	15.0	17.4	
Pond II	8.9	8.5	4.1
	2.2	4.4	
	11.1	12.9	
Pond III	16.0	18.6	1.7
	3.4	4.7	
	19.4	23.3	

$\bar{L}$ as a function of population density (Pond II omitted) : $\bar{L}$: $a_o = 17.92$, $a_1 = -1.13$, $n = 2$ (males)

$\bar{L}$: $a_o = 22.14$, $a_1 = -2.09$, $n = 2$ (females)

Maximum $\bar{L}$: $a_o = 20.99$, $a_1 = -0.94$, $n = 2$ (males)

$a_o = 25.43$, $a_1 = -1.26$, $n = 2$ (females)

Table 20 : Population density influence on $\bar{L}$ in field conditions.

Fig. 1 : Age distribution of I. elegans in the active population. (Denderleeuw, 1973).

Fig. 2 : Age distribution of P. nymphula in the active population. (based on CORBET 1952).

Fig. 3 : Immature and mature fractions of both sexes of I. elegans as a function of male population density.

Fig. 4 : Colour changes and polymorphism in female I. elegans.

Fig. 5 : Mating frequency in I. elegans as a function of the sex ratio, with indication of the different phases of the evolution cycle of the population.

Fig. 6 : Evolution of male $\bar{L}$ in I. elegans during the flight season at the Dunham ponds.

Fig. 7 : Evolution of female $\bar{L}$ in I. elegans during the flight season at the Dunham ponds.

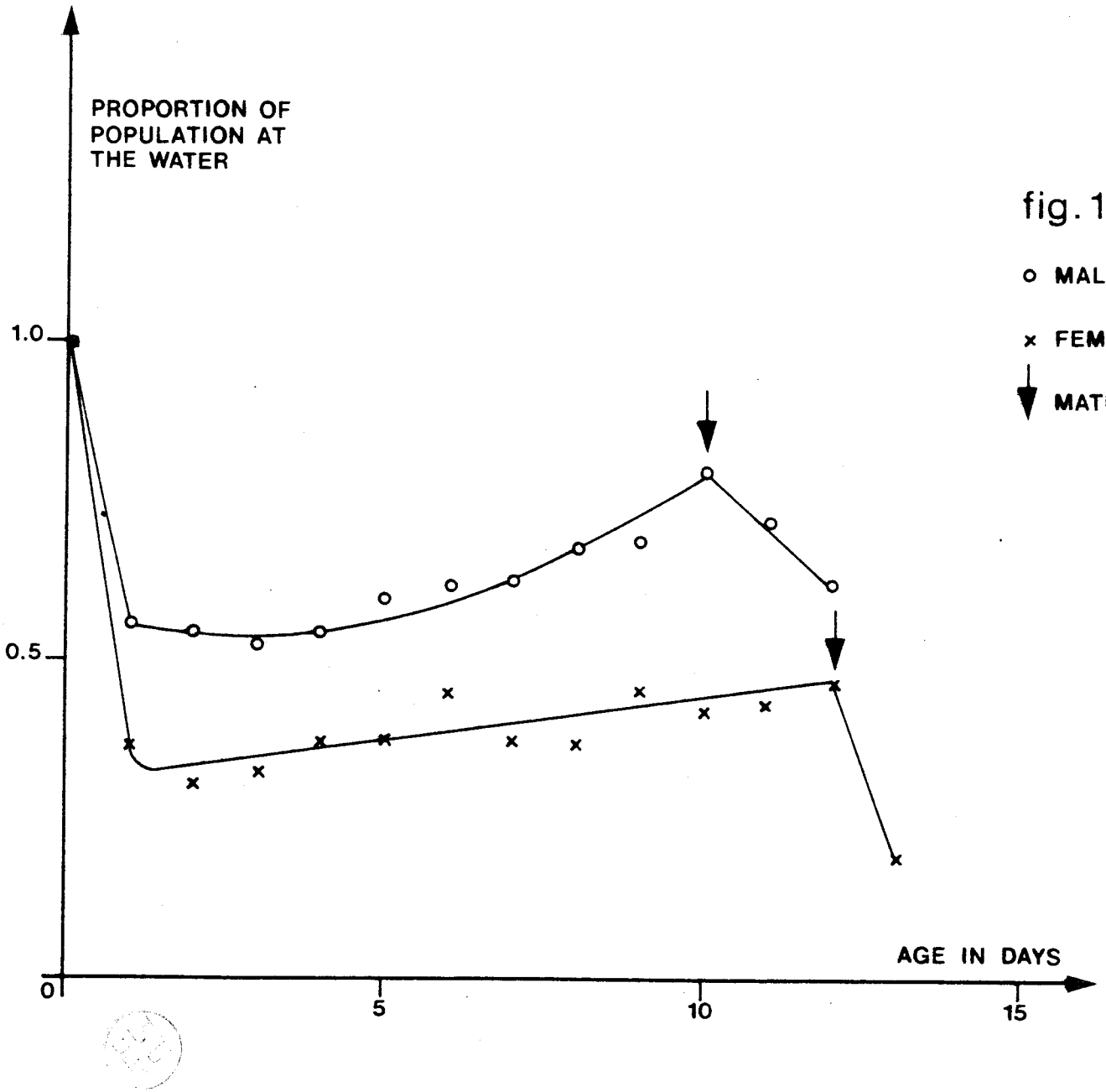


fig. 1.

o MALES

x FEMALES

MATURATION TIME

fig. 2.

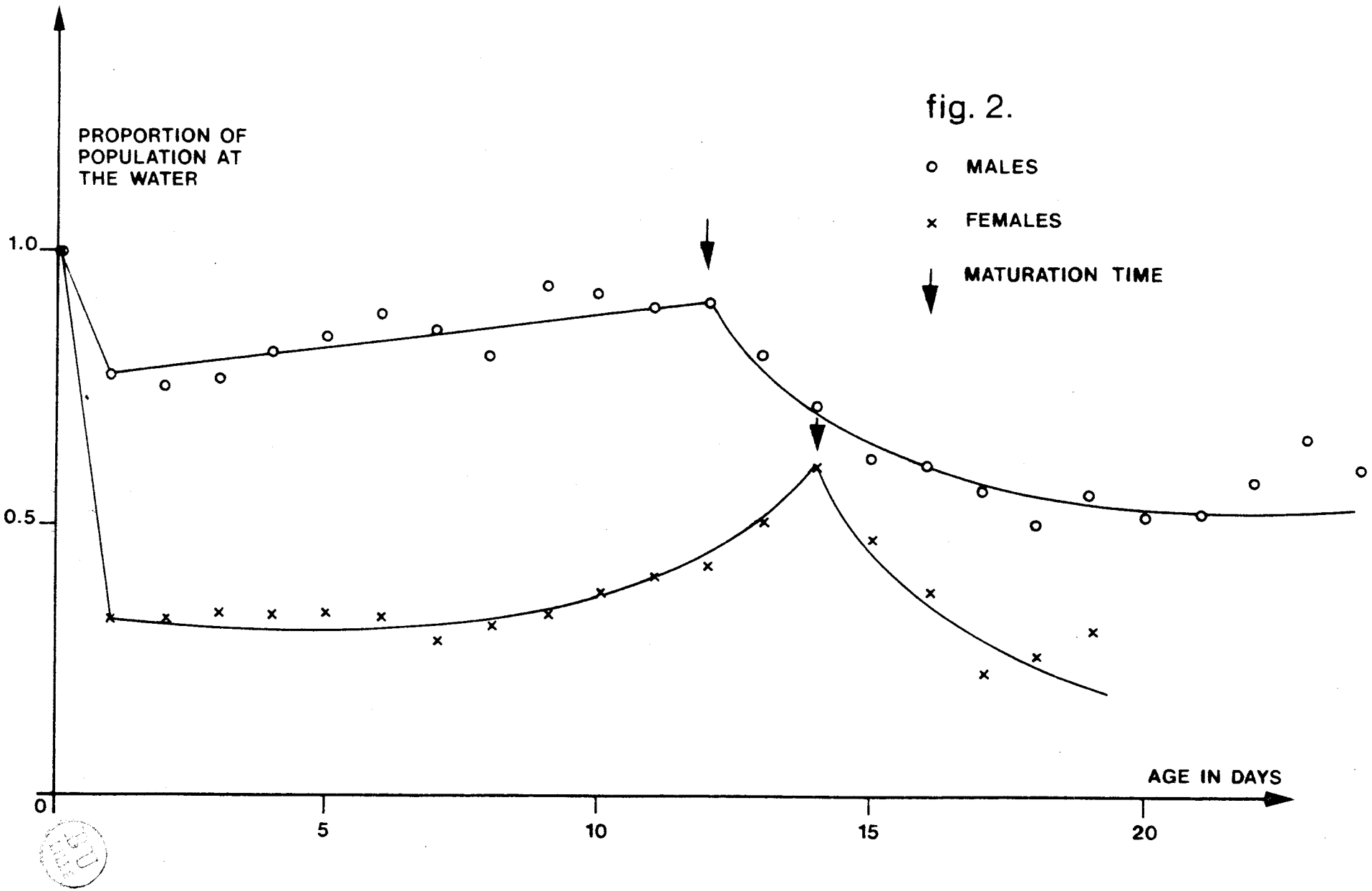

PROPORTION OF POPULATION AT THE WATER
1.0
0.5
0
MALES
FEMALES
MATURATION TIME
AGE IN DAYS
5
10
15
20

fig.3.

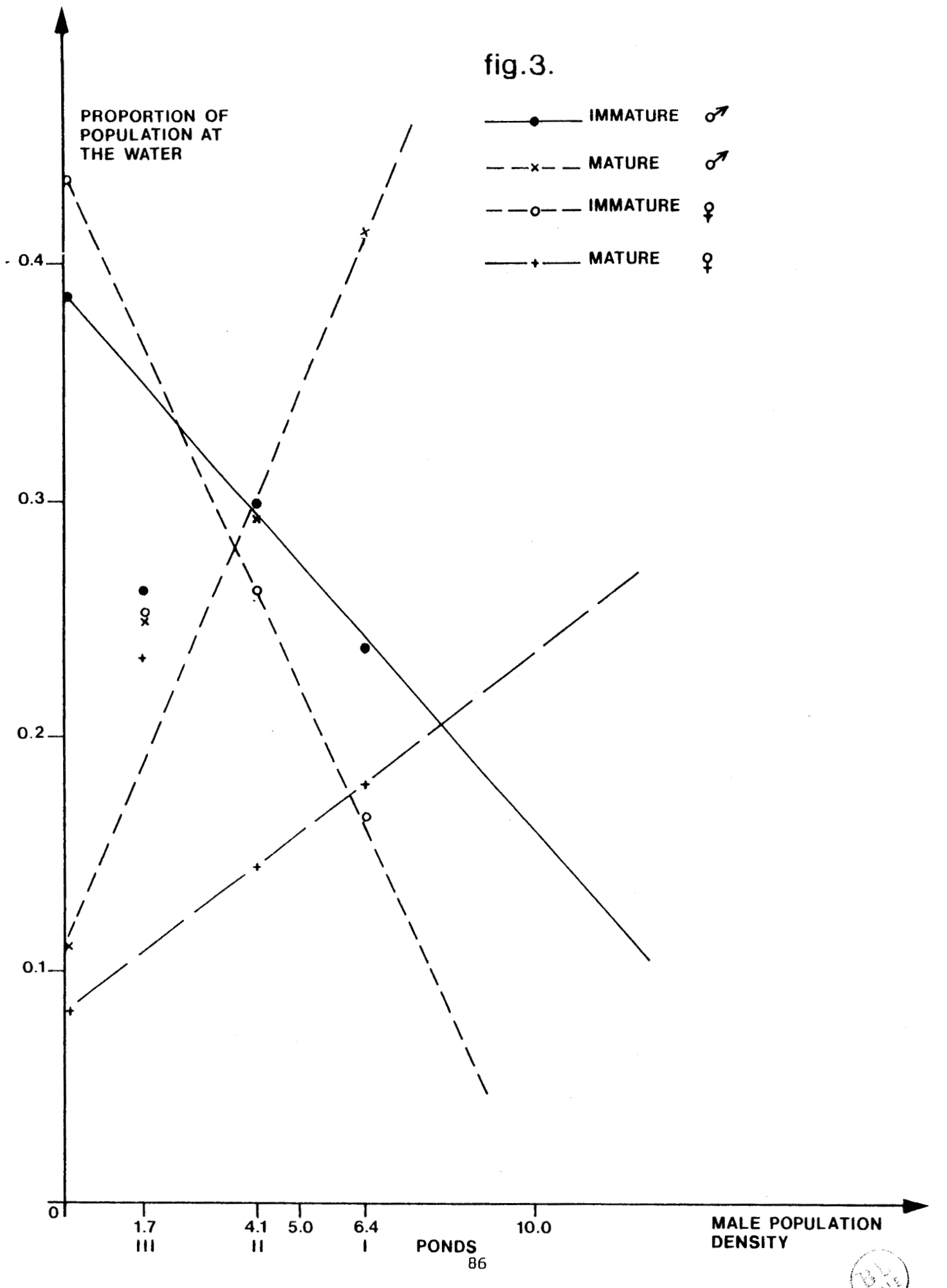
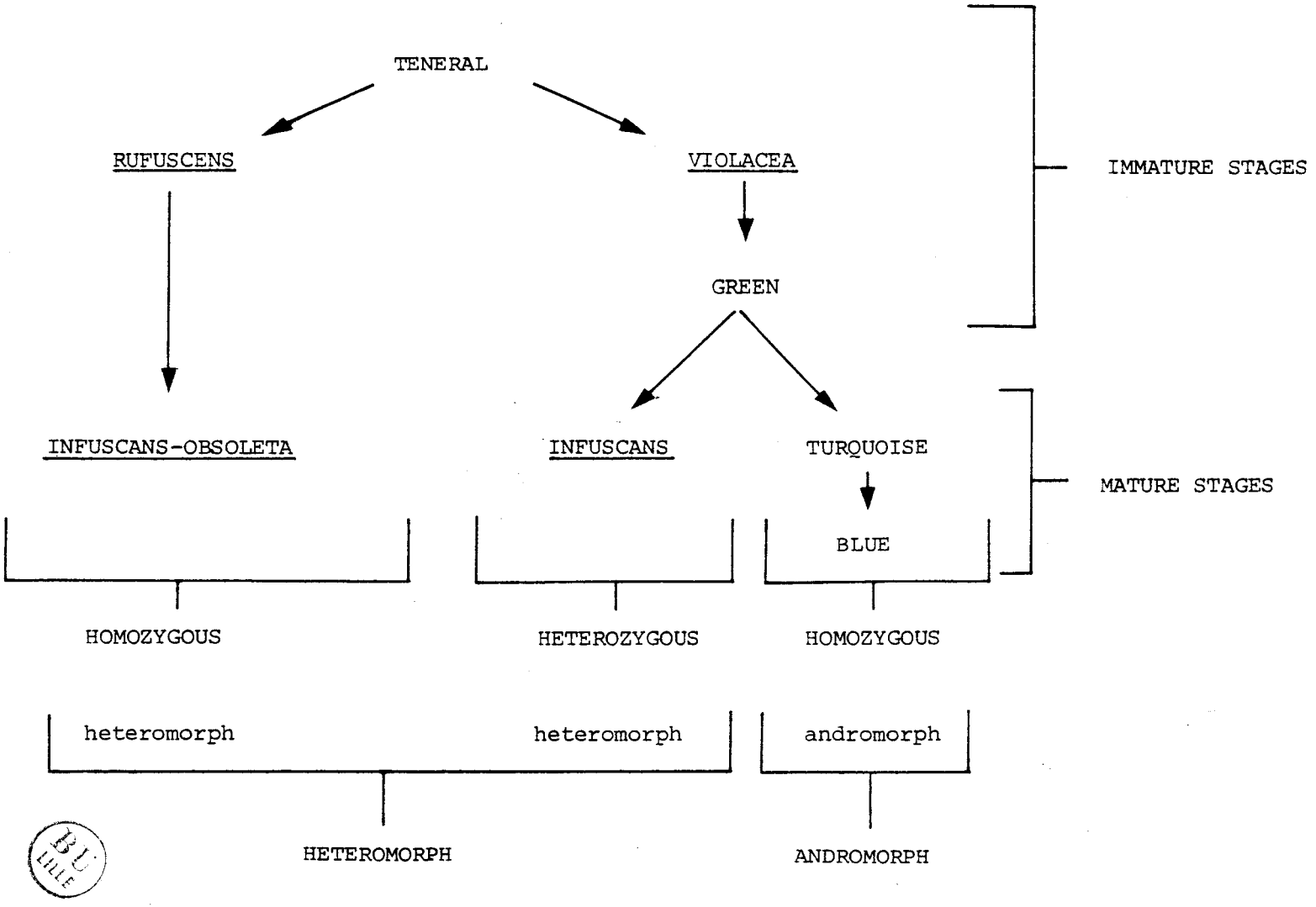


Fig. 4 Colour changes and polymorphism in female I. elegans



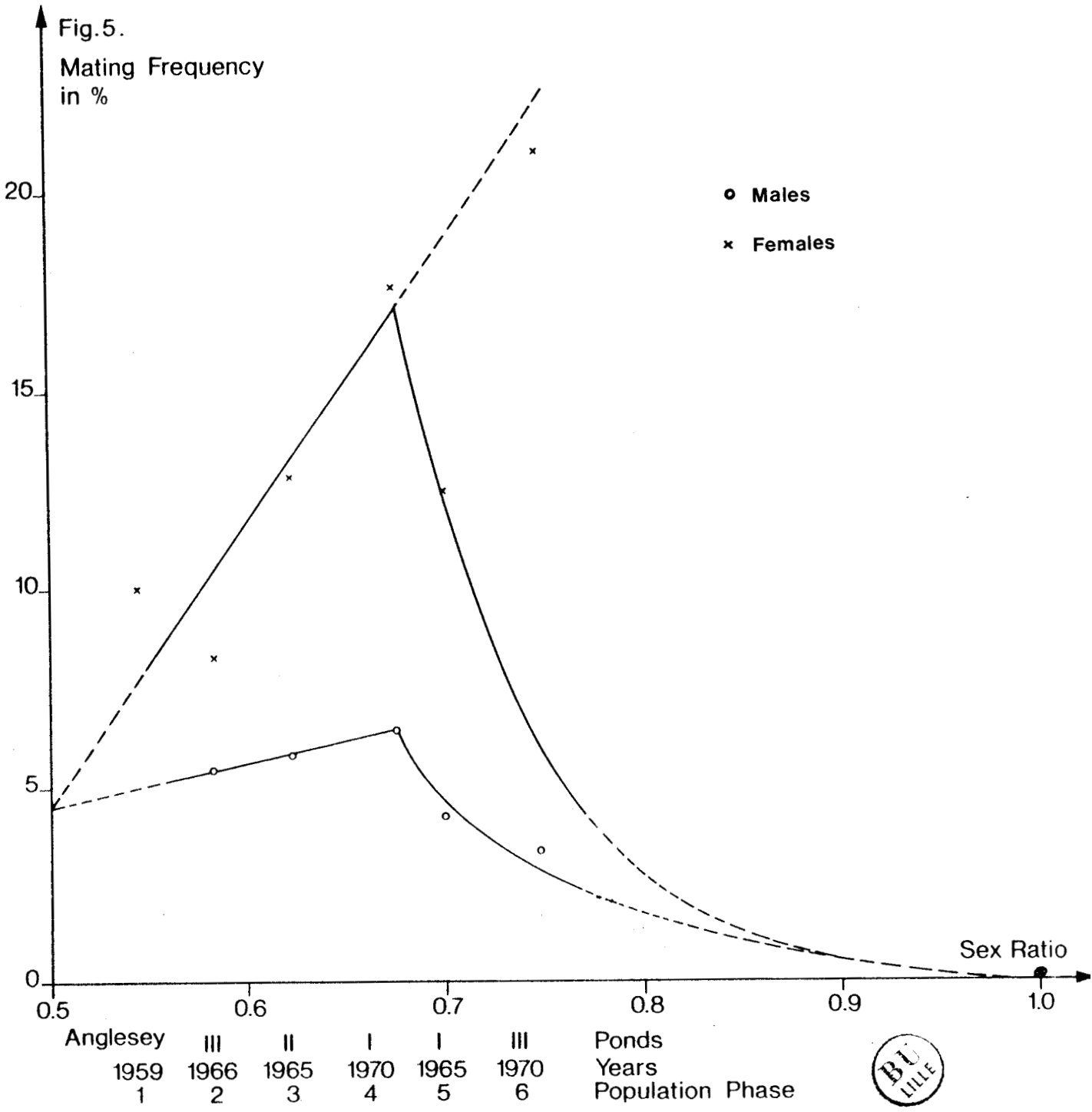


Fig.5.
Mating Frequency
in %
20
15
10
5
0
Males
Females
Sex Ratio
0.5
0.6
0.7
0.8
0.9
1.0
Anglesey
III
II
I
I
III
Ponds
1959
1966
1965
1970
1965
1970
Years
1
2
3
4
5
6
Population Phase

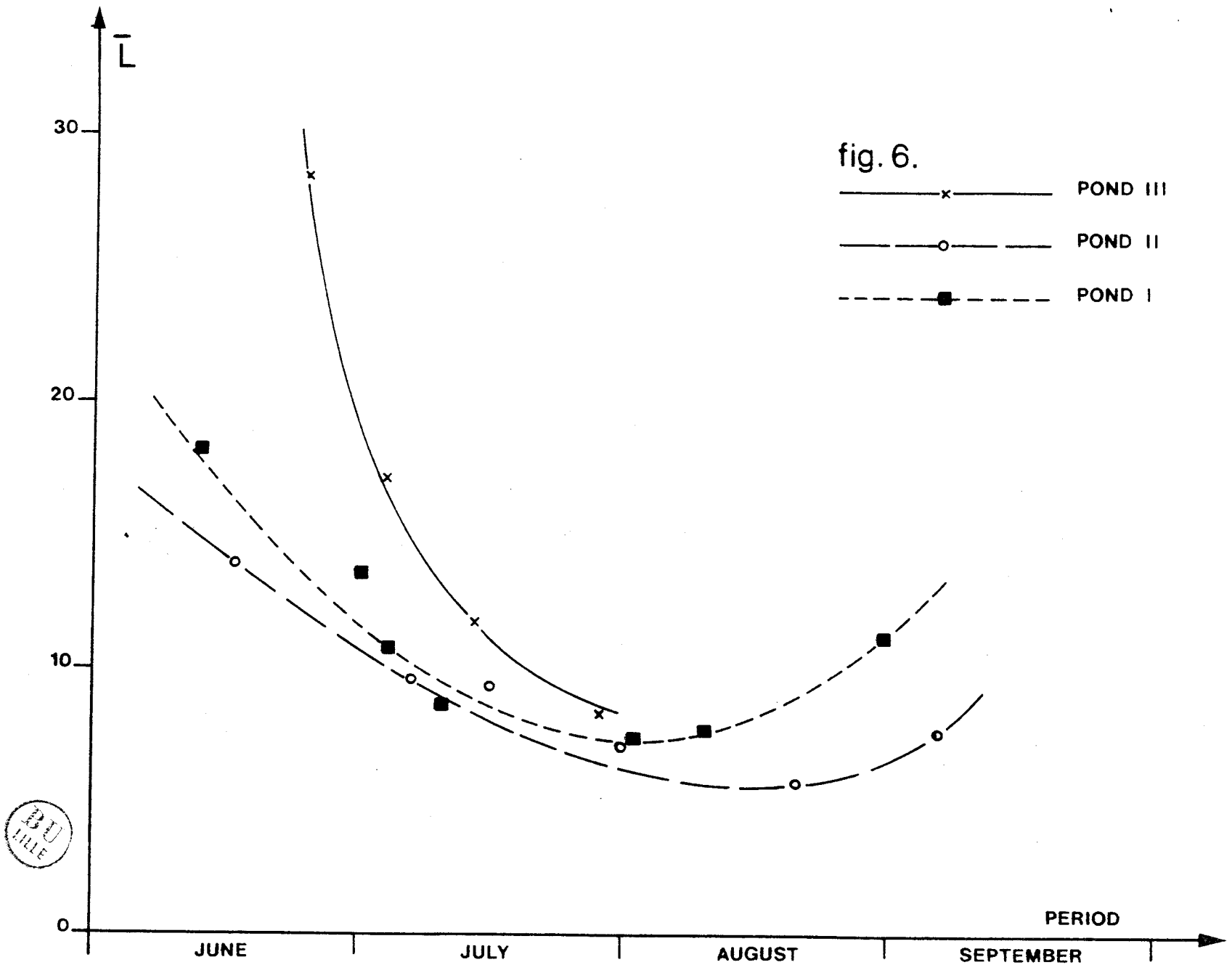


fig. 6.

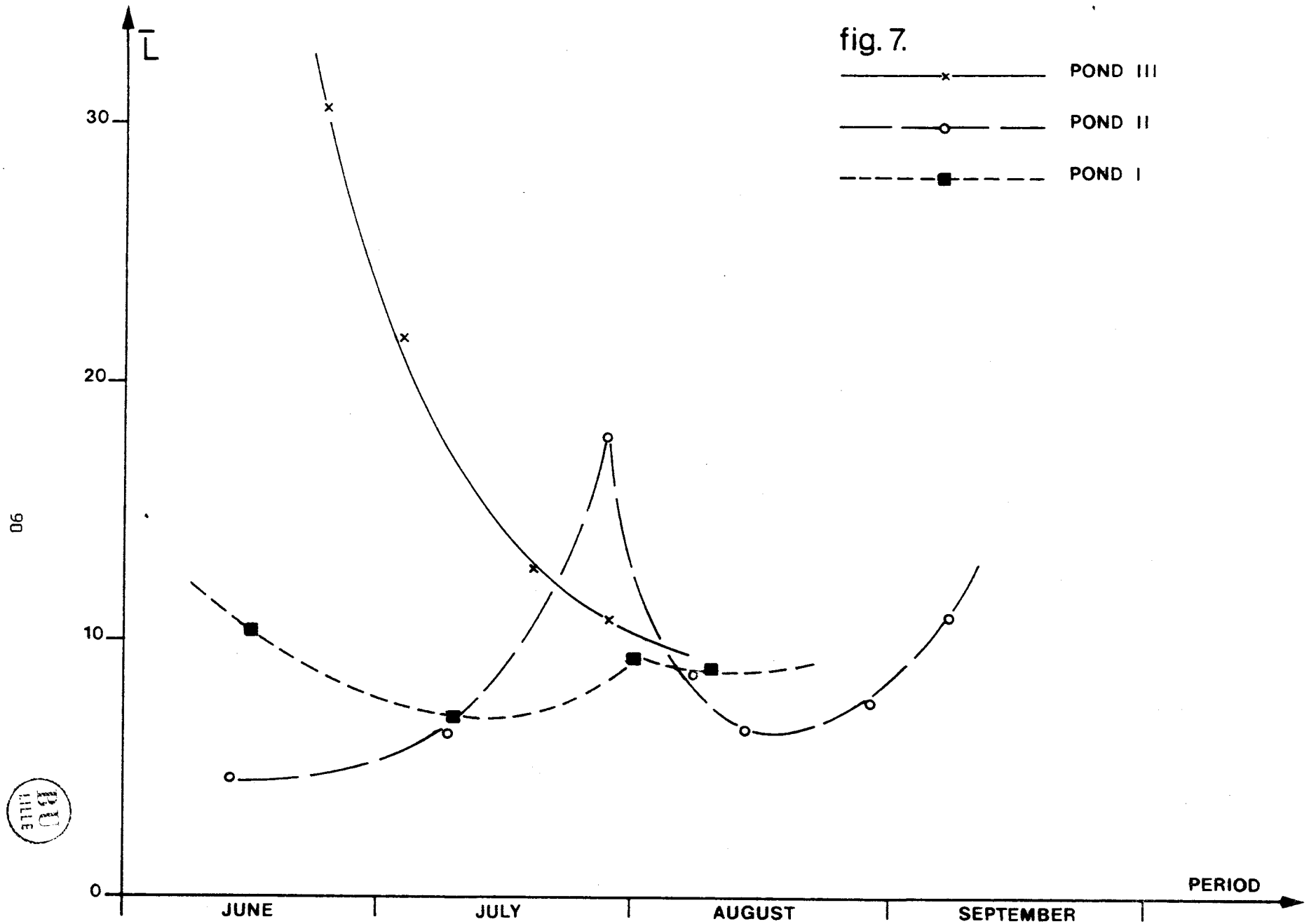


fig. 7.
POND III
POND II
POND I
L
30
20
10
0
JUNE
JULY
AUGUST
SEPTEMBER
PERIOD

ANNEXES

Odonatologica 3 (4): 261-263 *December 1, 1974*

AN INDIVIDUAL MARKING TECHNIQUE FOR ODONATA

B.O.N. HINNEKINT

Received July 29, 1974 / Accepted August 2, 1974

A technique for quick individual marking in the field was developed, using sharp-pointed waterproof "magic" markers, for putting an easily readable code on one hindwing.

INTRODUCTION

Most of the methods presently used in insect marking are slow and insufficiently stable for a study in which individual marking is needed. A review of the techniques used in Odonata was published by CORBET, LONGFIELD & MOORE (1960). These authors recommend the commonly used method of cellulose paint, as practised by MOORE (1952), CORBET (1952, 1960), PAJUNEN (1962) and PARR (1965). This is basically a good technique, but it is a bit slow and has one major disadvantage: the paint becomes rapidly viscous and sticky.

For marking individually a large number of animals an elaborate code is indispensable, so that e.g. marking the femurs (PAJUNEN, 1962) is out of the question and only the wings remain as a possibility.

THE NEW TECHNIQUE

Capture techniques are explained in full detail by PARR (1965). We also work in a team of two persons, one capturing the animals and passing them on to the second for marking and recording all necessary information.

Odonata are captured 10 to 20 at a time, using a butterfly net. They are removed from the net by grasping the top of the closed wings between thumb and fingers and then transferred to the other hand to hold them with head and thorax between thumb and two fingers. This permits to hold the wings against a

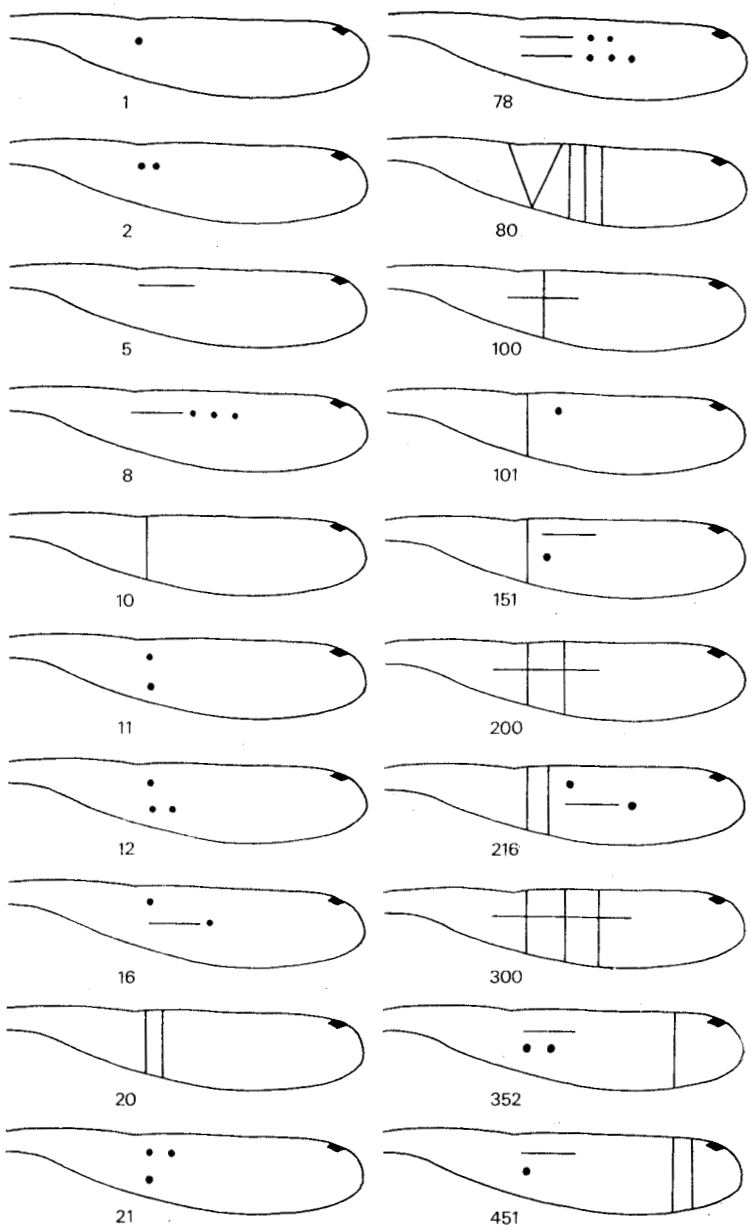


Fig. 1. Key to the code used in our individual marking technique for dragonflies.

solid surface to be marked by the second person on the underside of one hindwing using a sharp-pointed waterproof magic marker (as used in the laboratory to mark glasswork). The animals are released immediately hereafter.

Using only one wing for marking has the advantage that the code, applied at the time of capture, is read at recapture without having to spread the wings, which saves time and reduces possible damage.

The code used is shown in Figure 1. It is a modified Roman system, having a great relation with the Maya numbers. It is impossible to apply normal arabic numbers on the wings because the ink of the magic marker contracts on the wing surface. But a combination of points, stripes and eventually different colours, provides an elegant and fast solution. The following symbols were selected: a point for unity, a horizontal stripe for five, a vertical stripe for ten and two vertical stripes for twenty. For numbers above ten: use the upper side of the wing for the decades and the lower side for the units. In order to reduce the number of symbols we use for fifty, sixty, etc. the Roman numbers for five, six etc. One hundred is symbolised by a cross. For numbers above one hundred a vertical stripe is placed before the number, for those above two hundred, two vertical stripes. Above three hundred and four hundred, the vertical stripes are placed behind te number. Five hundred is about a limit for this code in small Odonata, though using several colours may extend its application considerably.

It is recommended not to use the tip of the wing, as care should be taken not to touch the marks with the fingers. The coloured substance of the magic markers is indeed soluble in the lipids of the skin. Capture or recapture, application of the code and writing down the information needed takes an average of a minute per animal. There is thus a considerable gain of time, as compared with previous techniques, beside the advantage of having at hand a powerful technique for individual recognizing of recaptured specimens.

ACKNOWLEDGEMENTS

The author has had the benefit of discussing his method with Dr. M.J. PARR (University of Salford, England). To Dr. H.J. DUMONT (University of Ghent, Belgium) he is indebted for criticizing the manuscript.

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MOORE, N.W., 1952. On the so-called "territories" of dragonflies (Odonata: Anisoptera). *Behaviour* 4 (2): 85-100.

PAJUNEN, V.I., 1962. Studies on the population ecology of Leucorrhinia dubia (v.d. Lind.) (Odonata: Libellulidae). *Ann. Zool. Soc. 'Vanamo'* 24 (4): 1-79.

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Données de l'expérience de marquage à Denderleeuw en août 1973.

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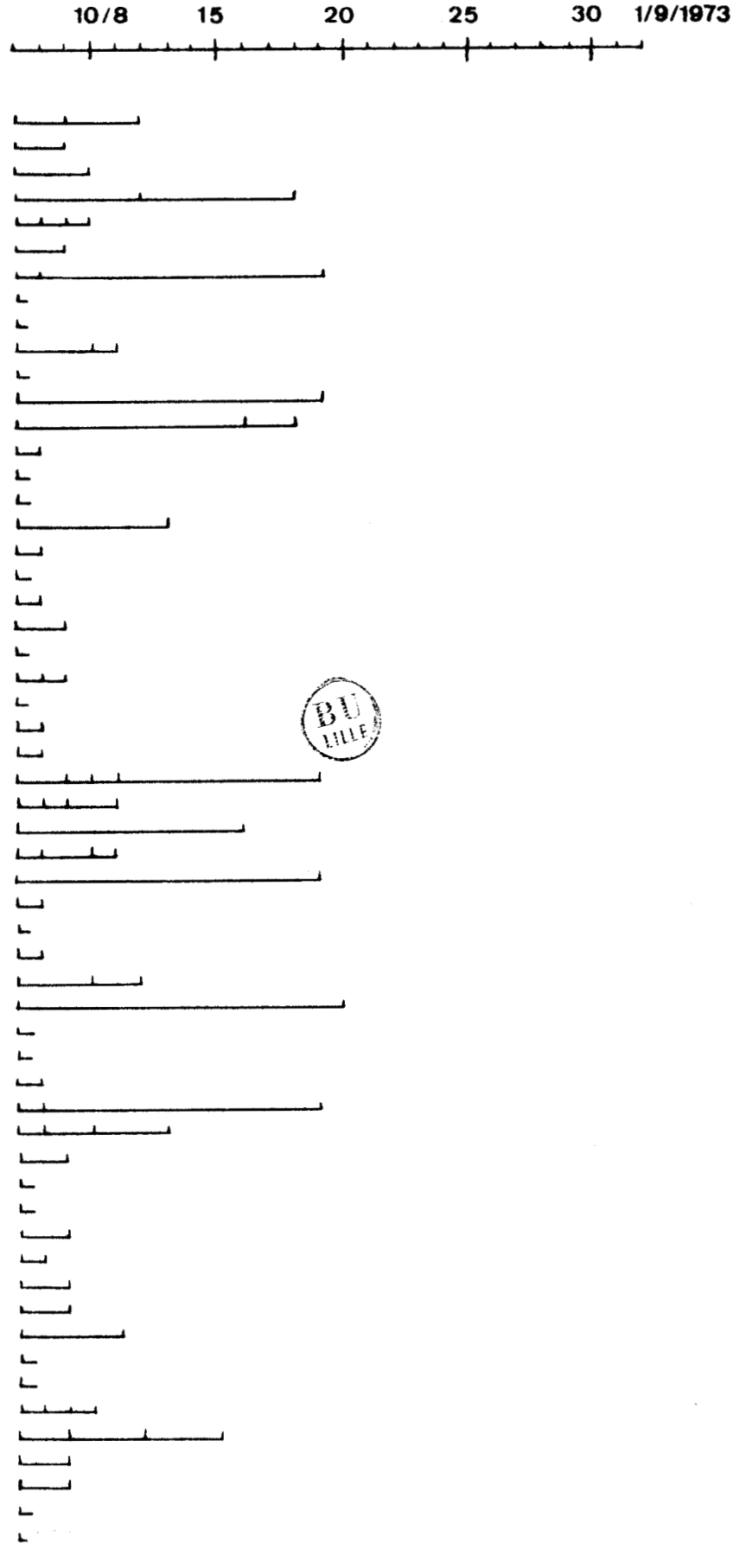

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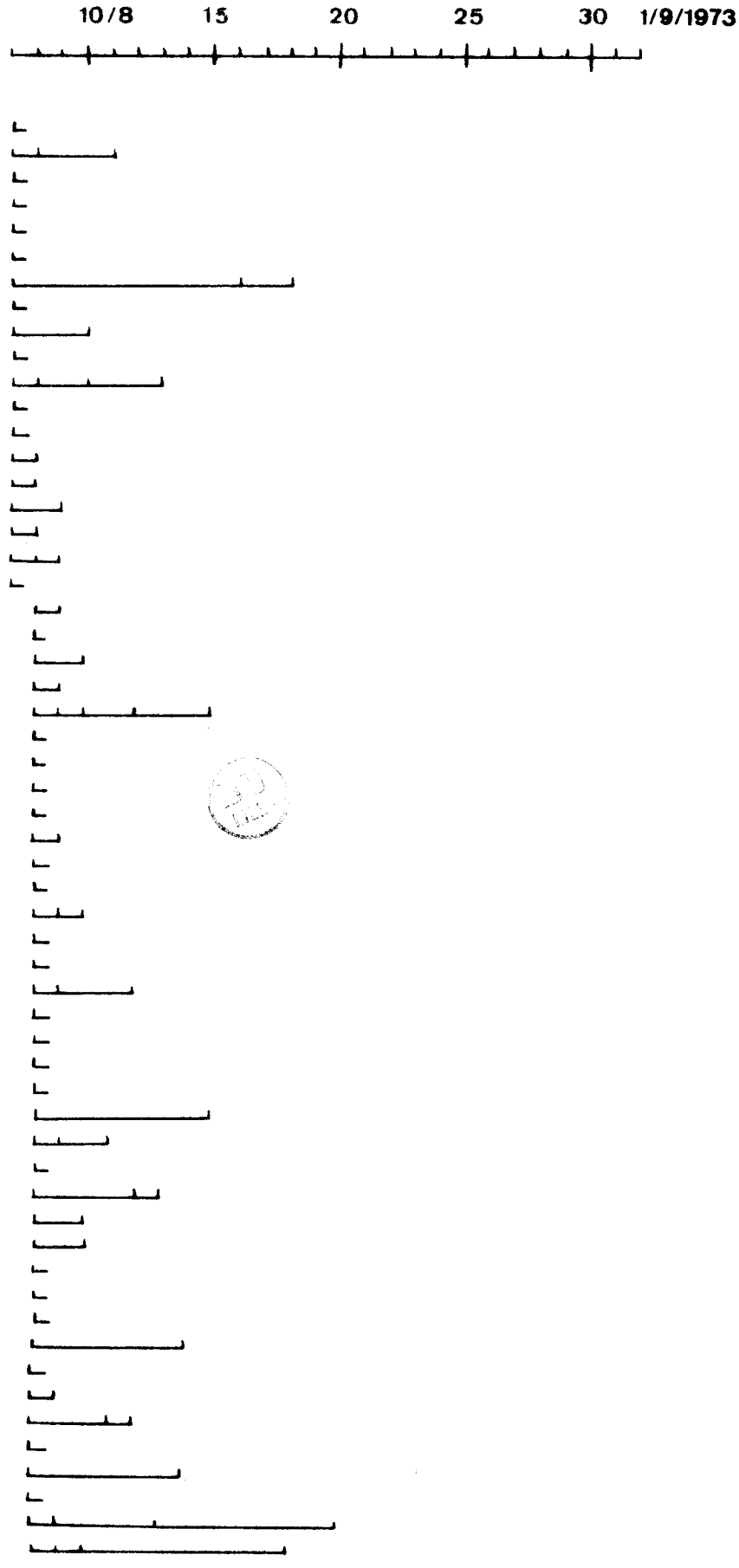

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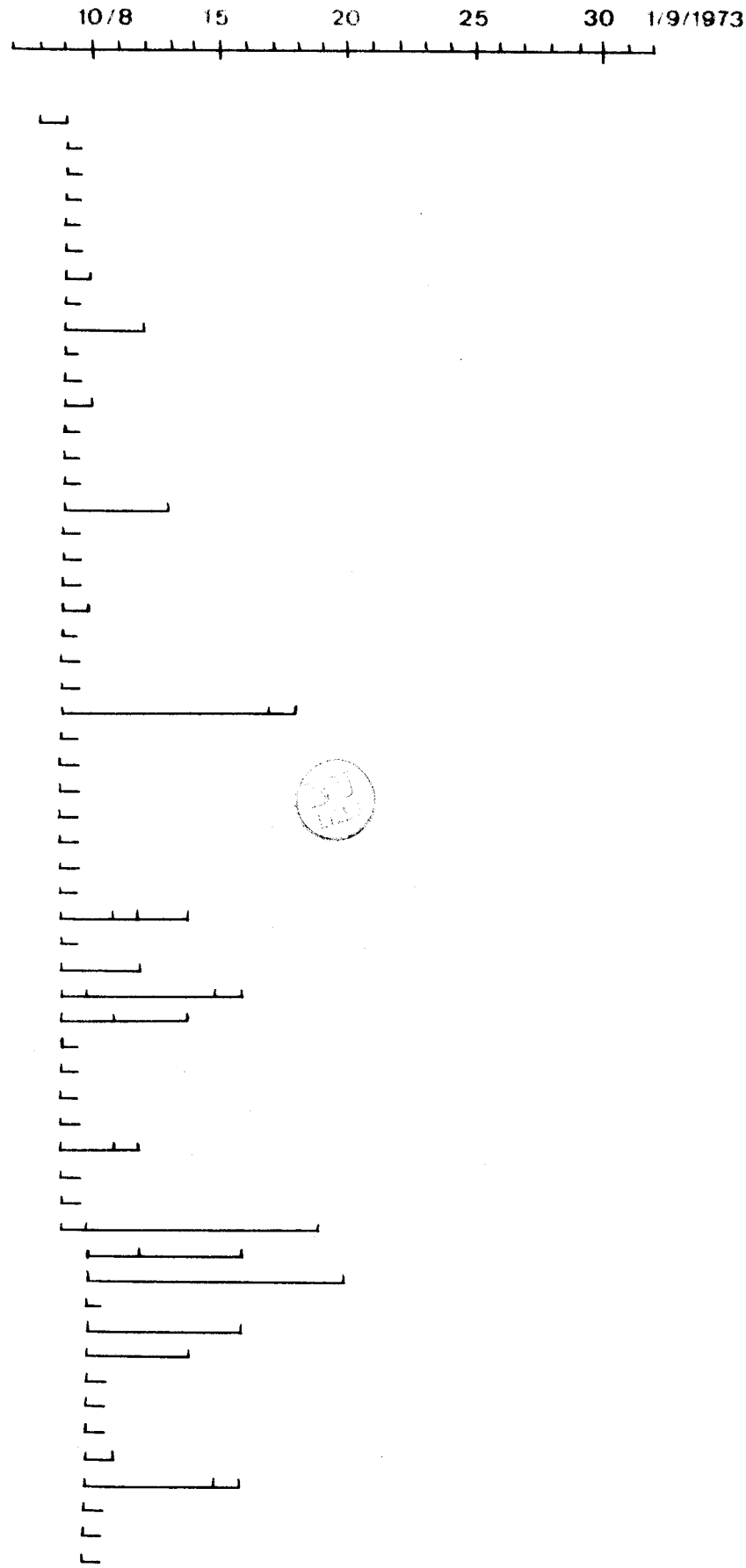

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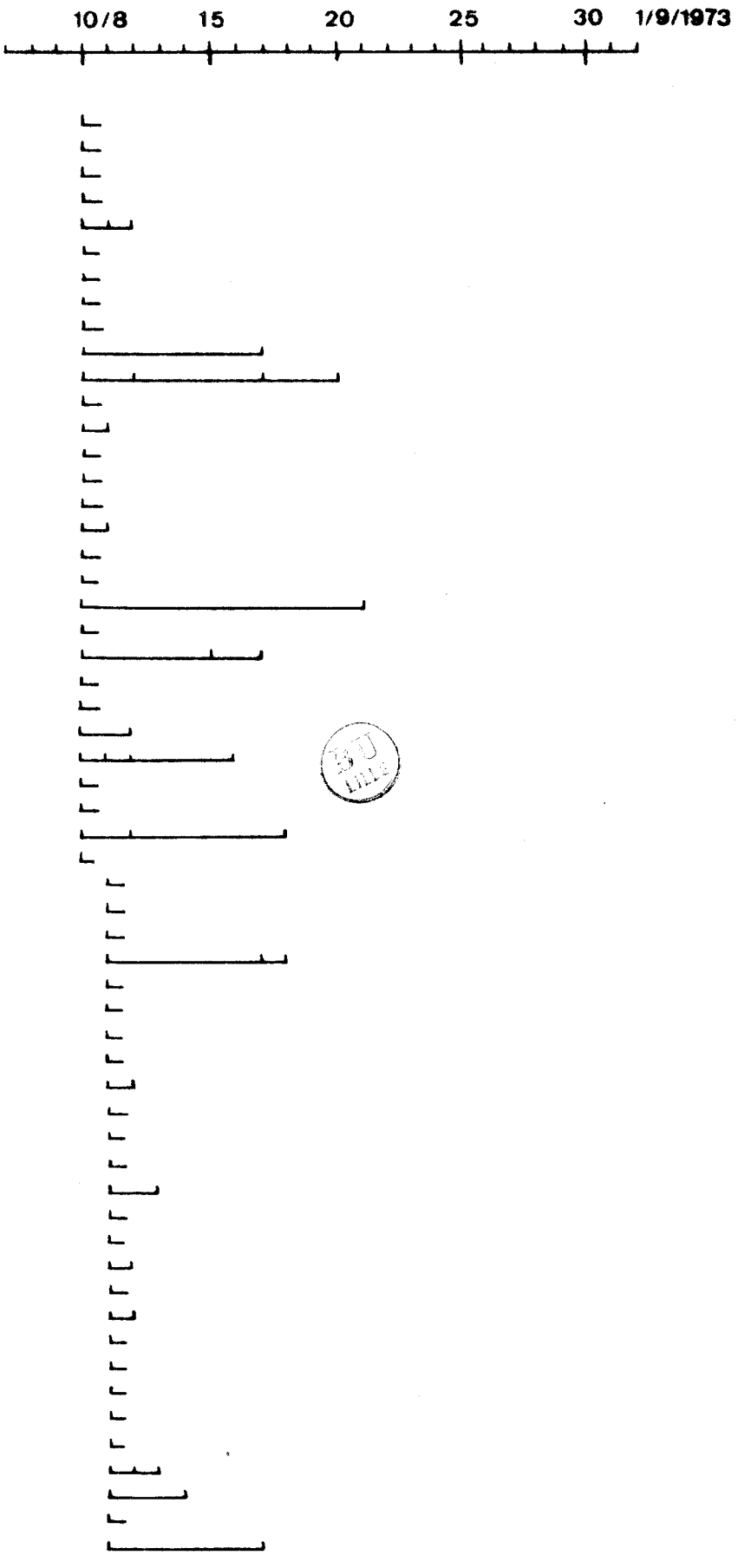

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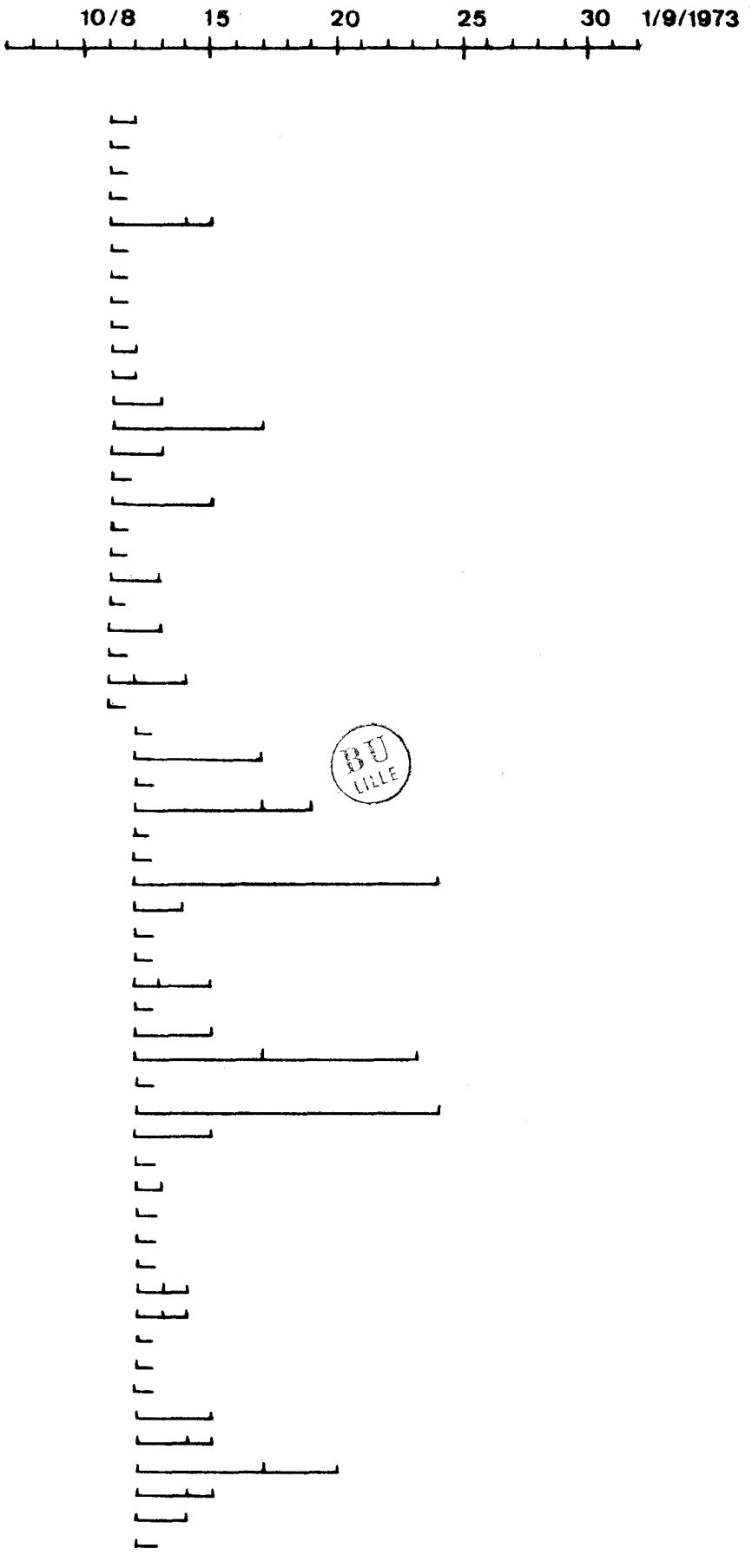

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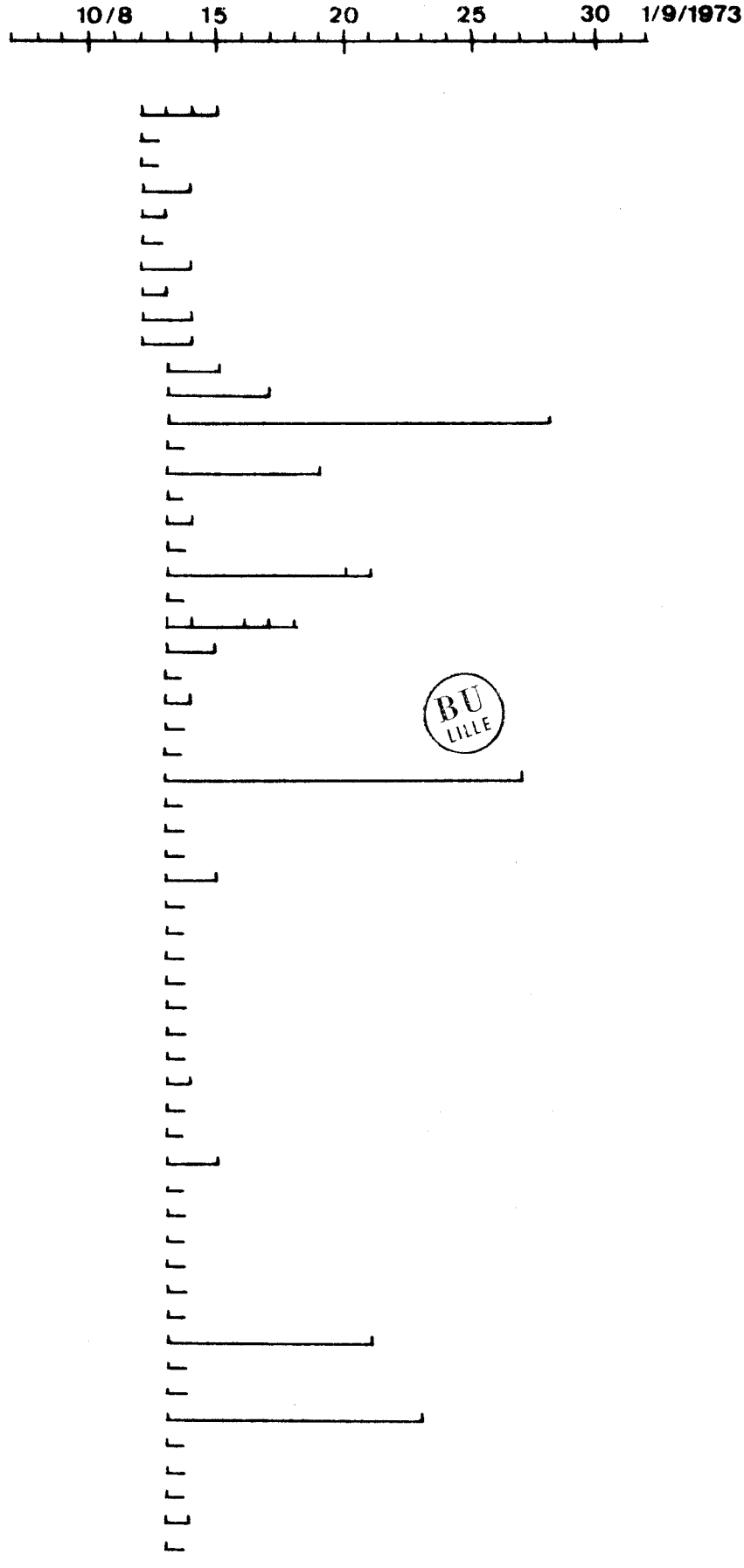

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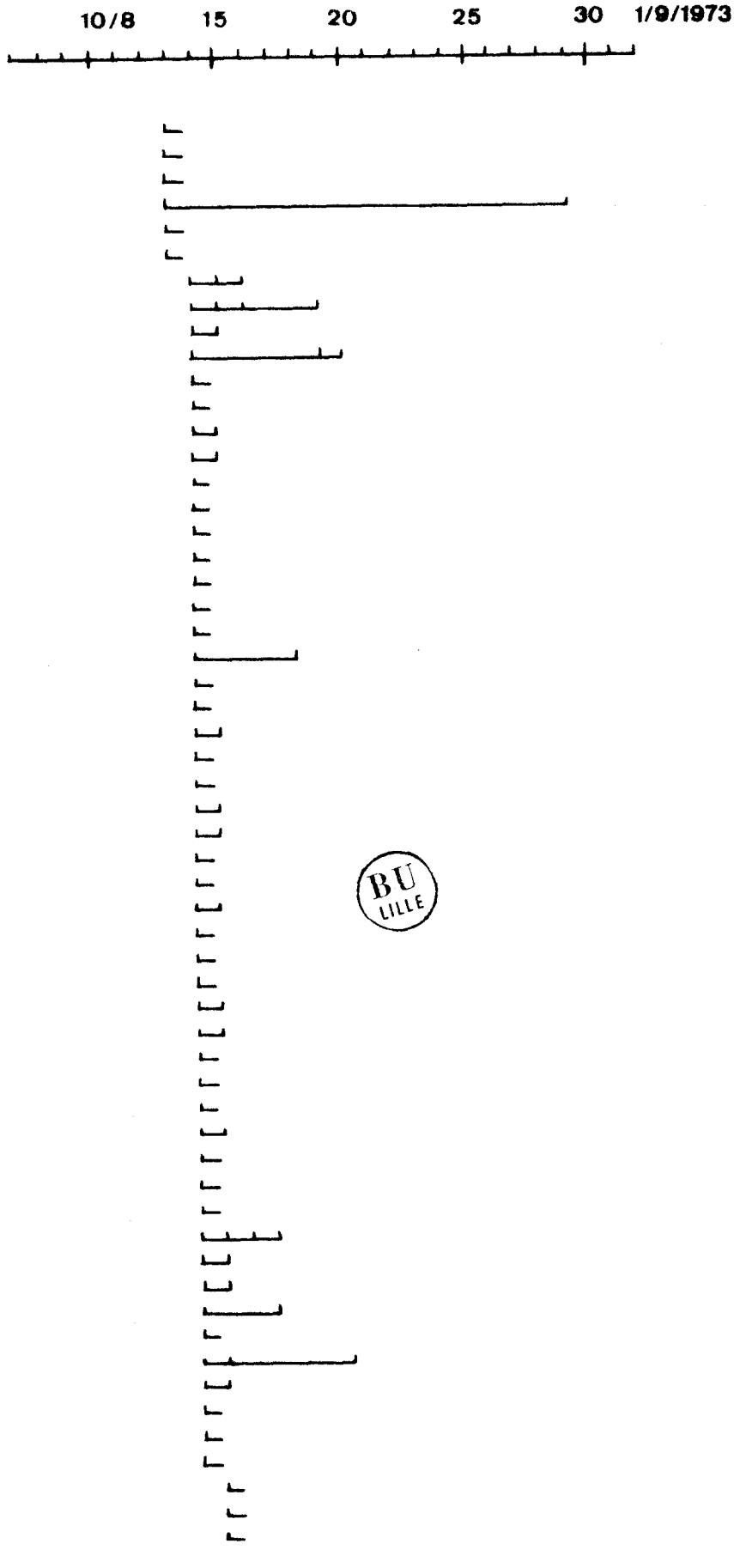

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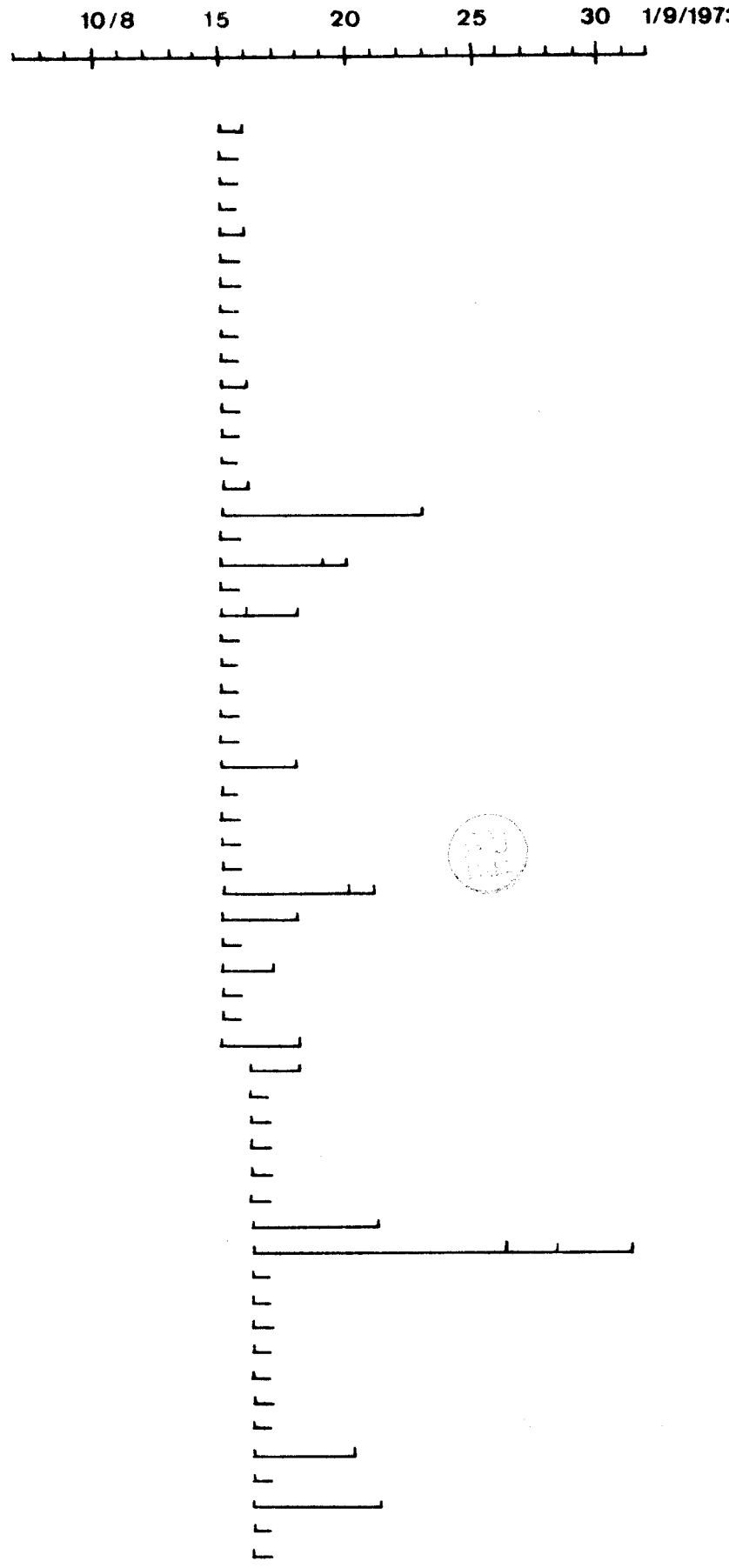

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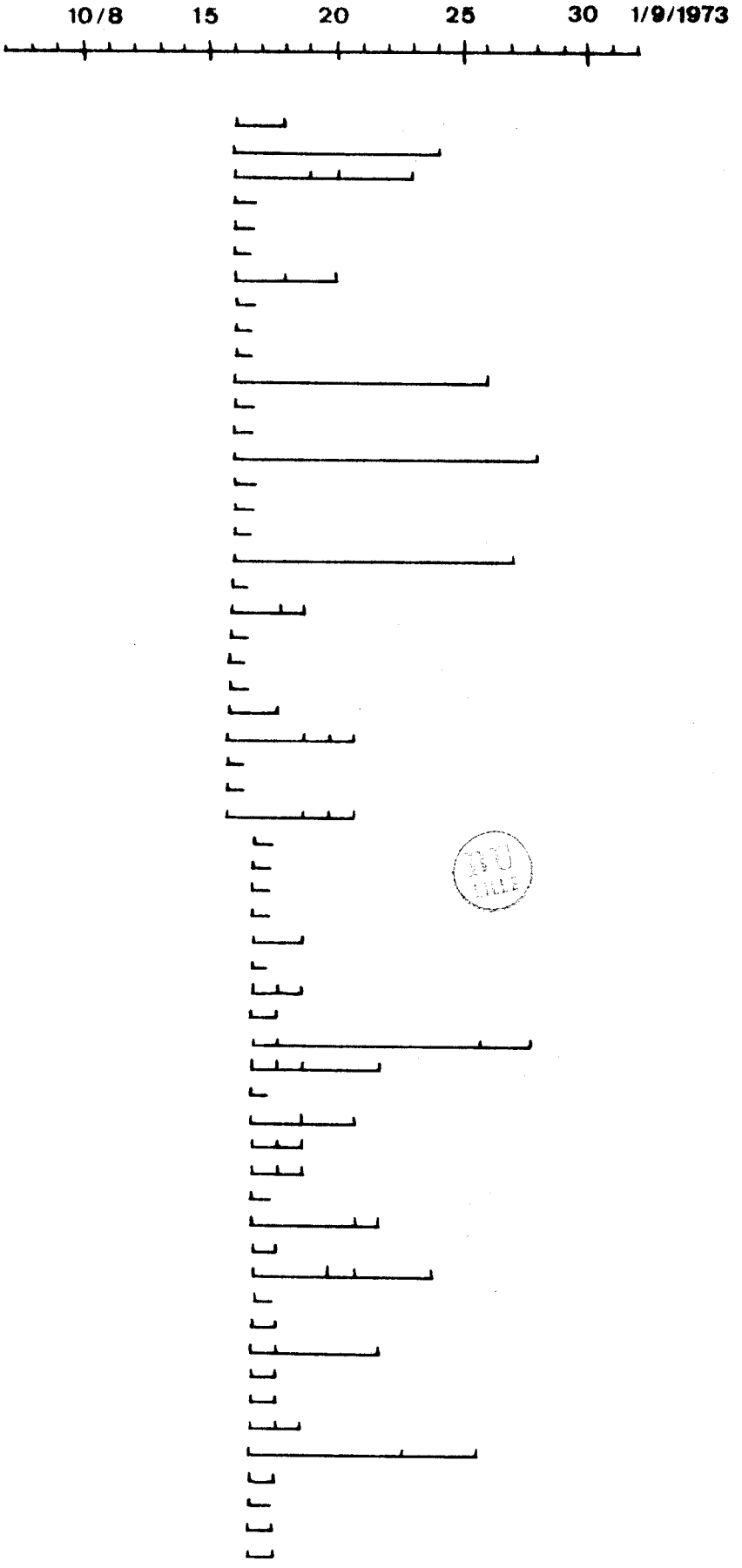

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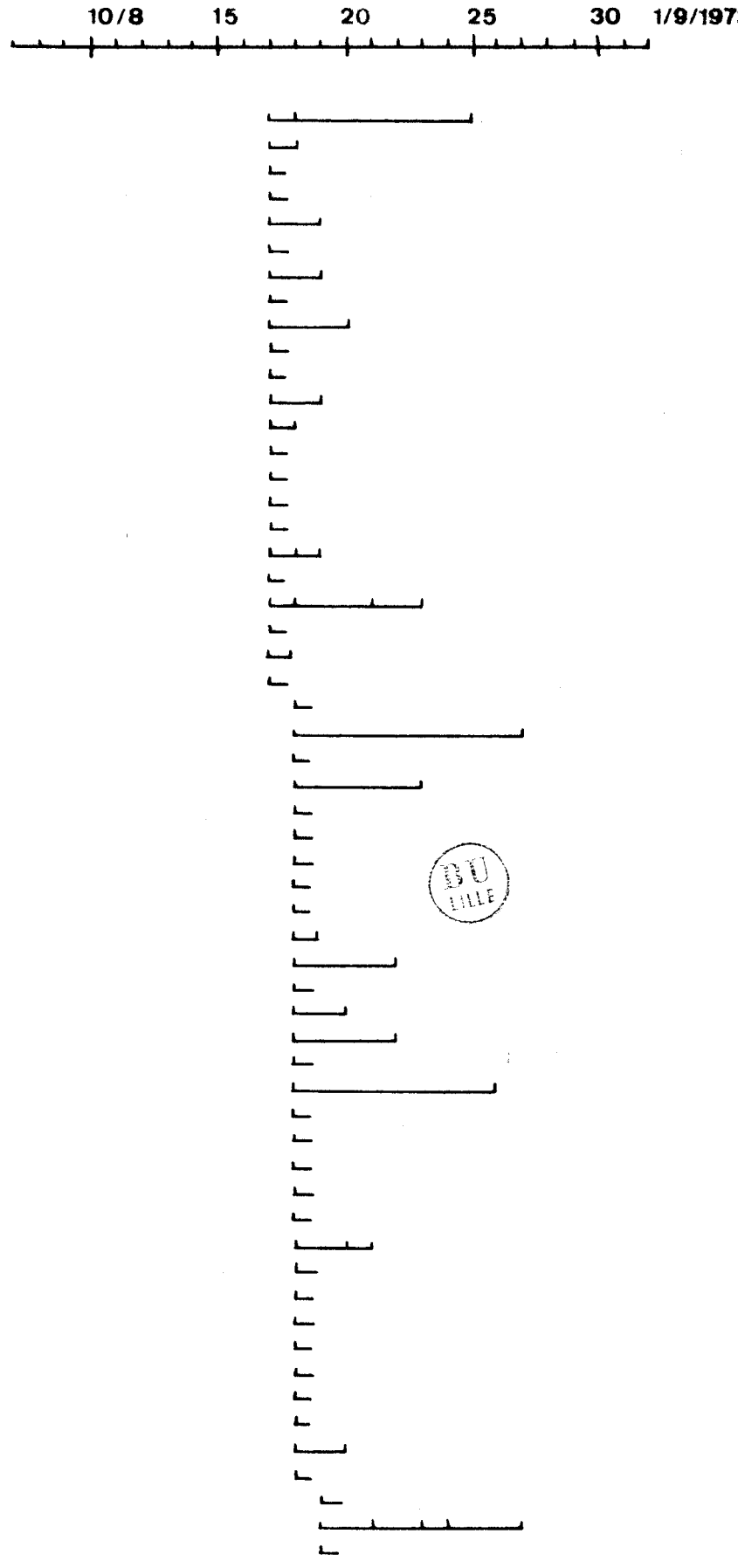

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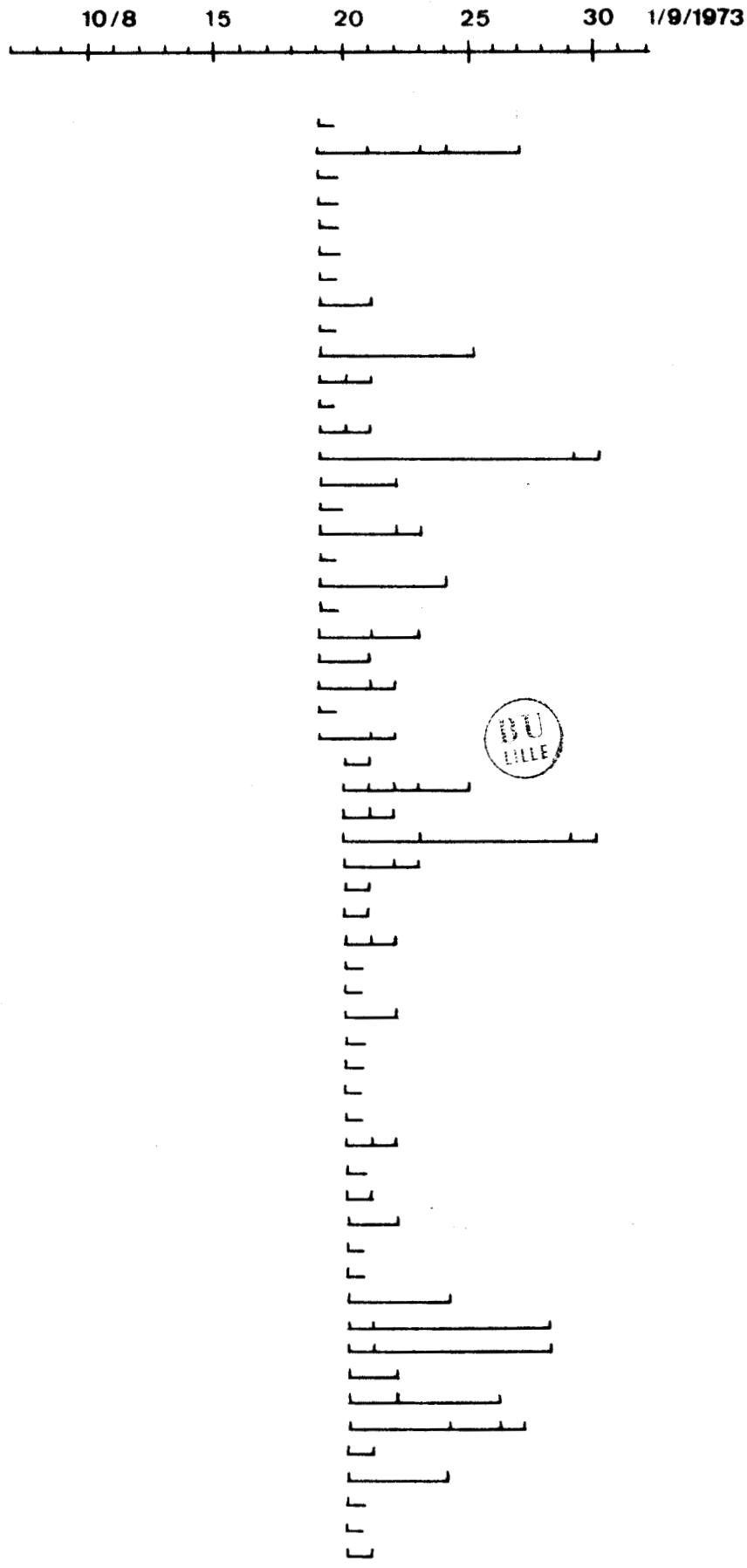

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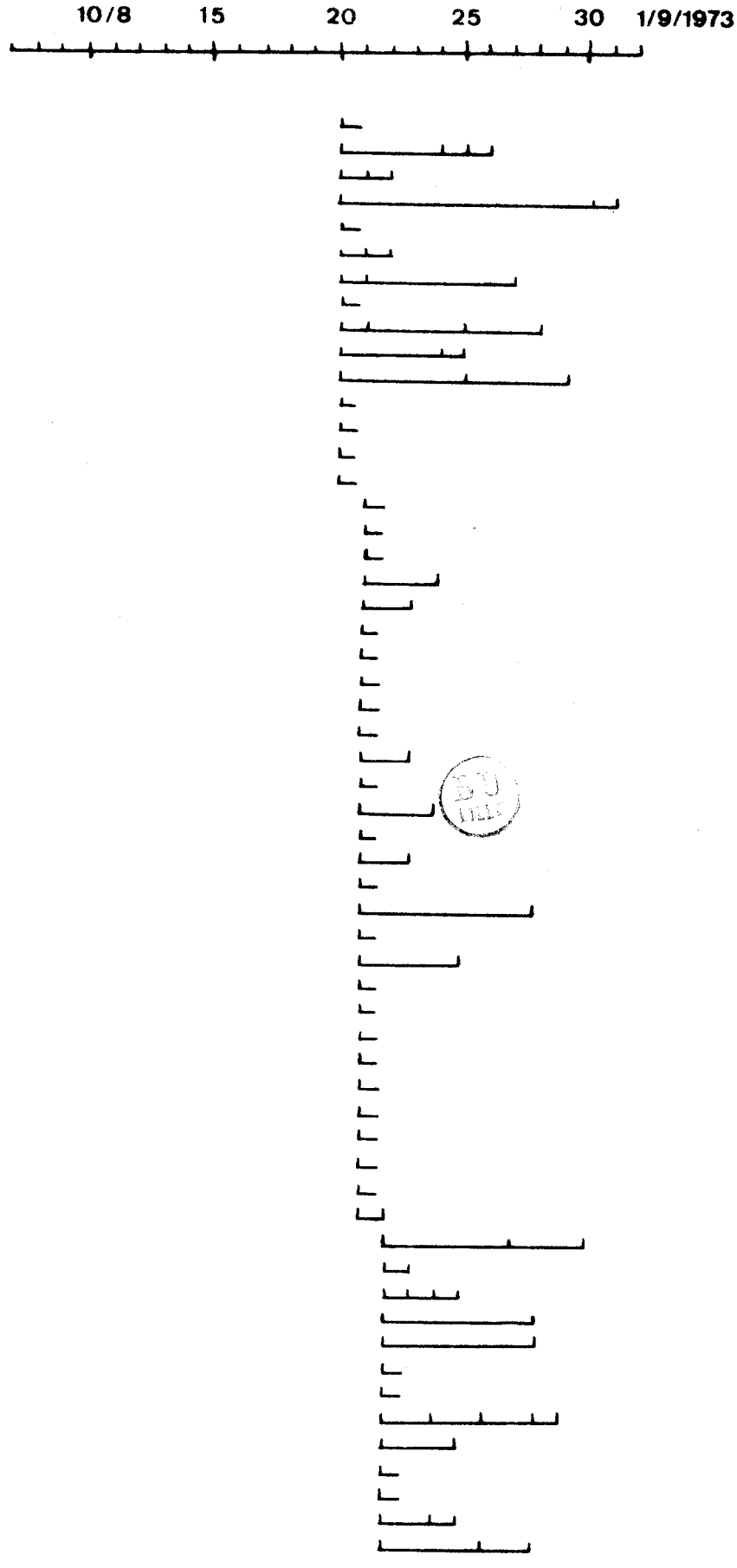

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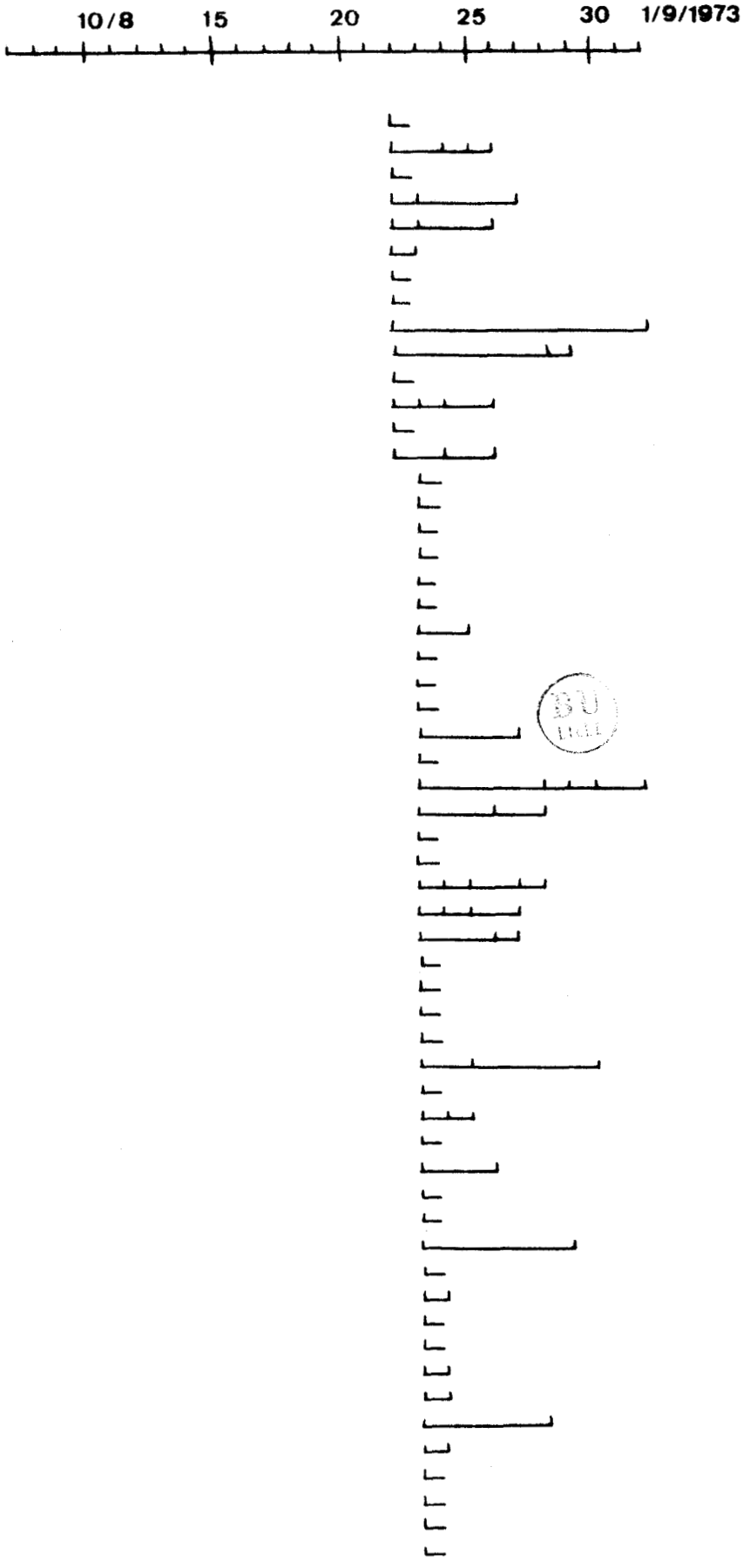

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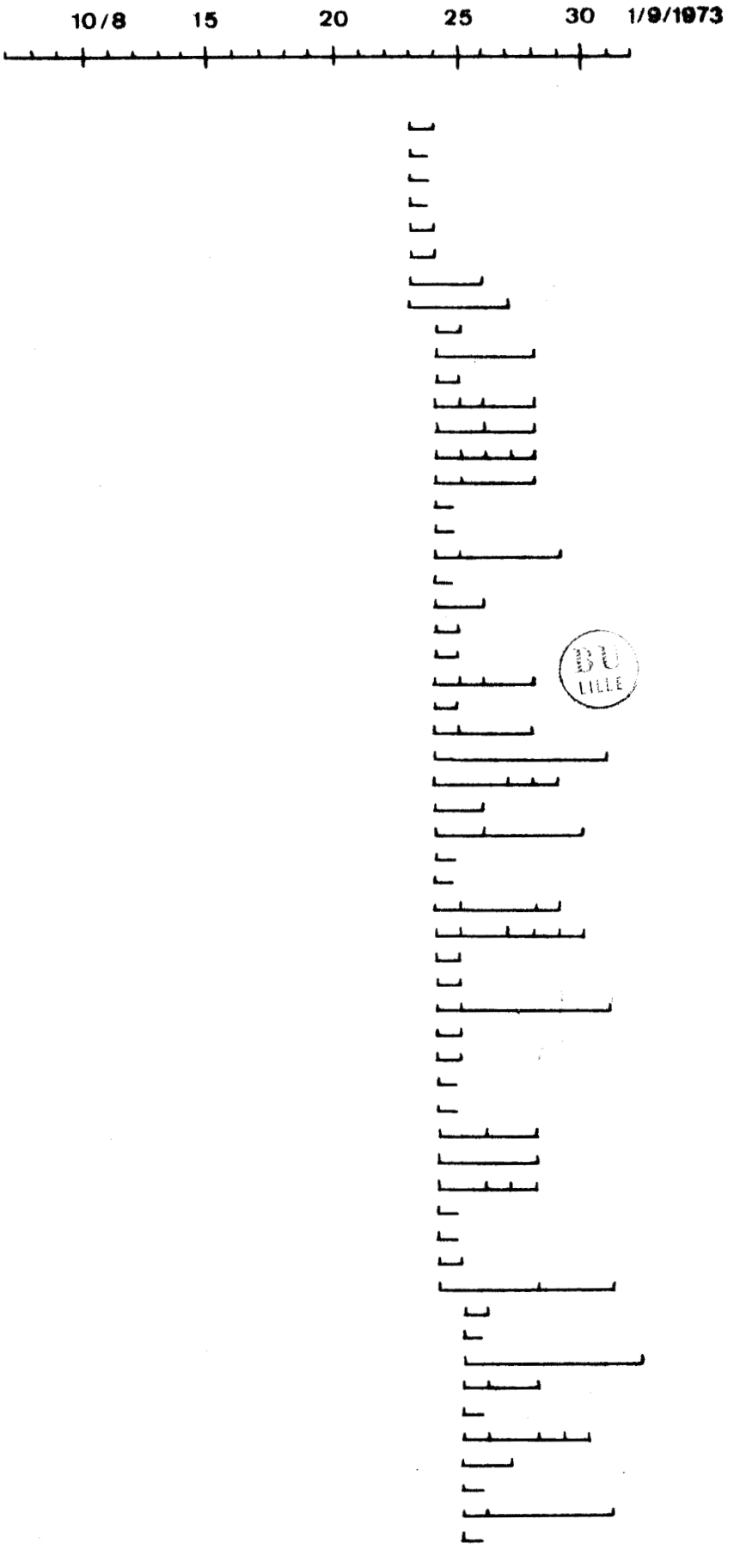

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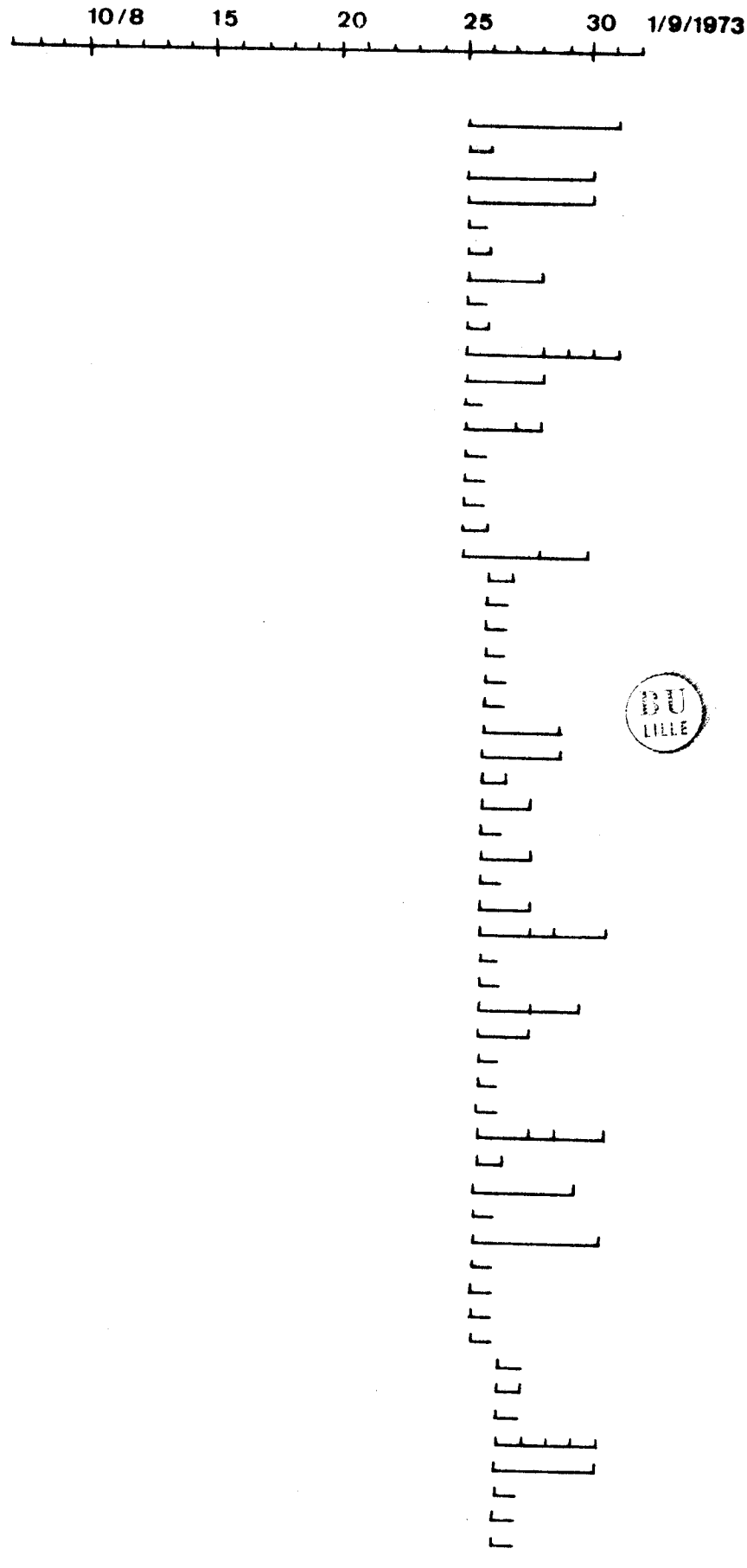

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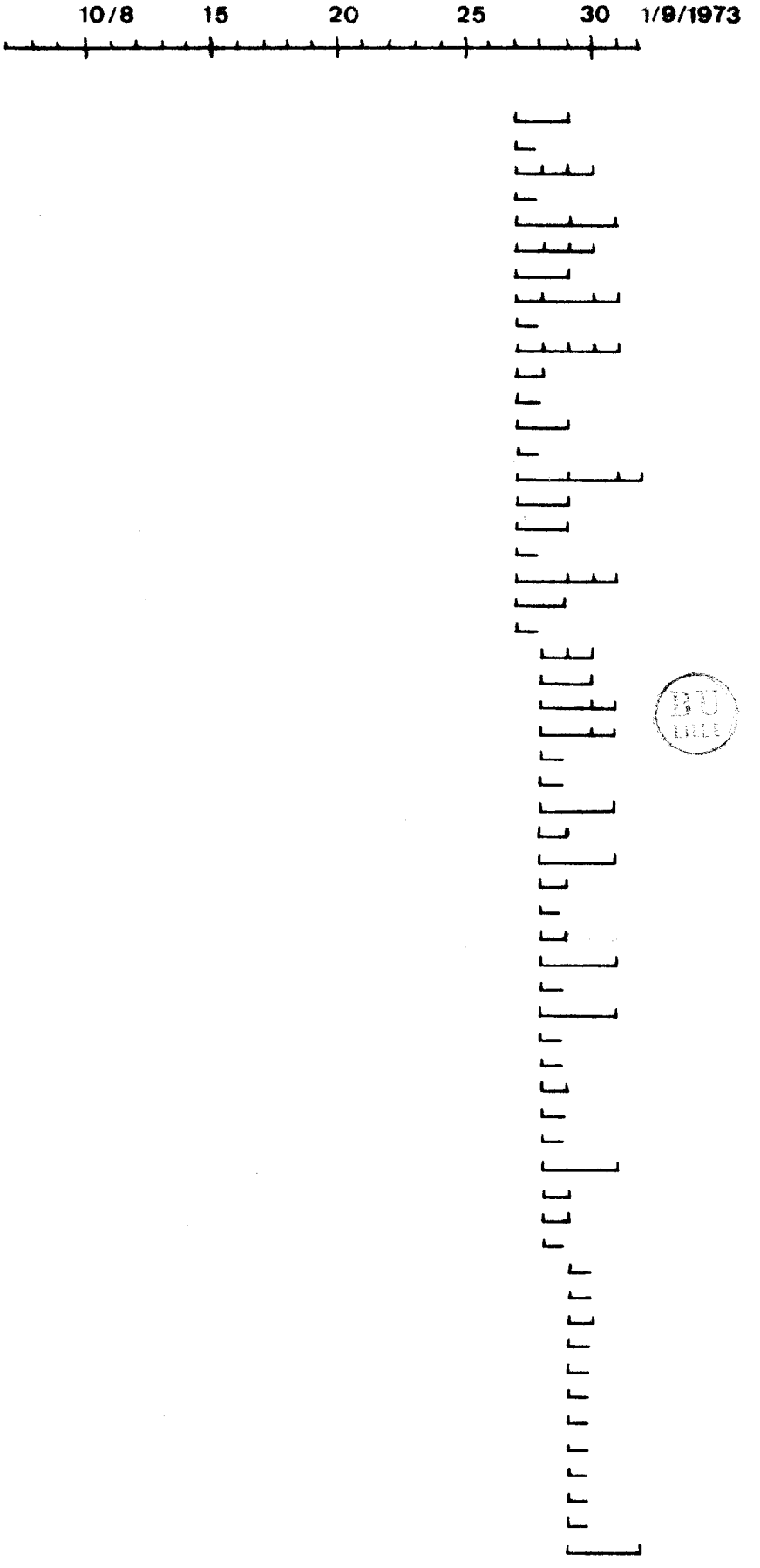

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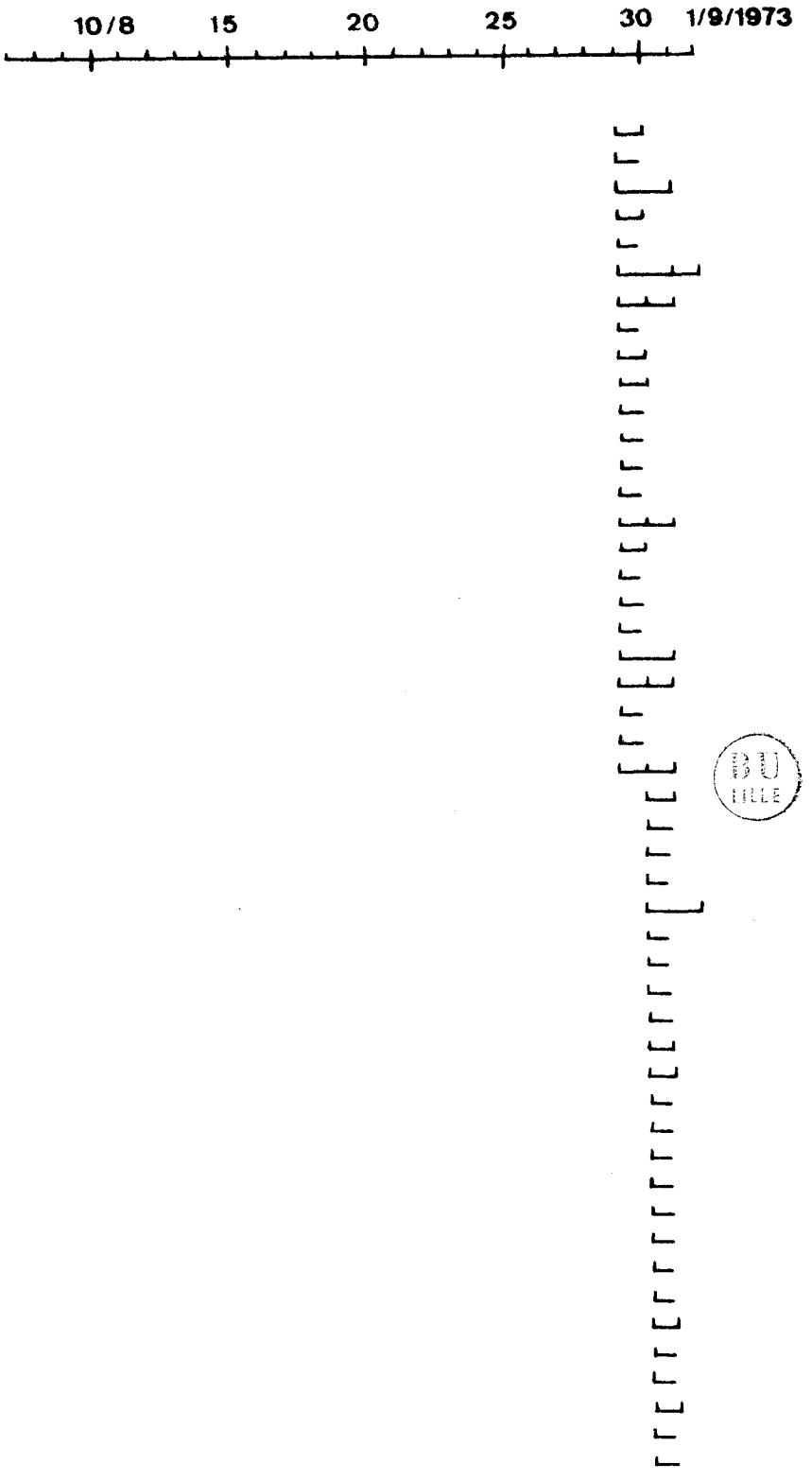

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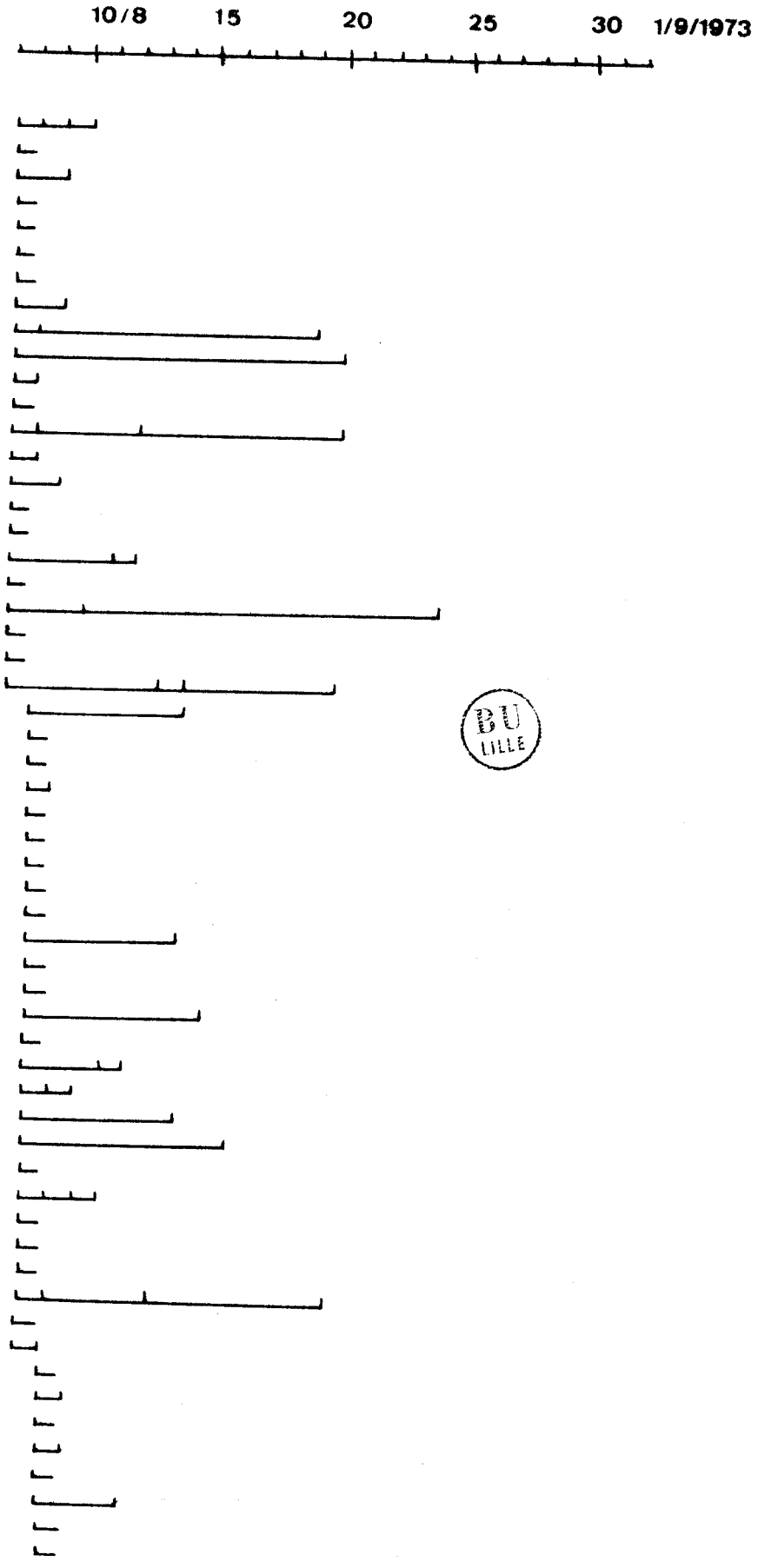

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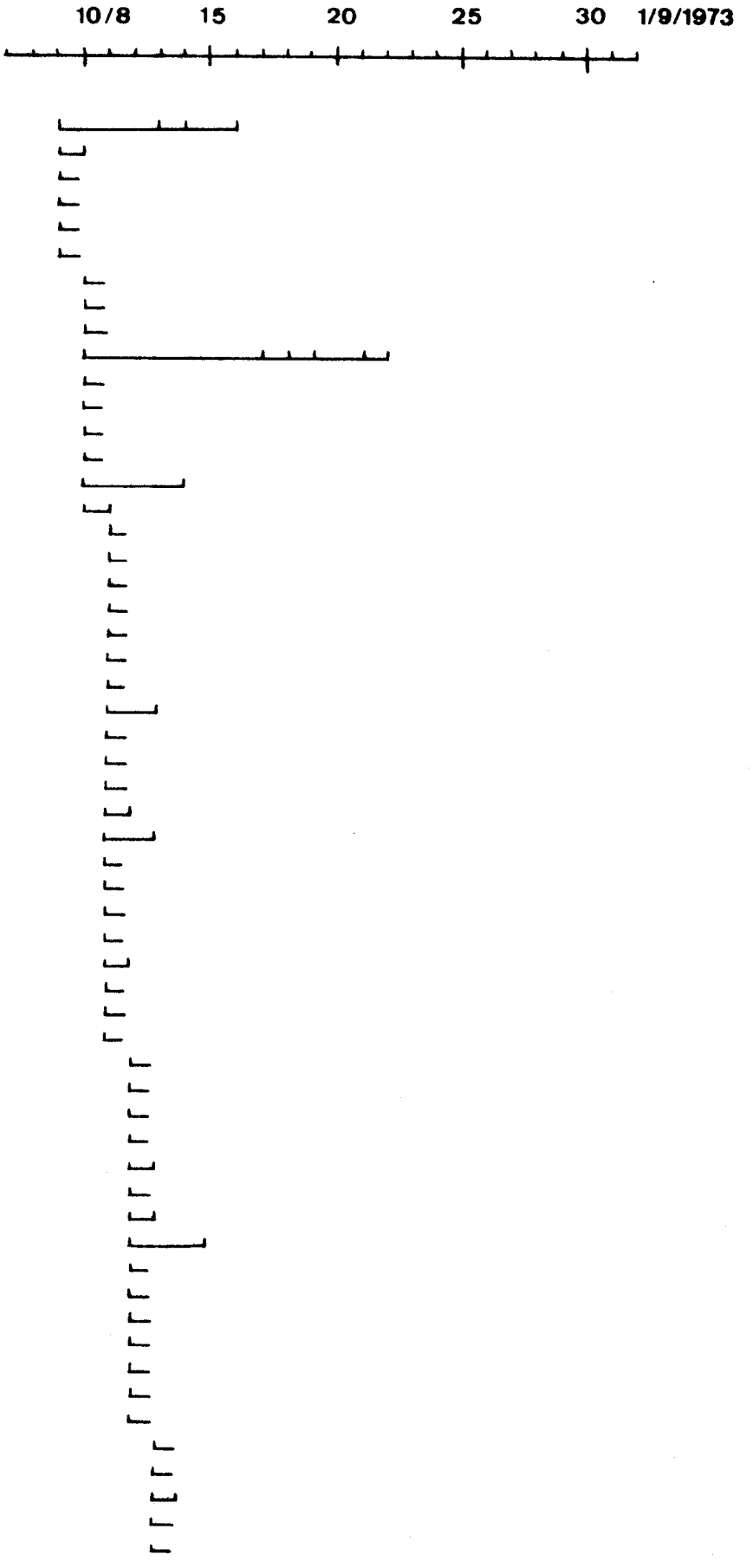

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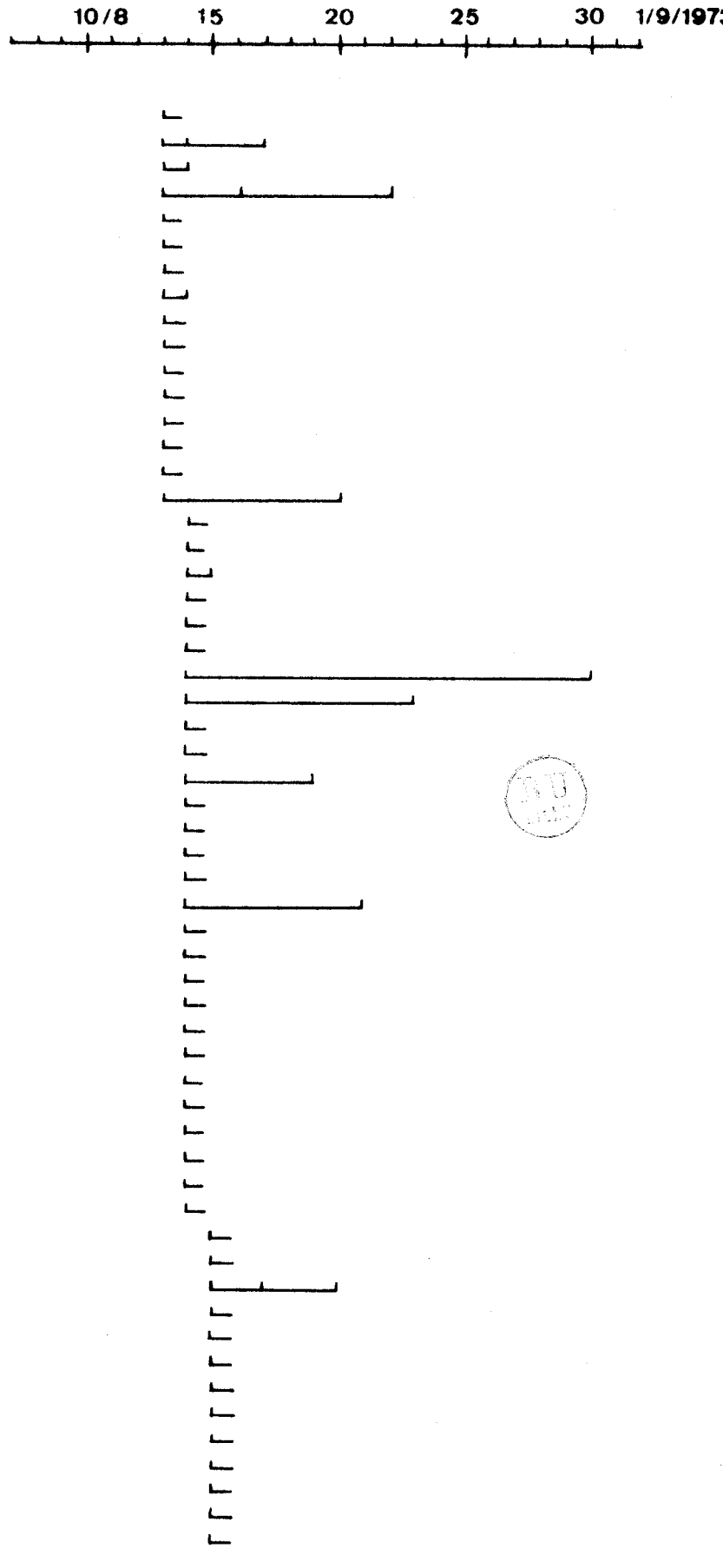

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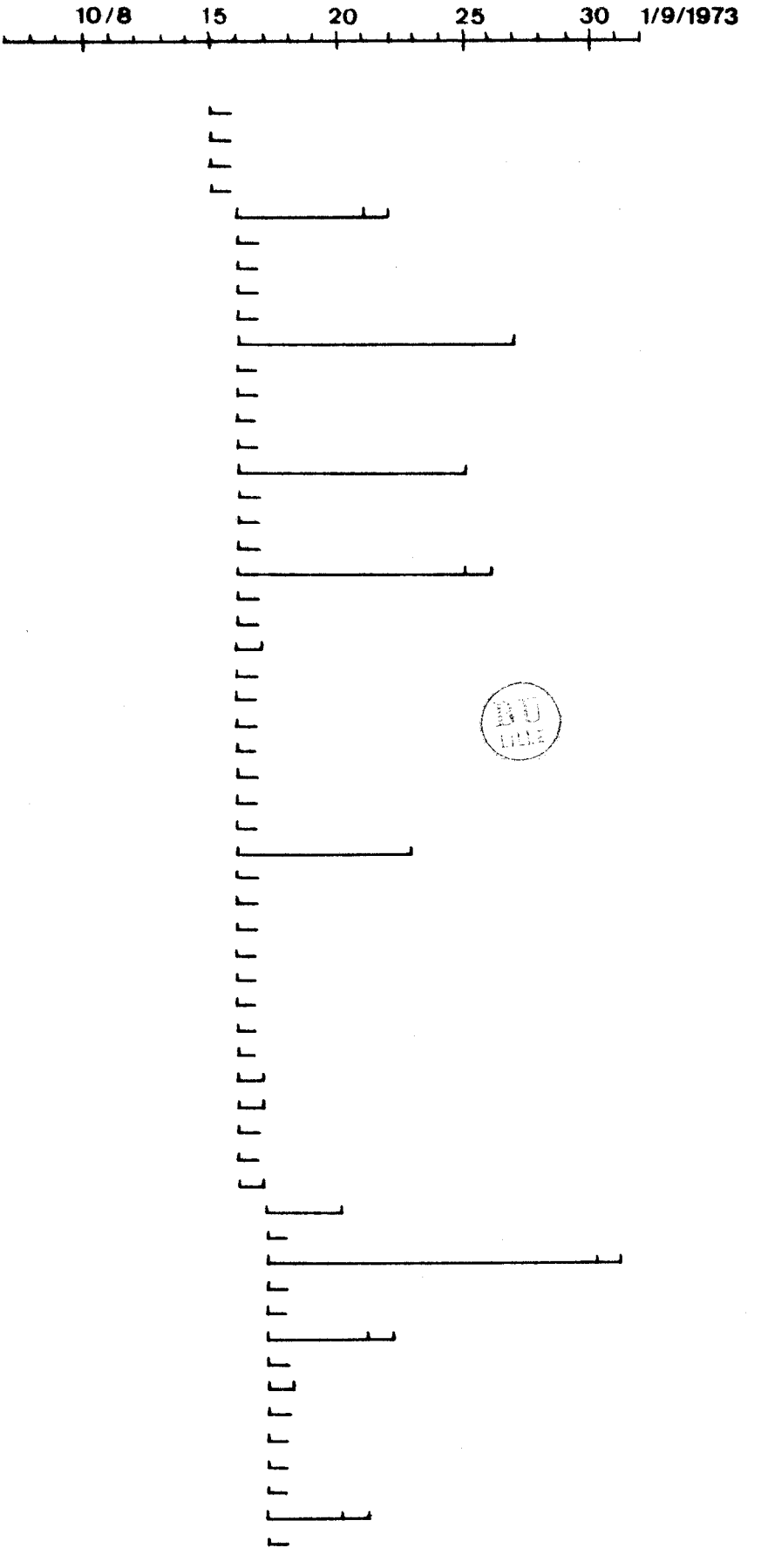

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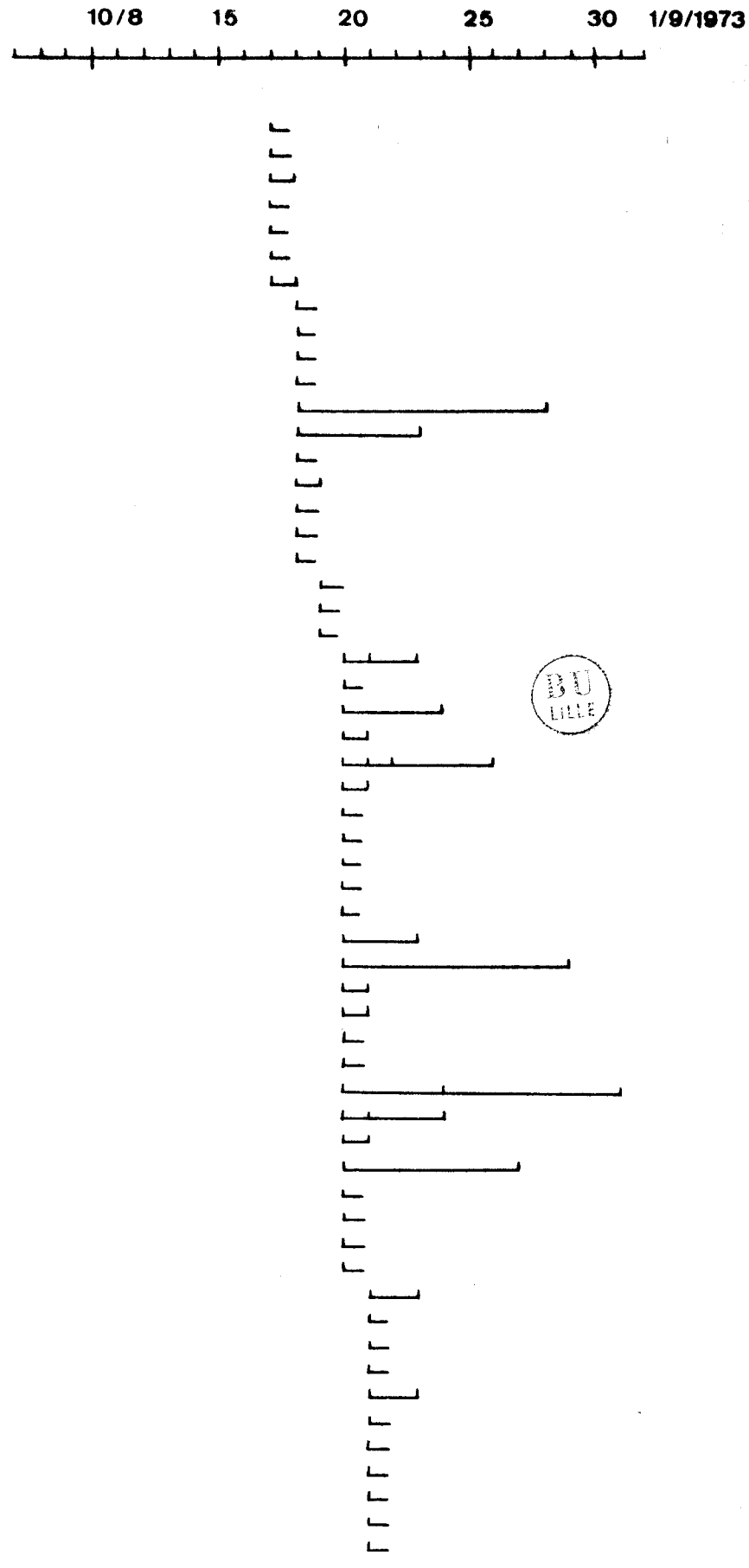

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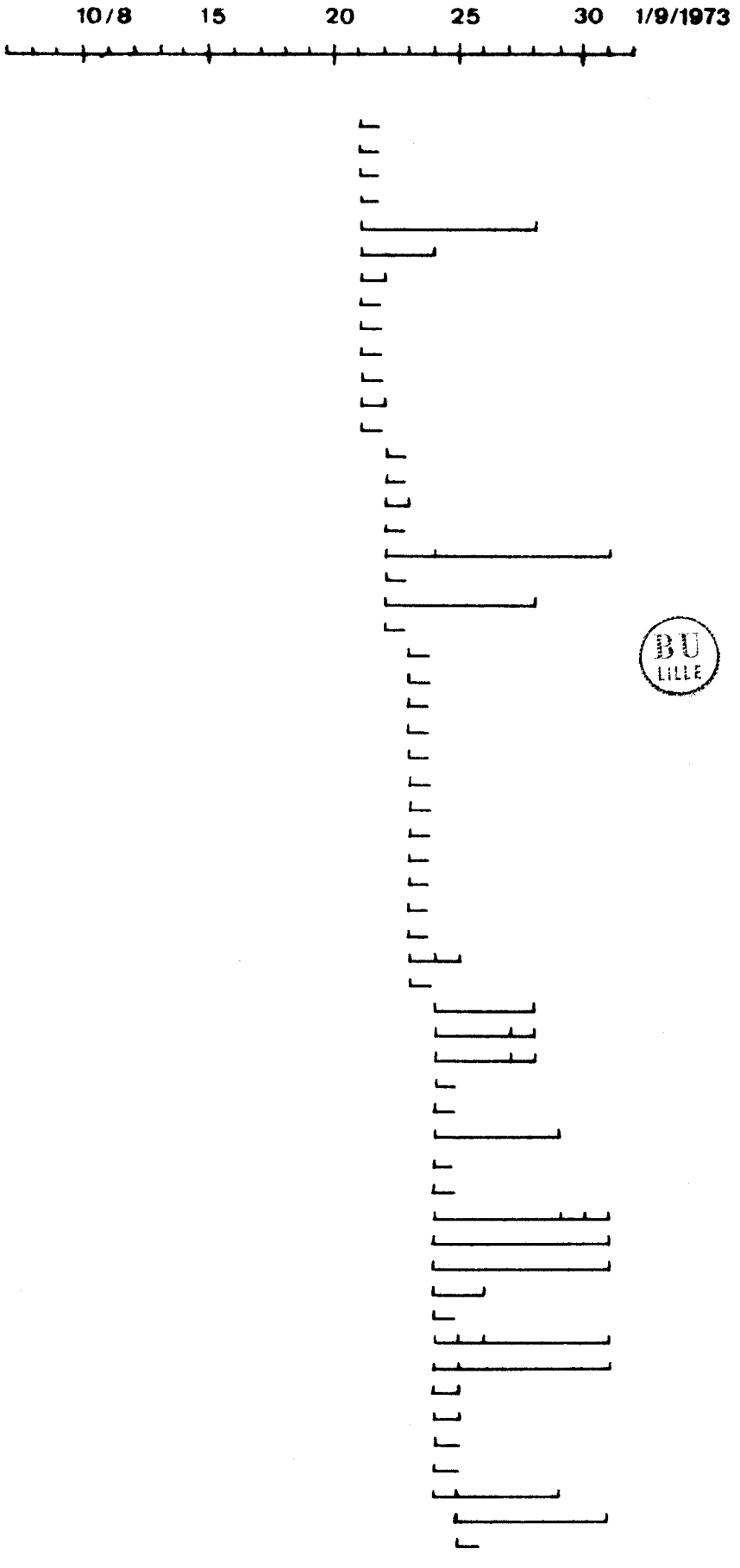

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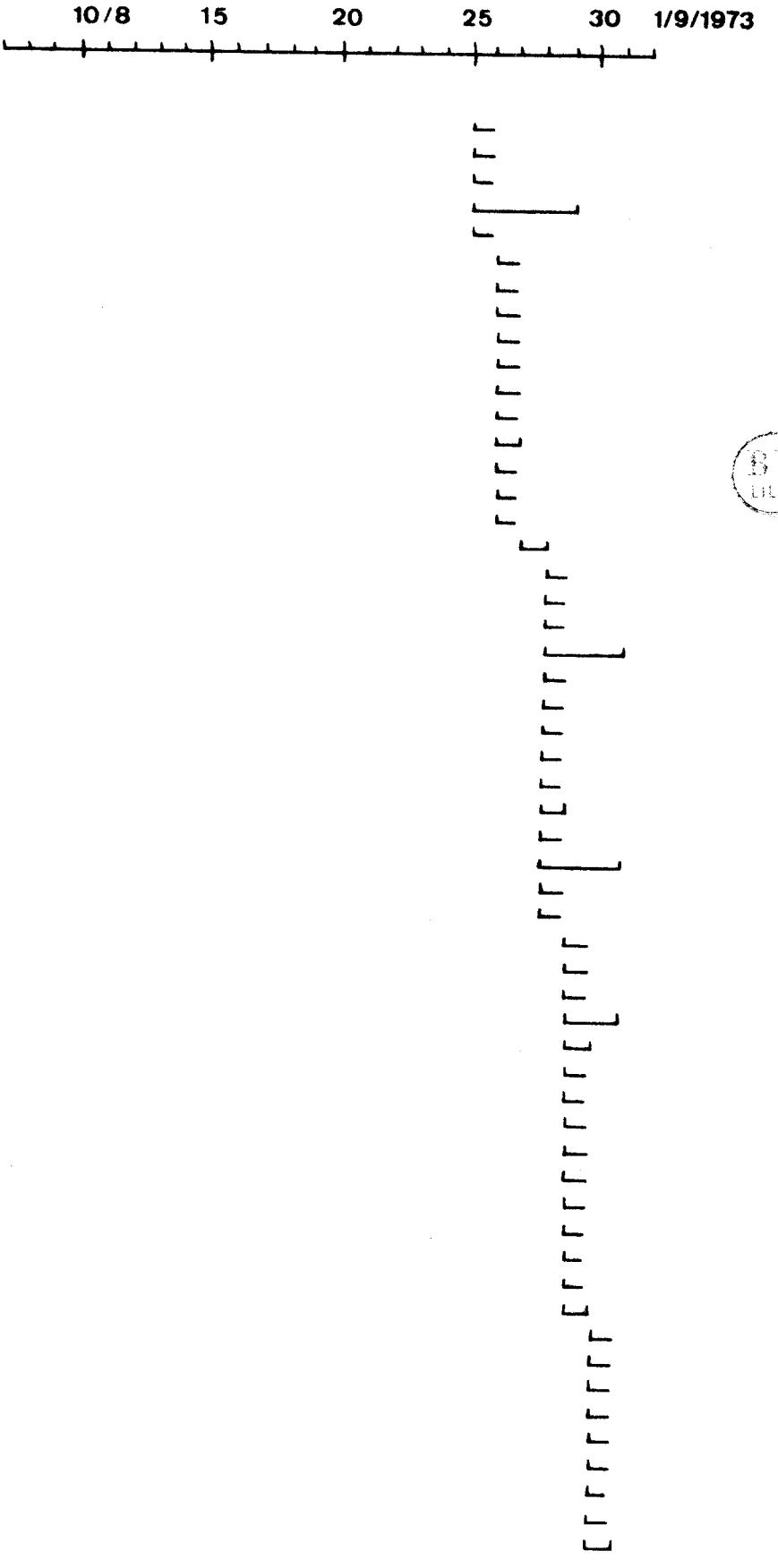

I. elegans (Mâles),

marquage août 1973

à Denderleeuw

Dates en août 1973																							Spécimens recapturés
																					30		
																				29	9	9	
																			28	7	5	12	
																		27	8	13	5	26	
																	26	4	6	5	2	17	
																25	8	2	7	2	5	24	
															24	19	9	4	14	4	2	52	
														23	10	6	5	5	4	2	2	34	
													22	6	6	4	6	2	5	2	1	32	
												21	2	5	2	1	0	0	1	0	0	11	
											20	15	11	3	4	5	4	3	1	2	2	50	
										19	2	8	4	3	2	1	0	1	0	1	1	23	
									18	1	3	1	2	1	0	0	1	1	0	0	0	10	
								17	21	11	2	5	3	2	1	1	2	0	1	0	0	49	
							16	0	5	4	5	4	0	1	1	0	2	1	2	0	0	25	
						15	5	1	4	1	2	1	0	1	0	0	0	0	0	0	0	15	
					14	18	3	2	1	2	2	0	0	0	0	0	0	0	0	0	0	28	
				13	5	4	2	2	1	1	1	2	0	2	0	0	0	0	1	1	0	22	
			12	7	11	7	0	4	0	1	1	0	0	1	2	0	0	0	0	0	0	34	
		11	8	6	4	2	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	24	
	10	5	6	0	1	2	4	3	1	0	2	1	0	0	0	0	0	0	0	0	0	25	
9	5	3	4	1	2	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	20	
8	11	6	2	4	2	2	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	31	
7	23	17	10	7	4	3	0	1	2	0	3	5	2	0	0	0	0	0	0	0	0	0	77
76	62	71	66	68	69	72	73	77	65	68	70	52	70	67	49	76	67	65	68	52	73	75	59

Spécimens Capturés

I. elegans (Femelles),

marquage en août 1973

à Denderleeuw

Dates en août 1973	Spécimens capturés	Spécimens recapturés
30	14	21
29	2	2
28	1	0	1
27	1	0	0	1
26	1	1	0	0	2
25	0	0	0	1	0	1
24	4	2	2	3	3	1	15
23	1	1	1	0	0	0	0	3
22	1	1	0	0	0	1	0	0	3
21	2	2	1	0	0	0	1	0	0	6
20	8	1	2	3	0	1	1	0	1	0	17
19	0	0	0	0	0	0	0	0	0	0	0	0
18	1	0	0	0	1	0	0	0	0	1	0	0	3
17	3	0	2	2	1	0	0	0	0	0	0	0	1	9
16	5	0	0	0	1	1	1	0	2	1	1	0	0	0	12
15	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2
14	1	0	0	0	0	1	1	0	1	0	0	0	0	0	0	1	5
13	4	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	8
12	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
11	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4
10	2	0	0	2	0	1	1	1	1	0	1	1	0	0	0	0	0	0	0	0	10
9	3	0	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
8	5	2	2	1	1	3	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	17
7	6	4	3	2	2	0	0	0	0	0	0	1	3	0	0	0	1	0	0	0	0	0	0	22
24	32	23	27	27	22	27	37	21	41	28	15	6	34	38	15	22	27	14	16	6	23	21	14	

Méthode de Fisher et Ford pour I. elegans

1. Dates au mois d'août 1973.
2. Nombre de jours.
3. Nombre de spécimens libérés.
4. $\bar{s}^{t}$
5. Spécimens marqués en date de la colonne 1, dont on suppose qu'ils seront encore en vie le 30 août 1973.
6. Nombre de spécimens marqués en date de la colonne 1 plus ceux des jours précédents, dont on suppose qu'ils seront encore en vie le 30 août 1973.
7. Nombre de jours que les spécimens marqués ont vécus.
8. Nombre d'observations de spécimens marqués.
9. Nombre de jours vécus observés.
10. Nombre de jours vécus extimés.
11. Différence entre le nombre de jours vécus observés et le nombre de jours vécus estimés.
12. Nombre de captures.
13. Estimation de la population en date de la colonne 14.
14. Date au mois d'août 1973.

Données selon la méthode de FISHER & FORD - mâles - $\bar{s} = 0.7420$

Date	t	n Libérés	$\bar{s}^t$	(3)x(4)	(5) de bas en haut	(6) de bas en haut	n Marqués observés	n Jours survécus	$\frac{(8).(7)}{(6)}$	(9)-(10)	n Capturés	$\frac{(6).(12)}{(8).(4)_{t-1}}$	Date
30	-	-	(1.0000)	-	-	-	-	-	-	-	-	-	-
29	1	75	0.7420	55.650	194.790	728.671	34	132	127.19	4.81	59	338.0	30
28	2	73	0.5506	40.194	139.140	533.881	39	146	149.64	- 3.64	75	360.6	29
27	3	52	0.4085	21.242	98.946	394.741	50	212	199.47	12.53	73	262.4	28
26	4	68	0.3031	20.611	77.704	295.795	23	99	87.55	11.45	52	430.1	27
25	5	65	0.2249	14.619	57.093	218.091	37	135	141.33	- 6.33	68	346.2	26
24	6	67	0.1669	11.182	42.474	160.998	37	86	140.25	-54.25	65	331.8	25
23	7	76	0.1238	9.409	31.292	118.524	28	93	106.05	-13.05	67	448.6	24
22	8	49	0.0919	4.503	21.883	87.232	25	100	99.66	0.34	76	537.4	23
21	9	67	0.0682	4.569	17.380	65.349	22	59	82.72	-23.72	49	421.2	22
20	10	70	0.0506	3.542	12.811	47.969	37	107	138.54	-31.54	67	340.2	21
19	11	52	0.0375	1.950	9.269	35.158	23	129	87.24	41.76	70	557.5	20
18	12	70	0.0279	1.953	7.319	25.889	27	132	95.51	36.49	52	375.9	19
17	13	68	0.0207	1.408	5.366	18.570	39	119	134.97	-15.97	70	345.2	18
16	14	65	0.0153	0.995	3.958	13.204	16	83	53.38	29.62	68	812.6	17
15	15	77	0.0114	0.878	2.963	9.246	17	66	53.05	12.95	65	740.5	16
14	16	73	0.0084	0.613	2.085	6.283	37	93	111.50	-18.50	77	380.6	15
13	17	72	0.0063	0.454	1.472	4.198	25	65	71.30	- 6.30	73	511.7	14
12	18	69	0.0046	0.317	1.018	2.726	19	51	50.88	0.12	72	612.3	13
11	19	68	0.0034	0.231	0.701	1.708	26	68	63.35	4.65	69	404.4	12
10	20	66	0.0026	0.172	0.470	1.007	17	45	36.42	8.58	68	552.9	11
9	21	71	0.0019	0.135	0.298	0.537	22	47	39.64	7.36	66	343.8	10
8	22	62	0.0014	0.087	0.163	0.239	28	45	41.06	3.94	71	217.5	9
7	23	76	0.0010	0.076	0.076	0.076	23	23	23.00	0.00	62	146.3	8
										1.30			

Données selon la méthode de FISHER & FORD – Femelles – $\bar{s} = 0.800$

Date	t	n Libérés	$\bar{s}^{t}$	(3)x(4)	(5) de bas en haut	(6) de bas en haut	n Marques observés	n Jours survécus	$\frac{(8)\times(7)}{(6)}$	(9)-(10)	n Capturés	$\frac{(6)\times(12)}{(8)\times(4)_{t-1}}$	Date
30	–	–	(1.0000)	–	–	–	–	–	–	–			
29	1	21	0.8000	16.800	77.657	416.966	5	37	26.85	10.15	14	217.4	30
28	2	23	0.6400	14.720	60.857	339.309	6	29	33.45	- 4.45	21	266.2	29
27	3	6	0.5120	3.072	46.137	278.452	8	38	48.28	-10.28	23	207.3	28
26	4	16	0.4096	6.554	43.065	232.315	5	25	26.97	- 1.97	6	100.9	27
25	5	14	0.3277	4.588	36.511	189.250	5	23	25.92	- 2.92	16	285.2	26
24	6	27	0.2621	7.077	31.923	152.739	7	15	33.49	-18.49	14	194.8	25
23	7	22	0.2097	4.613	24.846	120.816	7	35	34.04	0.96	27	365.6	24
22	8	15	0.1678	2.517	20.233	95.970	8	32	37.95	- 5.95	22	265.3	23
21	9	38	0.1342	5.100	17.716	75.737	7	36	29.93	6.07	15	226.2	22
20	10	34	0.1074	3.652	12.616	58.021	14	47	64.39	-17.39	38	255.2	21
19	11	6	0.0859	0.515	8.964	45.405	9	75	45.59	29.41	34	315.3	20
18	12	15	0.0687	1.031	8.449	36.441	3	22	12.94	9.06	6	196.7	19
17	13	28	0.0550	1.540	7.418	27.992	4	13	15.09	- 2.09	15	404.9	18
16	14	41	0.0440	1.804	5.878	20.574	8	18	28.00	-10.00	28	374.1	17
15	15	21	0.0352	0.739	4.074	14.696	2	14	7.21	6.79	41	1,898.1	16
14	16	37	0.0281	1.040	3.335	10.622	4	17	12.74	4.26	21	497.4	15
13	17	27	0.0225	0.608	2.295	7.287	9	30	28.58	1.42	37	335.8	14
12	18	22	0.0180	0.396	1.687	4.992	6	15	17.75	- 2.75	27	337.4	13
11	19	27	0.0144	0.389	1.291	3.305	7	22	17.92	4.08	22	225.4	12
10	20	27	0.0115	0.311	0.902	2.014	6	16	13.40	2.60	27	281.9	11
9	21	23	0.0092	0.212	0.591	1.112	8	16	15.05	0.95	27	173.4	10
8	22	32	0.0074	0.237	0.379	0.521	9	13	12.37	0.63	23	105.3	9
7	23	24	0.0059	0.142	0.142	0.142	6	6	6.00	0	32	102.3	8
										0.09			

Calcul de la moyenne du nombre de spécimens par jour selon la méthode de FISHER & FORD.

I. elegans, Mâles, $\bar{s}$ = 0.742, Denderleeuw 1973.

Date en août	n spécimens libérés le jour précédent	n marquages faits. $\bar{s}$	n Marquages présents par jour	n Captures	n m Marquages.Captures	m Recaptures
7	-	-	-	76	-	-
8	76	76 + 0.742	56.39	62	3,496	23
9	62	(56.39+62). 0.742	87.85	71	6,237	28
10	71	(87.85+71). 0.742	117.87	66	7,779	22
11	66	(117.87+66). 0.742	136.43	68	9,277	17
12	68	(136.43+68). 0.742	151.69	69	10,467	26
13	69	(151.69+69). 0.742	163.75	72	11,790	19
14	72	(163.75+72). 0.742	174.93	73	12,770	25
15	73	(174.93+73). 0.742	183.96	77	14,165	37
16	77	(183.96+77). 0.742	193.63	65	12,586	17
17	65	(193.63+65). 0.742	191.90	68	13,049	16
18	68	(191.90+68). 0.742	192.85	70	13,500	39
19	70	(192.85+70). 0.742	195.03	52	10,142	27
20	52	(195.03+52). 0.742	183.30	70	12,831	23
21	70	(183.30+70). 0.742	187.95	67	12,593	37
22	67	(187.95+67). 0.742	189.17	49	9,269	22
23	49	(189.17+49). 0.742	176.72	76	13,431	25
24	76	(176.72+76). 0.742	187.52	67	12,564	28
25	67	(187.52+67). 0.742	188.85	65	12,275	37
26	65	(188.85+65). 0.742	188.36	68	12,808	37
27	68	(188.36+68). 0.742	190.22	52	9,891	23
28	52	(190.22+52). 0.742	179.73	73	13,120	50
29	73	(179.73+73). 0.742	187.53	75	14,065	39
30	75	(187.53+75). 0.742	194.80	59	11,493	73
				1.610	369,598	690

Moyenne du nombre de spécimens par jour : $\frac{369,598}{690} = 535.65$

Calcul de la moyenne du nombre de spécimens par jour selon la méthode de FISHER & FORD

I. elegans, Femelles, $\bar{s}$ = 0.800, Denderleeuw 1973.

Date en août	n spécimens libérés le jour précédent	n marquages faits. $\bar{s}$	$\bar{n}$ Marquages présent par jour	n Captures	n Marquages. Captures	r Recaptures
7	-	-	-	24	-	-
8	24	24 + 0.800	19.20	32	614	6
9	32	(19.20+32). 0.800	40.96	23	942	9
10	23	(40.96+23). 0.800	51.17	27	1,382	8
11	27	(51.17+27). 0.800	62.53	27	1,688	6
12	27	(62.52+27). 0.800	71.62	22	1,576	7
13	22	(71.62+22). 0.800	74.90	27	2,022	6
14	27	(74.90+27). 0.800	81.52	37	3,016	9
15	37	(81.52+37). 0.800	94.82	21	1,991	4
16	21	(94.82+21). 0.800	92.66	41	3,799	2
17	41	(92.66+41). 0.800	106.93	28	2,968	8
18	28	(106.93+28). 0.800	107.94	15	1,619	4
19	15	(107.94+15). 0.800	98.35	6	590	3
20	6	(98.35+ 6). 0.800	83.48	34	2,838	9
21	34	(83.48+34). 0.800	93.98	38	3,571	14
22	38	(93.98+38). 0.800	105.58	15	1,584	7
23	15	(105.58+15). 0.800	96.46	22	2,122	8
24	22	(96.46+22). 0.800	94.77	27	2,559	7
25	27	(94.77+27). 0.800	97.42	14	1,364	7
26	14	(97.42+14). 0.800	89.14	16	1,426	5
27	16	(89.14+16). 0.800	84.11	6	505	5
28	6	(84.11+ 6). 0.800	72.09	23	1,658	8
29	23	(72.09+23). 0.800	76.07	21	1,597	6
30	21	(76.07+21). 0.800	77.66	14	1,087	5
				560	42,518	153

Moyenne du nombre de spécimens par jour : $\frac{42,518}{153} = 277,90$

Sex ratio à Denderleeuw en août 1973

Basé sur :	mâles	femelles	Sex ratio
Nombre de captures	1.610	560	0.74
Nombre d'individus	961	397	0.71
Estimation du nombre selon la méthode de FISHER & FORD	536	278	0.66

Calcul de la $\bar{L}_{LT}$ de la population d'Ischnura elegans d'Anglesey

Basé sur les données de LORD (1961) du 27/5 au 4/6

Mâles	t	Fréquence	
	1	34	$\bar{L} = 2.19$
	2	22	$S_x = 1.14$
	3	17	$S_{\bar{x}} = 0.12$
	4	17	$n = 90$
	4 ⊕	26	

Femelles	t	Fréquence	
	1	21	$\bar{L} = 2.41$
	2	12	$S_x = 1.16$
	3	18	$S_{\bar{x}} = 0.14$
	4	15	$n = 66$
	4 ⊕	18	

Calcul de la $\bar{L}_{LT}$ de la population d'Ischnura elegans d'Anglesey

Basé sur les données de LORD (1961) du 13/6 au 29/6

Mâles	t	Fréquence	
	1	11	$\bar{L} = 4.30$
	2	3	$S_x = 2.37$
	3	8	$S_{\bar{x}} = 0.30$
	4	12	$n = 61$
	5	11	
	6	7	
	7	2	
	8	1	
	9	6	
	9 ⊕	9	

Femelles	t	Fréquence	
	1	0	$\bar{L} = 5.11$
	2	4	$S_x = 2.17$
	3	1	$S_{\bar{x}} = 0.41$
	4	8	$n = 28$
	5	5	
	6	4	
	7	0	
	8	3	
	9	3	
	9 ⊕	1	

Calcul de la $\bar{L}_{LT}$ de la population d'Ischnura elegans de Pembrokeshire

(Basé sur les données de PARR (1969).

Mâles

t	Fréquence
1	24
2	13
3	22
4	15
5	12
6	9
6 ⊕ | 7	25 | 10
8	8
9	3
10	3
11	1

$\bar{L} = 3.05$

$S_x = 1.64$

$S_{\bar{x}} = 0.17$

$n = 95$

Femelles

t	Fréquence
1	6
2	10
3	6
4	6
5	2
6	0
6 ⊕ | 7	1 | 1

$\bar{L} = 2.60$

$S_x = 1.22$

$S_{\bar{x}} = 0.22$

$n = 30$

Correction de la $\bar{L}_{FF}$ des populations de Dunham (basé sur les données de PARR 1969).

Dunham pond I, 1965

Sexe	Période	$\bar{L}_{FF}$	t	$\bar{L}_{FF_c}$ (x)	Milieu de la période
Mâles	27/5–28/6	15.9	33	18.0	12/6
	11/6–20/7	12.6	40	13.4	1/7
	14/6–21/7	9.9	38	10.7	3/7
	24/6–23/7	7.4	30	8.7	9/7
	16/6–19/8	6.4	35	7.1	2/8
	21/7–27/8	7.1	38	7.6	9/8
	10/8–14/9	10.2	36	11.2	28/8
	Moyenne	9.9		11.0	
Femelles	1/6–29/6	8.7	29	10.3	15/6
	24/6–23/7	5.8	30	6.8	9/7
	16/7–12/8	7.7	28	9.3	30/7
	22/7–27/8	8.2	37	8.9	9/8
	Moyenne	7.6		8.8	

(x): Corrigé avec le facteur de correction correspondant avec t - 1.

Dunham pond II, 1965

Sexe	Période	$\bar{L}_{FF}$	t	$\bar{L}_{FF_c}$ (x)	Milieu de la période
Mâles	2/6–29/6	11.4	28	13.8	16/6
	18/6–23/7	8.7	36	9.5	6/7
	29/6–6/8	8.8	40	9.3	19/7
	16/7–13/8	5.9	29	7.0	30/7
	5/8–12/9	5.1	39	5.8	24/8
	19/8–22/9	7.0	35	7.7	5/9
	Moyenne	7.8		9.0	
Femelles	27/5–29/6	4.9	34	5.5	13/6
	23/6–23/7	5.4	31	6.2	8/7
	16/7–6/8	13.2	22	17.9	27/7
	21/7–23/8	7.6	34	8.5	7/8
	30/7–27/8	5.3	29	6.3	13/8
	12/8–12/9	6.6	32	7.5	28/8
	23/8–22/9	9.4	31	10.9	7/9
	Moyenne	7.5		9.0	

Dunham pond III, 1966

Sexe	Période	$\bar{L}_{FF}$	t	$\bar{L}_{FF_c}$ (x)	Milieu de la période
Mâles	6/6–11/7	25.8	36	28.3	24/6
	13/6–22/7	16.0	40	17.0	3/7
	23/6–2/8	11.0	41	11.6	13/7
	7/7–16/8	7.8	41	8.2	27/7
	Moyenne	15.2		16.3	
Femelles	6/6–15/7	28.6	40	30.5	26/6
	10/6–25/7	21.3	46	21.8	3/7
	28/6–8/8	12.2	42	12.8	19/7
	11/7–16/8	9.9	37	10.7	29/7
	Moyenne	18.1		19.0	

$\frac{\bar{L}_{c\sigma^{\prime}}}{\bar{L}_{c\varphi}}$ en relation avec le sex ratio

Basé sur les données de :	x sex ratio (captures)	y $\bar{L}_{c\sigma^{\prime}} / \bar{L}_{c\varphi}$
PARR's Dunham Ponds I	0.70	1.22
II	0.62	1.05
PARR – Pembrokeshire	0.67	1.16
LORD 1	0.52	0.97
LORD 2	0.59	1.05
En théorie	0.50	1.00

$y = a_o + a_1 x$

$a_o = 0.39$

$a_1 = 1.14$

$r^2 = 0.89$

$n = 6$

Les populations non-isolées qui comprennent aussi une partie de la zône neutre ne sont pas inclus. Il s'agit ici du sex ratio de la population active près de l'eau.

Période de maturation et fraction à l'eau

Denderleeuw 1973, I. elegans, mâles, $\bar{s} = 0.749$

t	n	$\sum n$	$\sum n.\bar{s}^{-i}$	Fraction à l'eau	$n.\bar{s}^{i}$	Δ
0	327	565	565	1.00	450	115
1	63	238	318	0.56	337	- 99
2	50	175	312	0.55	252	- 77
3	27	125	297	0.53	189	- 64
4	18	98	311	0.55	142	- 44
5	18	80	339	0.60	106	- 26
6	15	62	351	0.62	79	- 19
7	9	47	355	0.63	60	- 13
8	9	38	383	0.68	45	- 7
9	4	29	390	0.69	33	- 4
10	8	25	450	0.80	25	0
11	6	17	408	0.72	19	- 2
12	9	11	352	0.62	14	- 3
13	2	2	-		11	- 9
13 ⊕	4				11	

$565 - 450 = 115 \cong 90 + 9$

$\bar{L} = 3.98$

$S_x = 3.26$

$S_{\bar{x}} = 0.21$

Période de maturation et fraction à l'eau

Denderleeuw 1973, I. elegans, femelles, $\bar{s} = 0.780$

t	n	$\sum n$	$\sum n.\bar{s}^{-i}$	Fraction à l'eau	$Nn.\bar{s}^{i}$	Δ
0	180	252	252	1.00	180	72
1	25	72	92	0.37	140	- 72
2	7	47	77	0.31	110	- 63
3	5	40	84	0.33	85	- 45
4	7	35	95	0.38	67	- 32
5	2	28	97	0.38	52	- 24
6	9	26	115	0.46	41	- 15
7	4	17	97	0.38	32	- 15
8	1	13	95	0.38	25	- 12
9	3	12	115	0.46	19	- 7
10	2	9	108	0.43	15	- 6
11	1	7	108	0.43	12	- 5
12	4	6	118	0.47	9	- 3
13	2	2	51	0.20	7	- 5
13 ⊕	3				7	

$252 - 180 = 72 = 67 + 5$

$\bar{L} = 4.36$

$S_x = 3.66$

$S_{\bar{x}} = 0.43$

Période de maturation et fraction à l'eau.

P. nymphula (CORBET, 1952) mâles, $\bar{s}$ = 0.887 (t = 36 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	Fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	120	120	383	383	1.00	350	33
1	32	33	263	296	0.77	310	- 47
2	23	25	230	292	0.76	275	- 45
3	10	11	205	294	0.77	244	- 39
4	13	15	194	314	0.82	217	- 23
5	11	13	179	326	0.85	192	- 13
6	19	23	166	340	0.89	170	- 4
7	7	9	143	331	0.86	151	- 8
8	9	12	134	310	0.81	154	- 20
9	11	15	122	359	0.94	119	- 3
10	11	15	107	355	0.93	106	- 1
11	6	9	92	344	0.90	94	- 2
12	12	18	83	350	0.91	83	0
13	9	14	65	309	0.81	74	- 9
14	7	12	51	273	0.71	65	- 14
15	3	5	39	236	0.62	58	- 19
16	3	6	34	232	0.61	51	- 17
17	3	6	28	215	0.56	46	- 18
18	-	-	22	190	0.50	40	- 18
19	2	4	22	215	0.56	36	- 14
20	1	2	18	198	0.52	31	- 13
21	-	-	16	198	0.52	28	- 12
22	-	-	16	224	0.58	25	- 9
23	1	3	16	252	0.66	22	- 6
24	-	-	13	231	0.60	20	- 7
25	-	-	13	260	0.68	17	- 4
26	1	4	13	293	0.77	15	- 2
27	-	-	9	229	0.60	13	- 4
28	-	-	9	258	0.67	12	- 3
29	-	-	9	291	0.76	11	- 2
30	-	-	9	328	0.86	10	- 1
31	1	9	9	370	0.97	9	0
32	-	-	-	-	-	8	- 8
33	-	-	-	-	-	7	- 7
34	-	-	-	-	-	6	- 6
35	-	-	-	-	-	5	- 5

$383 - 350 = 33 \cong 42 + 5$

Γ = 7.01 8.86 $\rightarrow \bar{s}$ = 0.887

S_x = 5.40 7.02

$S_{\bar{x}}$ = 0.39 0.43

Période de maturation et fraction à l'eau.

P. nymphula (CORBET, 1952) femelles, $\bar{s}$ = 0.84375 (t = 36 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	Fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	115	115	160	160	1.00	110	50
1	8	8	45	53	0.33	93	- 48
2	4	4	37	52	0.33	78	- 41
3	5	5	33	55	0.34	66	- 33
4	4	5	28	55	0.34	56	- 28
5	3	4	23	54	0.34	47	- 24
6	4	5	19	53	0.33	40	- 21
7	1	1	14	46	0.29	33	- 19
8	1	1	13	51	0.32	28	- 15
9	1	1	12	55	0.34	24	- 12
10	1	1	11	60	0.38	20	- 9
11	1	1	10	65	0.41	17	- 7
12	-	-	9	69	0.43	14	- 5
13	-	-	9	81	0.51	12	- 3
14	2	3	9	97	0.61	10	- 1
15	1	2	6	77	0.48	9	- 3
16	1	2	4	61	0.38	7	- 3
17	-	-	2	36	0.23	6	- 4
18	-	-	2	42	0.26	5	- 3
19	1	2	2	50	0.31	4	- 2
20	-	-	-	-	-	4	- 4
21	-	-	-	-	-	3	- 3
22	-	-	-	-	-	3	- 3
23	-	-	-	-	-	2	- 2
24	-	-	-	-	-	2	- 2
25	-	-	-	-	-	2	- 2
26	-	-	-	-	-	1	- 1
27	-	-	-	-	-	1	- 1
28	-	-	-	-	-	1	- 1
29	-	-	-	-	-	1	- 1
30	-	-	-	-	-	1	- 1
31	-	-	-	-	-	1	- 1
32	-	-	-	-	-	-	-
33	-	-	-	-	-	-	-
34	-	-	-	-	-	-	-
35	-	-	-	-	-	-	-

$160 - 110 = 50 \cong 48 + 0$

$\bar{L}$ = 5.50 6.40 → $\bar{s}$ = 0.84375

S_x = 4.80 5.38

$S_{\bar{x}}$ = 0.78 0.80

Période de maturation et fraction à l'eau

I. elegans - mâles - Dunham POND I - 1965 (t = 110 jours)

t	n	n'	$\sum_{n'}$	$\sum n!\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	190	190	374	374	1.00	295	79
1	12	12	184	204	0.55	267	- 83
2	17	17	172	210	0.56	241	- 69
3	10	10	155	210	0.56	218	- 63
4	22	23	145	217	0.58	197	- 52
5	6	6	122	202	0.54	178	- 56
6	6	6	116	212	0.57	161	- 45
7	7	7	110	223	0.60	146	- 36
8	5	5	103	231	0.62	132	- 29
9	12	13	98	243	0.65	119	- 21
10	12	13	85	233	0.62	108	- 23
11	6	7	72	218	0.58	97	- 25
12	1	1	65	218	0.58	88	- 23
13	8	9	64	237	0.63	80	- 16
14	9	10	55	226	0.60	72	- 17
15	7	8	45	204	0.55	65	- 20
16	4	5	37	186	0.50	59	- 22
17	1	1	32	178	0.48	53	- 21
18	3	4	31	190	0.51	48	- 17
19	1	1	27	183	0.49	43	- 16
20	3	4	26	195	0.52	39	- 13
21	2	2	22	183	0.49	36	- 14
23	5	6	20	203	0.54	29	- 9
25	2	3	14	174	0.47	24	- 10
26	1	1	11	151	0.40	21	- 10
27	2	3	10	152	0.41	19	- 9
30	1	1	7	144	0.39	18	- 11
34	1	1	6	187	0.50	12	- 6
37	2	3	5	208	0.56	8	- 3
39	1	2	2	102	0.27	6	- 4
$\bar{L}$	9.69	10.43	$\rightarrow \bar{s} = 0.9041228$				
S_x	7.90	8.43					
$S_{\bar{x}}$	0.61	0.62					

$374 - 295 = 79 \cong 79 + 4$

Période de maturation et fraction à l'eau

I. elegans - mâles - Dunham POND II - 1965 (t = 120 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	580	580	913	913	1.00	660	253
1	33	33	333	376	0.41	584	- 251
2	35	36	300	383	0.42	517	- 217
3	34	35	264	380	0.42	458	- 194
4	30	31	229	373	0.41	405	- 176
5	26	27	198	364	0.40	359	- 161
6	12	13	171	355	0.39	318	- 147
7	26	28	158	371	0.41	281	- 123
8	13	14	130	344	0.38	249	- 119
9	15	16	116	347	0.38	221	- 105
10	3	3	100	338	0.37	195	- 95
11	6	7	97	370	0.41	172	- 75
12	9	10	90	388	0.42	153	- 63
13	5	6	80	390	0.43	135	- 55
14	4	5	74	407	0.45	120	- 46
15	4	5	69	428	0.47	106	- 37
16	2	2	64	449	0.49	94	- 30
17	7	8	62	492	0.54	83	- 21
18	11	13	54	483	0.53	74	- 20
19	-	-	41	415	0.45	65	- 24
20	5	6	41	469	0.51	58	- 17
21	3	4	35	452	0.50	51	- 16
22	1	1	31	452	0.50	45	- 14
23	1	1	30	494	0.54	40	- 10
24	5	6	29	539	0.59	35	- 6
25	8	10	23	483	0.53	31	- 8
26	3	4	13	309	0.34	28	- 15
28	1	1	9	273	0.30	22	- 13
32	2	3	8	394	0.43	13	- 5
36	3	4	5	401	0.44	8	- 3
38	1	1	1	102	0.11	6	- 5
$\bar{L}$	8.20	8.72 → $\bar{s}$ = 0.8853212					
S_x	7.66	7.99					
$S_{\bar{x}}$	0.44	0.44					

913 - 660 = 253 ≅ 246 + 5

Période de maturation et fraction à l'eau

I. elegans - mâles - Dunham POND III - 1966 (t = 72 jours)

t	n	n'	$\sum n'$	$\sum n'\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	60	60	191	191	1.00	167	24
1	6	6	131	140	0.73	156	- 25
2	9	9	125	143	0.75	146	- 21
3	6	6	116	141	0.74	137	- 21
4	2	2	110	143	0.75	128	- 18
5	4	4	108	150	0.79	120	- 12
6	6	7	104	155	0.81	112	- 8
7	8	9	97	154	0.81	105	- 8
8	5	6	88	149	0.78	98	- 10
9	2	2	82	149	0.78	92	- 10
10	3	3	80	155	0.81	86	- 6
11	2	2	77	159	0.83	81	- 4
12	3	4	75	166	0.87	76	- 1
13	1	1	71	168	0.88	71	0
14	1	1	70	177	0.93	66	4
15	3	4	69	186	0.97	62	7
17	3	4	65	200	1.05	54	11
18	5	7	61	200	1.05	51	10
19	2	3	54	190	0.99	48	6
20	3	4	51	191	1.00	45	6
21	1	1	47	188	0.98	42	5
22	8	12	46	197	1.03	39	7
23	1	1	34	155	0.81	37	- 3
24	1	1	33	161	0.84	34	- 1
25	1	1	32	167	0.87	32	0
26	4	6	31	173	0.91	30	1
27	2	3	25	149	0.78	28	- 3
28	3	5	22	140	0.73	26	- 4
30	4	7	17	123	0.64	23	- 6
32	2	4	10	43	0.23	20	- 10
34	1	2	6	57	0.30	18	- 12
36	1	2	4	43	0.23	15	- 9
39	1	2	2	26	0.14	13	- 11
$\bar{t}$	13.68	15.64	$\rightarrow \bar{s} = 0.9360614$				
S_x	10.07	10.52					
$S_{\bar{x}}$	0.99	0.92					

$191 - 167 = 24 \cong 14 + 11$

Période de maturation et fraction à l'eau

I. elegans - femelles - Dunham POND I - 1965 (t = 92 jours)

t	n	n'	$\sum n'$	$\sum n'\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	131	131	191	191	1.00	132	59
1	8	8	60	68	0.36	117	- 57
2	11	11	52	66	0.35	103	- 51
3	1	1	41	59	0.31	92	- 51
4	4	4	40	65	0.34	81	- 41
5	6	6	36	66	0.35	72	- 36
6	1	1	30	62	0.32	64	- 34
7	3	3	29	68	0.36	56	- 27
8	2	2	26	69	0.36	50	- 24
9	3	3	24	72	0.38	44	- 20
10	3	3	21	71	0.37	39	- 18
12	2	2	18	78	0.41	31	- 13
13	2	2	16	78	0.41	27	- 11
14	2	2	14	77	0.40	24	- 10
15	2	2	12	84	0.44	21	- 9
16	2	2	10	70	0.37	19	- 9
17	1	1	8	63	0.33	17	- 9
19	2	2	7	71	0.37	13	- 6
21	1	1	5	65	0.34	10	- 5
25	1	1	4	84	0.44	6	- 2
27	1	1	3	80	0.42	5	- 2
34	1	1	2	125	0.65	2	0
42	1	1	1	167	0.87	1	0
$\bar{L}$	8.72	8.72	$\rightarrow \bar{s} = 0.88532$				
S_x	8.51	8.51					
$S_{\bar{x}}$	1.10	1.10					

$191 - 132 = 59 \cong 57$

Période de maturation et fraction à l'eau

I. elegans - femelles - Dunham POND II - 1965 (t = 119 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	463	463	615	615	1.00	405	210
1	21	21	152	174	0.28	354	- 202
2	20	20	131	171	0.28	310	- 179
3	11	11	111	166	0.27	271	- 160
4	12	12	100	170	0.28	238	- 138
5	12	13	88	171	0.28	208	- 120
6	8	8	75	167	0.27	182	- 107
7	11	12	67	170	0.28	159	- 92
8	7	8	55	160	0.26	139	- 84
9	7	8	47	156	0.25	122	- 75
10	2	2	39	148	0.24	107	- 68
11	2	2	37	160	0.26	93	- 56
12	2	2	35	173	0.28	82	- 47
13	1	1	33	187	0.30	72	- 39
14	5	6	32	207	0.34	63	- 31
15	2	2	26	192	0.31	55	- 29
16	1	1	24	203	0.33	48	- 24
18	4	5	23	254	0.41	37	- 14
20	2	2	18	259	0.42	28	- 10
21	4	5	16	263	0.43	25	- 9
22	1	1	11	207	0.34	22	- 11
24	2	3	10	245	0.40	17	- 7
28	3	4	7	293	0.48	10	- 3
29	1	1	3	143	0.23	8	- 5
30	1	1	2	109	0.18	7	- 5
33	1	1	1	82	0.13	5	- 4
$\bar{t}$	7.57	8.01	$\rightarrow \bar{s} = 0.8751561$				
S_x	7.31	7.54					
$S_{\bar{x}}$	0.61	0.61					

$615 - 405 = 210 \cong 198 + 4$

Période de maturation et fraction à l'eau

I. elegans - femelles - Dunham POND III - 1966 (t = 72 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	73	73	163	163	1.00	133	30
1	3	3	90	95	0.58	126	- 36
2	2	2	87	97	0.59	119	- 32
3	5	5	85	101	0.62	112	- 27
5	3	3	80	106	0.65	100	- 20
6	1	1	77	108	0.66	95	- 18
7	7	8	76	113	0.69	89	- 13
10	5	6	68	120	0.74	75	- 7
11	4	5	62	116	0.71	71	- 9
12	4	5	57	112	0.69	67	- 10
13	2	2	52	109	0.67	64	- 12
14	1	1	51	101	0.62	60	- 9
15	2	3	50	117	0.72	57	- 7
16	3	4	47	116	0.71	54	- 7
17	4	5	63	165	1.01	51	12
18	10	13	58	161	0.99	48	10
19	1	1	45	132	0.81	45	0
20	3	4	44	137	0.84	43	1
21	2	3	40	131	0.80	40	0
22	1	1	37	129	0.79	38	- 1
23	4	6	36	132	0.81	36	0
24	1	2	30	117	0.72	34	- 4
25	2	3	28	115	0.71	32	- 4
26	1	2	25	109	0.67	30	- 5
27	2	3	23	106	0.65	29	- 6
28	1	2	20	98	0.60	27	- 7
29	1	2	18	93	0.57	26	- 8
30	1	2	16	88	0.54	24	- 8
31	1	2	14	81	0.50	23	- 9
34	1	2	12	82	0.50	19	- 7
35	1	2	10	72	0.44	18	- 8
36	1	2	8	61	0.37	17	- 9
39	1	2	6	55	0.34	15	- 9
41	1	2	4	41	0.25	13	- 9
45	1	2	2	26	0.16	10	- 8
$\bar{L}$	16.11	18.16	$\rightarrow \bar{s} = 0.944934$				
S_x	9.92	10.47					
$S_{\bar{x}}$	1.09	0.99					

$163 - 133 = 30 \cong 28 + 8$

Période de maturation et fraction à l'eau

E. cyathigerum – mâles – Dunham pond III – 1966 (t = 83 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	100	100	225	225	1.00	177	48
1	3	3	125	134	0.60	165	- 40
2	7	7	122	141	0.63	154	- 32
3	9	9	115	142	0.63	143	- 28
4	11	12	106	141	0.63	133	- 27
5	4	4	94	134	0.60	124	- 30
6	4	4	90	138	0.61	116	- 26
7	3	3	86	141	0.63	108	- 22
8	9	10	83	147	0.65	100	- 17
9	1	1	73	138	0.61	93	- 20
10	5	6	72	147	0.65	87	- 15
12	3	4	66	155	0.69	75	- 9
13	4	5	62	156	0.69	70	- 8
14	4	5	57	154	0.68	65	- 8
15	6	7	52	151	0.67	61	- 9
16	1	1	45	140	0.62	57	- 12
17	2	3	44	147	0.65	53	- 9
18	2	3	41	147	0.65	49	- 8
20	1	1	38	157	0.70	43	- 5
22	3	4	37	177	0.79	37	0
23	2	3	33	169	0.75	35	- 2
24	2	3	30	165	0.73	32	- 2
26	2	3	27	171	0.76	28	- 1
27	1	1	24	163	0.72	29	- 5
28	3	5	23	168	0.75	24	- 1
29	2	3	18	141	0.63	23	- 5
31	1	2	15	136	0.60	20	- 5
32	2	3	13	126	0.56	18	- 5
34	1	2	10	112	0.50	16	- 6
35	1	2	8	96	0.43	15	- 7
38	2	4	6	89	0.40	12	- 6
39	1	2	2	32	0.14	11	- 9
$\bar{L}$	12.59	14.58	$\rightarrow \bar{s} = 0.9314129$				
S_x	10.13	10.98					
$S_{\bar{x}}$	1.00	0.98					

$225 - 177 = 48 \cong 31 + 9$

Période de maturation et fraction à l'eau

C. puella - mâles - Dunham pond III - 1966 (t = 57 jours)

t	n	n'	$\sum n'$	$\sum n'.\bar{s}^{-i}$	fraction à l'eau	$Nm.\bar{s}^{i}$	Δ
0	83	83	198	198	1.00	158	40
1	3	3	115	123	0.62	148	- 33
2	9	9	112	128	0.64	139	- 27
3	11	12	103	125	0.63	130	- 27
4	7	8	91	118	0.59	122	- 31
5	1	1	83	115	0.58	114	- 31
6	5	6	82	121	0.61	107	- 25
7	1	1	76	120	0.60	100	- 24
8	3	3	75	126	0.63	94	- 19
9	2	2	72	129	0.65	88	- 16
10	7	8	70	134	0.67	83	- 13
12	4	5	62	135	0.68	72	- 10
13	2	3	57	133	0.67	68	- 11
14	1	1	54	134	0.67	64	- 10
15	4	5	53	140	0.70	60	- 7
17	2	3	48	145	0.73	52	- 4
18	2	3	45	145	0.73	49	- 4
20	2	3	42	154	0.77	43	- 1
24	1	2	39	185	0.93	33	6
26	3	6	37	200	1.00	29	8
27	2	4	31	179	0.90	27	4
28	3	6	27	166	0.83	26	1
29	2	4	21	138	0.69	24	- 3
30	1	2	17	119	0.60	23	- 6
31	1	2	15	112	0.56	21	- 6
33	2	5	13	111	0.56	19	- 6
36	1	3	8	83	0.42	15	- 7
45	1	5	5	93	0.47	8	- 3
$\bar{t}$	12.05	15.90	$\rightarrow \bar{s} = 0.937107$				
S_x	10.48	12.43					
$S_{\bar{x}}$	1.15	1.16					

$198 - 158 = 40 \cong 25 + 3$

Traitement d'adultes d'Ischnura elegans avec l'hormone juvenile (JH) et du farnésol (F) en 1974, 1975 et 1976.

(Dans la suite des tables 15 à 19).

Codes : ☒ : capture et traitement

☒ : mort

T : turquoise

B b : bleu

Traitement : 70 µg JH/éthanol – Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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27										T								B																						

A 56

Traitement : 70 µg JH/éthanol – Mâles (suite)

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
1							T						B																											
2							T									B																							
3																																							
4																																							
5																																							
6																																							
7																																							
8								T									B																						

A 57

Traitement : 100 µg JH/éthanol – Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
1										T	B																												
2				T				B																															
3					T				B																														
4				T																																		
5				T		B																																	
6							T																																
7																																							
8																																							
9																																							
10																																							

Traitement : 140 µg JH/éthanol - Mâles

No. sp.	Nombre de jours	Remarques
1		
2	Tb	
3		
4	T b	
5		
6		
7		
8		
9		
10		
11		
12		
13		
14	T	
15		
16		
17		
18		

Traitement : 200 µg JH/éthanol - Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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Traitement : 210 µg JH/éthanol – Mâles

No. sp.	Nombre de jours	Remarques
1	1 2 3 4	
2	1 2 3	
3	1 2 3	
4	1 2 3	
5	1 2 3	
6	1 2 3	
7	1 2 3	
8	1 2 3	
9	1 2 3 4	
10	1 2 3 4	
11	1 2 3	
12	1 2 3	
13	1 2 4	

Traitement : 280 µg JH/éthanol – Mâles

No. sp.	Nombre de jours	Remarques
1	1 2 4	
2	1 4	

Traitement : Témoin – Mâles

No. sp.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	~	~	42	Remarques
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A 61

Traitement : Témoin - Mâles (suite)

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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16														T																									

Traitement : Injection de 70 µg JH/éthanol - Mâles

(pas inclus dans les calculs)

No. sp.	Nombre de jours 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40	Remarques
1	TB	
2		
3	TB	
4		
5		
6	TB	
7		
8	TB	

Traitement : 35 µg F/éthanol - Mâles

No. sp.	Nombre de jours 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40	Remarques
1	T B	
2	T	
3		
4		
5	T B	
6	T B	
7		
8	T B	
9	T B	
10		
11		
12		
13		
14		
15		
16	T B	

Traitement : 70 µg F/éthanol - Mâles

No. sp.	Nombre de jours (1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40)	Remarques
1	TB	
2	TB	
3	TB	
4	TB	
5	TB	
6		
7		
8		
9		
10		
11		
12		
13		
14		
15		

Traitement : 140 µg F/éthanol - Mâles

No. sp.	Nombre de jours (1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39 40)	Remarques
1		
2		
3		
4	TB	

Traitement : 83 µg JH/huile de paraffine - Mâles

No. sp.	Nombre de jours	Remarques
1		
2		
3		
4		
5	T b	
6	T	
7	T	
8		
9		
10		
11		
12		
13		
14	T b	
15		
16	T	
17		
18	T b	
19		
20		
21	T	
22	T	
23		
24		
25	T b	
26	Tb	
27		

Traitement : 83 µg JH/huile de paraffine – Mâles (suite)

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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18																																							
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20								T							b																									

A 66

Traitement : 167 µg JH/huile de paraffine – Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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23																																							
24																																							

A 67

Traitement : 83 µg F/huile de paraffine - Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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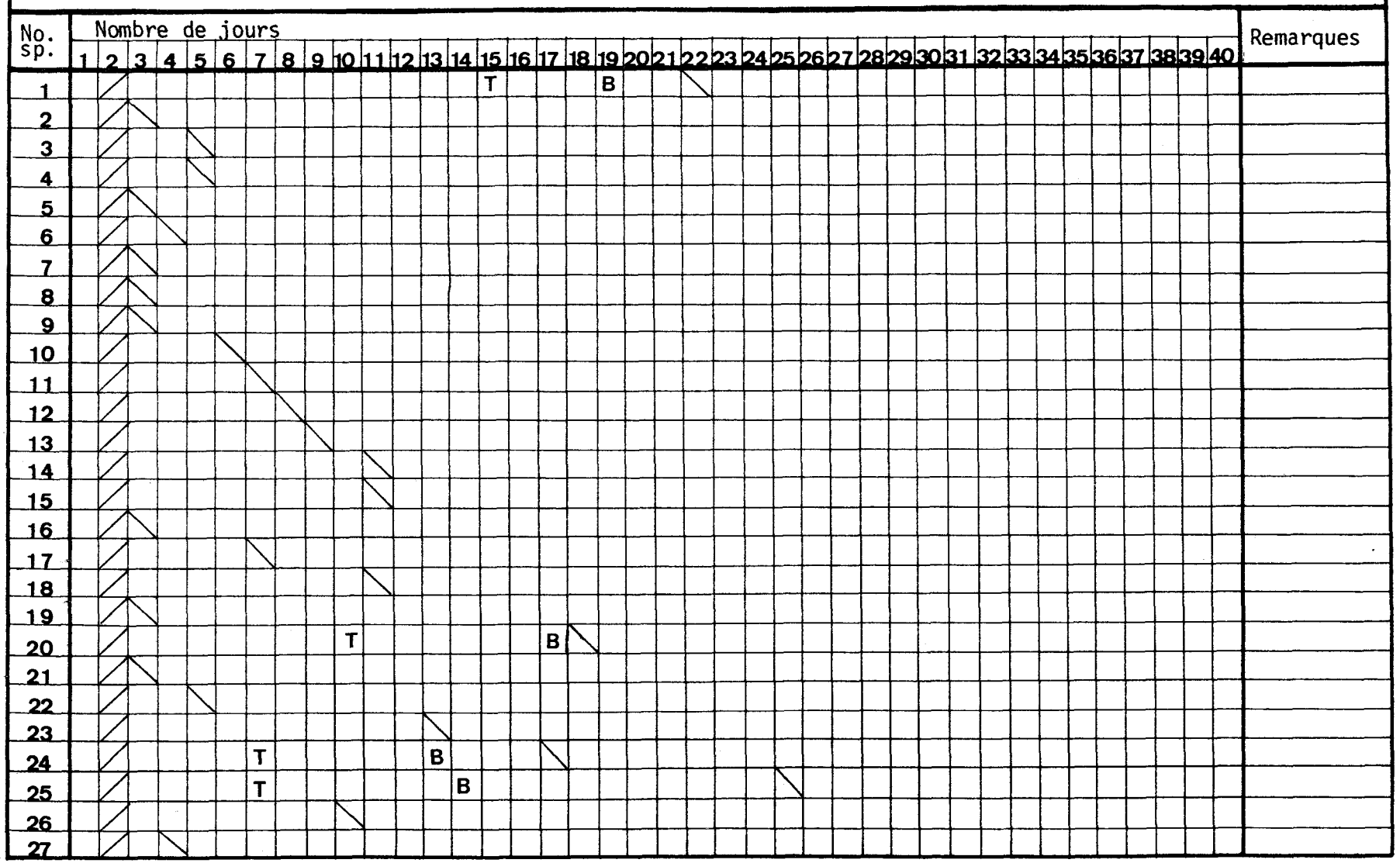
A 68

Traitement : 83 µg F/huile de paraffine - Mâles (suite 1)



Traitement : 83 µg F/huile de paraffine - Mâles (suite 2)

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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4																																							
5																																							

A 70

Traitement : 167 µg F/huile de paraffine - Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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Traitement : 167 µg F/huile de paraffine - Mâles (suite 1)

No. sp.	Nombre de jours																																								Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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Traitement : 167 µg F/huile de paraffine - Mâles (suite 2)

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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Traitement : 250 µg F/huile de paraffine en 3 doses - Mâles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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Traitement : 83 µg JH/huile de paraffine - Femelles

No. sp.	Nombre de jours	Remarques
1		
2		
3		
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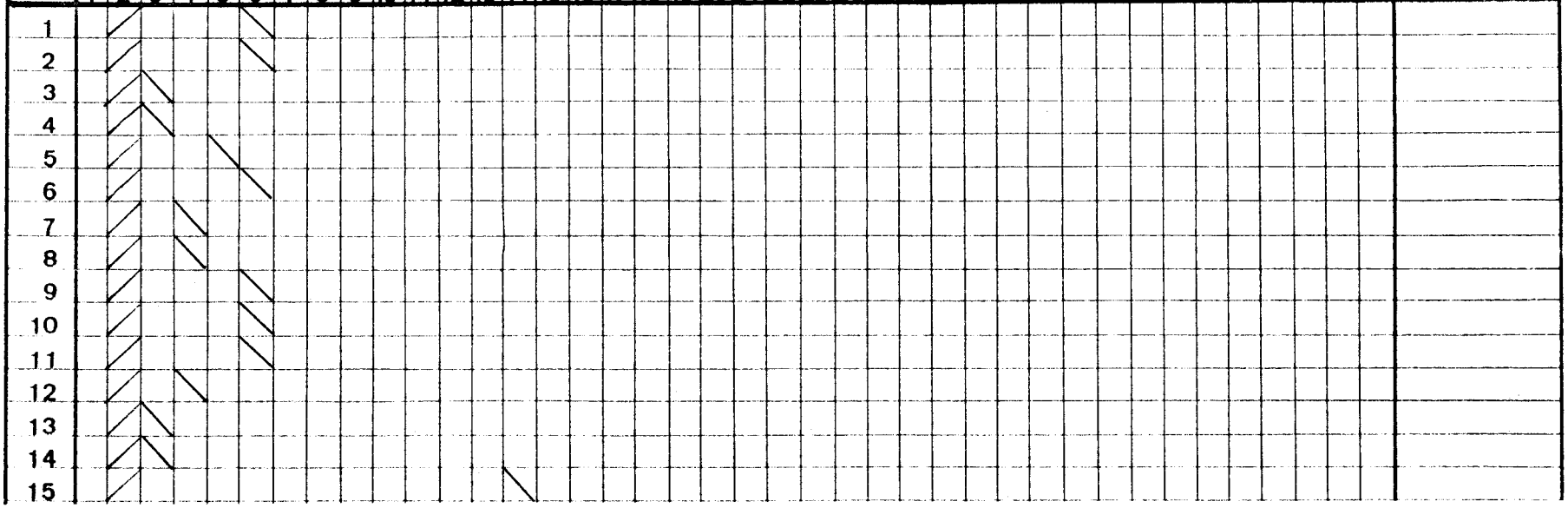
Traitement : 83 µg JH/huile de paraffine – Femelles (suite)



Traitement : 140 µg JH/éthanol – Femelles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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Traitement : Témoin - Femelles

No. sp.	Nombre de jours																																						Remarques
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	
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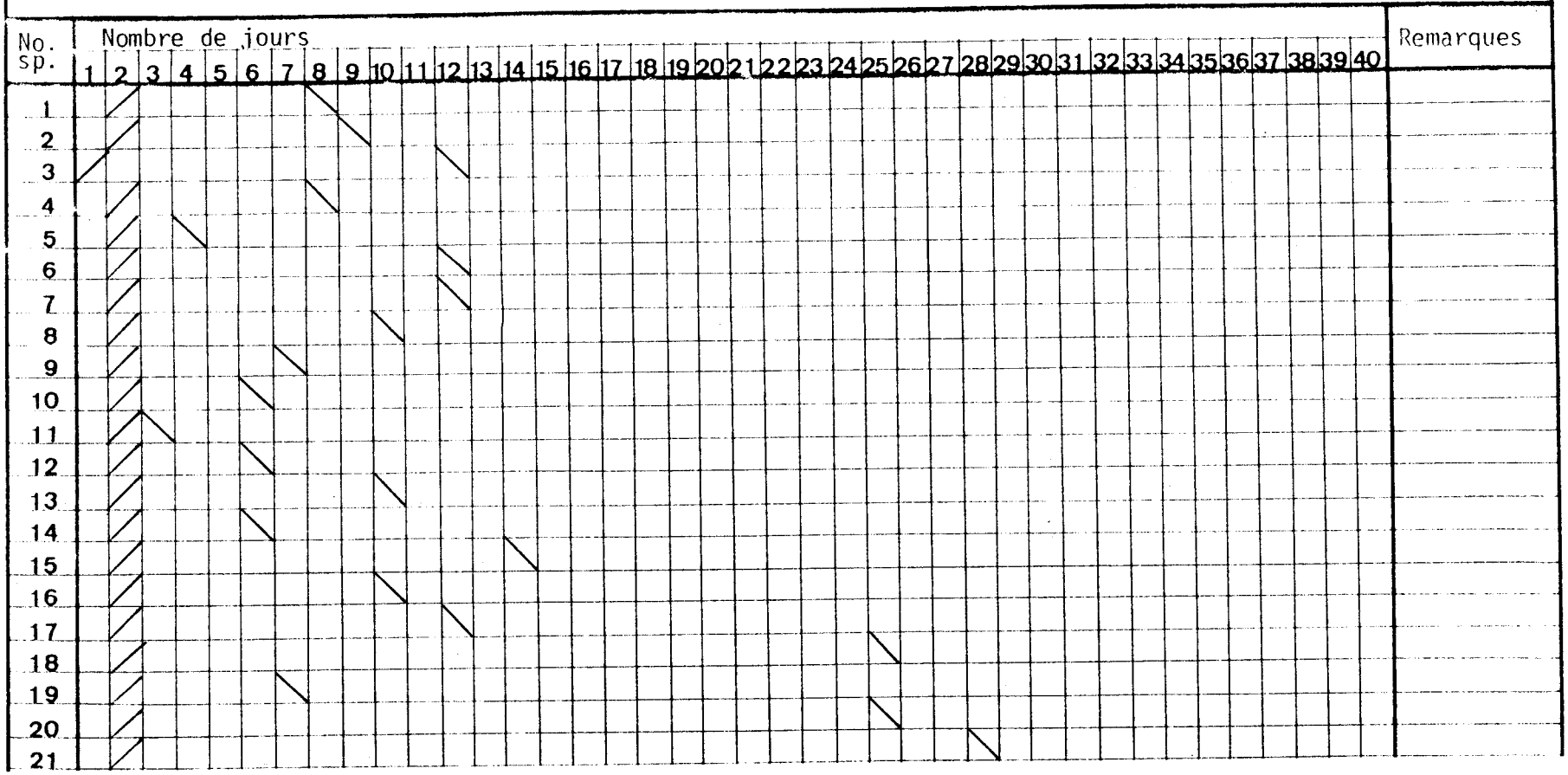
Traitement : **Témoin – Femelles (suite)**



Ischnura elegans : Distribution chi-quarré de la mortalité par période de 5 jours. (Mâles et Femelles)

O_i	Moyenne des classes	Temps (en classes de 5 jours)	Temps Sx^{-1}	P(x).n	E_i	P(x).n	E_i
		0	0	0		0	
33	3				50		23
		5	0.58	50.33		22.91	
18	8				15		17
		10	1.17	65.57		40.30	
20	13				9		13
		15	1.75	74.09		53.07	
10	18				5		9
		20	2.33	79.45		62.62	
5	23				3		7
		25	2.91	82.93		69.75	
3	28				3		6
		30	3.50	85.42		75.13	
1	33				2		4
		35	4.08	87.05		79.17	
1	38				1		3
		40	4.66	88.19		82.15	
1	43				1		2
		45	5.24	88.99		84.37	
				$\nu = 1$		$\nu = 2$	
				$\chi^2 = 26.65$		$\chi^2 = 14.44$	

O_i = observed frequency (fréquence observée)

E_i = expected frequency (fréquence espérée)

χ^2 = 16.9 (à 5 % et df = 9)

$\bar{x}$ = 10.63

n = 91

S_x = 8.58

Ischnura elegans : Distribution F de la mortalité par période de 5 jours (Mâles et Femelles)

O_i	Moyenne des classes	Temps (en classes de 5 jours)	Temps. Sx^{-1}	n- Q(x).n	E_i	n-Q(x).n	E_i	n-Q(x).n	E_i	n-Q(x).n	E_i	n-Q(x).n	E_i
		0	0										
33	3				38		37		39		39		39
		5	0.58	38.43		36.93		38.95		38.79		39.22	
18	8				21		19		21		21		21
		10	1.17	59.20		56.15		60.32		59.97		60.90	
20	13				11		11		12		12		12
		15	1.75	70.71		66.85		72.12		71.63		72.85	
10	18				7		6		7		7		7
		20	2.33	77.56		73.45		79.04		78.58		79.80	
5	23				4		4		4		4		4
		25	2.91	81.82		77.79		83.22		82.78		83.92	
3	28				3		3		3		3		3
		30	3.50	84.59		80.80		85.85		85.47		86.47	
1	33		5% grens		2		2		1		2		2
		35	4.08	86.39		82.90		87.50		87.15		88.03	
1	38				1		2		1		1		1
		40	4.66	87.62		84.44		88.57		88.29		89.02	
1	43				1		1		1		1		1
		45	5.24	88.47		85.60		89.23		89.05		89.65	
$\bar{x}$ = 10.63		χ^2 = 16.9		ν_1 = 2		2		2		2		2	
n = 91		(à 5 % et		ν_2 = 10		5		15		13		20	
S_x = 8.58		df = 9)		df = 9		9		9		9		9	
				χ^2 = 10.49		11.77		8.22		8.72		8.72	

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Ischnura elegans : Distribution F de la mortalité par période de 3 jours.

(Mâles et Femelles)

O_i	Moyenne des classes	Temps (en classes de 3 jours)	Temps. S_x^{-1}	n-Q(x).n	Ei
		0	0	0	
20	2				26
		3	0.35	26.35	
18	5				18
		6	0.70	44.40	
11	8				12
		9	1.05	56.94	
13	11				9
		12	1.40	65.79	
9	14				7
		15	1.75	72.12	
2	17				5
		18	2.10	76.71	
8	20				3
		21	2.45	80.08	
3	23				2
		24	2.80	82.57	
2	26				2
		27	3.15	84.44	
2	29				1
		30	3.50	85.85	
0	32				1
1		33	3.85	86.93	
2	35				1
		36	4.20	87.76	
0	38				1
0.5		39	4.55	88.40	
1	41				1
		42	4.90	88.90	

$\bar{x} = 10.63$

$n = 91$

$S_x = 8.58$

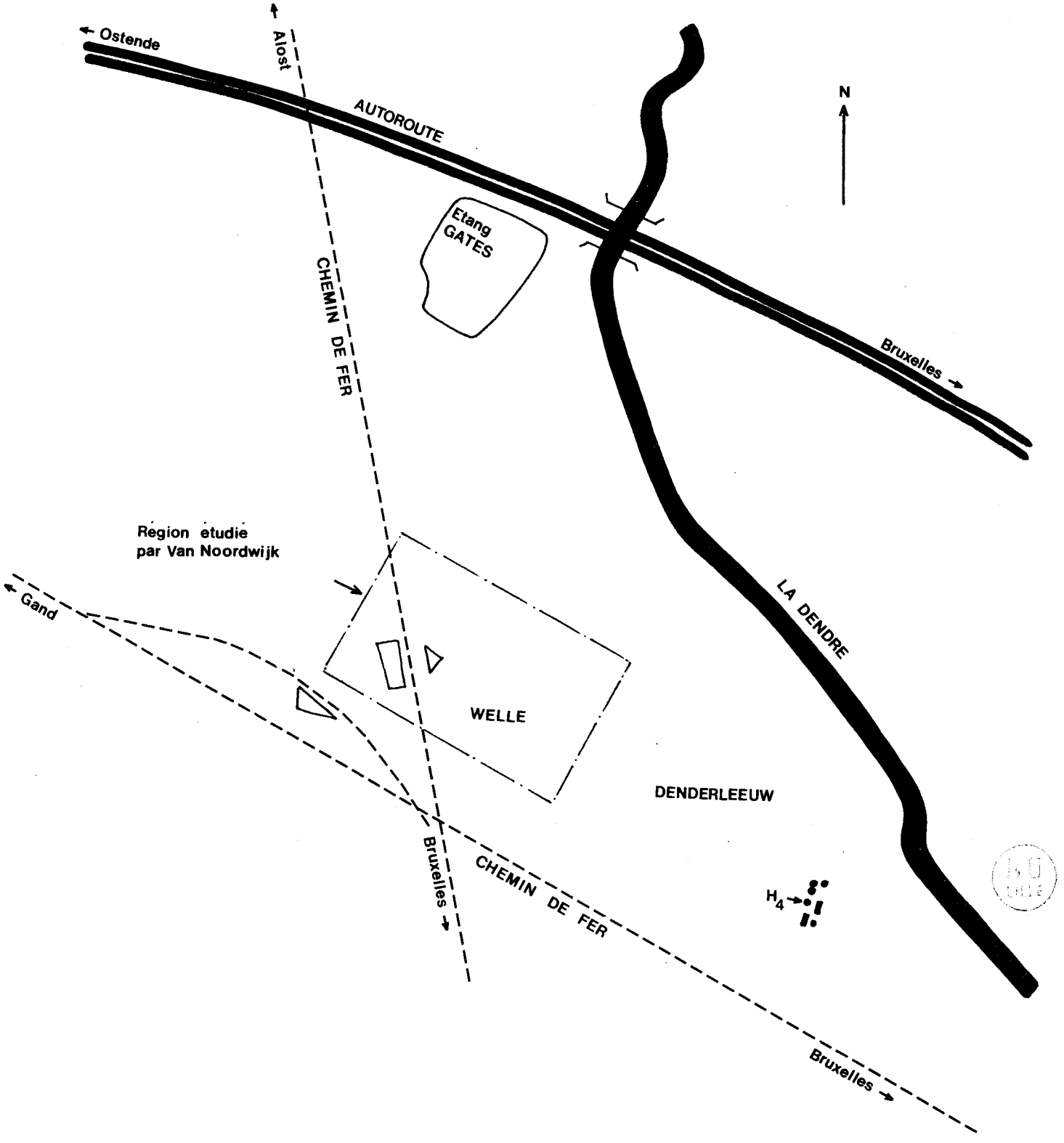
$\chi^2 = 22.4$ (à 5 % et df = 13)

$V_1 = 2$

$V_2 = 15$

$\chi^2 = 15.45$

Situation géographique des habitats étudiés

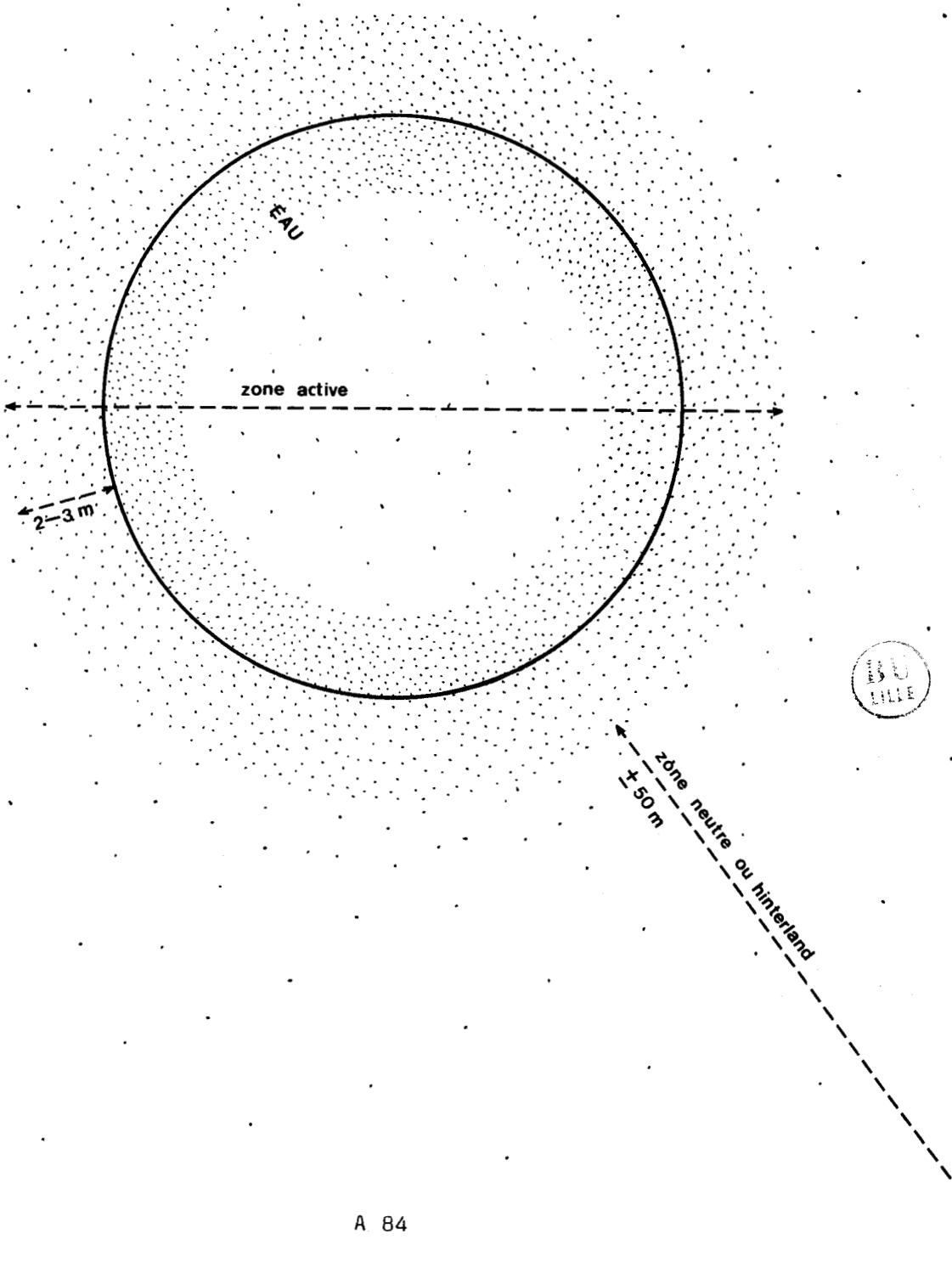


Carte d'après la carte NINOVE 30/4 de l'Institut Géographique Militaire.

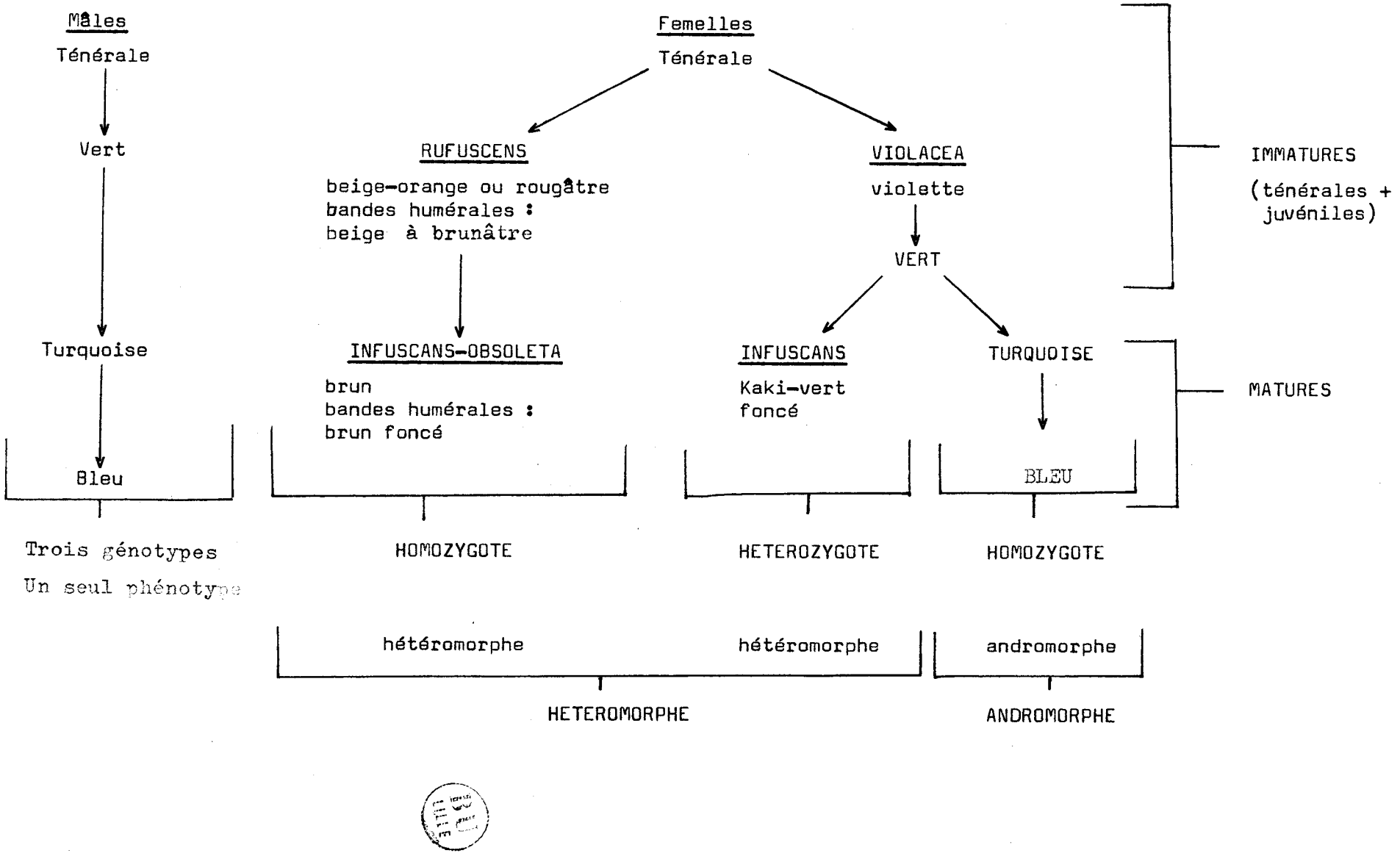
Echelle 1 : 10.000

Distribution d'une population d'Odonates

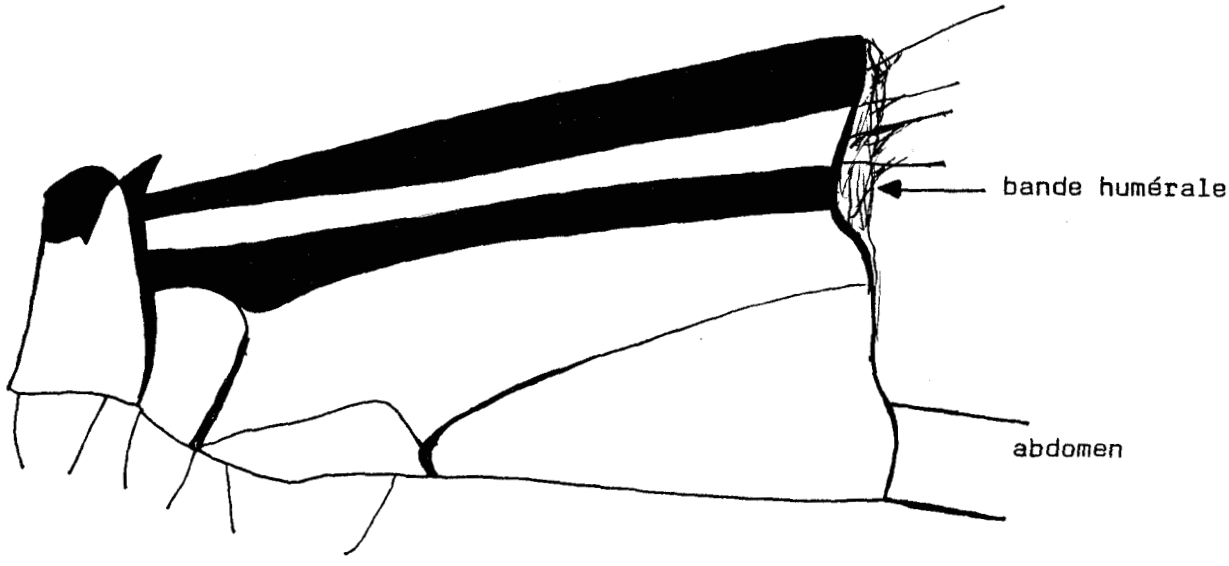
(Les distances dépendent fortement des caractéristiques topographiques)



Formes d'Ischnura e.elegans



Thorax d'Ischnura e.elegans



Changements de coloration : - le thorax, sauf la face dorsale et les bandes humérales
- les taches postoculaires
- le 8ème segment de l'abdomen

Les changements de coloration se produisent par le fait que des petits ilôts de pigments se créent et se répandent de plus en plus.