3

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Lifetable construction for the gorse seed weevil, *Apion ulicis* (Forster) (Coleoptera: Apionidae) before gorse pod dehiscence, and life history strategies of the weevil

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Abstract A lifetable of the pre-emergent stages for *Apion ulicis* (Forster) has been prepared from multi-cohort stage-frequency data and analysed using the Kiritani-Nakasuji-Manly method. This estimates the daily survival rate, the stage specific survival rate, the duration of each developmental stage in days, and the numbers entering each stage.
An age specific mortality table has been prepared. An Allee effect is observed between adult weight and the density of adults per pod. Mortality factors within gorse pods appear to be density dependent. The results are discussed in relation to larval life history strategies and the habit of egg clustering by ovipositing females.

Keywords *Apion ulicis*; Coleoptera; Apionidae; lifetable; multi-cohort stage frequency data; Kiritani-Nakasuji-Manly model; density dependent mortality; Allee effect; larval competition; egg clustering

INTRODUCTION

The analysis of insect census data and the construction of a lifetable is a necessary precursor to an inquiry into population regulation and fluctuation (Birley 1977), as it contributes to an understanding of the population dynamics of a species (Southwood 1978).

The aim of the lifetable is to show the effects of successive events in their natural order, by describing the survival of cohorts of individuals in relation to their lifestage (Varley et al. 1973). The lifetable shows variations in survival rates at different stages and how this affects numbers in later stages. The determination of these phenomena forms the basis of a key factor analysis. The key factor is the survival in the stage of the lifecycle that contributes most to the variation in overall population numbers. With further study, factors that affect survival at certain developmental stages can be elucidated. Key factor analysis can be applied to a population that has been observed for several generations (Manly 1990).

The gorse seed weevil was introduced into New Zealand in 1931 to biologically control gorse (*Ulex europaeus* L.) (Miller 1970). Female weevils oviposit inside gorse pods. The developing larvae consume the immature gorse seeds before completing their development within the pod. The adults are released from the pod when it dehisces.

A vertical lifetable for a single generation of *A. ulicis* was constructed from multi-cohort stage frequency data. Different developmental stages were sampled from the population over time with individuals entering the population for a substantial part of the sampling period.

A variety of methods are available for the analysis of insect stage frequency data from which lifetables can be prepared (Varley et al. 1973; Birley 1977; Mills 1981; Manly 1987). Manly (1974, 1990) has reviewed and compared these models and others commenting on the parameters estimated and the assumptions of each. For the construction of this lifetable, the Kiritani-Nakasuji-Manly (KNM) method of analysis (Manly 1990) was used. This method assumes that:

(i) The population being sampled is large enough for any changes in that population to act deterministically, provided that the survival rate per unit time is the same for all stages over the entire sampling period.

(ii) That sampling is started at or just after the time that individuals begin to enter stage one.

(iii) Population losses through migration are negligible.

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This model estimates the daily survival rate, stage specific survival rate, duration of each developmental stage in days, and the numbers entering each stage. These numerical estimates allow the postulation of interacting processes which affect the survival of developing weevils.

MATERIALS AND METHODS

In November 1989, a pilot study to determine the sample size was conducted on an 8 ha gorse site at Whitford in south Auckland. Three-hundred gorse pods were selected randomly and then examined under a stereo-microscope at ×10.5 magnification. All lifestages were recorded and the numbers combined for the calculation of sample size.

As the variance was larger than the mean, the distribution of eggs and larvae in infected pods was aggregated (Southwood 1978). Adherence to the negative binomial was tested using techniques described by Southwood (1978). The dispersion parameter k was determined at 0.454 by iterative solution of log

$$log(N/n_o) = klog(1+\bar{x}/k)$$

where N = total number of pods and n_o = number of empty pods.

k was used to calculate the U statistic

$$U = s^2-(\bar{x}\ +(\bar{x})^2/k)$$

As U was less than its standard error (–122.7< 17.96) the negative binomial adequately described the distribution (Southwood 1978). Optimal sample size was calculated as

$$n = (1/\bar{x}-1/k)/(E)^2$$

where E = the desired level of accuracy.

At the chosen level of accuracy ($E = 0.07$) the optimal sample was 476 pods. Every 7 days, 495 pods were collected at Whitford, returned to the laboratory, dissected, and examined microscopically. The number of each lifestage was recorded along with the number of larvae feeding on and within each seed. The head-capsules of larvae were measured under the stereomicroscope at × 25 magnification to ascertain instar number (Hoddle 1991a).

Adult weevils were weighed on a digital balance to determinewhether a relationship between adult weight and density existed. This was analysed using a General Linear Models Procedure on the upward and downward slope for each sex using SAS (Proc GLM, SAS Institue Inc 1987).

The biology of *A. ulicis* and this sampling regime satisfied the requirements of the KNM method of analysis for insect census data. The equations for the estimates made by this model were as follows:

The survival parameter:

$$X = -log_e(A_q^*/A_1^*)/(B_q^*-B_1^*) \qquad (1)$$

The stage-specific survival rate for Stage j:

$$W_j = A_{j+1}^*/A_j^* \qquad (2)$$

The duration of each stage:

$$a_j = -log_e(W_j)/X \qquad (3)$$

The number entering stage j:

$$M_j = A_j^*X \qquad (4)$$

To solve equations 1–4, A_j^*, D_j^* and B_j^* need to be determined. The variable estimates the area under the $F_j(t)$ curve (i.e., the cumulative sum for each column of the cumulative stage frequency table) where $h= t_n-t_1/(n-1)$, t=time, and F_{ij}= the sample frequency for the number in stage j or higher at time t_i.

The area under the $tF_j(t)$ curve is estimated by

$$D_j{*} = h\sum_{i=1}^{n} tF_{ij}$$

(i.e., the cumulative sum of time multiplied by each corresponding value from the appropriate column of the cumulative stage frequency table), and $B_j^*=D_j^*/A_j^*$.

RESULTS

The average level of pod infection attained by *A. ulicis* at Whitford over the sampling period was 16% (n=32, range 1.6%–42%). The frequency of each lifestage recorded on successive sampling occassion is shown in Table 1. The cumulative stage frequency table from this data is given in Table 2. These values were used to determine A_j^*, D_j^*, and B_j^* (Table 3).

The corresponding estimates from equations 1–4 in the methods section are shown in Table 4. The stage specific survival rate for adults cannot be determined as this value is dependent on A_j^* that follows that stage. Consequently, the duration of that stage is incalculable, being dependent on the value derived for the stage specific survival rate. Caging experiments by Forster (1977) indicate that upon emergence from pods, adults can live for approximately 12 months.

As the KNM model estimates the numbers entering each stage, an age specific mortality table can be

As the KNM model estimates the numbers entering each stage, an age specific mortality table can be prepared (Table 5) (Varley et al. 1973). Line 1 shows the changes in number during a single generation of *A. ulicis* at Whitford. Line 2 shows the numbers which die in the interval between each lifestage. The sum is the total number of individuals that die before the adult stage is reached. Line 3 shows the figures for percentage mortality, calculated in relation to the original egg number. When summed the resulting value is the proportion that died. Consequently, 11.5% of the eggs laid produced adults.

The succesive percentage mortality in each stage is the number of individuals alive at the beginning of that stage. The product of the fraction surviving gives the generation survival rate. The population values can be converted to log values, and the effects of the mortality can be expressed logarithmically as *k*-values. This is the difference between the logarithms of the

Table 1 Multi-cohort stage frequency data for *A. ulicis* collected every 7 days from Whitford, where E represents eggs, I_1 first instar larvae, I_2 second instar larvae, I_3 third instar larvae, P pupae, and A adults.

Date	E	I_1	I_2	I_3	P	A
31-7-90	0					
8-8-90	26					
15-8-90	149					
22-8-90	177					
29-8-90	417					
5-9-90	604					
12-9-90	777					
19-9-90	1151	0				
26-9-90	1447	22	0			
3-10-90	1656	72	4			
10-10-90	1217	151	20	0		
17-10-90	1192	894	45	25		
24-10-90	400	618	207	188	0	
31-10-90	238	261	521	374	16	0
7-11-90	81	89	130	457	65	7
14-11-90	30	13	8	324	113	18
21-11-90	5	9	5	197	346	67
28-11-90	0	3	6	187	372	260
5-12-90		12	16	177	324	345
12-12-90		0	0	37	230	590
19-12-90				0	65	607
26-12-90					0	147
2-1-91						56
9-1-91						0

Table 2 Cumulative stage frequency data for *A. ulicis* prepared from Table 1, where time is in days, E represents eggs, I_1 first instar larvae, I_2 second instar larvae, I_3 third instar larvae, P pupae, and A adults.

Time	E	I_1	I_2	I_3	P	A
0	0					
7	26					
14	149					
21	177					
28	417					
35	604					
42	777					
49	1151	0				
56	1469	22	0			
63	1732	76	4			
70	1388	171	20	0		
77	2156	964	70	25		
84	1413	1013	395	188	0	
91	1410	1172	911	390	16	0
98	829	748	659	529	72	7
105	506	476	463	455	131	18
112	629	624	615	610	413	67
119	828	828	825	819	632	260
126	874	874	862	846	669	345
133	857	857	857	857	820	590
140	672	672	672	672	672	605
147	147	147	147	147	147	147
154	56	56	56	56	56	56
161	0	0	0	0	0	0

Table 3 Estimates of A_j^*, D_j^*, and B_j^* prepared from the cumulative stage frequency table (Table 2). Where E represents eggs, I_1 first instar larvae, I_2 second instar larvae, I_3 third instar larvae, P pupae, and A adults.

Stage	A_j^*	D_j^*	B_j^*
E	127869	10368106	81.08
I_1	60900	6468588	106.22
I_2	45892	5251967	114.44
I_3	39158	4644465	118.61
P	25396	3229786	127.18
			132.65

Table 4 Estimates of the daily survival rate, stage specifc survival rate, duration of each stage, and the numbers entering each stage for *A. ulicis* at Whitford. E represents eggs, I_1 first instar larvae, I_2 second instar larvae, I_3 third instar larvae, P pupae, and A adults.

Stage	Daily survival rate	Stage specific survival rate	Duration of stage (in days)	Number entering stage
E	0.9580	0.4763	17.66	5369.22
I_1		0.7536	6.74	2557.19
I_2		0.8533	3.78	1927.01
I_3		0.6486	10.31	1644.24
P		0.5775	13.08	1066.38
A				615.78

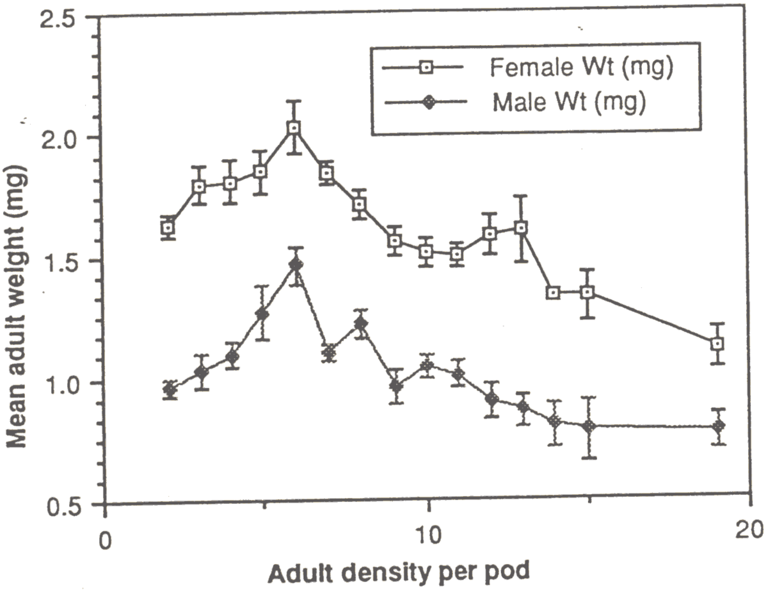

Fig. 1 The average weight of male and female weevils with standard error bars recorded from pods containing different densities of adults. The pods were collected from Whitford.

population before and after the mortality acts. The *k*-values can be summed since they act in sequence to give the generation mortality *K*. Mortality is highest from eggs to first instar larvae, whereas the highest rate of survival is seen at instar 2.

The *k* values from Table 5 can be tested for density dependent mortality (Southwood 1978). The regression co-efficients for log N_t (the number entering a specific larval stage) against log N_{t+1} (the number surviving that specific larval stage) (t=0.41 df=1 P>0.05)) and log N_{t+1} against $\log_t$ (t=0.27 df=1 P>0.05)) did not differ significantly from 1.0. Density dependent mortality was not statistically proven with this test (Southwood 1978).

The average number of larvae per seed was 2.47 ±0.12 (n=209 range 1–13), with a mean of 3.84 ±0.22 seeds (n=209 range 1–6) and 7.32 ±0.58 larvae (n=209 range 1–14) per pod.

The relationship between adult weight for males and females with density is non linear (Fig. 1). Each sex attains a maximum weight at a density of six weevils per pod. Either side of these maxima a decrease in body weight is observed. The upward slope for females did not differ significantly from zero (t=1.26 n=34 P>0.05). The upward male slope (t=2.36 n=34 $P\leq0.05$), the downward male slope (t=7.05 n=148 $P\leq0.05$), and the downward female slope (t=10.36 n=156 $P\leq0.05$) differed significantly from zero, indicating that a linear relationship existed between weight and density. Therefore, the relationship of adult weight to adult density per pod for *A. ulicis* exhibits an Allee effect (Allee et al. 1949) (Fig. 1).

DISCUSSION

The bionomics of *A. ulicis* have been studied previously (Davies 1928; Forster 1977) but neither author prepared a lifetable, determined the length of each developmental stage, or investigated factors regulating numbers in the pod during development. The survivorship of weevils within the pod is fundamental to the population dynamics of *A. ulicis*. Therefore, what causes the fluctuation of numbers for each lifestage in the pod?

The factors determining population trends within pods appear to be density dependent. Although this was not proved conclusively (an Allee effect was observed), failure to detect it does not prove its absence (Southwood 1978). It should be noted that key factors influencing population trends are not always density dependent (Hayes 1981).

Gourlay (1989) reports that ecto-parasitism of larvae by a *Pteromalus* spp. in New Zealand occurs and adult parasitism by the fungus *Hirsutella* has also been recorded (Forster 1977). Egg, larval, pupal, or adult parasitism were not observed. Gorse seed mortality caused by the fungus *Cladosporium cladoporiodes* resulting in the starvation of larvae is negligible, because of the low level of occurrance observed in the field (Hoddle 1991b). A small proportion of infected pods (0.39) picked in mid January 1990 contained dead adults. Since parasitism had not occurred death was assumed to have been caused by starvation, as the pods had failed to dehisce. This has been observed previously (Davies 1928; Miller 1970).

Adult weight has been used as an indicator of potential adult fitness in studies on the Curculionoidea (Mitchell 1975; Credland et al. 1986; Wilson 1988). In *A. ulicis,* adult weight for each sex is highest at a density of six adults per pod. This is the mean number of weevils per pod from other studies (Cowley 1983) and would appear to be related to the average egg cluster size laid by the female of 6.9 ±0.2 eggs per pod (Cowley 1983).

Either side of the observed maxima a decrease in body weight was evident. Below a larval density that produced six adults per pod, deleterious effects caused by under-crowding are assumed. At densities producing more than six adults, however, larval overcrowding and intra-specific competition affect adult fitness. This is the direct result of the number of eggs laid per pod.

As eggs were laid on a larval resource of limited carrying capacity, the number of eggs laid at each event affected the lifetime fitness of the females (Ives 1989). To optimise fitness, the most productive clutch size is the number of eggs per pod that maximises the number of fit (estimated by weight) adults emerging from that pod. This is known as the Lack solution (Smith & Lessells 1985).

The adaptive significance of egg clustering with respect to larval survival has been discussed extensively (Parker & Courtney 1984; Smith & Lessells 1985; Matsumoto 1990). Generally, for egg clusters larger or smaller than average, the larval survival rate for many species of insect decreases (Matsumoto 1990).

Apion ulicis larvae attain an optimum adult weight in larval aggregations that produce six adults per pod. This may result from the co-operative establishment of a feeding site, which produces feeding scars allowing individuals access to the inner tissues of the seed, and possibly a stronger stimulation for feeding (Matsumoto 1990). Evidence for this in *A. ulicis* is seen as more than one larva is found per seed. The adverse effects of physical conditions resulting from temperature and humidity can be reduced by larval aggregation (Matsumoto 1990).

A co-operative interaction of this nature would appear to be greatest at instar 1 and instar 2 as these stages exhibited the highest larval survival rates (Table 5). It is relevant to mention here that 52% of the eggs laid did not produce first instar larvae capable of establishing a feeding site. This may be caused in part by a high initial egg infertility as Cowley observed (1983). In larger than average clusters, larval mortality results because of concentrated predation and parasitism risks, or from the overloading of the larval resource (Matsumoto 1990). The latter can result in extermination of whole cohorts (Matsumoto 1990). This is probable for *A. ulicis* larvae as they are unable to move between patches. Consequently, the highest observable larval mortality occurs at instar 3 (Table 5). This intra-specific competition affects the ability to sequester enough reserves to complete pupal metamorphosis and a further decline in numbers is observed (Table 5).

Under such conditions larval competition is of two types, "contest" (attack) and "scramble" (avoid) (Smith & Lessells 1985) which are defined in terms of resource use and larval behaviour. These terms represent the extremes of an ecological continuum and intermediate processes can occur. The position of *A. ulicis* on the continuum is undetermined as the exact number of eggs or larvae per pod before pupae or adults being found is unknown. Intuitively, the scramble end of the continuum would seem likely, since eggs are laid in batches and on average more than one adult is produced per pod. The larval resource is often not exploited fully with seed fragments and occasionally whole seeds remaining in the pod. Clutch

Table 5 Age specific mortality table for *A. ulicis* within pods at Whitford, where E represents eggs, I_1 first instar larvae, I_2 second instar larvae, I_3 third instar larvae, P pupae, and A adults.

Line	E	I_1	I_2	I_3	P	A
(1) Population	5369	2557	1927	1644	1066	616
(2) No dying in interval	2812	630	283	578	450	Sum: 4753 dead
(3) % mortality	52.37	11.73	5.27	10.77	8.38	Sum: 88.52% mortality
(4) Successive % mortality	52.37	24.64	14.69	35.16	35.16	42.21
(5) Successive % survival	47.63	75.36	85.31	64.84	57.79	
(6) Fraction surviving	0.4763	0.7536	0.8531	0.6484	0.5779	Product 0.1147 (generation survival rate)
(7) Log Pop	3.73	3.41	3.28	3.22	3.03	2.79
(8) *k* value	0.32	0.13	0.06	0.19	0.24	Sum:K=0.94 (generation mortality)

size is related to the type of competition between larvae (Ives 1989).

The size of egg clusters may be affected by various factors beside those directly acting on larval mortality. Clutch size can be selected for by maximising the reproductive success of the maternal parent when viewed in relation to female fecundity and the cost to females of locating suitable oviposition sites (Courtney 1984; Parker & Courtney 1984; Parker & Begon 1986). Once egg clustering develops, the advantages of aggregation or the inter-dependence among members within a cluster (usually sibs) may evolve. This in turn would reinforce the selection of the female to cluster her eggs (Matsumoto 1990). Therefore, to maximise reproductive and lifetime fitness, female gorse seed weevils oviposit eggs in clusters. This optimises the effect of density dependent competition and maximises adult fitness with respect to weight.

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