

# A POPULATION STUDY OF A COLONY OF IMAGINAL *ISCHNURA ELEGANS* (VAN DER LINDEN) (ODONATA: COENAGRIIDAE) AT DALE, PEMBROKESHIRE

By M. J. PARR

*Biological Laboratories, Royal College of Advanced Technology, Salford*

## CONTENTS

I. INTRODUCTION	.. .. .	237
II. THE DAMSELFLY <i>Ischnura elegans</i> (Van der Linden)	.. .. .	238
III. THE HABITAT	.. .. .	241
IV. METHODS:		
(1) Field Procedure	.. .. .	242
(2) Analysis of Capture-recapture data	.. .. .	245
(3) Jackson's First Method (1948)	.. .. .	248
(4) Jackson's Second Method (1948)	.. .. .	254
(5) Fisher and Ford's Method (1947)	.. .. .	255
(6) Bailey's Triple-catch Method (1951)	.. .. .	262
(7) Jolly's Method (1965)	.. .. .	264
V. DISCUSSION:		
(1) Population Estimates	.. .. .	268
(2) Sex Ratio	.. .. .	275
(3) Longevity	.. .. .	276
(4) Female Polymorphism	.. .. .	277
ACKNOWLEDGEMENTS	.. .. .	280
REFERENCES	.. .. .	281

## I. INTRODUCTION

THE work described in this paper was undertaken to illustrate in detail capture-recapture methods of studying populations of an isolated insect community, and because few such studies have been carried out on zygopteran dragonflies having a long flying season. Furthermore, as the entomological fauna of Dale has been neglected a study of any of the commoner insects in the area would be useful.

Lincoln (1930) was the first to use a capture-recapture method for estimating the size of a population. His simple formula, the "Lincoln Index", was used for estimating the numbers of wild duck by an analysis of ringing returns. The capture-recapture method was later developed by Jackson (1948) during his extensive work on tsetse fly populations in Africa. This method has subsequently been elaborated and used for the analysis of populations of Odonata (Borror, 1934; Corbet, 1952; Johnson, 1962), Lepidoptera (Dowdeswell, Fisher and Ford, 1940 and 1949; Davis, Frazer and Tynan, 1958), Orthoptera (Richards and Waloff, 1954), as well as birds and other vertebrates, which occur in colonies and are easily trapped (Blackwell and Dowdeswell, 1951, and

Leslie and Chitty, 1951). These capture-recapture methods involve marking and releasing a given number of specimens and from the proportion of marked specimens recovered in subsequent samples various facts relating to the nature, size and changes in an animal population can be deduced, such as estimates of the number of individuals present in the colony each day or the total numbers of animals emerging (or individuals present) throughout the season can be calculated. Capture-recapture studies may also be designed to provide information on the genetic constitution of a natural population. This is well illustrated by the work of Sheppard (1951) on the relationship between colour and pattern forms of the polymorphic land snail *Helix* (= *Cepaea*) *nemoralis* and its predation by thrushes. Dowdeswell *et al.* (1949) working on Tean (Isles of Scilly) employed similar methods to study changes in populations of the butterfly *Maniola jurtina* and obtained detailed information on the differential survival rates of individuals in neighbouring colonies. We can say, therefore, that capture-recapture methods are valuable tools for studying ecological problems and micro-evolution in both the field and laboratory, providing the limitations of current analytical methods are recognized.

A colony of the damselfly *Ischnura elegans* (Van der Linden) centred on a chain of four ponds at Maryborough Farm (Map Reference No. SM 812048) situated on the Dale peninsula, Pembrokeshire (Fig. 1) was studied from 24th June–7th July, 1964. The damselfly *Pyrrhosoma nymphula* (Sulzer), studied by Corbet (1952), differs from *I. elegans* in that it is a true "spring species" with a diapause in the final larval instar, and in having a synchronized emergence in spring and early summer as well as a relatively short adult life. In contrast, *I. elegans* is a "summer species" lacking a diapause in the final instar and with an extended emergence period commonly lasting fifteen weeks.

## II. THE DAMSELFLY *Ischnura elegans* (VAN DER LINDEN)

This species is one of the most common and widely distributed dragonflies in the British Isles, rivalled perhaps, in this respect, only by *Pyrrhosoma nymphula* and *Enallagma cyathigerum* (Charp.). The adult *I. elegans* has been fully described by Longfield (1949 and 1960) and Lord (1961); it may be easily recognized by the distinctive colour patterns and slim body. The male has blue (adult) or apple-green (immature) sides to the thorax; a very slim abdomen, mostly greenish-black dorsally, with the 8th segment entirely cerulean blue; the pterostigma of the forewing is partly black and partly white. The female is markedly polymorphic with respect to colour and a number of different forms or varieties have been described by several authors (Killington, 1924; Fraser, 1956; Longfield, 1949 and 1960; and Lord, 1961). Andromorphic (= turquoise) females are virtually identical to the males, but have a more robust abdomen, a nearly unicoloured pterostigma and lack, of course, the accessory genitalia beneath the second segment of the abdomen. Other forms of the female differing widely from the male in pattern and in colour are known as heteromorphs. The two heteromorphs *infuscans* Campion and *infuscans-obsolata* Killington both have the 8th abdominal segment a dull, dark reddish-brown and also have the bright thoracic cerulean blue or apple-green of the andromorph replaced by duller colours. In *infuscans* the light colour of the thorax is olive-green or dull apple-green. *Infuscans-obsolata* has the light colour of the thorax a dull fawn or

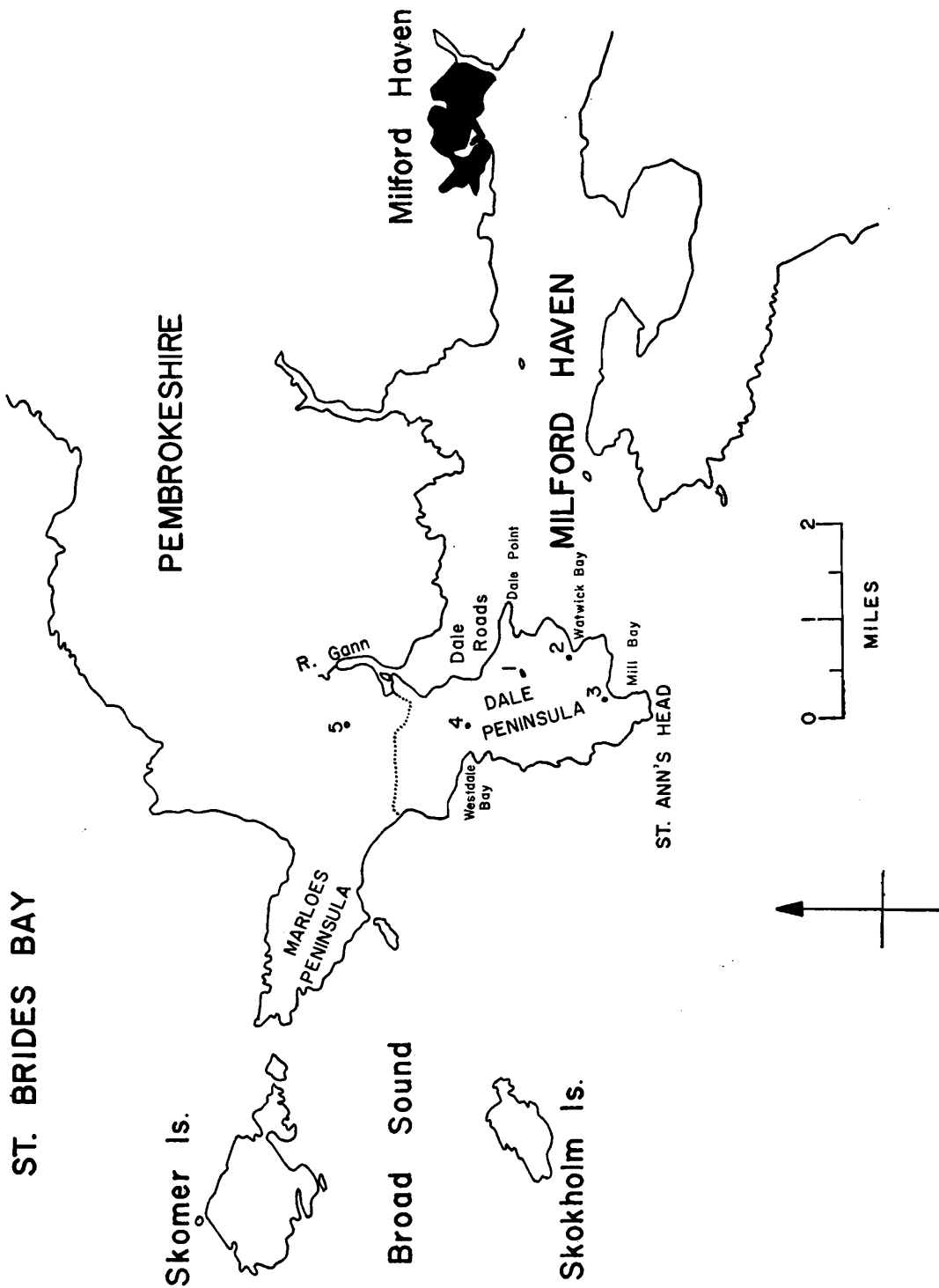


FIG. 1.

Map showing the location of the ponds mentioned in the text: 1, Maryborough Farm; 2, Watwick Bay; 3, Mill Bay; 4, Dale Castle; 5, Philbeach.

brownish-olive but without the well developed blackish humeral stripes which are present in the andromorph and in *infuscans*. Forms *rufescens* Stephens and *violacea* Selys have been shown by Lord (1961) to be immature stages; the former invariably maturing to *infuscans-obsolata* and the latter, usually via the green form, maturing to either the andromorph (turquoise) or *infuscans* form. *Rufescens* resembles *infuscans-obsolata* in colour-pattern but the light colour of the thorax is either salmon pink, reddish or orange-fawn, the actual colour apparently depending primarily on the age of the insect. The 8th abdominal segment is cerulean blue. *Violacea* has a colour pattern resembling that found in the andromorph and *infuscans* but the principal light colour of the thorax is generally violet, although some individuals are violet-green or violet-blue; the 8th abdominal segment is again mostly cerulean blue.

*I. elegans* breeds in weedy ditches, ponds, lakes or slow moving waters, especially favouring those with emergent vegetation and a good growth of tall grasses, nettles, etc. at the water's edge. The insect tolerates brackish conditions and may be found breeding very close to the sea-shore. The larvae live amongst submerged water plants and may be obtained by sweeping the vegetation with a stout net or from collections of water weed after being transferred into suitable containers, such as white enamelled dissecting trays. The colonies of this species may be very large and have ill-defined boundaries, especially when the breeding site is a large marsh with drainage ditches and surrounded by extensive areas of tall vegetation such as grasses and *Juncus*, or heather. Such colonies occur commonly on Anglesey, in the New Forest and in parts of Cheshire. In contrast, in breeding areas surrounded by closely grazed turf, with small amounts of tall vegetation, the insect colony may occur within quite sharply defined limits. Small ponds or bomb-craters in agricultural land frequently support small, virtually isolated populations of *I. elegans*. In the Dale colony, hedges act as effective barriers limiting the distribution of the insects even when these occur close to the water's edge. Where tall meadow-grass is succeeded by an equally tall growth of barley there is an effective colony boundary. In this case, the barley is probably too dense, whereas meadow-grasses provide sufficient protection when the insect is resting, and also space in between the grass stalks for flight and feeding. In windy weather, therefore, the insects are able to fly under relatively sheltered conditions when the temperatures permit. On the last day of the observations some specimens of *I. elegans* were flying between 9.45 a.m.—12.00 noon amongst grass stems when the wind speed exceeded 20 knots and the sky was overcast (see Table 1). On this date (7th July) freshening winds and heavy rain prevented any insect activity during the afternoon. It should be remembered, however, that although perfectly good colony boundaries may be recognized, as in the Maryborough population, the possibility of emigration and immigration cannot be ignored. Such dispersal movements may occur at various times in the life of the imaginal dragonfly (Corbet, 1962), but in species which do not regularly undertake long distance migrations (e.g. *I. elegans*) movement away from the parent colony probably occurs most often during the maturation period, which occupies the first one or two weeks of the insect's aerial life. When newly emerged specimens of *I. elegans* were caught and then released they invariably flew away from the ponds, whereas adult insects rarely behaved in this manner. Sexually immature

dragonflies show a negative response to water resulting in a virtual absence of these forms from the water's edge and the surrounding vegetation.

*I. elegans* was abundant in the Maryborough colony, but other species of Odonata were scarce. The two other species recorded during the period being *Coenagrion puella* (L.) and *Libellula depressa* L. The former comprised about a dozen sexually mature individuals, usually near the edge of the pond, very few being seen away from water. About 3 or 4 specimens of *L. depressa* were seen flying over pond No. 4 (see Fig. 2) during the period 25th–30th June, and two immature males were captured. The level of odonate interspecific interaction was therefore low at all four ponds.

There is no doubt that zygopteran dragonflies are often eminently suitable subjects for population analysis using the capture-recapture techniques because of their wide general distribution in Great Britain and the tendency to occur commonly in small, relatively isolated communities. A practical point of some importance is that damselflies, such as *Ichnura* and *Coenagrion*, are easily netted, thereby facilitating sampling work.

### III. THE HABITAT

The bedrock of the Dale peninsula is Devonian Old Red Sandstone marls with a central cap of glacial Boulder Clay (Dresser, 1959). The Boulder Clay extends from the south and west to Maryborough Farm itself, but the ponds are actually on Old Red Sandstone.

The Dale peninsula was found to be a good area for studying relatively isolated populations of zygopteran dragonflies. Movement of Zygoptera on to the Dale peninsula from other parts of Pembrokeshire is probably somewhat restricted as the peninsula neck is only approximately  $\frac{3}{4}$  mile wide at the narrowest part. Near this point, buildings and a wooded region are the dominant features. Standing water is scarce on the peninsula (Fig. 1). In addition to the Maryborough Farm site supporting the colony only four other permanent ponds were discovered in the area. As at Maryborough, two of the other ponds (Watwick and Mill Bay) were formed by damming small streams, apparently for the purpose of providing irrigation water for crops, particularly potatoes. The remaining pond (Castle Pond), situated near to Dale Castle, is small, exposed and provides cattle with drinking water. A new irrigation pond was constructed at Philbeach in June, 1964. Collecting at the nearest pond (Watwick) failed to reveal any movement of *I. elegans* from Maryborough; no specimens marked at Maryborough were seen at the Watwick pond during two visits made towards the end of the study period. Much of the peninsula consists of agricultural land serving to restrict the free distribution of individual damselflies from the various breeding areas at the ponds listed.

The four ponds at Maryborough Farm have been formed by the excavation of the bed of a small stream and the construction of earth and rock dams containing large-bore drainage pipes allowing water to flow from one pond to another, when the stream is swollen. At the time of this survey, the water level was rather low and water passed from one pond to the next by seepage through the dams. The progressive drops in water level from Ponds 1 to 4 were 2, 2 and

3½ feet respectively. No obvious exit for the water from Pond 4 could be seen and it seemed as if drainage from this pond was restricted. Each pond was at least 3 feet deep near the centre but shallower at the edges. Water plants were present in each of the ponds, the principal species being *Rorippa nasturtium-aquaticum* (L.) Hayek (watercress) and a filamentous algal "blanket weed", the latter forming floating mats on the surface. Duckweed, *Lemna minor* L., was also present. The adult dragonflies frequently rested on these plants, especially in fine, sunny periods. The distribution of the main vegetation types in the vicinity of the four ponds and the approximate boundary of the colony can be seen by reference to Fig. 2.

#### IV. METHODS

##### (1) *Field procedure*

In common with other British damselflies, *I. elegans*, flies most actively and is also most conspicuous in warm sunshine. A relatively high air temperature and lack of strong wind are associated with maximum activity in this insect. During the present study, *I. elegans* was seldom sufficiently active to allow many individuals to be captured before 9.0 a.m. (G.M.T.). On one day (4th July) the insects showed considerable activity by 8.30 a.m. when the wind speed was relatively low (11 knots at 8.0 a.m. at Dale Fort nearby) and the sun shone from early morning. In dull periods, when the air temperature remained above about 60° F. and there was little wind, the majority of the insects would cease active flight but they would still be easy to flush from vegetation and sampling could, therefore, continue under these sub-optimal conditions. On 25th June, the collecting and marking were done during the period 12.00–14.30 hours; on all other days, except 27th June when no field work was carried out, the work was done before 13.00 hours, generally occupying 2–3 hours.

Butterfly nets having 6 foot long handles were used to catch the daily sample. The sampling was random to the extent that every individual we could catch was taken, irrespective of age (teneral or adult) and sex, the whole area of the colony being covered as far as possible. Those individuals flying over the water or resting on low emergent vegetation were more difficult to capture unharmed than those over land. This is because the dragonflies tend to fly very low over the water surface and in attempting capture with a wet, heavy net there is danger of causing damage to the delicate insect. The wings and head suspension are most likely to be damaged in this way, particularly in teneral insects. However, during the present study the insects were successfully marked if handled carefully. Observations on freshly marked and released teneral *I. elegans* failed to reveal wing damage or any degree of abnormal behaviour.

When disturbed, damselflies usually fly a few yards *downwind*, but *I. elegans*, *Coenagrion puella* and *Enallagma*, like other Zygoptera, can fly against a strong breeze, before returning to their original site. When collecting damselflies, it is desirable to walk *downwind* in order to catch the maximum number possible in a given time. The captured dragonflies should be boxed separately until they are subsequently marked and released. It is, however, advisable not to separate the individuals taken flying in tandem or *in copula*. It was found that cardboard pillboxes having a diameter of 6.5 cm. and depth of 5.5 cm. served as very satisfactory receptacles for the insects. Generally the insects did not need to be

Table 1. Dale Fort Weather Statistics, 13th June-7th July, 1964.

Date	Cloud (8ths)	Wind		Temp. °F.		Barom. pressure	Rain (ins.)	Sun total	Sun 0800-1000 GMT.
		Dir.	Spd. kts.	Max.	Min.				
June 13	6	16	14	53	53	1,005.2	0.13	10.5	Yes
14	5	29	11	57	50	1,012.1	0.04	3.2	Yes
15	6	29	10	57	50	1,016.0	0.0	10.8	Yes
16	2	25	10	56	52	1,019.0	0.04	6.5	Yes
17	8	—	0	62	53	1,014.8	0.0	3.1	No
18	8	29	13	60	49	1,013.4	0.0	9.1	No
19	6	36	23	58	50	1,013.8	0.0	15.0	Cloud 0800-0900, Sun from 0900
20	3	34	17	57	48	1,018.0	0.0	11.8	Yes
21	7	29	6.5	58	49	1,018.4	0.0	0.8	No
22	7	36	5.5	61	53	1,016.9	0.01	2.9	No
23	6	32	11	61	53	1,016.6	0.0	5.9	No
24	6	36	6.5	66	49	1,024.1	0.0	8.2	No
25	0	18	2	71	50	1,025.8	0.0	7.3	Yes
26	0	11	2	70	53	1,021.6	tr.	11.9	Yes
27	8	20	11	70	57	1,019.3	0.0	2.6	No
28	6	29	8	65	56	1,022.4	tr.	1.9	?
29	1	34	17	62	52	1,026.7	0.0	7.7	Yes
30	6	27	6	64	52	1,027.0	0.0	15.0	Yes
July 1	8	34	20	66	53	1,028.7	0.0	10.8	Yes
2	5	34	8	67	53	1,027.0	0.0	5.8	Yes
3	6	29	10	64	54	1,021.9	0.0	3.7	No
4	1	02	11	62	51	1,021.0	0.0	13.0	Yes
5	4	34	10	61	49	1,020.3	0.0	7.7	No
6	5	02	16	62	53	1,020.5	0.0	10.8	Yes
7	7	23	23	61	53	1,011.8	0.05*	0.0	No

Readings at 0900 GMT. Rainfall and maximum temperature thrown back.

\* Reading at 1800 hours.

Wind direction in accordance with modified compass scale:

09—East  
18—South  
27—West  
36—North

handled whilst being boxed. When a specimen was marked or examined the box was opened and the insect lightly grasped by the wings with finger and thumb, care being taken not to let the insect escape. When the box top was lifted, the imprisoned dragonflies frequently exhibited thanatosis (death-feigning), but some were active for a short time before they could be held in the manner described. If all four wings are lightly held together, the insect can exercise little effective movement and marking is easily carried out. When handling teneral damselflies it is important not to hold the wings tightly as this can damage the soft veins and stimulate the insect to make vigorous attempts to escape thereby damaging the wings. It is also of importance to have clean, dry fingers when handling teneral damselflies; damp or sticky fingers are more likely to injure the soft wings.

*I. elegans* was marked by placing small spots of rapid-drying cellulose paint on the wings; this method of marking insects was first suggested by Brett (1936). Paint suitable for this purpose is sold in small tins as model aeroplane 'dope'

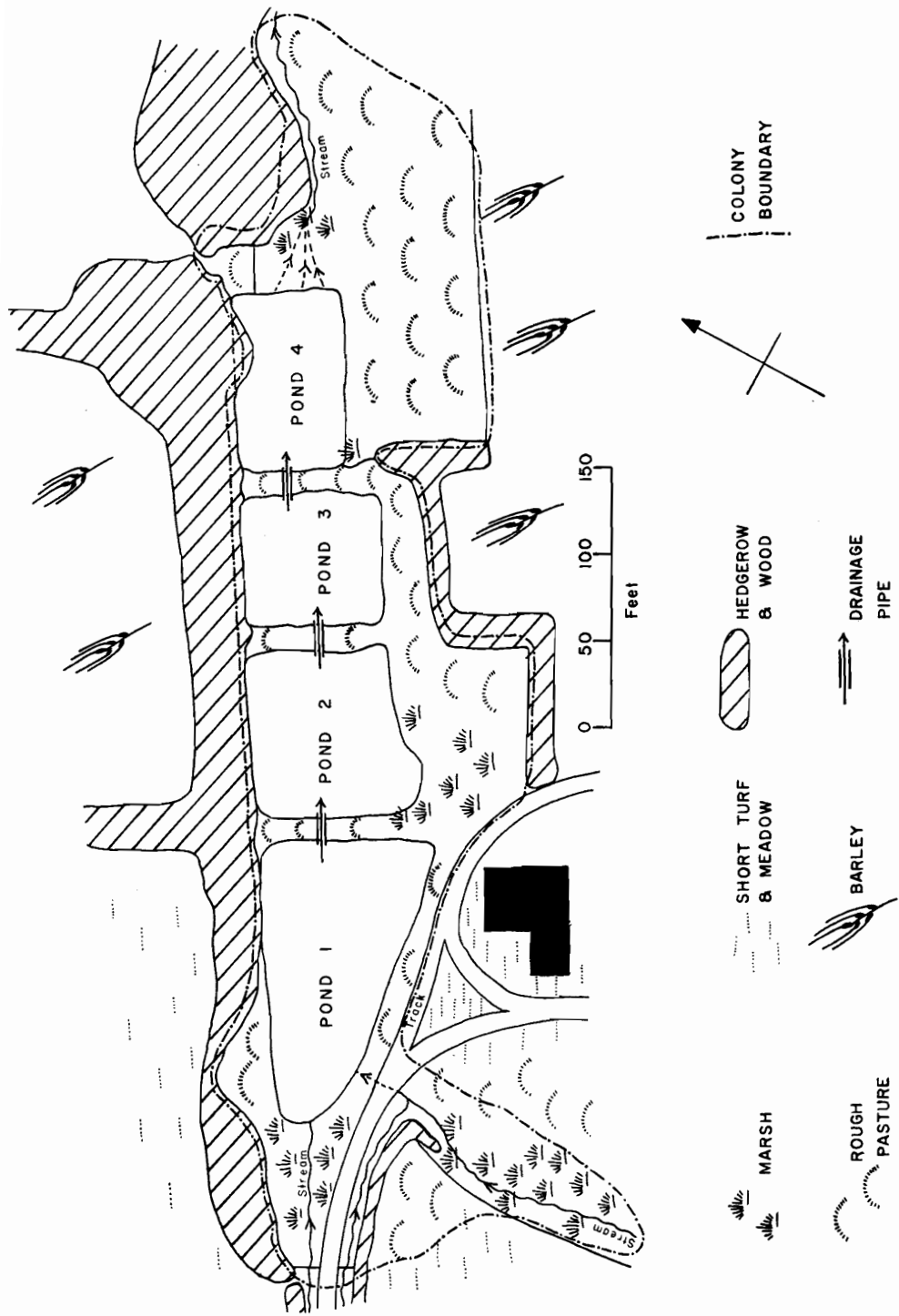


FIG. 2.

The area occupied by the Maryborough Farm colony of *Ischnura elegans* in 1964.



and in touch-up kits for cars. The paint was applied by a pointed piece of wire or a slender grass stem and placed on the underside of the hind wings. A particular colour placed on either the left or right wings was used to denote a specific date; e.g. an orange dot on the right side indicated the insect was first caught on 2nd July. It might be expected that the fore and hind wings could be used to denote different dates, but in practice this system was found to be too difficult to operate as the hindwings generally cover the forewings when the insect, with its wings folded above the thorax, is held between the fingers. The colours used during the period 25th June–7th July, 1964, were orange, yellow, green, blue, white, grey and brown. By using light and dark shades of the same colour for different dates and marking the femora as well as the wings, it would be possible to employ this particular technique for a considerably longer period than that covered in this study. Alternatively, more complicated marking systems may be devised allowing each individual to receive a unique mark. The cellulose paint dries in a matter of seconds; however, it was noticed that many individuals (not all) at first attempted to remove the paint from the wings by rubbing movements of the abdomen. If paint was applied too thickly or as too large a spot there was a tendency for it to become smeared on the sides of the abdomen. The successful application of a small mark necessitated frequent cleaning of the marking wire and occasional thinning of the paint. In practice it was found most convenient to capture, mark and release the damselflies from a specific area occupied by the colony, before continuing the work in another part. The insects were thus held captive for only a relatively short time and the number of individuals captured more than once in a particular day was small. However, the recapture of adult specimens within minutes of being marked at distances up to 150 yards away proves that marked damselflies are capable of quickly distributing themselves freely in the population during fine weather. The damselfly, *Pyrrosoma nymphula*, is also known to randomize rapidly (Corbet, 1952). Individuals incapable of normal flight after capture and marking were not released. It can be seen by reference to Tables 2 and 3 that this was an infrequent occurrence. Marking, recording and releasing were mostly carried out as soon as a batch of approximately 30 insects had been captured: this would generally be done twice or thrice during each day's collecting period. The recording procedure adopted involved the separate recording of the sexes, noting of the different female colour forms (after 1st July) and, of course, the various date specific marks borne by many individuals. Unmarked insects would be recorded in an appropriate column ( $\sigma$  or  $\text{♀}$ ) and marked with paint before release. A male insect caught bearing a green mark on the left side and blue and white marks on the right side was recorded as having been previously captured on 28th and 30th June and 1st July. However, it is important to remember that the three marks so recorded represent a single damselfly; a note was, therefore, always made of the many insects caught bearing multiple marks.

## (2) Analysis of Capture-Recapture Data

The estimation of the size of an isolated animal population depends on the principle that if a sample of  $s_1$  specimens is caught, marked, released and allowed to become distributed at random throughout the population, then if a



second sample of  $s_2$  specimens contains  $m$  marked individuals, the total population size,  $P$ , can be estimated as

$$\hat{P} = \frac{s_1 s_2}{m} \quad (1)$$

This simple procedure (the Lincoln Index) has been elaborated and refined to provide a greater degree of accuracy and more information by a number of workers since Lincoln's original work published in 1930. The process now generally adopted involves repeated sampling (although not necessarily daily) and knowing how often and on what dates a specimen has previously been caught. The data obtained by such capture, marking and recapture techniques can be conveniently presented in the form of triangular trellis tables first used by Dowdeswell, Fisher and Ford (1940). Tables 2 and 3 are trellis diagrams showing recapture data obtained for *I. elegans* during 1964. The dates form a horizontal row along the top and the captures and releases are entered in the left and right borders of the table respectively. The recaptures, representing marks, are entered in the body of the table; where the number of individuals recaptured differs from the number of marks recaptured the former are placed in parenthesis (see below for further explanation). For example, Table 2 shows that on 25th June, 78 male *I. elegans* were captured (top left of table) and that 77 were successfully marked and released (bottom right of table). On 2nd July, 83 specimens were captured and 83 released. This table shows, in the row running obliquely downwards to the left from 2nd July, that of the 83 insects captured on that date, 7 had been previously marked on 1st July, 7 on 30th June, 5 on 29th June, 4 on 28th June, 3 on 26th June and 3 on 25th June. Similarly, near the centre of the table the figure 6 indicates that on 3rd July, 6 individuals were caught which had been marked previously on 29th June, when 58 damselflies were released and that these 6 marked specimens were taken in a sample of 67 which were all successfully marked and released. Table 3 records that none of the 37 female insects released on 30th June were recaptured on the next day when a sample of 26 was taken; this is indicated by the figure 0. Tables 2 and 3 record both the number of marks and number of individuals recaptured. We need to know the actual number of both sexes recaptured in order to estimate the average length of life of the imagines. Reference to Table 3 illustrates this point. On 29th June, when 34 female *Ischnura* were captured, one of the five recaptured had been previously marked on 25th and 28th June. The number of recaptures recorded for 28th June are, therefore, reduced by one and in the diamond immediately below 28th and 29th June the figures 4 (3) are written. Therefore, of the 5 female insects recaptured on the 29th June (when a total of 34 was caught), 1 survived 4 days (from 25th June), 1 three days (from 26th June) and 3 one day (from 28th June). A dot (.) indicates that no captures, recaptures or releases could be made, in this case because no collecting was done on 27th June.

From the records thus obtained estimates were calculated of the daily populations of male and female imagines of *I. elegans* in the Dale colony studied, using several of the different methods devised to analyse capture-recapture data.

(3) *Jackson's First Method* (1948)

In order to obtain accurate estimates of an animal population using the Lincoln Index it is essential to comply with following conditions which are implicit in equation (1):

(i) That the marked animals distribute themselves freely in a random fashion with respect to the remainder of the population in the time between release and recapture.

(ii) That marked and unmarked animals behave similarly and that on subsequent occasions any marked individual has the same chance of being captured as any other member of the population.

(iii) That the number initially caught equals the number caught on a second occasion.

(iv) That the population does not alter numerically between release and recapture due to death or immigration or birth (may = emergence) or emigration.

These points will now be considered in turn.

The question of homogeneous redistribution of marked individuals in relation to the remainder of the population can only be resolved by careful study of the factors obtaining in specific cases. In the present study, it was found that sampling and releasing in three or four areas within the colony boundary led to rapid randomization of marked *I. elegans*, providing weather conditions were suitable. It may be extremely difficult to be sure that marked specimens will behave in the same manner as unmarked ones. Observations on *Ischnura* indicate that the application of cellulose paint to the wings may result in some degree of discomfort as many specimens attempted to clean the wings with the abdomen immediately after the paint was used. However, the behaviour of marked specimens soon returned to normal and several were seen feeding and copulating within minutes of being marked. It is much more difficult to ensure that any marked insect has an equal chance of being captured as unmarked individuals. The marking system employed may make marked specimens more conspicuous to predators or to the person carrying out sampling. Predation (except possibly by spiders) does not seem to be an important factor affecting the survival rate of *Ischnura*, but damselflies marked with white and orange paint were more conspicuous than those with green or brown spots. Sampling must be as random as possible and, therefore, the sighting of a marked insect should not lead to excessive efforts to secure it again, whilst unmarked individuals are ignored. If the number initially caught does not equal the number caught on a second occasion the third condition can be met by correcting the value of the number recaptured to the figure expected if 100 animals had been caught on each occasion. In general terms the corrected recapture values ( $y$ ) may be calculated thus:

$$y = \frac{R}{I} \times \frac{100}{M} \times \frac{100}{C} \quad (2)$$

where

C = number captured.

M = number marked and released.

R = number recaptured.

Table 3. *Ischnura elegans* (♀). Numbers captured and released. Individuals (in parentheses) and marks recaptured entered in body of Table

JUNE										JULY										
25	26	27	28	29	30	1	2	3	4	5	6	7	1	2	3	4	5	6	7	
6	0	.	.	4	4	0	0	3	5	2	0	.	.	.	3	5	1	2	0	.
12	.	1	.	(3)	(3)	1	0	0	(3)	1	0	50	.	.	1	1	1	0	38	
.	.	1	1	3	1	3	0	3	4	1	0	.	.	0	1	4	1	0	.	
.	1	1	1	1	1	(2)	2	3	0	2	0	.	.	3	0	0	0	0	.	
36	1	0	0	.	(0)	1	3	0	0	0	33	.	.	0	0	0	0	0	33	
34	1	0	0	.	1	0	0	0	0	0	33	.	.	0	0	0	0	0	33	
37	0	1	0	1	.	0	0	0	0	24	.	.	.	0	0	0	24	.	.	
26	0	0	0	0	.	0	0	0	0	26	.	.	.	1	0	0	26	.	.	
24	0	0	0	0	0	.	0	0	0	37	.	.	.	0	0	0	37	.	.	
33	0	0	0	0	0	0	0	0	34	.	.	.	.	0	0	0	34	.	.	
33	33	33	33	33	33	33	33	36	.	.	.	.	.	0	0	36	.	.	.	
40	40	40	40	40	40	40	40	11	.	.	.	.	.	0	0	.	.	.	.	
50	50	50	50	50	50	50	6	.	.	.	.	.	.	0	0	.	.	.	.	
10	10	10	10	10	10	10	.	.	.	.	.	.	.	0	0	.	.	.	.	
6	6	6	6	6	6	6	.	.	.	.	.	.	.	0	0	.	.	.	.	

Table 4. *I. Ischnura elegans* ( $\delta$ ). Corrected recapture frequencies

JUNE										JULY																			
25	26	27	28	29	30	1	2	3	4	5	6	7	25	26	27	28	29	30	1	2	3	4	5	6	7				
a <sub>1</sub>	a <sub>2</sub>	b <sub>1</sub>	c <sub>1</sub>	d <sub>1</sub>	e <sub>1</sub>	f <sub>1</sub>	g <sub>1</sub>	h <sub>1</sub>	i <sub>1</sub>	j <sub>1</sub>	k <sub>1</sub>	l <sub>1</sub>	m <sub>1</sub>	a <sub>1</sub>	a <sub>2</sub>	b <sub>1</sub>	c <sub>1</sub>	d <sub>1</sub>	e <sub>1</sub>	f <sub>1</sub>	g <sub>1</sub>	h <sub>1</sub>	i <sub>1</sub>	j <sub>1</sub>	k <sub>1</sub>	l <sub>1</sub>	m <sub>1</sub>		
78	7.083	a <sub>2</sub>	b <sub>2</sub>	c <sub>2</sub>	d <sub>2</sub>	e <sub>2</sub>	f <sub>2</sub>	g <sub>2</sub>	h <sub>2</sub>	i <sub>2</sub>	j <sub>2</sub>	k <sub>2</sub>	l <sub>2</sub>	m <sub>2</sub>	78	7.083	a <sub>2</sub>	b <sub>2</sub>	c <sub>2</sub>	d <sub>2</sub>	e <sub>2</sub>	f <sub>2</sub>	g <sub>2</sub>	h <sub>2</sub>	i <sub>2</sub>	j <sub>2</sub>	k <sub>2</sub>	l <sub>2</sub>	m <sub>2</sub>
55	a <sub>3</sub>	b <sub>3</sub>	c <sub>3</sub>	d <sub>3</sub>	e <sub>3</sub>	f <sub>3</sub>	g <sub>3</sub>	h <sub>3</sub>	i <sub>3</sub>	j <sub>3</sub>	k <sub>3</sub>	l <sub>3</sub>	m <sub>3</sub>	55	a <sub>3</sub>	b <sub>3</sub>	c <sub>3</sub>	d <sub>3</sub>	e <sub>3</sub>	f <sub>3</sub>	g <sub>3</sub>	h <sub>3</sub>	i <sub>3</sub>	j <sub>3</sub>	k <sub>3</sub>	l <sub>3</sub>	m <sub>3</sub>		
63	a <sub>4</sub>	b <sub>4</sub>	c <sub>4</sub>	d <sub>4</sub>	e <sub>4</sub>	f <sub>4</sub>	g <sub>4</sub>	h <sub>4</sub>	i <sub>4</sub>	j <sub>4</sub>	k <sub>4</sub>	l <sub>4</sub>	m <sub>4</sub>	63	a <sub>4</sub>	b <sub>4</sub>	c <sub>4</sub>	d <sub>4</sub>	e <sub>4</sub>	f <sub>4</sub>	g <sub>4</sub>	h <sub>4</sub>	i <sub>4</sub>	j <sub>4</sub>	k <sub>4</sub>	l <sub>4</sub>	m <sub>4</sub>		
58	a <sub>5</sub>	b <sub>5</sub>	c <sub>5</sub>	d <sub>5</sub>	e <sub>5</sub>	f <sub>5</sub>	g <sub>5</sub>	h <sub>5</sub>	i <sub>5</sub>	j <sub>5</sub>	k <sub>5</sub>	l <sub>5</sub>	m <sub>5</sub>	58	a <sub>5</sub>	b <sub>5</sub>	c <sub>5</sub>	d <sub>5</sub>	e <sub>5</sub>	f <sub>5</sub>	g <sub>5</sub>	h <sub>5</sub>	i <sub>5</sub>	j <sub>5</sub>	k <sub>5</sub>	l <sub>5</sub>	m <sub>5</sub>		
50	a <sub>6</sub>	b <sub>6</sub>	c <sub>6</sub>	d <sub>6</sub>	e <sub>6</sub>	f <sub>6</sub>	g <sub>6</sub>	h <sub>6</sub>	i <sub>6</sub>	j <sub>6</sub>	k <sub>6</sub>	l <sub>6</sub>	m <sub>6</sub>	50	a <sub>6</sub>	b <sub>6</sub>	c <sub>6</sub>	d <sub>6</sub>	e <sub>6</sub>	f <sub>6</sub>	g <sub>6</sub>	h <sub>6</sub>	i <sub>6</sub>	j <sub>6</sub>	k <sub>6</sub>	l <sub>6</sub>	m <sub>6</sub>		
45	a <sub>7</sub>	b <sub>7</sub>	c <sub>7</sub>	d <sub>7</sub>	e <sub>7</sub>	f <sub>7</sub>	g <sub>7</sub>	h <sub>7</sub>	i <sub>7</sub>	j <sub>7</sub>	k <sub>7</sub>	l <sub>7</sub>	m <sub>7</sub>	45	a <sub>7</sub>	b <sub>7</sub>	c <sub>7</sub>	d <sub>7</sub>	e <sub>7</sub>	f <sub>7</sub>	g <sub>7</sub>	h <sub>7</sub>	i <sub>7</sub>	j <sub>7</sub>	k <sub>7</sub>	l <sub>7</sub>	m <sub>7</sub>		
83	a <sub>8</sub>	b <sub>8</sub>	c <sub>8</sub>	d <sub>8</sub>	e <sub>8</sub>	f <sub>8</sub>	g <sub>8</sub>	h <sub>8</sub>	i <sub>8</sub>	j <sub>8</sub>	k <sub>8</sub>	l <sub>8</sub>	m <sub>8</sub>	83	a <sub>8</sub>	b <sub>8</sub>	c <sub>8</sub>	d <sub>8</sub>	e <sub>8</sub>	f <sub>8</sub>	g <sub>8</sub>	h <sub>8</sub>	i <sub>8</sub>	j <sub>8</sub>	k <sub>8</sub>	l <sub>8</sub>	m <sub>8</sub>		
67	a <sub>9</sub>	b <sub>9</sub>	c <sub>9</sub>	d <sub>9</sub>	e <sub>9</sub>	f <sub>9</sub>	g <sub>9</sub>	h <sub>9</sub>	i <sub>9</sub>	j <sub>9</sub>	k <sub>9</sub>	l <sub>9</sub>	m <sub>9</sub>	67	a <sub>9</sub>	b <sub>9</sub>	c <sub>9</sub>	d <sub>9</sub>	e <sub>9</sub>	f <sub>9</sub>	g <sub>9</sub>	h <sub>9</sub>	i <sub>9</sub>	j <sub>9</sub>	k <sub>9</sub>	l <sub>9</sub>	m <sub>9</sub>		
63	a <sub>10</sub>	b <sub>10</sub>	c <sub>10</sub>	d <sub>10</sub>	e <sub>10</sub>	f <sub>10</sub>	g <sub>10</sub>	h <sub>10</sub>	i <sub>10</sub>	j <sub>10</sub>	k <sub>10</sub>	l <sub>10</sub>	m <sub>10</sub>	63	a <sub>10</sub>	b <sub>10</sub>	c <sub>10</sub>	d <sub>10</sub>	e <sub>10</sub>	f <sub>10</sub>	g <sub>10</sub>	h <sub>10</sub>	i <sub>10</sub>	j <sub>10</sub>	k <sub>10</sub>	l <sub>10</sub>	m <sub>10</sub>		
94	a <sub>11</sub>	b <sub>11</sub>	c <sub>11</sub>	d <sub>11</sub>	e <sub>11</sub>	f <sub>11</sub>	g <sub>11</sub>	h <sub>11</sub>	i <sub>11</sub>	j <sub>11</sub>	k <sub>11</sub>	l <sub>11</sub>	m <sub>11</sub>	94	a <sub>11</sub>	b <sub>11</sub>	c <sub>11</sub>	d <sub>11</sub>	e <sub>11</sub>	f <sub>11</sub>	g <sub>11</sub>	h <sub>11</sub>	i <sub>11</sub>	j <sub>11</sub>	k <sub>11</sub>	l <sub>11</sub>	m <sub>11</sub>		
82	a <sub>12</sub>	b <sub>12</sub>	c <sub>12</sub>	d <sub>12</sub>	e <sub>12</sub>	f <sub>12</sub>	g <sub>12</sub>	h <sub>12</sub>	i <sub>12</sub>	j <sub>12</sub>	k <sub>12</sub>	l <sub>12</sub>	m <sub>12</sub>	82	a <sub>12</sub>	b <sub>12</sub>	c <sub>12</sub>	d <sub>12</sub>	e <sub>12</sub>	f <sub>12</sub>	g <sub>12</sub>	h <sub>12</sub>	i <sub>12</sub>	j <sub>12</sub>	k <sub>12</sub>	l <sub>12</sub>	m <sub>12</sub>		
31	a <sub>13</sub>	b <sub>13</sub>	c <sub>13</sub>	d <sub>13</sub>	e <sub>13</sub>	f <sub>13</sub>	g <sub>13</sub>	h <sub>13</sub>	i <sub>13</sub>	j <sub>13</sub>	k <sub>13</sub>	l <sub>13</sub>	m <sub>13</sub>	31	a <sub>13</sub>	b <sub>13</sub>	c <sub>13</sub>	d <sub>13</sub>	e <sub>13</sub>	f <sub>13</sub>	g <sub>13</sub>	h <sub>13</sub>	i <sub>13</sub>	j <sub>13</sub>	k <sub>13</sub>	l <sub>13</sub>	m <sub>13</sub>		
77	a <sub>14</sub>	b <sub>14</sub>	c <sub>14</sub>	d <sub>14</sub>	e <sub>14</sub>	f <sub>14</sub>	g <sub>14</sub>	h <sub>14</sub>	i <sub>14</sub>	j <sub>14</sub>	k <sub>14</sub>	l <sub>14</sub>	m <sub>14</sub>	77	a <sub>14</sub>	b <sub>14</sub>	c <sub>14</sub>	d <sub>14</sub>	e <sub>14</sub>	f <sub>14</sub>	g <sub>14</sub>	h <sub>14</sub>	i <sub>14</sub>	j <sub>14</sub>	k <sub>14</sub>	l <sub>14</sub>	m <sub>14</sub>		

Tables 4 and 5 show the calculated recapture values for male and female *I. elegans*. For example, near the centre of Table 4 can be seen the figure 7.678 in diamond  $d_6$  which is calculated from the 3 recaptures recorded in the corresponding position in Table 2, the 63 insects captured on 4th July and the 62 insects marked and released on 28th June, according to the equation given

above. Table 4 shows that recapture percentages usually show a trend with time (positive or negative) towards smaller percentages, meaning that there are progressively fewer marked animals surviving in each subsequent sample of 100. Jackson termed the series running to the bottom-left of the Table the *Negative series* and that running to the bottom-right the *Positive series* (although he, in fact, did not use the triangular trellis figure). The trellis figure shows how percentage frequencies may be used to distinguish changes due to the emergence or immigration of new individuals from those due to death or emigration. Consider  $f_2$  and  $g_1$  in Table 4. These values occur respectively at two days after day  $f$  (30th June) and one day after day  $g$ , or in each case at day  $h$ . The values  $f_2$  and  $g_1$  represent the percentage of the total catch on day  $h$  (2nd July), provided by every 100 damselflies marked on day  $f$  and day  $g$  respectively. If no deaths or emigration had occurred from day  $f$  to day  $g$ , then 100 individuals marked on day  $f$  would have formed the same proportion of the catch on day  $h$  as would 100 damselflies marked on day  $g$ . Therefore, the difference observed between  $f_2$  and  $g_1$  should be due to the death or emigration of some of the insects marked on day  $f$  by day  $g$ . As  $f_2$  would otherwise have equalled  $g_1$ , it can be seen that the number of deaths per every  $g_1$  insect from day  $f$  to day  $g$  must have been  $g_1 - f_2$ . This gives a rate per individual of  $\frac{g_1 - f_2}{g_1} = 1 - \frac{f_2}{g_1}$ ; that is, for every

insect surviving on day  $f$ ,  $1 - \frac{f_2}{g_1}$  of an insect has died by day  $g$ . Similarly, considering  $f_1$  and  $f_2$ , if no emergences or immigration had occurred from day  $g$  to day  $h$  then 100 damselflies marked on day  $f$  would have formed the same proportion of the catch on day  $h$  as day  $g$ , as they would be dying at the same rate as the unmarked individuals. Therefore the differences between  $f_2$  and  $f_1$  may be due to dilution of the marked proportion by new emergences or immigration from day  $g$  to day  $h$ . Since  $f_2$  otherwise would be expected to equal  $f_1$ , the  $f_1$  insects recorded on day  $h$  include only  $f_2$  old individuals, and therefore  $f_1 - f_2$  new emergences or immigrations. This is a rate per damselfly of  $\frac{f_1 - f_2}{f_1} = 1 - \frac{f_2}{f_1}$ ; which indicates that for every insect surviving on day  $h$ ,  $1 - \frac{f_2}{f_1}$

of an insect has emerged or immigrated to the colony since day  $g$ . That is to say, if the adjusted frequencies in rows running to bottom-left are relatively constant (except for sampling errors) this is a clear indication that individuals are not being lost through death or emigration. Similarly, if the percentage recapture frequencies in rows running to the bottom-right show no definite trend, then no new individuals are being added to the population by birth (or emergence) or immigration. Examination of Table 4 shows, however, that the corrected recapture values decline both to the south-west as well as to the south-east, indicating that during the study period the male population of *I. elegans* was losing individuals by death and/or emigration and was gaining individuals by emergence and/or immigration. Far less reliance can be placed on the data provided by Table 5 (corrected recapture frequencies for female *I. elegans*) because of the general low level of recaptures and smaller total numbers of insects released. The fourth condition may be by-passed by extrapolation from a series of adjusted recapture frequencies  $y_1, y_2, y_3, \dots, y_n$  so

Table 5. *Ischnura elegans* (♀). Corrected recapture frequencies

JUNE					JULY								
25	26	27	28	29	30	1	2	3	4	5	6	7	
a <sub>0</sub>	a <sub>1</sub>	b <sub>1</sub>	c <sub>1</sub>	d <sub>1</sub>	e <sub>1</sub>	f <sub>1</sub>	g <sub>1</sub>	h <sub>1</sub>	i <sub>1</sub>	j <sub>1</sub>	k <sub>1</sub>	l <sub>1</sub>	m <sub>1</sub>
6	0.0	a <sub>2</sub>	b <sub>2</sub>	c <sub>2</sub>	d <sub>2</sub>	e <sub>2</sub>	f <sub>2</sub>	g <sub>2</sub>	h <sub>2</sub>	i <sub>2</sub>	j <sub>2</sub>	k <sub>2</sub>	0.0
12	a <sub>3</sub>	b <sub>3</sub>	c <sub>3</sub>	d <sub>3</sub>	e <sub>3</sub>	f <sub>3</sub>	g <sub>3</sub>	h <sub>3</sub>	i <sub>3</sub>	j <sub>3</sub>	k <sub>3</sub>	0.0	50
	4629	a <sub>4</sub>	b <sub>4</sub>	c <sub>4</sub>	d <sub>4</sub>	e <sub>4</sub>	f <sub>4</sub>	g <sub>4</sub>	h <sub>4</sub>	i <sub>4</sub>	j <sub>4</sub>	0.0	38
36	4902	a <sub>5</sub>	b <sub>5</sub>	c <sub>5</sub>	d <sub>5</sub>	e <sub>5</sub>	f <sub>5</sub>	g <sub>5</sub>	h <sub>5</sub>	i <sub>5</sub>	j <sub>5</sub>	0.0	33
34	4504	a <sub>6</sub>	b <sub>6</sub>	c <sub>6</sub>	d <sub>6</sub>	e <sub>6</sub>	f <sub>6</sub>	g <sub>6</sub>	h <sub>6</sub>	i <sub>6</sub>	j <sub>6</sub>	0.0	33
37	0.0	a <sub>7</sub>	b <sub>7</sub>	c <sub>7</sub>	d <sub>7</sub>	e <sub>7</sub>	f <sub>7</sub>	g <sub>7</sub>	h <sub>7</sub>	i <sub>7</sub>	j <sub>7</sub>	0.0	24
26	0.0	a <sub>8</sub>	b <sub>8</sub>	c <sub>8</sub>	d <sub>8</sub>	e <sub>8</sub>	f <sub>8</sub>	g <sub>8</sub>	h <sub>8</sub>	i <sub>8</sub>	j <sub>8</sub>	0.0	26
24	0.0	a <sub>9</sub>	b <sub>9</sub>	c <sub>9</sub>	d <sub>9</sub>	e <sub>9</sub>	f <sub>9</sub>	g <sub>9</sub>	h <sub>9</sub>	i <sub>9</sub>	j <sub>9</sub>	0.0	34
33	0.0	a <sub>10</sub>	b <sub>10</sub>	c <sub>10</sub>	d <sub>10</sub>	e <sub>10</sub>	f <sub>10</sub>	g <sub>10</sub>	h <sub>10</sub>	i <sub>10</sub>	j <sub>10</sub>	0.0	36
33	0.0	a <sub>11</sub>	b <sub>11</sub>	c <sub>11</sub>	d <sub>11</sub>	e <sub>11</sub>	f <sub>11</sub>	g <sub>11</sub>	h <sub>11</sub>	i <sub>11</sub>	j <sub>11</sub>	0.0	11
40	0.0	a <sub>12</sub>	b <sub>12</sub>	c <sub>12</sub>	d <sub>12</sub>	e <sub>12</sub>	f <sub>12</sub>	g <sub>12</sub>	h <sub>12</sub>	i <sub>12</sub>	j <sub>12</sub>	0.0	6
50	0.0	a <sub>13</sub>	b <sub>13</sub>	c <sub>13</sub>	d <sub>13</sub>	e <sub>13</sub>	f <sub>13</sub>	g <sub>13</sub>	h <sub>13</sub>	i <sub>13</sub>	j <sub>13</sub>	0.0	10
36	0.0	a <sub>14</sub>	b <sub>14</sub>	c <sub>14</sub>	d <sub>14</sub>	e <sub>14</sub>	f <sub>14</sub>	g <sub>14</sub>	h <sub>14</sub>	i <sub>14</sub>	j <sub>14</sub>	0.0	36
33	0.0	a <sub>15</sub>	b <sub>15</sub>	c <sub>15</sub>	d <sub>15</sub>	e <sub>15</sub>	f <sub>15</sub>	g <sub>15</sub>	h <sub>15</sub>	i <sub>15</sub>	j <sub>15</sub>	0.0	36
33	0.0	a <sub>16</sub>	b <sub>16</sub>	c <sub>16</sub>	d <sub>16</sub>	e <sub>16</sub>	f <sub>16</sub>	g <sub>16</sub>	h <sub>16</sub>	i <sub>16</sub>	j <sub>16</sub>	0.0	36
33	0.0	a <sub>17</sub>	b <sub>17</sub>	c <sub>17</sub>	d <sub>17</sub>	e <sub>17</sub>	f <sub>17</sub>	g <sub>17</sub>	h <sub>17</sub>	i <sub>17</sub>	j <sub>17</sub>	0.0	36
33	0.0	a <sub>18</sub>	b <sub>18</sub>	c <sub>18</sub>	d <sub>18</sub>	e <sub>18</sub>	f <sub>18</sub>	g <sub>18</sub>	h <sub>18</sub>	i <sub>18</sub>	j <sub>18</sub>	0.0	36
33	0.0	a <sub>19</sub>	b <sub>19</sub>	c <sub>19</sub>	d <sub>19</sub>	e <sub>19</sub>	f <sub>19</sub>	g <sub>19</sub>	h <sub>19</sub>	i <sub>19</sub>	j <sub>19</sub>	0.0	36
33	0.0	a <sub>20</sub>	b <sub>20</sub>	c <sub>20</sub>	d <sub>20</sub>	e <sub>20</sub>	f <sub>20</sub>	g <sub>20</sub>	h <sub>20</sub>	i <sub>20</sub>	j <sub>20</sub>	0.0	36
33	0.0	a <sub>21</sub>	b <sub>21</sub>	c <sub>21</sub>	d <sub>21</sub>	e <sub>21</sub>	f <sub>21</sub>	g <sub>21</sub>	h <sub>21</sub>	i <sub>21</sub>	j <sub>21</sub>	0.0	36
33	0.0	a <sub>22</sub>	b <sub>22</sub>	c <sub>22</sub>	d <sub>22</sub>	e <sub>22</sub>	f <sub>22</sub>	g <sub>22</sub>	h <sub>22</sub>	i <sub>22</sub>	j <sub>22</sub>	0.0	36
33	0.0	a <sub>23</sub>	b <sub>23</sub>	c <sub>23</sub>	d <sub>23</sub>	e <sub>23</sub>	f <sub>23</sub>	g <sub>23</sub>	h <sub>23</sub>	i <sub>23</sub>	j <sub>23</sub>	0.0	36
33	0.0	a <sub>24</sub>	b <sub>24</sub>	c <sub>24</sub>	d <sub>24</sub>	e <sub>24</sub>	f <sub>24</sub>	g <sub>24</sub>	h <sub>24</sub>	i <sub>24</sub>	j <sub>24</sub>	0.0	36
33	0.0	a <sub>25</sub>	b <sub>25</sub>	c <sub>25</sub>	d <sub>25</sub>	e <sub>25</sub>	f <sub>25</sub>	g <sub>25</sub>	h <sub>25</sub>	i <sub>25</sub>	j <sub>25</sub>	0.0	36
33	0.0	a <sub>26</sub>	b <sub>26</sub>	c <sub>26</sub>	d <sub>26</sub>	e <sub>26</sub>	f <sub>26</sub>	g <sub>26</sub>	h <sub>26</sub>	i <sub>26</sub>	j <sub>26</sub>	0.0	36
33	0.0	a <sub>27</sub>	b <sub>27</sub>	c <sub>27</sub>	d <sub>27</sub>	e <sub>27</sub>	f <sub>27</sub>	g <sub>27</sub>	h <sub>27</sub>	i <sub>27</sub>	j <sub>27</sub>	0.0	36
33	0.0	a <sub>28</sub>	b <sub>28</sub>	c <sub>28</sub>	d <sub>28</sub>	e <sub>28</sub>	f <sub>28</sub>	g <sub>28</sub>	h <sub>28</sub>	i <sub>28</sub>	j <sub>28</sub>	0.0	36
33	0.0	a <sub>29</sub>	b <sub>29</sub>	c <sub>29</sub>	d <sub>29</sub>	e <sub>29</sub>	f <sub>29</sub>	g <sub>29</sub>	h <sub>29</sub>	i <sub>29</sub>	j <sub>29</sub>	0.0	36
33	0.0	a <sub>30</sub>	b <sub>30</sub>	c <sub>30</sub>	d <sub>30</sub>	e <sub>30</sub>	f <sub>30</sub>	g <sub>30</sub>	h <sub>30</sub>	i <sub>30</sub>	j <sub>30</sub>	0.0	36
33	0.0	a <sub>31</sub>	b <sub>31</sub>	c <sub>31</sub>	d <sub>31</sub>	e <sub>31</sub>	f <sub>31</sub>	g <sub>31</sub>	h <sub>31</sub>	i <sub>31</sub>	j <sub>31</sub>	0.0	36
33	0.0	a <sub>32</sub>	b <sub>32</sub>	c <sub>32</sub>	d <sub>32</sub>	e <sub>32</sub>	f <sub>32</sub>	g <sub>32</sub>	h <sub>32</sub>	i <sub>32</sub>	j <sub>32</sub>	0.0	36
33	0.0	a <sub>33</sub>	b <sub>33</sub>	c <sub>33</sub>	d <sub>33</sub>	e <sub>33</sub>	f <sub>33</sub>	g <sub>33</sub>	h <sub>33</sub>	i <sub>33</sub>	j <sub>33</sub>	0.0	36
33	0.0	a <sub>34</sub>	b <sub>34</sub>	c <sub>34</sub>	d <sub>34</sub>	e <sub>34</sub>	f <sub>34</sub>	g <sub>34</sub>	h <sub>34</sub>	i <sub>34</sub>	j <sub>34</sub>	0.0	36
33	0.0	a <sub>35</sub>	b <sub>35</sub>	c <sub>35</sub>	d <sub>35</sub>	e <sub>35</sub>	f <sub>35</sub>	g <sub>35</sub>	h <sub>35</sub>	i <sub>35</sub>	j <sub>35</sub>	0.0	36
33	0.0	a <sub>36</sub>	b <sub>36</sub>	c <sub>36</sub>	d <sub>36</sub>	e <sub>36</sub>	f <sub>36</sub>	g <sub>36</sub>	h <sub>36</sub>	i <sub>36</sub>	j <sub>36</sub>	0.0	36
33	0.0	a <sub>37</sub>	b <sub>37</sub>	c <sub>37</sub>	d <sub>37</sub>	e <sub>37</sub>	f <sub>37</sub>	g <sub>37</sub>	h <sub>37</sub>	i <sub>37</sub>	j <sub>37</sub>	0.0	36
33	0.0	a <sub>38</sub>	b <sub>38</sub>	c <sub>38</sub>	d <sub>38</sub>	e <sub>38</sub>	f <sub>38</sub>	g <sub>38</sub>	h <sub>38</sub>	i <sub>38</sub>	j <sub>38</sub>	0.0	36
33	0.0	a <sub>39</sub>	b <sub>39</sub>	c <sub>39</sub>	d <sub>39</sub>	e <sub>39</sub>	f <sub>39</sub>	g <sub>39</sub>	h <sub>39</sub>	i <sub>39</sub>	j <sub>39</sub>	0.0	36
33	0.0	a <sub>40</sub>	b <sub>40</sub>	c <sub>40</sub>	d <sub>40</sub>	e <sub>40</sub>	f <sub>40</sub>	g <sub>40</sub>	h <sub>40</sub>	i <sub>40</sub>	j <sub>40</sub>	0.0	36
33	0.0	a <sub>41</sub>	b <sub>41</sub>	c <sub>41</sub>	d <sub>41</sub>	e <sub>41</sub>	f <sub>41</sub>	g <sub>41</sub>	h <sub>41</sub>	i <sub>41</sub>	j <sub>41</sub>	0.0	36
33	0.0	a <sub>42</sub>	b <sub>42</sub>	c <sub>42</sub>	d <sub>42</sub>	e <sub>42</sub>	f <sub>42</sub>	g <sub>42</sub>	h <sub>42</sub>	i <sub>42</sub>	j <sub>42</sub>	0.0	36
33	0.0	a <sub>43</sub>	b <sub>43</sub>	c <sub>43</sub>	d <sub>43</sub>	e <sub>43</sub>	f <sub>43</sub>	g <sub>43</sub>	h <sub>43</sub>	i <sub>43</sub>	j <sub>43</sub>	0.0	36
33	0.0	a <sub>44</sub>	b <sub>44</sub>	c <sub>44</sub>	d <sub>44</sub>	e <sub>44</sub>	f <sub>44</sub>	g <sub>44</sub>	h <sub>44</sub>	i <sub>44</sub>	j <sub>44</sub>	0.0	36
33	0.0	a <sub>45</sub>	b <sub>45</sub>	c <sub>45</sub>	d <sub>45</sub>	e <sub>45</sub>	f <sub>45</sub>	g <sub>45</sub>	h <sub>45</sub>	i <sub>45</sub>	j <sub>45</sub>	0.0	36
33	0.0	a <sub>46</sub>	b <sub>46</sub>	c <sub>46</sub>	d <sub>46</sub>	e <sub>46</sub>	f <sub>46</sub>	g <sub>46</sub>	h <sub>46</sub>	i <sub>46</sub>	j <sub>46</sub>	0.0	36
33	0.0	a <sub>47</sub>	b <sub>47</sub>	c <sub>47</sub>	d <sub>47</sub>	e <sub>47</sub>	f <sub>47</sub>	g <sub>47</sub>	h <sub>47</sub>	i <sub>47</sub>	j <sub>47</sub>	0.0	36
33	0.0	a <sub>48</sub>	b <sub>48</sub>	c <sub>48</sub>	d <sub>48</sub>	e <sub>48</sub>	f <sub>48</sub>	g <sub>48</sub>	h <sub>48</sub>	i <sub>48</sub>	j <sub>48</sub>	0.0	36
33	0.0	a <sub>49</sub>	b <sub>49</sub>	c <sub>49</sub>	d <sub>49</sub>	e <sub>49</sub>	f <sub>49</sub>	g <sub>49</sub>	h <sub>49</sub>	i <sub>49</sub>	j <sub>49</sub>	0.0	36
33	0.0	a <sub>50</sub>	b <sub>50</sub>	c <sub>50</sub>	d <sub>50</sub>	e <sub>50</sub>	f <sub>50</sub>	g <sub>50</sub>	h <sub>50</sub>	i <sub>50</sub>	j <sub>50</sub>	0.0	36
33	0.0	a <sub>51</sub>	b <sub>51</sub>	c <sub>51</sub>	d <sub>51</sub>	e <sub>51</sub>	f <sub>51</sub>	g <sub>51</sub>	h <sub>51</sub>	i <sub>51</sub>	j <sub>51</sub>	0.0	36
33	0.0	a <sub>52</sub>	b <sub>52</sub>	c <sub>52</sub>	d <sub>52</sub>	e <sub>52</sub>	f <sub>52</sub>	g <sub>52</sub>	h <sub>52</sub>	i <sub>52</sub>	j <sub>52</sub>	0.0	36
33	0.0	a <sub>53</sub>	b <sub>53</sub>	c <sub>53</sub>	d <sub>53</sub>	e <sub>53</sub>	f <sub>53</sub>	g <sub>53</sub>	h <sub>53</sub>	i <sub>53</sub>	j <sub>53</sub>	0.0	36
33	0.0	a <sub>54</sub>	b <sub>54</sub>	c <sub>54</sub>	d <sub>54</sub>	e <sub>54</sub>	f <sub>54</sub>	g <sub>54</sub>	h <sub>54</sub>	i <sub>54</sub>	j <sub>54</sub>	0.0	36
33	0.0	a <sub>55</sub>	b <sub>55</sub>	c <sub>55</sub>	d <sub>55</sub>	e <sub>55</sub>	f <sub>55</sub>	g <sub>55</sub>	h <sub>55</sub>	i <sub>55</sub>	j <sub>55</sub>	0.0	36
33	0.0	a <sub>56</sub>	b <sub>56</sub>	c <sub>56</sub>	d <sub>56</sub>	e <sub>56</sub>	f <sub>56</sub>	g <sub>56</sub>	h <sub>56</sub>	i <sub>56</sub>	j <sub>56</sub>	0.0	36
33	0.0	a <sub>57</sub>	b <sub>57</sub>	c <sub>57</sub>	d <sub>57</sub>	e <sub>57</sub>	f <sub>57</sub>	g <sub>57</sub>	h <sub>57</sub>	i <sub>57</sub>	j <sub>57</sub>	0.0	36
33	0.0	a <sub>58</sub>	b <sub>58</sub>	c <sub>58</sub>	d <sub>58</sub>	e <sub>58</sub>	f <sub>58</sub>	g <sub>58</sub>	h <sub>58</sub>	i <sub>58</sub>	j <sub>58</sub>	0.0	36
33	0.0	a <sub>59</sub>	b <sub>59</sub>	c <sub>59</sub>	d <sub>59</sub>	e <sub>59</sub>	f <sub>59</sub>	g <sub>59</sub>	h <sub>59</sub>	i <sub>59</sub>	j <sub>59</sub>	0.0	36
33	0.0	a <sub>60</sub>	b <sub>60</sub>	c <sub>60</sub>	d <sub>60</sub>	e <sub>60</sub>	f <sub>60</sub>	g <sub>60</sub>	h <sub>60</sub>	i <sub>60</sub>	j <sub>60</sub>	0.0	36
33	0.0	a <sub>61</sub>	b <sub>61</sub>	c <sub>61</sub>	d <sub>61</sub>	e <sub>61</sub>	f <sub>61</sub>	g <sub>61</sub>	h <sub>61</sub>	i <sub>61</sub>	j <sub>61</sub>	0.0	36
33	0.0	a <sub>62</sub>	b <sub>62</sub>	c <sub>62</sub>	d <sub>62</sub>	e <sub>62</sub>	f <sub>62</sub>	g <sub>62</sub>	h <sub>62</sub>	i <sub>62</sub>	j <sub>62</sub>	0.0	36
33	0.0	a <sub>63</sub>	b <sub>63</sub>	c <sub>63</sub>	d <sub>63</sub>	e <sub>63</sub>	f <sub>63</sub>	g <sub>63</sub>	h <sub>63</sub>	i <sub>63</sub>	j <sub>63</sub>	0.0	36
33	0.0	a <sub>64</sub>	b <sub>64</sub>	c <sub>64</sub>	d <sub>64</sub>	e <sub>64</sub>	f <sub>64</sub>	g <sub>64</sub>	h <sub>64</sub>	i <sub>64</sub>	j <sub>64</sub>	0.0	36
33	0.0	a <sub>65</sub>	b <sub>65</sub>	c <sub>65</sub>	d <sub>65</sub>	e <sub>65</sub>	f <sub>65</sub>	g <sub>65</sub>	h <sub>65</sub>	i <sub>65</sub>	j <sub>65</sub>	0.0	36
33	0.0	a <sub>66</sub>	b <sub>66</sub>	c <sub>66</sub>	d <sub>66</sub>	e <sub>66</sub>	f <sub>66</sub>	g <sub>66</sub>	h <sub>66</sub>	i <sub>66</sub>	j <sub>66</sub>	0.0	36
33	0.0	a <sub>67</sub>	b <sub>67</sub>	c <sub>67</sub>	d <sub>67</sub>	e <sub>67</sub>	f <sub>67</sub>	g <sub>67</sub>	h <sub>67</sub>	i <sub>67</sub>	j <sub>67</sub>	0.0	36
33	0.0	a <sub>68</sub>	b <sub>68</sub>	c <sub>68</sub>	d <sub>68</sub>	e <sub>68</sub>	f <sub>68</sub>	g <sub>68</sub>	h <sub>68</sub>	i <sub>68</sub>	j <sub>68</sub>	0.0	36
33	0.0	a <sub>69</sub>	b <sub>69</sub>	c <sub>69</sub>	d <sub>69</sub>	e <sub>69</sub>	f <sub>69</sub>	g <sub>69</sub>	h <sub>69</sub>	i <sub>69</sub>	j <sub>69</sub>	0.0	36
33	0.0	a <sub>70</sub>	b <sub>70</sub>	c <sub>70</sub>	d <sub>70</sub>	e <sub>70</sub>	f <sub>70</sub>	g <sub>70</sub>	h <sub>70</sub>	i <sub>70</sub>	j <sub>70</sub>	0.0	36
33	0.0	a <sub>71</sub>	b <sub>71</sub> </										



that we can find the percentage recapture frequency  $y_0$  for date  $t_0$ , assuming recapture was possible immediately after release. Now in order to estimate  $y_0$ , it is first necessary to calculate an *ingress rate* or *egress rate per individual per day* (respectively  $r_+$  or  $r_-$ , depending on whether it is obtained from a positive or negative series) which is the pooled or smoothed estimate  $r_+ = \frac{y_n}{y_n - 1}$  or  $r_- = \frac{y_n}{y_n + 1}$ , where  $y$  is the corrected recapture frequency for day  $n-1$ , day  $n$ , or day  $n+1$ .

When recaptures were made on only a few dates, say 3 or 4,  $r$  may be estimated from the following equation:

$$r_+ \text{ (or } r_-) = \frac{y_2 + y_3 + \dots + y_n}{y_1 + y_2 + \dots + y_{n-1}} \quad (3)$$

When there are sufficient values of  $y$ , the estimate is smoothed further by using the equation

$$r_+ \text{ (or } r_-) = \sqrt{\frac{y_3 + y_4 + y_5 + \dots + y_n}{y_1 + y_2 + y_3 + \dots + y_{n-2}}} \quad (\text{Andrewartha, 1961}) \quad (4)$$

We can now find  $y_0$  from the equation

$$y_0 = \frac{y_1 + y_2 + \dots + y_{n-1}}{r_+ \text{ (or } r_-)} - (y_1 + y_2 + \dots + y_{n-2}) \quad (5)$$

and therefore the population on date  $t_0$  may be calculated in accordance with equation (1):

$$\hat{P}_0 = \frac{100}{I} \times \frac{100}{y_0}$$

For example, using this method the population of male *I. elegans* on 28th June ( $P_4$ ) may be estimated as follows:

$$\begin{aligned} r_+ d_0 &= \sqrt{\frac{d_3 + d_4 + d_5 + d_6 + d_7 + d_8}{d_1 + d_2 + d_3 + d_4 + d_5 + d_6}} \\ &= \sqrt{\frac{14 \cdot 34 + 7 \cdot 773 + 12 \cdot 04 + 7 \cdot 678 + 5 \cdot 147 + 7 \cdot 869}{27 \cdot 81 + 16 \cdot 13 + 14 \cdot 34 + 7 \cdot 773 + 12 \cdot 04 + 7 \cdot 678}} \\ &= \sqrt{\frac{54 \cdot 85}{85 \cdot 76}} \\ &= 0 \cdot 7999 \\ d_0 &= \frac{d_1 + d_2 + d_3 + d_4 + d_5 + d_6 + d_7}{r_+ d_0} - (d_1 + d_2 + d_3 + d_4 + d_5 + d_6) \\ &= \frac{90 \cdot 908}{0 \cdot 7999} - (85 \cdot 761) \\ &= 27 \cdot 839. \end{aligned}$$

$$\begin{aligned} \text{Hence, } \hat{P}_a \text{ (28th June)} &= \frac{100}{1} \times \frac{100}{27 \cdot 84} \\ &= \underline{\underline{359 \cdot 2}}. \end{aligned}$$

(4) *Jackson's Second Method* (1948)

This method also utilizes the fractions of the form  $\frac{y}{y_{n+1}}$  and  $\frac{y}{y_{n-1}}$  for estimating  $r_-$  and  $r_+$  respectively, as in the earlier method. When suitable data are available, the variance of  $r$  can be considerably reduced by smoothing, e.g. the values for  $r$  for 30th June (Table 4) may be calculated:

$$r_+ f_0 = \frac{e_2 + d_3}{e_1 + d_2},$$

$$r_- f_0 = \frac{e_2 + e_3 + e_4 + e_5 + e_6 + e_7}{f_1 + f_2 + f_3 + f_4 + f_5 + f_6}.$$

Then the male populations for that date may be estimated from the equations

$$\hat{P}_t = \frac{10^4 r_+}{f_1}, \quad \text{or} \quad \hat{P}_t = \frac{10^4 r_-}{e_1}.$$

As no sampling was carried out on 27th June and no recaptures are recorded in diamonds  $a_6$  and  $b_4$  the data for calculating  $r_+ f_0$  is sparse and it may be expected that the use of the series  $r_-$  would lead to a more reliable population estimate. Substituting the corrected recapture values in the foregoing equations, we obtain the following estimates for the population number on 30th June for males:

$$\begin{aligned} r_- f_0 &= \frac{7 \cdot 663 + 10 \cdot 39 + 15 \cdot 44 + 13 \cdot 68 + 3 \cdot 667 + 2 \cdot 103}{26 \cdot 67 + 16 \cdot 87 + 11 \cdot 94 + 15 \cdot 87 + 4 \cdot 255 + 4 \cdot 879} \\ &= \frac{52 \cdot 94}{80 \cdot 48} \\ &= 0 \cdot 6577 \\ \hat{P}_t &= \frac{10^4 \cdot 0 \cdot 6577}{6 \cdot 896} \\ &= \underline{\underline{954 \cdot 0}}; \end{aligned}$$

and for the positive series

$$\begin{aligned} r_+ f_0 &= \frac{7 \cdot 663 + 14 \cdot 34}{6 \cdot 869 + 16 \cdot 13} \\ &= 0 \cdot 9552 \\ \hat{P}_t &= \frac{10^4 \cdot 0 \cdot 9552}{26 \cdot 67} \\ &= \underline{\underline{358 \cdot 2}}. \end{aligned}$$

(5) *Fisher and Ford's Method* (1947)

The most detailed account of the Fisher and Ford (1947) capture-recapture method and the arithmetical treatment of the data so obtained has been given by Ford (1953). However, in view of the fact that this particularly useful paper is not easily accessible, the present opportunity has been taken to redescribe it. Tables 2 and 3 provide the basic data which allow Tables 6 and 7 to be constructed. Column 2 shows the interval from each day of release to 7th July, the last day on which captures were made; this is denoted as  $t$  days. Column 3 shows the number of daily releases. Column 4 shows the daily survival rate adopted (which is here 0.816 for males and 0.711 for females), expressed as a decimal and raised to the corresponding power of  $t$ . The survival rates (i.e. corresponding to a daily rate of elimination of 18.4 per cent for males and 28.9 per cent for females) are obtained by reducing to nothing, or nearly so, the difference (column 11) between the *observed* total days of survival (column 9) and the *expected* (column 10). The method for doing this is explained below. The total days of survival observed may be calculated *for each day* by the following procedure. Consider, for example, 29th June when 58 male damselflies were caught (Table 2). A total of 15 marks (*not* individuals) were recaptured on that date; one marked on 25th June, i.e.  $1 \times 4$  days survival, 4 marked on 26th June, i.e.  $4 \times 3$  days survival, and 10 marked on 28th June, i.e.  $10 \times 1$  days survival, giving a total of 26 days observed survival for the 29th June (see Tables 2 and 6). To obtain the entries in column 5, the entries in column 4 are multiplied by the corresponding ones in column 3; this gives the number of marks from given dates expected to be flying on 7th July. Therefore, at any intermediate date, e.g.  $t$  days, before 7th July the number of marks expected to be in existence will be the sum of these entries (i.e. in column 5) for releases *prior to that date*, divided by  $0.816^t$ , in the case of males in this example. Hence we can calculate the

number of male marks available for capture on 2nd July as  $\frac{59.052}{0.816^5} = 164.4$

(see also Tables 8 and 9). Column 6 contains the number of marks from given dates plus those previously expected to be available on 7th July, and is, therefore, obtained by progressively summing the entries in column 5 from the bottom.

In column 7 are found the entries from the previous column, summed from the bottom. This is done as we wish to calculate the average number of days between marking and recapture and hence estimate the total time interval between release and recapture (column 10) in order to estimate a death-rate. For example, on 30th June the average number of days between previous

marking and recapture on that date is expected to be  $\frac{87.507}{33.722}$ ; this multiplied

by the number of actual recaptures for this date, 8 (column 8), gives the estimated expected survival in days, 20.75 (column 10). It will be seen that such calculations are made *along the same line*, so that entries in columns 6 and 7 are dated relative to column 1 (i.e. 29th June in this case) and entries for column 8 relative to column 14 (30th June). The expected survival in days, 20.75, which we have calculated for 30th June may be compared with the actual total number of days survived for these insects, namely 17 (column 9).

Table 6. *Data for Fisher and Ford's Method—Male*

1	2	3	4	5	6	7
Date	t	Releases	% survival as decimal and raised to corresponding power of t.	Number of marks from given dates expected to be flying on 7th July. Col. 3 × 4	Number of marks from given dates and those previous expected to be flying on 7th July. Col. 5 Σ from bottom	Entries in Col. 6 weighted with days survived by marks. Col. 6 Σ from bottom
7	—	—	(1·0000)	—	—	—
6	1	81	0·8160	66·100	281·702	1,050·531
5	2	94	0·6659	62·580	215·602	768·829
4	3	63	0·5434	34·230	153·022	553·227
3	4	67	0·4434	29·710	118·792	400·205
2	5	83	0·3618	30·030	89·082	281·413
1	6	45	0·2953	13·280	59·052	192·331
30	7	50	0·2409	12·050	45·772	133·279
29	8	58	0·1966	11·400	33·722	87·507
28	9	62	0·1604	9·947	22·322	53·785
27	10	—	—	—	12·375	31·463
26	11	53	0·1068	5·662	12·375	19·088
25	12	77	0·08718	6·713	6·713	6·713

Table 7. *Data for Fisher and Ford's Method—Female*

1	2	3	4	5	6	7
Date	t	Releases	% survival as decimal and raised to corresponding power of t	Number of marks from given dates expected to be flying on 7th July. Col. 3 × 4	Number of marks from given dates and those previous expected to be flying on 7th July. Col. 5 Σ from bottom	Entries in Col. 6 weighted with days survived by marks. Col. 6 Σ from bottom
7	—	—	(1·0000)	—	—	—
6	1	50	0·7110	35·5500	90·4203	245·8765
5	2	38	0·5055	19·2090	54·8703	155·4562
4	3	33	0·3594	11·8602	35·6613	100·5859
3	4	33	0·2555	8·4315	23·8011	64·9246
2	5	24	0·1817	4·3608	15·3696	41·1235
1	6	26	0·1292	3·3592	11·0083	25·7539
30	7	37	0·0919	3·4003	7·6496	14·7456
29	8	34	0·0653	2·2202	4·2493	7·0960
28	9	36	0·0464	1·6704	2·0291	2·8467
27	10	—	—	—	0·3587	0·8176
26	11	11	0·0235	0·2585	0·3587	0·4589
25	12	6	0·0167	0·1002	0·1002	0·1002

*schmura elegans*—Daily Survival Rate of 81·6%

8	9	10	11	12	13	14
Recaptures	Total days observed survival	Expected survival in days. $\frac{\text{Col. 8} \times \text{Col. 7}}{\text{Col. 6}}$	Excess of Col. 9 over Col. 10	Captures	Estimated daily population Nos. $\frac{\text{Col. 6} \times \text{Col. 12}}{\text{Col. 8} \times \text{Col. 4}}$	Date
7	25	26·12	— 1·12	31	1,248·0	7
37	137	131·90	+ 5·10	82	585·4	6
38	137	137·40	— 0·40	94	568·4	5
39	141	131·40	+ 9·60	63	353·2	4
28	102	88·44	+ 13·56	67	489·7	3
29	91	94·42	— 3·42	83	467·2	2
13	27	37·86	— 10·86	45	536·6	1
8	17	20·75	— 3·75	50	875·0	30
15	26	36·15	— 10·15	58	438·9	29
7	20	17·78	+ 2·22	63	694·5	28
3	3	3	0·0	55	1,153·0	27
			+ 0·78			26

*schmura elegans*—Daily Survival Rate of 71·1%

8	9	10	11	12	13	14
Recaptures	Total days observed survival	Expected survival in days. $\frac{\text{Col. 8} \times \text{Col. 7}}{\text{Col. 6}}$	Excess of Col. 9 over Col. 10	Captures	Estimated daily population Nos. $\frac{\text{Col. 6} \times \text{Col. 12}}{\text{Col. 8} \times \text{Col. 4}}$	Date
0	—	—	—	10	∞	7
5	10	14·1658	— 4·1658	50	771·73	6
6	16	16·9235	— 0·9235	40	470·31	5
12	28	32·7336	— 4·7336	33	182·12	4
7	18	18·7295	— 0·7295	33	283·59	3
6	19	14·0370	+ 4·9030	24	242·34	2
2	5	3·8553	+ 1·1447	26	769·70	1
8	15	13·3594	+ 1·6406	37	224·61	30
6	11	8·4176	+ 2·5824	34	176·08	29
2	5	4·5537	+ 0·4463	36	139·1	28
0	—	—	—	12	∞	27
						26
			+ 0·2246			

The excess of observed survival over expected survival (here  $-3.75$ ) appears in column 11 and is summed at the foot ( $+0.78$  for *I. elegans* males;  $+0.2246$  for females). The daily captures are entered in column 12 and dated in relation to column 14. As stated previously, the daily survival rate relevant in each particular analysis is arrived at by reducing approximately to nothing the difference between the observed and expected total of days survived. Several trials must be made in order to determine which survival rate is most appropriate. This can be done by selecting about four survival rate values and plotting graphically the total excess (positive and/or negative) calculated for each case. The calculation of the excess for each trial, as in Tables 6 and 7, using a different survival rate is a somewhat tedious process using logarithm tables, but, of course, may be considerably speeded-up using a desk calculator; Fig. 3 illustrates the use of this method for determining the appropriate survival rate for *I. elegans* females at Dale in 1964. It will be seen that trials were made assuming survival rates of 0.6 per cent, 0.7 per cent, 0.75 per cent and 0.8 per cent giving the respective excesses of  $+17.7539$ ,  $+2.0471$ ,  $-6.503$  and  $-15.4315$ . The point of intersection of the curve so produced with the abscissa (approximately 0.711) gives a total excess of only 0.2246 in column 11. It should be noted that the line running through the four points on the graph is *not* straight.

It is now possible to utilize the data in Tables 6 and 7 to obtain the daily population estimates which appear in column 13 and which are dated with reference to column 14. The entries in column 13 are calculated by multiplying the corresponding entry in column 12 (dated to the same day, i.e. column 14) with that in column 6 (dated to the previous day) and dividing the product by the number in column 8 (dated to column 14) multiplied by that in column 4 (dated relative to column 14). Therefore, it will be noticed that 3 of the items used in calculating the entries in column 13 are *on the same line* (columns 6, 8 and 12,) whilst that in column 4 is found on the line *above*. For example, the figure of 875.0 as the estimated number of male *I. elegans* for 30th June is obtained thus:

$$\frac{50 \times 33.722}{8 \times 0.2409} = 875.0. \text{ When calculating the population for 7th July in this}$$

instance, or for the *last day* of any set of observations it is, of course, necessary to assume a survival rate of 1.0, i.e. 100 per cent survival for that day.

In order to obtain a more accurate estimate of the *average* daily population size for the period in question, it is necessary first to know how many marks the individuals carry during a given period of their existence. The number of marked insects surviving on the second day should be the number released on the previous day multiplied by the percentage survival rate expressed as a decimal. Similarly, the number of marks present in the population on the third day should equal the number of marks present on the previous day, plus the number of releases for that day, multiplied by the survival rate. This procedure is repeated for each subsequent day. The necessary calculations and the marks carried in the male and female populations of *I. elegans* are presented in Tables 8 and 9. To find the average daily population for the period 25th June-7th July the number of marks present each day (as computed in Tables 8 and 9) are multiplied by captures for that day. These products are then summed and the total divided by the number of marks recaptured over the whole period

Total excess  
col. II

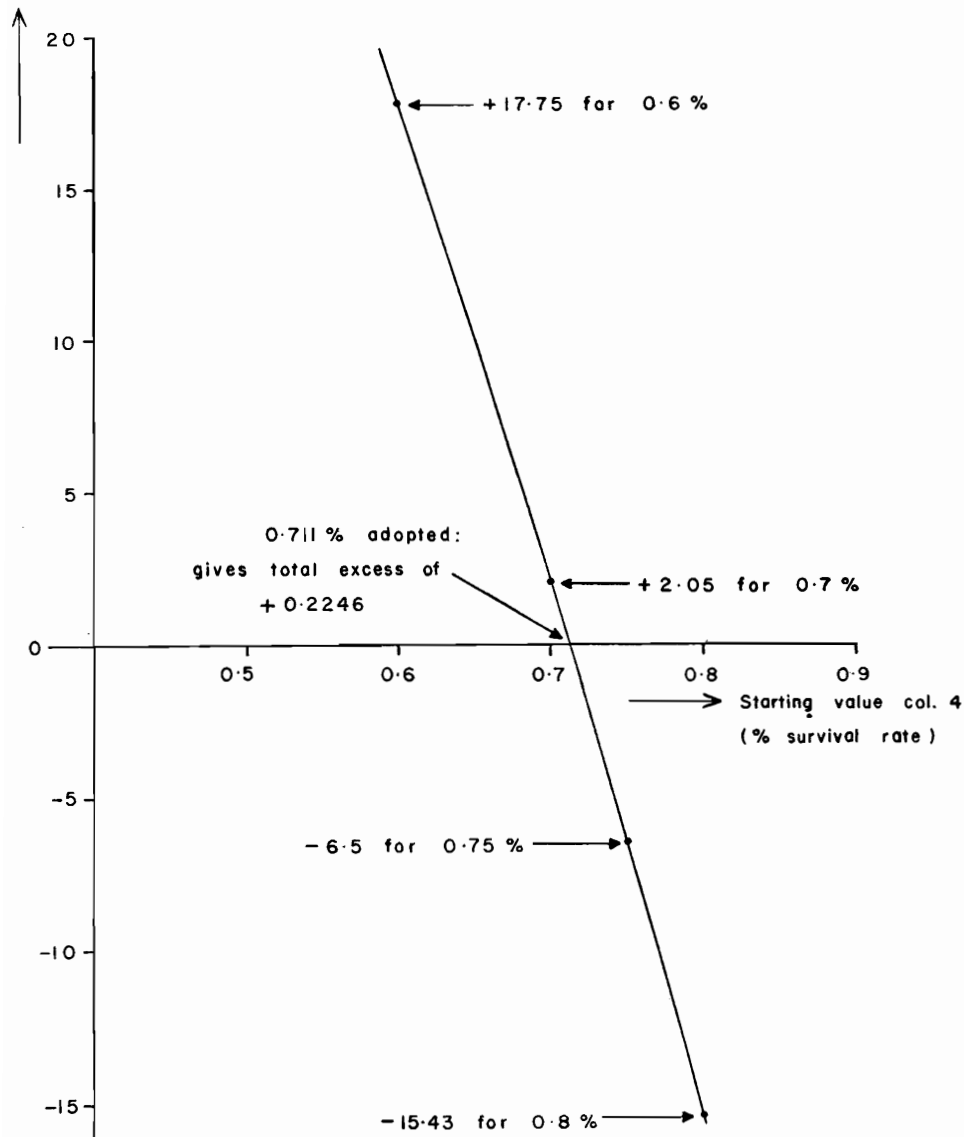


FIG. 3.

The determination of the appropriate survival rate for *Ischnura elegans* females for use in Fisher & Ford's method.

Table 8. *Estimated Number of Marks Present per day*

Date	Releases on <i>previous day</i>	Previous marks $\times$ survival rate	Marks present per day
MALES: Survival rate of 81.6%			
June	25	—	—
	26	77	62.83
	27	53	94.50
	28	—	77.10
	29	62	113.50
	30	58	139.90
July	1	50	155.00
	2	45	163.20
	3	83	200.90
	4	67	218.60
	5	63	229.80
	6	94	264.20
	7	81	281.70
FEMALES: Survival rate of 71.1%			
June	25	—	—
	26	6	4.266
	27	11	10.86
	28	—	7.72
	29	36	31.07
	30	34	46.27
July	1	37	59.21
	2	26	60.59
	3	24	60.15
	4	33	66.21
	5	33	70.53
	6	38	77.13
	7	50	90.36

(Tables 8 and 9). For example, it may be seen that for male *I. elegans* at Dale the marks  $\times$  captures totalled 121,634, which when divided by 224 marks recaptured gives an average daily population of 547.47. To estimate the total emergence during the study period, it is necessary to sum all the daily population sizes *except* the last and multiply the total by the daily elimination rate; the product so obtained is then added to the estimated population for the final day. In the case under consideration, allowance has to be made for the fact that no estimate is available for the actual population number of 27th June, for which the figure for the average daily population may be utilized. The total emergence of males and females during the sampling period may be calculated as shown in Table 10. It will be noticed that the total emergence numbers of females may only be estimated for the period 28th June–6th July inclusive as no recaptures were obtained on 26th, 27th June and 7th July.

An estimate of the longevity (average length of life,  $L$ ) can be obtained from the expression

$$\hat{L} = \frac{1}{1-p}$$



Table 9. Average Daily Population (Ref. Table 8)

Date	Marks in population/day	Captures	Marks $\times$ Captures	Recaptures	
MALES					
June	26	62.83	55	3,456	3
	27	94.50	—	—	—
	28	77.10	63	4,858	7
	29	113.50	58	6,583	15
	30	139.90	50	6,995	8
July	1	155.00	45	6,975	13
	2	163.20	83	13,550	29
	3	200.90	67	13,460	28
	4	218.60	63	13,770	39
	5	229.80	94	21,590	38
	6	264.20	82	21,660	37
	7	281.70	31	8,734	7
			121,634	224	
Average daily male population			= 121,634 $\div$ 224		
			= 547.47		
FEMALES					
June	26	4.266	12	51	0
	27	10.86	—	—	—
	28	7.72	36	278	2
	29	31.07	34	1,057	6
	30	46.27	37	1,711	8
July	1	59.21	26	1,539	2
	2	60.59	24	1,454	6
	3	60.15	33	1,985	7
	4	66.21	33	2,185	12
	5	70.53	40	2,822	6
	6	77.13	50	3,857	5
	7	90.36	10	904	0
			17,843	54	
Average daily female population			= 17,843 $\div$ 54		
			= 330.43		
Male % of population			= 62.37%		

where  $p$  is the probability of survival, i.e. the daily survival rate adopted. By this method the longevity of the two sexes may be estimated thus:

$$\text{Males: } \hat{L} = \frac{1}{0.184} = 5.4 \text{ days.}$$

$$\text{Females: } \hat{L} = \frac{1}{0.289} = 3.5 \text{ days.}$$

An alternative method is to sum the total number of days survived by all individual insects and divide this figure by the total number of insects (*not*

Table 10. Calculation of Total Emergence Numbers (Data obtained by the Fisher and Ford Method)

Date		Males	Females
June	26	1,153·0	∞
	27	547·5*	—
	28	694·5	139·1
	29	438·9	176·1
	30	875·0	224·6
July	1	536·6	769·7
	2	467·2	242·3
	3	489·7	283·6
	4	353·2	182·1
	5	568·4	470·3
	6	585·4	
		Total 6,709·4	Total 2,487·8
Totals multiplied by elimination rates:			
		$6,709·4 \times 0·184 = 1,235·0$	$2,487·8 \times 0·289 = 719·1$
July	6		$+ 771·7 = 1,490·8$
	7	$+ 1,248·0 = 2,483·0$ 62·48% males for period 28th June–5th July	

\* Average daily population: see Table 9.

marks) recaptured, as shown in Tables 2, 3 and 11. Using the second method, *I. elegans* males survived on the average 3·5 days and females 2·4 days between first being marked and finally being recaptured. In all probability the first method outlined here gives reasonably accurate estimates for this particular case, whereas the second one provides approximations which are too low. This will be discussed further in a later section. The data in Table 11 allow survival curves (Fig. 4) to be drawn for both sexes. Numbers of individuals surviving (expressed as a percentage of the total) are plotted against numbers of days survived. The survivorship curve for *I. elegans* females is clearly steeper than for males, as in *Pyrrosoma nymphula* studied by Corbet (1952).

#### (6) Bailey's Triple-catch Method (1951)

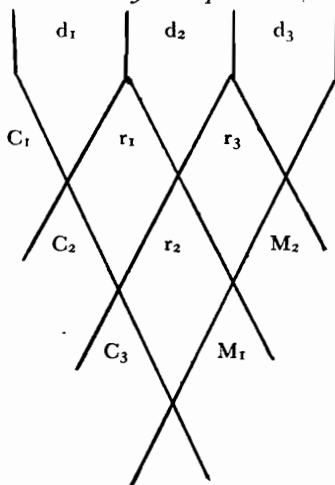
This is the simplest of the various methods of analysis of capture-recapture data described in this paper. As we have seen, the analysis of a large triangular trellis diagram of the type devised by Dowdeswell, Fisher and Ford (1940) allows daily estimates of population size to be calculated, but unfortunately it is very difficult to know how much precision can be attached to the results obtained. Bailey's method has the advantages of being simple to carry out and allows variances to be easily calculated.

Table 12 illustrates the use of this method.  $C_1$ ,  $C_2$  and  $C_3$  represent numbers captured on three successive days,  $d_1$ ,  $d_2$  and  $d_3$ ;  $M_1$  and  $M_2$  are the numbers

Table 11. Distribution of observed intervals between first and last captures of individuals and the calculation of average survival times. (Data from Tables 2 and 3)

Males				Females			
Number of Males		Days Survival	Total	Number of Females		Days Survival	Total
44	×	1	= 44	15	×	1	= 15
22	×	2	= 44	13	×	2	= 26
35	×	3	= 105	11	×	3	= 33
21	×	4	= 84	5	×	4	= 20
12	×	5	= 60	2	×	5	= 10
9	×	6	= 54	1	×	6	= 6
10	×	7	= 70	1	×	7	= 7
8	×	8	= 64				
3	×	9	= 27				
3	×	10	= 30				
1	×	11	= 11				
168		Totals	593	44		Totals	117
$\frac{593}{168} = 3.5$ Days Survival				$\frac{117}{44} = 2.4$ Days Survival			

Table 12. Bailey's Triple-catch Method



released on dates  $d_1$  and  $d_2$ , and  $r_1$ ,  $r_2$  and  $r_3$  numbers recaptured on the dates  $d_2$  and  $d_3$ . Bailey shows that the population on date  $d_2$  may be estimated from equation (6), providing the  $r$  values are all large:

$$\hat{P}_{d_2} = \frac{M_2 r_2 C_2}{r_1 r_3} \quad (6)$$

or, if the  $r$  values are more moderate we may use the approximately unbiased estimate

$$\widehat{Pd}_2 = \frac{M_2(C_2+1)r_2}{(r_1+1)(r_3+1)} \quad (7)$$

The large sample variances for equation (6) may be calculated from

$$\widehat{V}(Pd_2) = Pd_2^2 \left( \frac{1}{r_1} + \frac{1}{r_2} + \frac{1}{r_3} - \frac{1}{C_2} \right) \quad (8)$$

and the approximately unbiased estimate of variance for equation (7) may be obtained from

$$\widehat{V}(Pd_2) = Pd_2^2 - \frac{M_2^2(C_2+1)(C_2+2)r_3(r_3-1)}{(r_1+1)(r_1+2)(r_3+1)(r_3+2)} \quad (9)$$

Therefore, we may estimate the male population of *I. elegans* on 4th July using Table 2 and equation (7) thus

$$\begin{aligned} \widehat{P}_1 &= \frac{63(63+1)6}{(10+1)(8+1)} \\ &= \underline{\underline{244.4}} \end{aligned}$$

and the corresponding variance

$$\begin{aligned} \widehat{V}(P_1) &= 244.4^2 - \frac{63^2(63+1)(63+2)5(5-1)}{(11)(12)(9)(10)} \\ &= 31,905. \end{aligned}$$

Therefore, the standard error is calculated as

$$\begin{aligned} \text{S.E.} &= \sqrt{31,905} \\ &= 178.8. \end{aligned}$$

#### (7) *Jolly's Method* (1965)

This method has been developed for use in the majority of capture-recapture problems involving a 'single' population. A 'single' population, in Jolly's sense, is one occupying a single area within the boundaries of which the animals are free to move and to intermingle with others of the same species. Jolly shows that for a homogeneous population, subject to both death and immigration, a very simple solution exists for the maximum likelihood equations he derives in the early part of his paper. In practice, of course, a homogeneous population hardly or, perhaps, never exists, but this objection applies equally to the other capture-recapture techniques developed.

In all methods previously discussed, as in Jolly (1963), a deterministic survival (or death) rate is assumed. That is, any group or subgroup of the population is regarded as having been subject to an exact survival rate per unit interval of time. Whereas in Jolly's present (stochastic) method the symbol  $\phi$  is the *probability* of an animal in the  $i$ th sample surviving until the time of capture of the  $i+1$  sample. For this purpose death and emigration are synonymous. Each population sample is assumed to be random, and after marking and release the animals are understood to have redistributed themselves so that they have

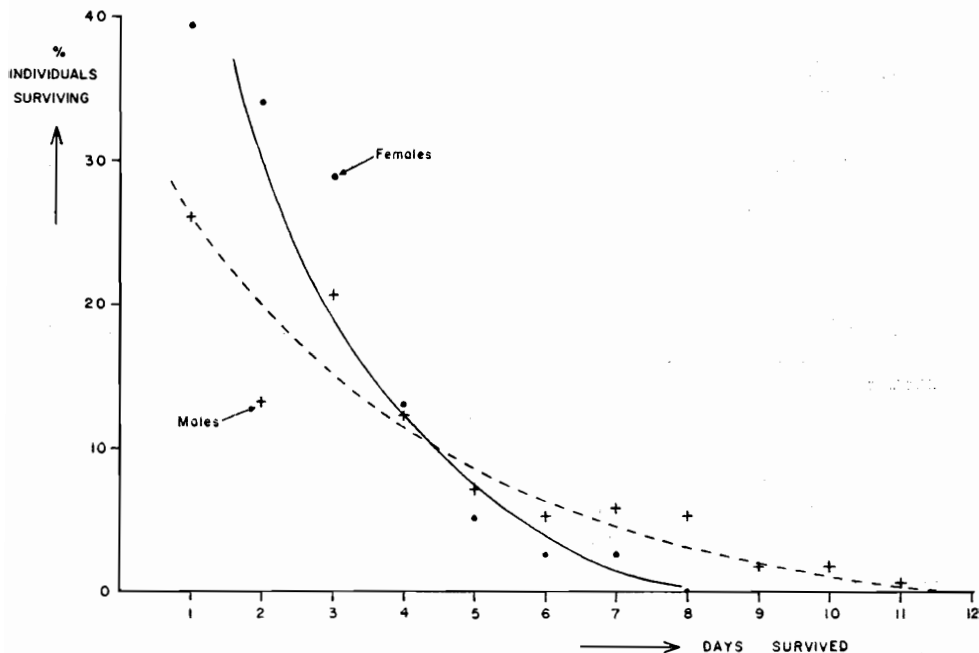


FIG. 4.

Survival curves for *Ischnura elegans* at Dale, 1964.

the same chance as any others of being recaptured. In this method the time intervals between successive samples do not have to be equal, nor is there any restriction on the length of time between samples. It is necessary to mark each specimen released so that it may be individually recognized if recaptured later. Alternatively, as in this study, one may employ a system of recording multiple recaptures (i.e. insects marked and released more than once) in order that the data may be arranged for analysis using this particular method.

Jolly shows that in order to estimate the total population ( $N_i$ ), the rate of egress (= probability of death or emigration), ( $\phi_i$ ), and the rate of ingress (= number of new animals joining the population through emergence or immigration), ( $B_i$ ), all that is required is the information contained in the series of estimates  $\hat{\alpha}_i$  and  $\hat{M}_i$ . Jolly defines these terms as:

$N_i$  = Total number in the population when the  $i$ th sample is captured.  
This moment in time is referred to as time  $i$ .

$\phi_i$  = Probability that an animal alive at the moment of *release* of the  $i$ th sample will survive till the time of capture of the  $i+1$ th sample (emigration and death being synonymous for this purpose).

$B_i$  = Number of new animals joining the population in the interval between the  $i$  and  $i+1$ th samples and alive at time  $i+1$ .



Tables 13a and 14a show the same data as Tables 2 and 3, but re-classified so that the dates at the head of the columns are the dates on which the insects were last previously captured.

For example, in the sample of 45 males collected on 1st July, one was previously captured and marked on 29th and 30th June, but only the capture on 30th June is scored for the purposes of this table as this date represents the one on which the insect was last previously captured. The columns are summed to give  $R_i$ . Table 13b is constructed by summing from the left the figures in each row in Table 13a, not counting the  $n_i$  and  $s_i$  columns. The top entry (in parenthesis) in each column is  $m_{i+1}$ . The total of the  $i-1$ th column, omitting the top entry, gives  $Z_i$ . For example,  $Z_{30}$  (= 33) is found by summing all but the top entry in column 4. The top entry, in parenthesis, in column 4 is 8 and this is  $m_{30}$ . The various estimates of population parameters may be obtained by substituting the relevant values in equations 10 to 15. These procedures will be illustrated by reference to males on 2nd July.

Table 14a. *Jolly's Method. Females*

$n_i$	$s_i$	June																
6	6	25																
12	11	0	26															
36	36	1	1	28														
34	34	0	1	4	29													
37	37	1	0	2	4	30	July											
26	26	0	0	1	1	0	1											
24	24	0	0	1	0	3	0	2										
33	33	0	0	1	1	2	0	3	3									
33	33	0	0	0	0	1	3	1	5	4								
40	38	0	0	1	0	0	0	0	4	1	5							
50	50	0	0	0	0	0	0	0	2	1	2	6						
10	—	0	0	0	0	0	0	0	0	0	0	0	7					
$R_i =$		2	2	10	6	6	3	4	11	2	2	0	—					

Table 14b

	June											July							
	25																		
	(0)	26																	
	1	(2)	28																
	0	1	(5)	29															
	1	1	3	(7)	30	July													
	0	0	1	2	(2)	1													
	0	0	1	1	4	(4)													
	0	0	1	2	4	4													
	0	0	0	0	1	4													
	0	0	1	1	1	1													
	0	0	0	0	0	0													
	0	0	0	0	0	0													
$Z_{i+1} =$	2	2	7	6	10	9	6	7	3	0	0	—							

$\uparrow$   
 $Z_i = Z_3$

$$\widehat{\alpha}_i = \frac{m_i}{n_i} \quad (i = 2, 3, \dots, n). \quad (10)$$

$$\widehat{\alpha}_2 = \frac{23}{83} = 0.2771.$$

$$\widehat{M}_1 = \frac{s_i Z_i}{R_i} + m_i \quad (i = 2, 3, \dots, n-1) \quad (11)$$

$$\widehat{M}_2 = \frac{83 \times 33}{27} + 23 = 124.4.$$

$$\widehat{N}_i = \frac{M_i}{\alpha_i} \quad (i = 2, 3, \dots, n-1) \quad (12)$$

$$\widehat{N}_2 = \frac{124.4}{0.2771} = \underline{\underline{448.8}}.$$

$$\widehat{\phi}_i = \frac{M_{+i}}{M_i - m_i + s_i} \quad (i = 1, 2, \dots, n-2) \quad (13)$$

$$\widehat{\phi}_2 = \frac{156.4}{124.4 - 23 + 83} = 0.8481$$

$$\widehat{B}_i = N_{i+1} - \phi_i (N_i - n_i + s_i) \quad (i = 2, 3, \dots, n-2) \quad (14)$$

$$\widehat{B}_2 = 551.4 - 0.8481(448.8 - 83 + 83) = 171.1.$$

Table 15 gives the daily estimates of the population parameters mentioned above. The final column in Table 15 gives the *approximate* standard errors for the population estimate,  $\widehat{N}_i$ . The term  $V(\widehat{N}_i/N_i)$  actually represents only the errors of estimation in  $\widehat{N}_i$ , but in practice these are only slightly different from a true estimate of variance for  $\widehat{N}_i$ ,  $V(\widehat{N}_i)$ . For 2nd July we may evaluate  $V(\widehat{N}_i/N_i)$  as follows:

$$V(\widehat{N}_i/N_i) = N_i (N_i - n_i) \left( \frac{M_i - m_i + s_i}{M_i} \left( \frac{1}{R_i} - \frac{1}{s_i} \right) + \frac{1 - \alpha_i}{m_i} \right) \quad (15)$$

$$\begin{aligned} V(\widehat{N}_2/N_2) &= 448.8 (448.8 - 83) \left( \frac{124.4 - 23 + 83}{124.4} \left( \frac{1}{27} - \frac{1}{83} \right) + \frac{1 - 0.2771}{27} \right) \\ &= 10,910 \end{aligned}$$

The S.E. is therefore

$$\begin{aligned} &\sqrt{10,910} \\ &= 104.5. \end{aligned}$$

## V. DISCUSSION

### (1) Population Estimates

Table 16 allows comparison of the daily population estimates for both sexes of *I. elegans* calculated by the methods of Fisher and Ford, Jackson, Bailey and Jolly. Considerable variation is shown in the estimates thus obtained using these different methods. This may be explained by consideration of both the data and

ERRATA

read

M<sub>i+1</sub>  
M<sub>i</sub> - m<sub>i</sub> + s<sub>i</sub>

p. 268, line 7: for



Table 15. Population Parameters obtained using Jolly's Method (1965)

Date	$\hat{\alpha}_i$	$\hat{M}_i$	$\hat{N}_i$	$\hat{\phi}_i$	$\hat{B}_i$	$\sqrt{V(\hat{N}_i/N_i)}$
MALES						
June 25	—	0	—	1.0710	—	—
26	0.0545	82.5	1,514.0	0.4319	-52.4	992.5
27	—	—	—	—	—	—
28	0.09526	57.2	600.7	1.1210	-181.3	257.3
29	0.2586	126.9	490.8	0.5296	+305.7	161.0
30	0.1600	90.5	565.6	1.1990	+36.5	208.4
July 1	0.2222	158.8	714.6	0.6417	-8.8	263.0
2	0.2771	124.4	448.8	0.8481	+171.1	104.5
3	0.2836	156.4	551.4	1.1800	-87.9	149.4
4	0.4287	241.2	562.8	0.4960	+166.5	182.2
5	0.3085	137.5	445.6	0.9184	+226.1	138.0
6	0.2927	186.0	635.4	—	—	484.2
7	0.1935	—	—	—	—	—
FEMALES						
June 25	—	—	—	—	—	—
26	—	0	—	0.8363	—	—
27	—	—	—	—	—	—
28	0.0556	9.2	165.6	1.0340	+132.5	132.0
29	0.1471	44.67	303.7	0.5837	+50.1	180.2
30	0.1892	43.0	227.3	1.2140	+877.1	123.5
July 1	0.0769	88.67	1,153.0	0.5146	-245.5	1,053.0
2	0.1667	58.0	347.9	0.3205	+6.3	234.6
3	0.2121	25.0	117.8	2.4500	+125.6	48.59
4	0.3031	125.5	414.2	0.4241	+175.7	314.3
5	0.1500	63.0	420.0	—	—	369.7
6	0.1000	—	—	—	—	—
7	—	—	—	—	—	—

the methods of analysis employed. Figs. 5 and 6 show the generally good correlation between estimates obtained with Fisher and Ford's, and Jolly's methods. In the case of males the most serious discrepancy is probably the appearance of a peak on 30th June with Fisher and Ford's technique, whereas this peak is delayed until 1st July and is reduced in the Jolly estimates. The respective female estimates of Fisher and Ford, and Jolly show very good agreement with reference to trends, but there is a considerable numerical difference in the size of the estimated peak occurring on 1st July. Both Jolly's and Fisher and Ford's methods are valuable in that they allow maximum use of the data collected. If the first day of sampling is termed day 1, estimates of population size may be obtained for days 2, 3, ..., n (Fisher and Ford) and 2, 3, ..., n-1 (Jolly), except for days when there is a *nil* catch for marking and release. In both these methods sampling may be carried out at either regular or irregular intervals to suit the requirements of a particular set of conditions. Whereas Fisher and Ford's method assumes the adoption of a deterministic survival rate for the period of the observations, Jolly's method does not; the latter may, therefore, be expected to give more realistic results with populations suspected of undergoing fluctuation.

Table 16. *A comparison of population estimates obtained using different methods*

Date	Jackson I (1948)		Jackson II (1948)		Fisher & Ford (1947)	Bailey (1951) Pop. Nos. S.E.		Jolly (1965) Pop. Nos. $\sqrt{V(\hat{N}/N)}$	
	r+	r-	r+	r-		Nos.	S.E.	Nos.	$\sqrt{V(\hat{N}/N)}$
MALES									
June 26	—	—	—	<b>940·8</b>	1,153·0	—	—	1,514·0	992·5
27	—	—	—	—	—	—	—	—	—
28	359·2	—	356·7	—	694·5	—	—	600·7	257·3
29	<b>1,108·0</b>	—	903·8	<b>426·4</b>	438·9	518·5	344·1	490·8	161·0
30	327·9	—	358·7	954·0	875·0	242·9	198·1	565·6	208·4
July 1	325·7	372·1	422·5	383·6	536·6	258·8	146·2	714·6	263·0
2	831·1	<b>403·2</b>	848·3	483·2	467·2	373·5	257·5	448·8	104·5
3	227·8	898·4	465·6	834·3	489·7	414·1	227·6	551·4	149·4
4	—	590·3	354·2	446·8	353·2	244·4	134·4	562·8	182·2
5	—	739·1	<b>486·2</b>	—	568·4	228·9	151·3	445·6	138·0
6	—	<b>1,068·0</b>	701·8	—	585·4	172·4	—	635·4	484·2
7	—	—	—	—	1,248·0	—	—	—	—
FEMALES									
June 28	<b>210·0</b>	—	324·1	—	139·1	—	—	165·6	132·0
29	<b>194·9</b>	—	<b>260·1</b>	253·2	176·1	142·8	103·3	303·7	180·2
20	—	—	—	132·7	224·6	—	—	227·3	123·5
July 1	—	—	—	—	769·7	—	—	1,153·0	1,053·0
2	—	—	154·5	—	242·3	—	—	347·9	234·6
3	109·9	—	149·4	—	283·6	46·8	—	117·8	48·59
4	—	<b>160·4</b>	—	677·4	182·1	374·0	279·6	414·2	314·3
5	—	—	455·7	—	470·3	259·7	—	420·0	369·7
6	—	2,169·0	—	—	771·7	—	—	—	—

The bold type figures in the Jackson columns indicate those values having the greatest reliability.

tuations or changes of survival rate in the course of days or weeks. The use of Jolly's method has an added advantage in that the calculations, necessary for estimation of population numbers, may be rapidly carried out, but, as has been already indicated, estimates by Fisher and Ford's method are tedious without the use of a calculating machine. No simple way of establishing the error of population densities obtained by this latter technique exists, but variances may be found for Jolly's parameters  $N_i$ ,  $\phi_i$ , and  $B_i$ , as well as other parameters having lesser importance in this context. Jolly (personal communication) has pointed out that the high value of the standard error of  $\hat{N}_i$ , of 26th June (males) is mainly due to the low number of marked insects ( $m_i$ ) captured on that date.

Figs. 5 and 6 also show the daily population estimates obtained using Bailey's Triple-catch Method. There can be little doubt that these estimates are highly unreliable and that the trends shown here are false, as the incidence of recaptures was too low in this study to allow the method to operate efficiently. The true standard errors of these estimates may be considerably higher than those given, on account of the approximative deterministic model and the rather small numbers of recaptures (Jolly, 1965, personal communication). This method may be expected to give accurate estimates only when the r, C and M

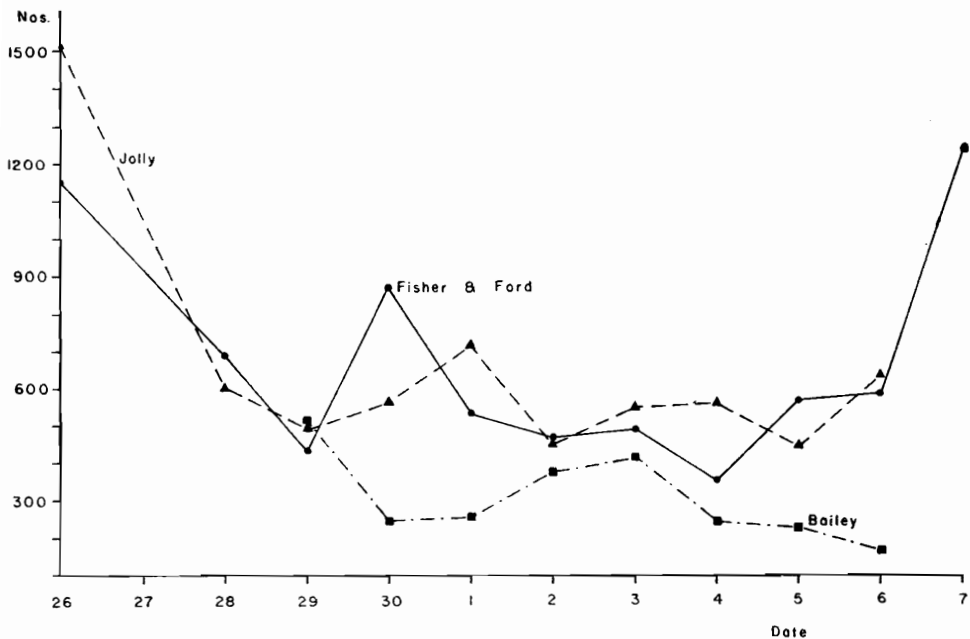


FIG. 5.

Male population trends obtained using the Fisher & Ford, Jolly and Bailey methods.

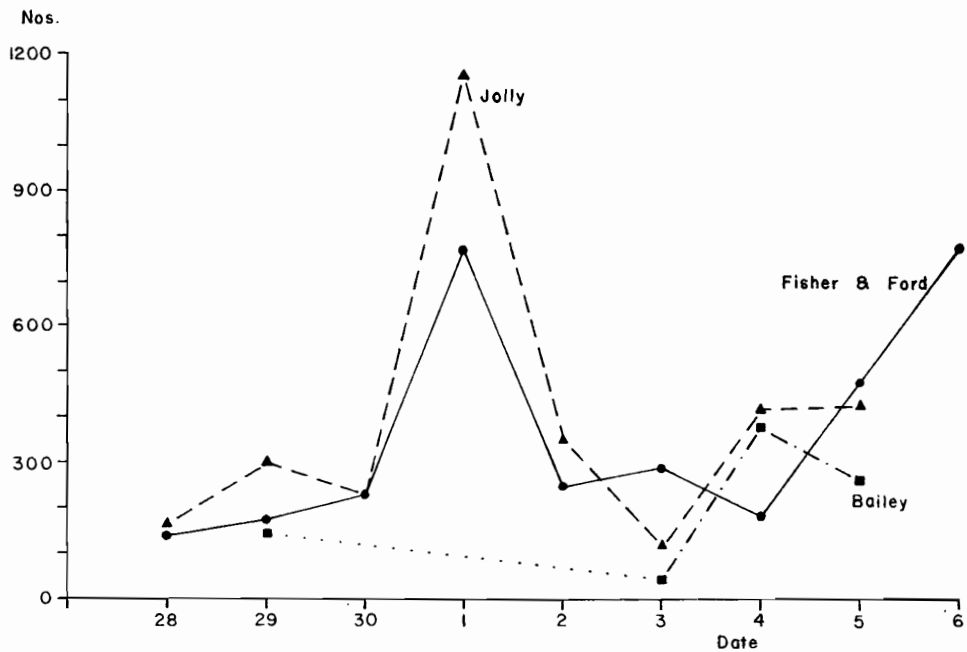


FIG. 6.

Female population trends obtained using the Fisher & Ford, Jolly and Bailey methods.

values (Table 12) are all large. In such cases the Triple-catch Method would be convenient to use as results could be obtained very quickly.

Figs. 7 and 8 compare respectively the two series of  $r_+$  estimates and two series of  $r_-$  estimates of Jackson's (1948) methods with the daily population densities obtained by Fisher and Ford's method. One of the principal requirements in order that Jackson's methods may be applied to the analysis of capture-recapture data is that the sampling should be at *regular* intervals. If, as on 27th June, sampling is completely curtailed on any day, or no recaptures are recorded for diamonds near the top half of the trellis diagram (see Tables 4 and 5) it may be impossible to obtain estimations using Jackson's methods. For example, Jackson's First Method ( $r_-$ ) may not be used on the *Ischnura* (male) data until 1st July. This is because no sampling was carried out on 27th June and due to the absence of any recaptures for diamond  $b_4$ . As Jackson points out, the reliability of his methods also depends on, for example, the series  $e_1, e_2, \dots, e_8$ , and  $e_1, d_2, c_3, \dots, a_5$  (Tables 4 and 5) declining in a geometrical progression. The latter series (i.e. those running from top right to bottom left) should always decline in this manner, provided that death is random with respect to age, and also that the sampling area is large enough to exclude an increasing proportion of re-immigration. It would seem rather unlikely that, in fact, death is random with age in damselflies. Teneral and the oldest individuals probably suffer more severely from the effects of bad weather than "middle-aged" insects. However, considerable work is needed to solve this problem.

The two  $r_+$  methods of Jackson give very similar results, but there is only correspondence with Fisher and Ford's method for the period 3rd-6th July (males) when the second  $r_+$  series shows fairly close agreement. On 29th June the  $r_+$  series both show large peaks which do not occur with any of the other methods used. The standard error for  $r_+$  (second method) on this date is 0.1835, which gives the estimated population limits as between 637.9 and 1,170.0. It can be seen that the lower limit of this estimate overlaps the upper limit of Jolly's estimate, which is 651.8, the standard error being 161.0 (Table 16). There are several reasons why the large estimates of the male populations for 29th June obtained using Jackson's  $r_+$  methods may be spurious. The data available for calculating  $r_+$  (II) are very sparse, owing to no sampling on 27th June and there being *nil* recaptures recorded in diamond  $b_4$ . The corrected recaptures recorded in diamond  $e_1$  (6.896) are strikingly low compared with other recapture values. This can be seen to be of importance when the methods of calculating the estimated populations using the  $r_+$  and  $r_-$  (II) methods are compared. The calculated  $r$  values are multiplied by 10,000 and divided by the *single* relevant corrected recapture value. For males on 29th June, this is either 27.81 for  $r_-$  or 6.896 for  $r_+$ , and consequently even relatively large differences in the respective  $r$  values are not sufficient to mask the apparently large sampling error or 6.896 corrected recaptures in diamond  $e_1$ . It can be seen that the series of male corrected recaptures  $e_1, e_2, \dots, e_7$  do not decline in geometrical progression and therefore the population estimate of 1,108.0 for 29th June obtained by Jackson's first method ( $r_+$ ) is of very doubtful value. Similarly, it can be shown that various population estimates of males using  $r_+$  calculated for 30th June-3rd July and using  $r_-$  for 30th June,

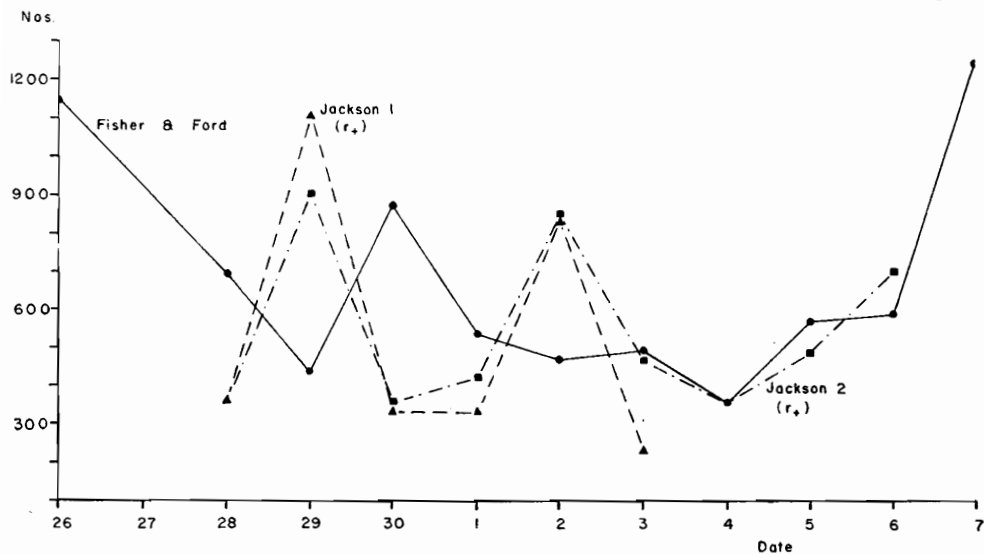


FIG. 7.

Male population trends obtained using Jackson's First and Second methods ( $r_+$ ) and Fisher & Ford's method.

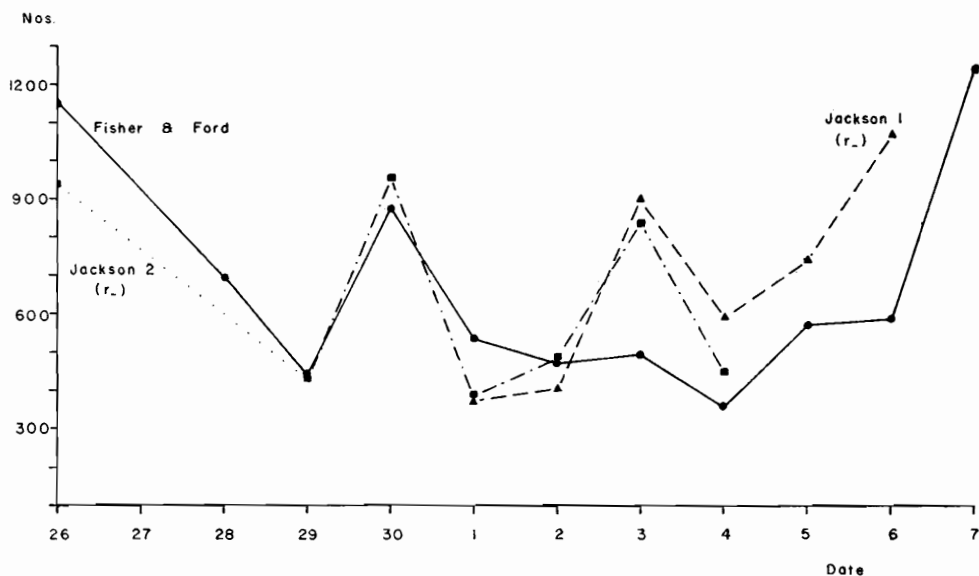


FIG. 8.

Male population trends using Jackson's First and Second methods ( $r_-$ ) and Fisher & Ford's method.

1st July, 3rd July, 5th and 6th July, are likely to be inaccurate. It is impossible to place much confidence in the male population trends as indicated by Jackson's methods, but nevertheless certain of the estimated densities would seem to be meaningful, notably those appearing in bold type in Table 16. The corrected recapture data for females are very largely unsuitable for analysis using Jackson's methods owing to the low recapture values recorded and, in particular, the absence of recoveries in the lower part of the table (Table 5). The only female population estimates obtained by these methods on which some reliance may be placed appear in bold type in Table 16; it is impossible to determine any positive trends from this information. Glasgow (1953) has shown that relatively low recapture values obtained from large tsetse-fly populations yield population density estimates which may exhibit considerable lack of correlation with respect to  $r$  values. However, Blower (1964), working with grasshoppers, has demonstrated that the analysis of a relatively small population yielding a high recapture rate gives comparable densities by the Jackson (I and II) and Fisher and Ford methods. It would seem, therefore, that Jackson's methods are particularly applicable in the case of populations producing a large percentage of recaptures and when a considerable proportion of the population is caught in each sample, but should be avoided when it is not possible to do this.

These analyses appear to indicate that the methods of Jolly (1965) and Fisher and Ford (1947) provide the best indication of population trends and actual densities for these particular sets of data. In the case of male *I. elegans*, distinct apparent population peaks, as calculated by the Jolly, and Fisher and Ford methods, can be seen for 26th June and 7th July, with a lesser one on 30th June or 1st July (Table 16 and Fig. 5); in contrast, the female population peaks occurred on 1st July and 6th July (Table 16 and Fig. 6). The Anglesey colony of *I. elegans* studied by Lord (1961) showed some similar daily variations. This is, perhaps, not altogether unexpected in a species having a very long flying season which commonly extends from early May to mid-September. So far as is known, *I. elegans* has no true larval diapause and eggs laid throughout the summer produce larvae within a few weeks. However, Corbet (in Corbet *et al.*, 1960) has suggested that certain species with long flying seasons may lay non-diapause eggs early in the summer, but diapause eggs later. It seems possible that this situation could obtain for *I. elegans*. Larvae emerging early in the summer will have attained a much larger size by the onset of winter than those hatching from the egg in late summer. The largest and oldest larvae will, therefore, produce the first imagines in the succeeding summer and these earliest emergences will be followed by the appearance of a succession of imaginal damselflies throughout the summer. Therefore, it would appear that the life history of *I. elegans* together with some other British species of damselflies and also the Libellulid dragonfly *Sympetrum striolatum* (Charp.) occupies approximately twelve months, that is to say, it is univoltine (Corbet, 1958). It would seem likely that a variety of external environmental factors could inhibit metamorphosis of the final instar larva. A spell of inclement weather involving rain, lack of sun, strong wind or low temperatures, especially early in the morning when most emergences occur (Lord, 1961) could result in the accumulation of numbers of fully developed larvae in the pond. The next spell of

fine morning weather would result in the sudden appearance of large numbers of fresh imagines. Corbet (1952), working with *Pyrrhosoma nymphula*, came to the conclusion that the three distinct emergence peaks he recorded probably represented a dispersed single peak owing to unfavourable weather on two days. The flying season of *P. nymphula* is short, generally in the region of one month, which indicates that imaginal emergence is synchronized to a considerable degree due to the occurrence of a diapause affecting the last larval instar the previous autumn. In contrast, it is not clear whether or not *I. elegans* undergoes a true diapause, but most probably growth of the various larval stages is interrupted by dormancy caused by low autumn and winter temperatures. This simple slowing down and interruption of larval development of *I. elegans* will not result in synchronization of larval development and, consequently, the flying season in *any one colony* extends over about 4 months. The male population trends shown by the Dale colony during the period 26th June–7th July, 1964, may be explained partly by reference to Table 1. Suppose the population numbers were relatively depressed during the time 28th June–5th July, and density was at a normally high level at the beginning and end of the study period; such a situation could have resulted from a spell of unfavourable weather, which would have limited emergences some days earlier. The weather records for Dale Fort show that the sun did not shine on any of the mornings (sunrise to 9.0 or 10.0 a.m.) during the period 17th June–24th June, except for 20th June, when there was certainly some sun. This succession of dull mornings would have depressed emergences of imagines from the ponds, as Lord (1961) has shown that most individuals of this species emerge early in the morning (before 10.0 a.m.) and only when the sun is shining. The increase in the male population indicated on 30th June or 1st July corresponds well with the single sunny morning, 20th June, in the otherwise cloudy period 17th–24th June (the sun shone from 0900 hours on 19th June), if we assume that the maturation period of *I. elegans* during this time was roughly 10–11 days. During the maturation period the damselflies avoid water and are, therefore, not generally seen in the colony area at this time; the length of this period depends to some extent at least on temperature. Johnson (1962) states that the maturation period for the damselfly *Hetaerina americana* in Texas may be about 6 days and Corbet (1952) estimates the maturation period for *Pyrrhosoma nymphula* in England as about 15 days.

## (2) Sex Ratio

In common with other studies on British damselflies (Corbet, 1952; Lord, 1961) it was found that there was a large excess of male imagines both actually captured (65.55 per cent males) and estimated to be flying (63.14 per cent males) (Fisher and Ford's method). In each daily sample males caught exceeded females recorded by a considerable margin, ranging from 82.1 per cent to 57.48 per cent. It will be seen that the percentage of males estimated to be flying during the period 28th June–6th July varies considerable from day to day (Table 17). On two dates, 1st July and 6th July, the percentage of males falls well below 50 per cent of the estimated flying population. These apparent anomalies may, in fact, represent the true situation, and can be explained by

Table 17. *Sex ratios of imagines*

Date	Numbers captured			Estimated numbers flying*		
	Males	Females	Male %	Males	Females	Male %
June 25	78	6	92.41	—	—	—
26	55	12	82.10	1,153.0	∞	—
27	—	—	—	—	—	—
28	63	36	63.63	694.5	139.1	83.33
29	58	34	63.04	438.9	176.1	71.36
30	50	37	57.48	875.0	224.6	79.53
July 1	45	26	63.37	536.6	769.7	41.11
2	83	24	77.57	467.2	242.3	65.86
3	67	33	67.00	489.7	283.6	63.31
4	63	33	65.61	353.2	182.1	65.97
5	94	40	70.15	568.4	470.3	54.70
6	82	50	62.11	585.4	771.7	43.15
7	31	10	75.61	1,248.0	∞	—
Average percentage of Males for period 28th June–1st July, 65.55				Average percentage of Males for period 28th June–1st July, 63.14		

\* Fisher and Ford method.

the assumption that, on the two dates in question, a large influx of new, unmarked females into the population resulted in the movement away from the main colony area of many already established females. In consequence, the number of marked individuals in any colony area fell sharply and, furthermore, this was followed by continued adjustment of the numbers of females present, as a result of intraspecific interaction. Hence, males still outnumber females captured on 1st July and 6th July and the high numbers of females estimated to be flying on these dates represents, in some measure, numbers present in the colony plus a number which had recently moved away.

### (3) Longevity

As previously described, the average length of life of male and female *I. elegans* at Dale can be estimated by two methods which give different results (Table 18). Calculations from the respective male and female survival rates give longevitys of 5.4 and 3.5 days. Lord (1961) obtained survival times for

Table 18. *Average longevity*

	Calculated from survival rate. (Fisher and Ford.)	Estimated from observed days survived.
	$\hat{L} = \frac{1}{1-p}$	
Male	5.4 days	3.5 days
Female	3.5 days	2.4 days



*I. elegans* of 5.5 and 6.2 days (males) and 5.3 and 4.3 days (females); and for *Pyrrhosoma nymphula* of 4.0 days (males and females) using the same method. As in the present study, she marked both teneral and adult forms. In contrast, Corbet (1952) working with *Pyrrhosoma*, estimated the average longevity as about 6.7 days for both sexes when only sexually mature imagines were marked. It seems reasonable to suggest that the expectation of life varies at different periods of imaginal life and in particular that teneral individuals are more likely to succumb than older immature imagines and sexually mature (adult) insects. Very old individuals must, again, be expected to show a high death rate. The relatively high average expectation of life obtained by Corbet for *P. nymphula* may, therefore, be ascribed to some extent at least, to the non-inclusion of tenerals in his study. The low estimated longevity obtained for *I. elegans*, by the second method of dividing the total number of days survived by all individual insects by the total number of insects recaptured, is almost certainly due to the sampling period being too short. The limitation of the sampling period precluded the possibility of the observation of any insects older than 12 days; in fact, the observed maximum time survived by any specimen was 11 days by a male marked on 25th June. Lord observed that *I. elegans* kept in the laboratory lived for up to 41 days and Corbet (1952) obtained a maximum survival value of about 31 days for *P. nymphula* in the field. Therefore, the survival curves obtained for *I. elegans* at Dale (Fig. 4) do not give a true indication of the maximum expectation of life for either sex, although the higher female death rate is evident from the steeper curve compared with that of the male. Corbet similarly recorded a higher female death rate for *Pyrrhosoma*.

#### (4) Female Polymorphism

The work of Lord (*loc. cit.*) in Anglesey, has shown that the female polymorphism of *I. elegans* appears to be a complicated phenomenon, probably under genetic control (Fig. 9). Preliminary investigations would appear to

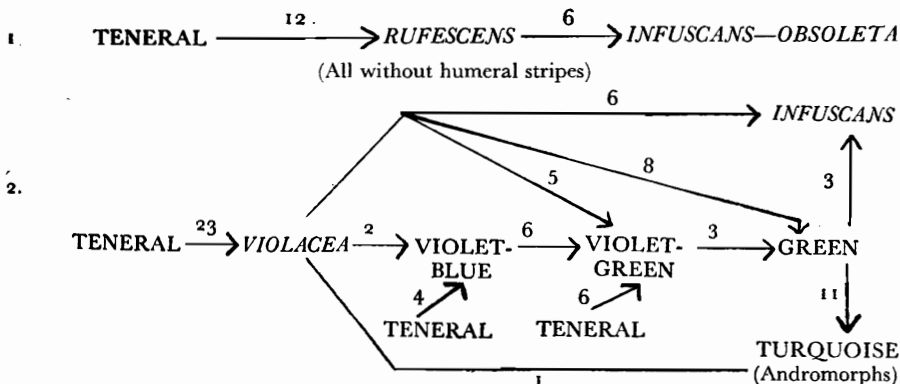


FIG. 9.

The Colour Polymorphism and Colour Changes in *I. elegans* females (after Lord, 1961). Numbers represent actual observed changes in individuals. (Anglesey population, 1960.)

indicate that the proportions of the colour varieties differ in different colonies (Table 19). Whereas *infuscans-obsolata* was the commonest variety (42.2 per cent) at Pentre berw, Anglesey in 1959/60, it was the most uncommon form at Dale in 1964 (7.3 per cent) and at a pond in Anglesey in 1959/60 (14.0 per cent). The turquoise andromorphs constituted 56.6 per cent of the female population at Dale, but only 38.5 per cent at Pentre berw. Sixty per cent of the pond population in Anglesey were *infuscans*, whereas at Dale and Pentre berw the percentage for this form was only 36.0 and 19.3 respectively.

Table 19. *Female Colour Polymorphs of I. elegans in three colonies in Pembrokeshire and Anglesey*

		Anglesey-Ditch (Lord, 1959/60)		Anglesey-Pond (Lord, 1959/60)		Pembrokeshire- Ponds (1964)	
		Numbers captured	%	Numbers captured	%	Numbers captured	%
Mature	{ Andromorphs ..	178	38.5	26	26.0	93	56.7
	{ <i>Infuscans</i> ..	89	19.3	60	60.0	59	36.0
	{ <i>Infuscans-obsolata</i> ..	195	42.2	14	14.0	12	7.3
	Totals ..	462	100.0	100	100.0	164	100.0
Immature	{ Green ..	?	—	?	—	25	28.4
	{ <i>Violacea</i> ..	36	—	27	—	23	26.1
	{ <i>Rufescens</i> ..	21	—	7	—	23	26.1
	{ Teneral ..	?	—	?	—	17	19.4
	Totals ..	57	—	34	—	88	100.0

Table 20 shows the actual numbers of female *I. elegans* caught for each colour variety at Dale in 1964, together with percentages in parenthesis. Lord also found that the *violacea* and green forms are immature stages which ultimately develop into either *infuscans* or andromorphs. The data of Table 20 and Fig. 10 is consistent with these findings. For the purposes of the present study, forms *violacea* (strict sense), violet-green and violet-blue are all classified as *violacea*. When the daily combined percentages of andromorphs and *infuscans* are plotted with green forms and *violacea* it can be seen that there is a close inverse relationship between the numbers of presumed immature stages and adults of these forms (Fig. 10).

Colour polymorphism is a phenomenon common to the females of many species of the genus *Ischnura*, as well as to other genera of Zygoptera. The Australian *I. heterosticta* Burm. has females of at least two distinct forms: an andromorph and heteromorph similar to *infuscans* of *I. elegans* (Tillyard, 1905a). The North American *I. verticalis* Say, studied by Grieve (1937) is recorded as having at least four colour varieties, with the male resembling one of them. Grieve (*loc. cit.*) suggests that in the case of *I. verticalis* the colour forms may represent different geographic races as only one type (a heteromorph) was present in the vicinity of Ithaca, New York, whereas other forms were present in various parts of North America over an extensive geographic range. However, in the British Isles it would appear that all three mature colour forms of

Table 20. Daily captures of female polymorphs

Date	Female totals	Adult			Immature			
		Turquoise Andromorphs	<i>Infuscans</i>	<i>Infuscans-obsolata</i>	Green	<i>Violacea</i>	<i>Rufescens</i>	<i>Teneral</i> †
June 30	37	5(13.5)	1(2.7)	1(2.7)	11(29.7)	12(32.4)	7(18.9)	0(0.0)
July 1	26	10(38.5)	2(7.7)	5(19.2)	5(19.2)	3(11.5)	1(3.8)	0(0.0)
2	24	5(20.8)	8(33.3)	4(16.7)	3(12.5)	2(8.3)	0(0.0)	2(8.3)
3	33	10(30.3)	9(27.3)	2(6.1)	3(9.1)	0(0.0)	4(12.1)	5(15.2)
4	33	14(42.4)	11(33.3)	0(0.0)	2(6.1)	1(3.0)	0(0.0)	5(15.2)
5	40	18(45.0)	10(25.0)	2(5.0)	1(2.5)	1(2.5)	5(12.5)	3(7.5)
6	50	27(54.0)	13(26.0)	1(2.0)	0(0.0)	2(4.0)	5(10.0)	2(4.0)
7	10	4(40.0)	3*(30.0)	0(0.0)	0(0.0)	2(20.0)	1(10.0)	0(0.0)

\* Includes one specimen, presumed to be young *infuscans*, having *infuscans* thorax and blue 8th abdominal segment.

† Unclassifiable.

Percentages in parenthesis.

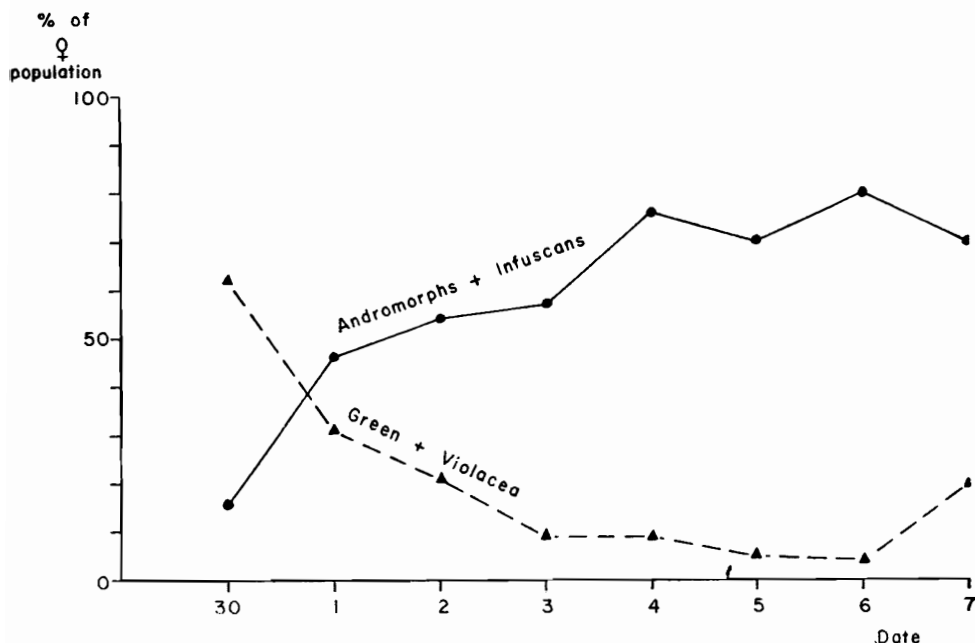


FIG. 10.

Daily combined percentages of andromorphs and *infuscans* plotted with green and *violacea*.

*I. elegans* occur in most, if not all, localities and, therefore, an explanation in terms of geographic races is not possible in this case. Furthermore, the differences in the percentages of the three female colour forms in three colonies in Wales remain wholly unexplained. There is clearly great scope for more detailed ecological and genetical studies of colour polymorphism in the genus *Ischnura*.

#### ACKNOWLEDGEMENTS

I wish to thank Mr. T. J. Gaskell, Dr. E. J. Popham, Professor P. M. Sheppard, Dr. P. S. Corbet, Miss C. Longfield and Mr. J. G. Blower for helpful and generous discussions in the course of the preparation of this paper. I am particularly grateful to Mr. G. M. Jolly for the use of the draft of his paper (1965) and for considerable assistance in the interpretation of recapture data. My thanks are also due to Mr. J. H. Barrett (Warden) and the staff of Dale Fort Field Centre, Mr. W. G. Morris (Maryborough Farm), Miss C. M. Wagner and my wife for their valuable help. It is a pleasure to record that the field work during the period 25th June–30th June was carried out with the co-operation of Miss B. M. Buck, Miss C. J. Kerr, Mr. P. T. White, Mr. R. A. P. Pearson, Mr. J. Rogerson, and Mr. A. R. Ash, all students of the Royal College of Advanced Technology, Salford, Lancashire.

## REFERENCES

- ANDREWARTHA, H. G. (1961). *Introduction to the Study of Animal Populations*. Methuen, London.
- BAILEY, N. T. J. (1951). On estimating the size of mobile populations from recapture data. *Biometrika*, **38** (3 & 4), 293-306.
- BAILEY, N. T. J. (1952). Improvements in the interpretation of recapture data. *J. anim. Ecol.*, **21**, 120-127.
- BLACKWELL, J. A. and DOWDESWELL, W. H. (1951). Local movement in Blue Tits. *British Birds*, **44**, 397-404.
- BLOWER, J. G. (1964). The estimation of animal numbers (The Lincoln Index). *Symposium—Ecology as a quantitative study* (Harris College, Preston, Lancs.). Cyclostyled.
- BORROR, D. J. (1934). Ecological studies of *Argia moesta* Hagen (Odonata: Coenagrionidae) by means of marking. *Ohio J. Sci.*, **34**, 97-108.
- BORROR, D. J. (1948). Analysis of repeat records of banded White-throat Sparrows. *Ecol. Monogr.*, **18**, 411-430.
- BRETT, G. A. (1936). Marking *Vanessa atalanta*. *Entomologist*, **69**, 263.
- CALVERT, P. P. (1915). The dimorphism or dichromatism of the females of *Ischnura verticalis*. *Ent. News*, **26**, 62-68.
- CORBET, P. S. (1951). The emergence and sex ratio of *Anax imperator* Leach (Odon., Aeshnidae). *Ent. mon. Mag.*, **87**, 176-179.
- CORBET, P. S. (1952). An adult population study of *Pyrrosoma nymphula* (Sulzer): (Odonata: Coenagrionidae). *J. anim. Ecol.*, **21** (2), 206-222.
- CORBET, P. S. (1954). Seasonal regulation in British dragonflies. *Nature, Lond.*, **174**, 655.
- CORBET, P. S. (1958). Temperature in relation to seasonal development of British dragonflies (Odonata). *Proc. Tenth Int. Congress of Entomology*, **2**, 755-758.
- CORBET, P. S. (1962a). Age-determination of adult dragonflies (Odonata). *XI Internationaler Kongress für Entomologie, Wien, 1960*, **3**, 287-289.
- CORBET, P. S. (1962b). *A Biology of Dragonflies*. Witherby, London.
- CORBET, P. S., LONGFIELD, C. and MOORE, N. W. (1960). *Dragonflies*. Collins, New Naturalist, London.
- COWLEY, J. (1938). Quantitative methods of local entomofaunistic survey. *Entomologist*, **71**, 8-12.
- DAVIS, G. A. N., FRAZER, J. F. D. and TYNAN, A. M. (1958). Population numbers in a colony of *Lysandra bellargus* Rott. (Lepidoptera: Lycaenidae) during 1956. *Proc. R. ent. Soc. Lond.* (A), **33** (1-3), 31-36.
- DOBSON, R. M. (1962). Marking techniques and their application to the study of small terrestrial animals. In: *Progress in Soil Zoology*, ed. Murphy, P. W., 228-239. Butterworths, London.
- DOWDESWELL, W. H. (1959). *Practical Animal Ecology*. Methuen, London.
- DOWDESWELL, W. H., FISHER, R. A. and FORD, E. B. (1940). The quantitative study of populations in the Lepidoptera. I. *Polyommatus icarus* Rott. *Ann. Eugen., Lond.*, **10**, 123-136.
- DOWDESWELL, W. H., FISHER, R. A. and FORD, E. B. (1949). The quantitative study of populations in the Lepidoptera. II. *Maniola jurtina* L. *Heredity*, **3**, 67-84.
- DRESSER, B. J. (1959). Land use and farm practice in the parish of Dale. *Field Studies*, **1** (1), 1-23.
- FISHER, R. A. and FORD, E. B. (1947). The spread of a gene in natural conditions in a colony of the moth *Panaxia dominula* L. *Heredity*, **1**, 143-174.
- FORD, E. B. (1953). The experimental study of evolution. *Australian and New Zealand Association for the Adv. of Sci.*, **33**, 143-154.
- FRASER, F. C. (1956). Odonata. *R. ent. Soc. Lond., Handbooks for the identification of British Insects*, **1** (10), 1-49.
- GARDNER, A. E. (1954). A note on the colour variation of *Ischnura elegans* (Van der Linden) (Odon: Coenagrionidae). *Ent. Gaz.*, **5** (2), 82-84.
- GEORGE, M. (1961). The flowering plants and ferns of Dale, Pembrokeshire. *Field Studies*, **1** (3), 1-24.
- GLASGOW, J. P. (1953). The extermination of animal populations by artificial predation and the estimation of populations. *J. anim. Ecol.*, **22**, 32-46.
- GRIEVE, E. G. (1937). Studies on the biology of the damselfly *Ischnura verticalis* Say, with notes on certain parasites. *Ent. amer.*, **17** (3), 121-152.
- JACKSON, C. H. N. (1948). The analysis of a tsetse-fly population. III. *Ann. Eugen. Lond.*, **14** (2), 91-108.

- JOHNSON, C. (1962). A description of territorial behaviour and a quantitative study of its function in males of *Hetaerina americana* (Fabricius) (Odonata: Agrilidae). *Canad. Ent.*, **94** (2), 178-190.
- JOLLY, G. M. (1963). Estimates of population parameters from multiple recapture data with both death and dilution—deterministic model. *Biometrika*, **50** (1 and 2), 113-128.
- JOLLY, G. M. (1965). Explicit estimates from capture—recapture data with both death and immigration—stochastic model. *Biometrika* **52** (1 and 2), 225-247.
- KILLINGTON, J. (1924). *Ischnura elegans*, Lind: Its general colour phases and its mature varieties and aberrations. *Entomologist*, **54**, 273-278.
- LESLIE, P. H. and CHITTY, D. (1951). Population estimates of the vole *Microstus agrestis* assuming deterministic survival rate. *Biometrika*, **38**, (3 and 4), 269-292.
- LINCOLN, F. C. (1930). Calculating waterfowl abundance on the basis of banding returns. *Circ. U.S. Dept. Agric.* No. 118, pp. 1-4.
- LONGFIELD, C. (1949). *The Dragonflies of the British Isles*. Warne, London.
- LORD, P. M. (1961). *A study of the colour varieties of some damselflies*. Ph.D. Thesis, University of Wales.
- LYON, M. B. (1915). The supposed dimorphic female of *Ischnura verticalis* Say. *Ent. News*, **26**, 59-62.
- MACLEOD, J. (1958). The estimation of numbers of mobile insects from low-incident recapture data. *Trans. R. ent. Soc. Lond.*, **110** (13), 363-392.
- MOORE, N. W. (1962). Population density and atypical behaviour in male Odonata. *Nature, Lond.*, **194**, 503-504.
- MOORE, N. W. (1964). Intra- and interspecific competition among dragonflies (Odonata). *J. Anim. Ecol.*, **33**, 49-71.
- RICHARDS, O. W. and WALOFF, N. (1954). Studies on the biology and population dynamics of British grasshoppers. *Anti-Locust Bull.*, **17**, Brit. Mus. (Nat. Hist.). 182 pp.
- SHEPARD, P. M. (1951). Fluctuations in the selective value of certain phenotypes in the polymorphic land snail *Cepaea nemoralis* (L.). *Heredity*, **5**, 125-143.
- TILLYARD, R. J. (1905a). On dimorphism in the female of *Ischnura heterosticha* Burm. *Proc. Linn. Soc. N.S.W.* (1905-1906), **30**, 302-306.
- TILLYARD, R. J. (1905b). On the supposed numerical preponderance of the males of Odonata. *Proc. Linn. Soc. N.S.W.* (1905-1906), **30**, 344-349.
- WOLFE, L. S. (1952). A study of the genus *Uropetala* Selys from New Zealand. *Trans. Roy. Soc. N.Z.*, **80** (3 and 4), 245-275.