ECOLOGY OF MEDITERRANEAN SNAILS IN SOUTHERN AUSTRALIAN AGRICULTURE: A STUDY OF *CERNUELLA VIRGATA* AND *COCHLICELLA ACUTA* ON THE YORKE PENINSULA

VANESSA L. CARNE

Thesis submitted for the degree of

Doctor of Philosophy

in

The University of Adelaide

Faculty of Sciences

School of Agriculture and Wine

The University of Adelaide

South Australia

AUGUST 2003

VOLUME 2 OF 2

CHAPTER VI

FACTORS THAT INFLUENCE MOVEMENT OF INDIVIDUAL *CERNUELLA VIRGATA* AND *COCHLICELLA ACUTA*: WITH PARTICULAR FOCUS ON ADULT *CERNUELLA VIRGATA* IN BARLEY

6.1 INTRODUCTION

Models can contribute to our understanding of ecological systems (Kareiva, 1989; Hillborn and Mangle, 1997; Schmitz, 2001). This is especially true for complex processes such as dispersal (Turchin, 1997; 1998). In addition to their utility as tools for describing dispersal, models can also provide a means for examining and generating hypotheses about the causes and consequences of dispersal (Nathan, 2001). Quantitative information on dispersal should be a key element in designing and evaluating management strategies for mobile invertebrate pests (Turchin and Thoeny, 1993).

Passive diffusion represents the simplest process of dispersal, involving no biological complications such as interactions among individuals (Kareiva, 1982). Simple diffusion assumes that reproduction and dispersal determine migration rate (Clark, 1998). It is based on the random motion of individuals (Jorné and Safriel, 1979). Despite this simplified approach, diffusion models have gained acceptance as the standard theoretical tool with which to examine patterns of dispersal and the consequences of that dispersal (Okubo, 1980; Okubo and Levin, 2002).

Movement models can be classified as either analytical or simulation, simple or detailed, stochastic or deterministic and by their mathematical structure (i.e. whether variables such as population density, space and time are discrete or continuous) (Turchin, 1998). The simplest diffusion models cannot be exactly right for any organism in the real world as animals' behaviour and their environment are far too complicated to be described by elegantly simple diffusion models (Okubo and Levin, 2002). Thus, more complex simulation models are necessary to explain the displacement of real organisms. Simulation models can predict the effects of variation in temperature, precipitation and other factors on population dynamics (Marin et al, 1998).

The goal of modelling can be either forecasting or prediction. Forecasting is weaker than prediction, and uses the knowledge of past behaviour of the system to forecast its future state. Forecasting will fail if the system's dynamics change (Turchin, 1997), which is especially relevant in agricultural systems that are very dynamic. Prediction anticipates a situation that was not encountered in the past. In general, prediction requires a mechanistic understanding of the system. Deriving parameter estimates from real data sets under a variety of conditions can then be used to develop mechanistic models. The ability to predict is an ultimate goal and the most powerful test to which a model could be subjected.

Mathematical models in population and community ecology have often been criticized for not being testable (DeAngelis, 1988; Peters, 1991; Murdoch et al, 1992). This is because they contain concepts, variables and parameters that cannot be measured or observed in nature (Peters, 1991). Others have noted that the level of replication, and levels of spatial and temporal scales of manipulation required for appropriate tests are impractical in most systems (Steinberg and Kareiva, 1996; Englund and Cooper, 2002). These limitations must be considered when developing simulation models to forecast dispersal of invertebrates.

Specifically, the aims of this chapter were:

I. To determine the climatic and non-climatic factors that are associated with movement of adult and juvenile *C. virgata* and *C. acuta* in crop and medic habitats, and

II. To build a simulation model that forecasts the net displacement for a population of adult *C. virgata* in barley.

6.2 MATERIALS AND METHODS

6.2.1 Identification of factors that influence movement

The population dynamics of the Mediterranean snails on the Yorke Peninsula (Chapter 3) and their breeding behaviour (Chapter 4) are related to temperature and rainfall. Therefore, it was highly probable that climatic factors would be associated with movement of individual snails. Thirteen climatic and ten non-climatic variables were tested to determine the factors that influenced movement length for adult and juvenile *C. virgata* and *C. acuta* in barley and medic (Table 6.1). Air temperature, soil temperature, relative humidity and rainfall were measured at the field site throughout the dispersal trials. Minimum, maximum and mean temperatures were selected as climatic variables to be tested. Individual snails were treated as random variables in the statistical model to eliminate random variance. Additionally, the previous movement length and turning angle were examined to determine any patterns in the snail movements. Statistical models showed that adult and juvenile *C. virgata* and *C. acuta* behaved differently in different vegetation types, and over the duration of the season (months). Consequently, species, age classes and vegetation types were analysed separately.

Movement length was modelled against climatic and non-climatic variables using PROC MIXED (SAS Institute, Cary, North Carolina), which estimates the unknown parameters using normal distribution maximum likelihood or restricted maximum likelihood (Mazumdar, et al, 1999; As described in Chapter 3). All variables were put into the maximal model. Effects estimated to be zero or non-significant were progressively dropped from the model and their effects were determined using the AIC value (Akaike, 1974). The final model included all statistically significant terms. The aim was to have only one of each representative variable, eg mean or maximum temperature, not both.

The remaining significant terms indicated those variables that explained movement length and were used in the simulation model. Predicted mean displacement was much larger than observed (Chapter 5). It was thought that day one data might not be representative of natural snail movement due to handling, marking and possible density dependence of conspecifics. By eliminating observed day one data from the analysis, AIC values decreased, indicating that these models were more valid than those that included day one data.

Table 6.1. Daily climatic and non-climatic variables that were measured (see Chapter 5) and tested to determine which of these factors influence movement length of adult and juvenile *C. virgata* and *C. acuta* in barley and medic.

Climatic	Non-climatic
Minimum air temperature (°C)	Individual snail
Maximum air temperature (°C)	Species
Mean air temperature (°C)	Age class: adult / juvenile
Maximum soil temperature (°C)	Plant type: barley / medic
Minimum soil temperature (°C)	Days after release
Mean soil temperature (°C)	Month released
Maximum relative humidity	Replicate within release
Minimum relative humidity	Turning angle (°)
Mean relative humidity	Previous turning angle (°)
Relative humidity at 9 am	Previous movement length (cm)
Relative humidity at 3 pm	
Presence or absence of rainfall (mm)	
Total rainfall (mm)	

6.2.2 Simulation model

An individual-based simulation model was developed to investigate the long-term redistribution of *C. virgata* populations. The simulation model developed in this chapter was tested against empirical displacement data ('model testing', Englund and Moen, 2003).

The model was used to forecast the net displacement (the straight-line distance from the beginning to the end point of a path (Turchin, 1997)) of a population of individual snails over a given period of time. The integration of dispersal data with climatic data was used to forecast how far snail populations could disperse during their active season.

A simulation model was developed in MATLAB (Student version 5.3.0.14912a (R11) MathWorks, 1999) that forecasted net displacement of *C. virgata* at a given time after release. Simulations were performed for 10 000 individuals, for movements made one, two, three, four and five days after release.

The assumptions made for the simulation model of the displacement of *C. virgata* in barley were:

I. Snails do not move through simple diffusion;
II. Snails show no homing behaviour;
III. The distribution of daily distances moved does not change throughout the breeding season (June-September) when the snails are active;
IV. The structure of habitat is homogeneous;
V. Rainfall and minimum temperature are correlated;
VI. The presence or absence of rainfall is important, not the total amount of rain.
VII. Weather conditions vary randomly across the active season of snails

Based on the results from the statistical model, the simulation model was developed using the variables that were associated with adult *C. virgata* movement (Figure 6.1). These variables were included in the model to forecast movement length over a given time period. Turning angles needed to be taken into account as adult *C. virgata* does not move in a continuous straight line, nor does its dispersal conform to simple diffusion, and therefore the correlated random walk does not apply to this species (see Chapter 5). Turning angles were assigned the frequency as observed in the field, as turning angles were biased for adult *C. virgata* in barley. Therefore, while the model randomly chose the turning angles; the frequency with which they were chosen was based on observed field data. The simulation model (Box 6.1) to forecast snail displacement was run for days one through five (as measured in the field) for 10 000 individuals. However, the number of days (life) over which snail movement is followed can be set to any desired figure. In the model, each snail starts at the origin (xx, yy), and movement is followed from there. Random statements to seed the random uniform distribution and random normal distribution are included in this model.

Beyond having a method that generates random values from a reasonable distribution for each vital rate, it is also necessary to make these random variables correlated. A realistic correlation is one in which there is statistical correlation but not absolute rigidity (Morris and Doak, 2002). The problem with this is generating the correlation while allowing each vital rate to vary according to its own probability distribution. Therefore, the 'Beta distribution', using normally distributed variables and cumulative distribution functions, was used (Morris and Doak, 2002). The subroutine 'SnailWeatheraCorr' generates a matrix of within-year, auto- and cross-correlated (with one time step) weather variables. This subroutine was adapted from Morris and Doak, (2002; Box 8.6; pp 284).

The weather parameters, minimum temperature and rainfall were placed in a positive semi-defined matrix for within year correlation. To fully parameterise a matrix model, information is required on three things: the mean value for each vital rate, the variability in each of these rates, and the covariance or correlation between each pair of rates (Morris and Doak, 2002). An issue regarding correlation of vital rates is correlation across time. Autocorrelation is correlation in the sequential values of a vital rate caused by environmental factors that are correlated between successive measurement periods. Similarly, cross-correlation is correlation of different rates across time steps (Morris and Doak, 2002). Rainfall and minimum temperature are relatively easy to measure and therefore deemed most appropriate for this model. The frequency of rain and also the minimum temperature were calculated for the data set. The model uses the within-year and between-year correlations of rain and minimum temperature; this was necessary because rainfall on a particular day is highly correlated with both temperature and rainfall. The probability of a rainfall event of a particular day is dependent on whether it rained the previous day. Minimum temperature and rainfall data entered into the model were based on measurements made from April through September over two years (2001-2002). Therefore, the model forecasts movement of adult *C. virgata* based on the average temperature and rainfall over the snail's active season, and is not adjusted for within season variation.

Model parameters based on a statistical model that included total rainfall resulted in a simulation model that forecasted unrealistically high movement lengths. A better fit was obtained when rainfall was treated as a binary variable. This is possibly because there were a limited range of rainfall values due to a small number of actual raindays. Therefore, the presence or absence of rainfall was given values of 1 and 0, respectively.

Once the climatic variables and initial move length are calculated, the program computes future movement lengths using a regression equation where:

aa = -12.03 (coefficient for intercept)
bb = 6.04 (coefficient for minimum temperature)
cc = 25.48 (coefficient for rainfall)
dd = 0.615 (coefficient for previous movement length)
ee = -7.405 (coefficient for rainfall x minimum temperature)
ff = -0.289 (coefficient for rainfall x previous movement length)
Such that if rainfall is = 0 then

Movement length (no rainfall) = aa + bb x minimum temperature + dd x previous movement length

Or, if rainfall = 1, then:
Movement length (rainfall) = movement length (no rainfall) + cc + ee x minimum temperature + ff x previous movement length

Because forecasted movement lengths were sometimes negative (since the intercept of the regression was negative), movement length was set to ≥ 0 for this model.

The file 'Stdnormcdf.m' was used to define rainfall cumulative distribution function and its confidence limits to calculate the standard normal cumulative distribution function. This file is a built in MATLAB function (Appendix 7).

Key distributions for vital rates are the beta and stretched beta-distributions (Morris and Doak, 2002). Spread predictions that ignore variance contain an order of magnitude bias (Clark et al, 2001). A stretched beta distribution is constrained to be between zero and a maximum number, and is therefore more appropriate than a normal distribution, because movement length cannot be a negative value and the standard deviation is very large (P. Doak, pers. comm.). A stretched beta-distribution is a rescaled beta-distribution that has self-defined minimum and maximum values, expanding the range of the usual beta (0 to 1) to fit the interval that makes biological sense for the movement rate being modelled. Because it is bound by these limits, this version of a beta-distribution can allow more realistic simulations compared to the lognormal distribution in which there is no upper limit (Morris and Doak, 2002). Therefore, a stretched beta-distribution was used. The stretched beta file defines the function 'stretchbetaval' that returns stretched beta-distributed values (Appendix 8).

The stretched beta-distribution is adapted from the MATLAB function 'betaval' which returns beta-distribution value with a specified Cumulative distribution function value (Morris and Doak, 2002) (Appendix 9). There are three methods that allow for random simulation of random beta value, however, only one simulates beta values that are correlated with other vital rates (Morris and Doak, 2002). This is the one that is presented in this simulation model. For a beta-distribution with parameters a and b (which are transformations of the mean and variance) and some p value between 0 and 1, this function gives the probability that a randomly chosen value from the distribution will be less than or equal to p, a probability referred to as $F(p|a,b)$ (Morris and Doak, 2002).'Betaval' takes a random $F(p|a,b)$ value along with the mean and standard deviation of the beta-distribution to simulate beta values that are correlated with each other (Morris and Doak, 2002).

The simulation model in this chapter forecasts movement length of adult *C. virgata* in barley as summarised in Figure 6.1. In addition to the initial movement length, the direction of movement needs to be determined. The initial direction that the snail takes is randomly selected, while movement length is dependent on the climatic parameters and previous movement length. After the initial movement is determined, the subsequent turning angle is picked from the distribution of observed turning angles. Movement length and direction of movement are then used to calculate the position of the snail after its next move (Box 6.1). These data are then put into a matrix, and displayed as the program progresses.

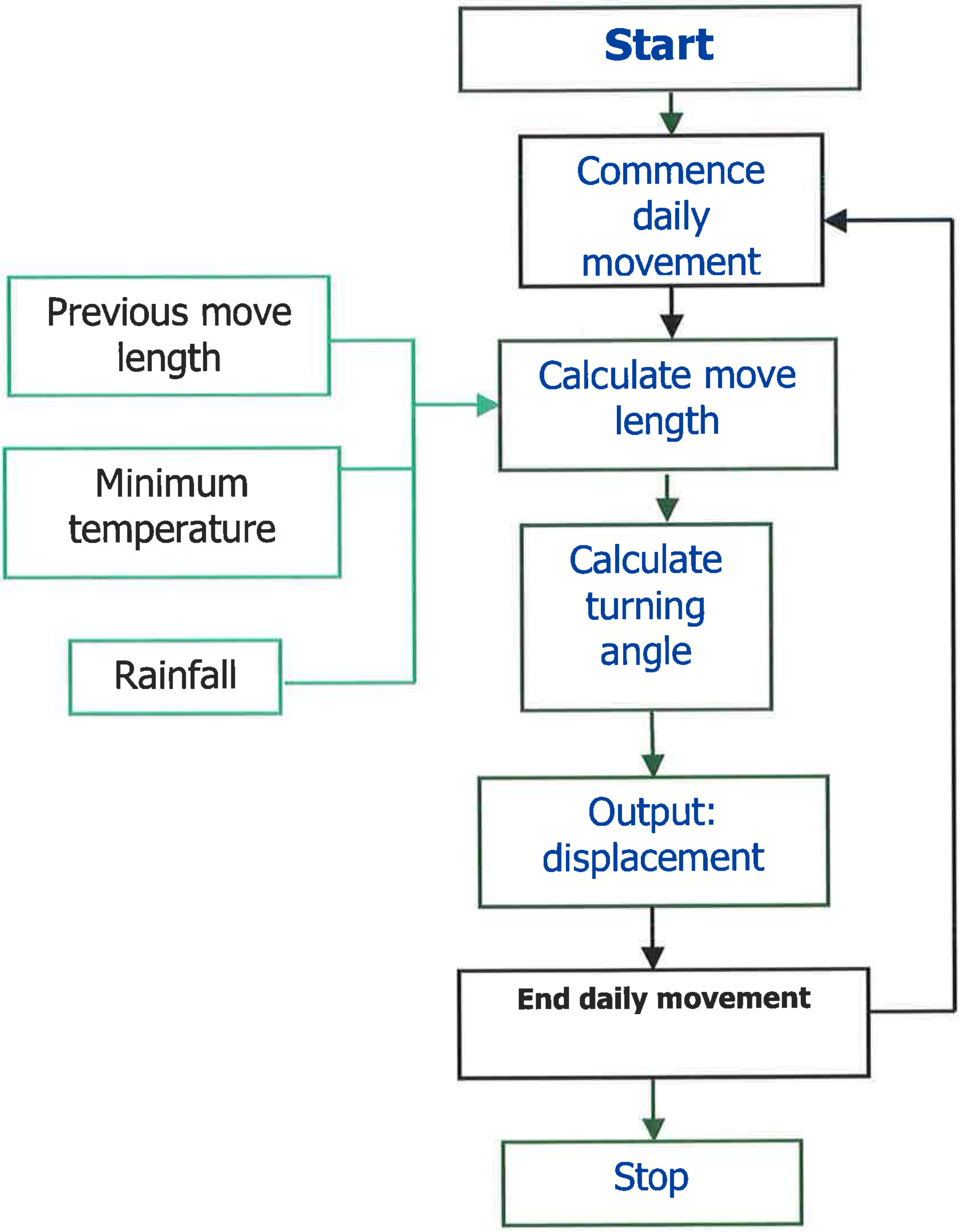

Figure 6.1. A flow diagram representing how the simulation model forecasts the movement length of adult *C. virgata* in barley, and how the parameters in the model are included.

Box 6.1. Simulation model, written in MATLAB. (Student version 5.3.0.14912a (R11) MathWorks, 1999), that forecasts movement length for adult *C. virgata* in a barley crop.

```
%snailnolnmove.m
%this program simulates the movement of snails

%**********currently setting it up for CV ADULTS in BARLEY*****************
%observed displacements for snails during june, july, sept trails combined
%mean=66.62, stdev=60.35, n=343

clear all;

%******************************************************************

%specifying user defined parameters
life = 10;    %this specifies the number of days over which we want to follow snail
movement
inds = 10 000   %this specifies the number of individuals for whom we simulate movement

%******************************************************************
%calculating snail movement
for snail = 1:inds;
  xx=0; %each snail starts at the origin and we follow movement from there
  yy=0;

%******************************************************************

  rand('state',sum(100*clock)); %seeds the random uniform distribution
  randn('state',sum(100*clock)); %seeds random normal distribution

%******************************************************************

  %SnailWeatherCorr: this subroutine generates sets of within-year,
  % auto- and cross-correlated (with one time step) for weather variables.

  %****************Subroutine Parameters**********************
  % parameters for min_temp and rainfall:
  weathmeans= [9.35, 0]; % means, zero is place-holder for rain
  weathvars=       [6.69, 0]; % variances (not standard deviations)
    % positive semi-definite matrix for within year correlations
  % (corrected if original was not good):
  corrin=...
    [1          -0.10;
    -0.10          1]      ;

      % then the auto- and cross-correlations for one step.
  % The form should be columns of v1(t), v2(t), etc...and rows of v1(t+1), v2(t+1), etc..
  % where v1(t) is  % weather variable 1 in year t
```

Box 6.1. cont

```
corrout=[...
      0.32            -0.02;
    -0.19       0.56];

    yrspan = 50;
  % this is the number of years of correlation info to use to simulate the correlation pattern
  % more years are better. 50 is quite accurate.
  tmax = 60;        % number of years of vital rates to simulate;

  %*********************************************************************

  np = length(weathmeans);
  results = [];
    %--------creating and using the big correlation matrix, M----
  % this set of loops makes the big correlation matrix (M) with multi-year correlations: the
% if statements are used to estimate the correct correlations with increasing time lags,
% always assuming that all long-time-lag correlations are only caused by within-year and
% one-time-step correlations
  for ii = 1:yrspan;
    for jj=1:yrspan;
      if ii==jj, litmx = corrin;
      else litmx =corrout; end;
      expo=1;
      if ii > jj, expo = ii-jj; litmx = (litmx)^expo; end;
      if ii < jj expo = jj-ii;  litmx = (litmx')^expo; end;
      for ip=1:np;
        for jp = 1:np;
          M(ip+np*(ii-1),jp+np*(jj-1)) = litmx(ip,jp);
        end; % jp
      end; % ip
    end; % jj
  end; % ii

  % get the eigenvalues for calculating the M12 matrix (here called zfull):
  [W,D] = eig(M); % getting the eigenvalues and vectors
    % now, a check for negative eigenvalues -- if you have them,
  % it sets negatives and small positive values = 0
  check = min(min(D));        % are the smallest eigenvalues negative?
  if check < 0
    %disp('The min eigenvalue is < 0. Eigenvalues are:')
    %disp(diag(D))
    %disp('hit enter to continue with approximation')
    pause
    maxneg = max(max(abs(D(find(D<=0)))));
    % maxneg is the largest negative eigenvalue
    D(find(abs(D<=maxneg))) = 0; % set the negatives = 0
```

Box 6.1. cont.

```
  %disp('Corrected eigenvalues are:')
  %disp(diag(D))
  newfullmx = W*newD*W'; % make a corrected matrix
  for ii=1:np % change from covariance’s to correlations
    for jj=1:np
      if newfullmx(ii,ii) ==0 | newfullmx(jj,jj)==0;
        newfullmx(ii,jj) =0;
      else
        newfullmx(ii,jj) = ...
          newfullmx(ii,jj)/((newfullmx(ii,ii)*newfullmx(jj,jj))^0.5);
      end;
    end;
  end;
  [W,D] = eig(newfullmx);
end; %check < 0

M12 = W*abs(D.^0.5)*W';       % the M^(1/2) matrix
sz = length(M12); % the total number of lines in M12

% get the lines from the middle of M12 to use to generate correlations
startcase = (round(yrspan/2)*np +1);
zvalold=real(M12(startcase:(startcase+np-1),:));
zvalnew=real(M12((startcase+np):(startcase+2*np-1),:));
clear M12 W D; % clearing memory
% zvalold and zvalnew are each one year of rows in M12

% to start the whole thing off, calculate a first set of
% normals, then multiply with zvalold to get correlated normals:
newns = randn(sz,1);
oldxy = zvalold*newns;
%-----end of: creating and using the big correlation matrix------

normresults = [];  weatherresults = [];

for tt=1:tmax % a loop to make multiple sets of rates
  %disp('time is'); disp(tt);
  %update the uncorrelated random normals
  newns = [newns((np+1):sz); randn(np,1)];
  % make the new set of correlated normals
  newxy= zvalnew*newns;
  normresults = [normresults; oldxy', newxy']; % save results
  oldxy = newxy;       % make the new correlated rates old

  % now convert correlated normals to the correct distributions for temp and rainfall

  temp = weathmeans(1)+sqrt(weathvars(1)).*newxy(1);

  %this codes rainfall as yes or no given that rains 34.7% of time
```

Box 6.1. cont.

```
        if stdnormcdf(newxy(2))<0.347; rain=1; else rain=0; end;
    %this puts the results in a matrix
    weatherresults = [weatherresults;temp, rain];

  end; % tt

  %this can be used to display info from subroutine and check its functioning
  %disp('the input correlations (all rates and one step')
  %disp('correlations) are:');
  %disp([corrin corrout';corrout,corrin])
  %disp('the correlations of the normals are:')
  %disp(corrcoef(normresults));
  %disp('the within-year correlations of the vital rates are:');
  %disp(corrcoef(weatherresults));
  %disp('the input means and variances were');
  %weathmeans, weathvars
  %disp('means and variances of the simulated rates are:')
  %meanrates = mean(weatherresults)
  %variances = var(weatherresults)
  %************************************************************
  %end of SnailWeatherCorr subroutine

    %pick an initial move length from the distribution of all move lengths
  %mean=29.48 stdev=42.107 n=1397
  %because move length can not be negative a normal distribution is not appropriate
  %and given the huge stdev many values would be negative with a normal distribution
  %therefore I use a stretched beta distribution with min=0, max=500
  %disp('initial movel picked from stretched beta')
  movel=stretchbetaval(29.48, 42.107, 0, 500, rand),


  %the initial direction that the snail takes is randomly selected
  rr=rand;
  dir = rr*360;

    for day =1:life;
    pmove=movel;
    temp=weatherresults(day,1);
    rain=weatherresults(day,2);
    movelength is then dependent on the climate parameters and previous movelength,
    aa = -12.03;        %coefficient for intercept
    bb = 6.04;            %coefficient for temp
    cc = 25.48;            %coefficient for rainfall
    dd = 0.615;            %coefficient for prevmove
    ee =  -7.405;        %coefficient for rf*temp
    ff = -0.289;        %coefficient for rf*pmove
```

Box 6.1 cont

```
  movel=aa+bb*temp+dd*pmove;
  if rain==0;
    movel=movel+cc+ee*temp+ff*pmove;
  else;
  end;

  if movel>0; movel=movel;
  else movel=0;
  end;

      %turning angle is picked from the distribution of turning angles
  ta=[15 45 75 105 135 165 195 225 255 315 345];
  fr_ta=[.07 .06 .07 .08 .09 .13 .1 .12 .09 .07 .07 .05];
  cumfr_ta=[.07 .13 .2 .27 .36 .5 .6 .72 .81 .88 .95 1];
  rr=rand;
  num_ta=sum(rr>=cumfr_ta)+1;
  tang=(num_ta*30)-15;

  dir=dir + tang;
  if dir>360; %compass direction can't be greater than 360 so have to correct for this
    dir = dir - 360;
  else
    dir=dir;
  end;

  %now take the movelength and direction to calculate new position after move
  xx = xx + movel*sin(dir);
  yy = yy + movel*cos(dir);

  %put these data into a matrix, rows contain: day, temp, rain, x, y, and movel
  dist(1,day)=day;
  dist(2,day)=temp;
  dist(3,day)=rain;
  dist(4,day)=xx;
  dist(5,day)=yy;
  dist(6,day)=movel;

  %this will display the day number as the program progresses
  %disp('day number=');
  %disp(day);
  day=day+1;

end;
%disp(dist);
displ=sqrt(xx^2+yy^2);
ddspl(1,snail)=displ;
meanres=mean(dist');
```

Box. 6.1.cont.

```
  disp('mean day, temp, rain, xx, yy, movel');
  disp(meanres);
  %this will display the number of a snail just completed so that we can track if the
 % program is proceeding

  snail=snail+1;
end;

disp('Final displacements');
disp(ddspl');
mdisp=mean(ddspl);
disp('mean displacement');
disp(mdisp);
```

The model output was analysed and graphed in Microsoft Excel for Windows 2000. Descriptive statistics were calculated for the output of the simulation models for days one through five. Further to this, a regression line was fitted to the mean, median and maximum values for days one through five. Based on the regression equation, predictions for displacement from the origin for adult *C. virgata* in barley are given for days 10, 20, 30, 60, 90 and 120.

In order to provide an initial validation of the simulation model, day five observed data were plotted against forecasted data. Displacement data for June, July and September 2002 data were combined and compared to the forecasted values from the model. These data were used because the variables entered into the model were based on the average for 2002 field data. Additionally, data from June, July and September 2002 adult *C. virgata* in barley for day five were compared to the forecasted values from the simulation model separately to examine the variation within the season.

6.3 RESULTS

6.3.1 Identification of factors that influence movement

Mixed model analyses were used to identify the climatic and non-climatic variables that were predicted individual snail movement. Adult and juvenile, *C. virgata* and *C. acuta*, in barley and medic were analysed separately, thus, there were a total of eight models produced (Table 6.2-6.9). The value for the intercept was not significantly different from zero for all analysis of movement, and therefore not presented in the tables.

The climatic variables that increased movement length of adult and juvenile *C. virgata* and *C. acuta* in barley and medic were minimum temperature and rainfall. Minimum temperature on its own was associated with the movement length of adult *C. virgata* in barley (Table 6.2) and medic (Table 6.3). However, the interaction between minimum temperature and rainfall were associated with movement by adult *C. virgata* in barley (Table 6.2); and adult *C. acuta* in barley (Table 6.4) and medic (Table 6.5). The interaction between minimum temperature and rainfall were also associated with the movement length of juvenile *C. virgata* in barley (Table 6.6), juvenile *C. acuta* in barley (Table 6.8) and juvenile *C. acuta* in medic (Table 6.9). That is, for all treatments across species, except for juvenile *C. virgata* in barley (Table 6.7), minimum temperature was positively associated with movement length.

Temperature and rainfall were associated with the population dynamics of adult *C. virgata*, *C. acuta* and *T. pisana* (see Chapter 3). It was therefore expected that these factors would be related to snail movement. Snails require moisture for activity. Additionally, snails are exothermic, and therefore dependent on temperature for movement. It therefore follows that cooler minimum temperatures would limit snail activity, whereas warmer minimum temperatures would increase this. Interactions between minimum temperature and rainfall are also expected to drive snail movement as these variables are often correlated with each other.

Non-climatic variables were also used to forecast movement of *C. virgata* and *C. acuta*, however, these factors often interacted with rainfall. Previous movement length, or the interaction between previous movement length and rainfall or turning angle, were associated with each of adult and juvenile *C. virgata* and *C. acuta* in barley and medic (Tables 6.2-6.9). Previous movement length was correlated with the movement length of adult *C. virgata* (Tables 6.2 and 6.3) and *C. acuta* (Tables 6.4 and 6.5) in barley and medic. Previous movement length was positively associated with movement of juvenile *C. virgata* in barley (Table 6.6), and *C. acuta* in barley (Table 6.8) and medic (Table 6.9). The fact that previous movement length was associated with movement of snails indicates some snails are generally more active than others. Similarly, the interaction with rainfall indicates that rainfall drives movement, and that more active snails are more likely to move greater distances with rainfall than those that are less active.

The interaction between previous movement length and turning angles explain dispersal of adult *C. acuta* in medic (Table 6.5) and juvenile *C. acuta* in barley (Table 6.8). It is vital to remember that movement data were taken on a daily basis, and therefore dispersal data represent displacement from the origin each day, rather than incorporating movement across all days.

The climatic and non-climatic factors associated with dispersal, that were consistent between adult and juvenile *C. virgata* and *C. acuta*, and between medic and barley, were temperature, rainfall, previous movement length and turning angles. However, the combinations of variables and the association between these variables and movement length differed for adult and juvenile *C. virgata* and *C. acuta*, and between medic and barley. Therefore, species, age classes and habitat type need to be assessed separately, and separate models are required for each. The simulation model presented in this chapter was based on adult *C. virgata* in barley.

Table 6.2. Solution for fixed effects from mixed model analysis on the factors that were associated with the movement length of adult *C. virgata* in a barley crop in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Minimum air temperature (°C)	6.04	997	1.93	0.0035
Rainfall	25.48	997	8.93	0.0046
Previous movement length	0.62	997	12.7	<0.0001
Minimum air temperature x Rainfall	-7.41	997	10.11	<0.0001
Previous movement length Rainfall	-0.29	997	14.24	<0.0001

Table 6.3. Solution for fixed effects from mixed model analysis on the factors that were associated with the movement length of adult *C. virgata* in medic in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Rainfall	29.33	814	8.32	<0.0001
Minimum air temperature	1.83	814	12.70	0.0008
Previous movement length	0.38	814	3.37	<0.0001

Table 6.4. Solution for fixed effects from mixed model analysis on the factors that were associated with the movement length of adult *C. acuta* in a barley crop in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Rainfall	-19.79	521	-6.71	<0.0001
Minimum air temperature x rainfall	2.82	521	8.23	<0.0001
Previous movement length	0. 35	521	10.16	<0.0001

Table 6.5. Solution for fixed effects from mixed model analysis on the factors that were associated with the movement length of adult *C. acuta* in medic in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Minimum air temperature x no rainfall	1.94	319	2.48	0.0135
Previous movement length x previous turning angle	0.0005	319	2.18	0.0298

Table 6.6. Solution for fixed effects from mixed model analysis on the factors that were associated with the movement length of juvenile *C. virgata* in a barley crop in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Minimum air temperature x rainfall	0.37	101	0.25	0.0232
Previous movement length x previous turning angle	-0.00186	101	-3.91	0.0002

Table 6.7. Solution for fixed effects from mixed model analysis on the factors that associated with the movement length of juvenile *C. virgata* in medic in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Previous movement length	0.020	37	1.96	0.0477
Mean air temperature	24.07	37	3.34	0.0019
Mean soil temperature	-80.85	37	-4.69	<0.0001
Previous turning angle	0.12	37	3.37	0.0017

Table 6.8. Solution of fixed effects from mixed model analysis on the factors that were associated with the movement length of juvenile *C. acuta* in a barley crop in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	t	P > |t|
Minimum air temperature x rainfall	0.70	101	0.38	0.0426
Previous movement length	0.355	101	3.28	<0.0014

Table 6.9. Solution for fixed effects from mixed model analysis on the factors that were associated with the movement length of juvenile *C. acuta* in medic in 2002 at Minlaton, Yorke Peninsula, South Australia.

Effect	Estimate	DF	*t*	P >|t|
Minimum air temperature x no rainfall	-0.18	44	-0.07	0.0261
Previous movement length	0.49	44	5.69	<0.0001

The simulation model forecasts movement length of *C. virgata* using the variables that proved to be significant in the statistical model (Table 6.2). In order to show how the simulation model forecasts adult *C. virgata* movement, a range of minimum air temperature and previous movement length scenarios are given (Table 6.10), either with or without rainfall. Of the scenarios presented, the greatest movement is predicted when minimum air temperature is 8°C and rainfall occurs. The same temperature and previous movement in the absence of rainfall however yields a forecasted movement length of 0 cm.

Table 6.10. Forecasted movement length based on the variation of previous movement length, minimum temperature and rainfall.

Previous movement length (cm)	Minimum temperature (°C)	Rainfall?	Forecasted movement length (cm)
31.6	4	No	5.0
31.6	4	Yes	44.4
31.6	8	No	0
31.6	8	Yes	81.7
60	8	No	9

6.3.2 Simulation model

The displacement curve generated by the simulation model increased with each consecutive day (Figure 6.2). Half of the individuals in the simulation were forecasted to remain within 20 cm of their origin on day one, 30 cm on day two, 40 cm on day three, 50 cm on day four and 60 cm on day five (Table 6.11). The reason for such large movement on day one relative to day two is because on day one, there are no turning angles involved. Therefore, the displacement on day one is their movement measured in one direction. However, on days two through five, displacement would include the effects of turning angles, hence would include *C. virgata* not dispersing from the origin in one direction. With each consecutive day, the distribution of displacement of *C. virgata* from the origin increased (Figure 6.2).

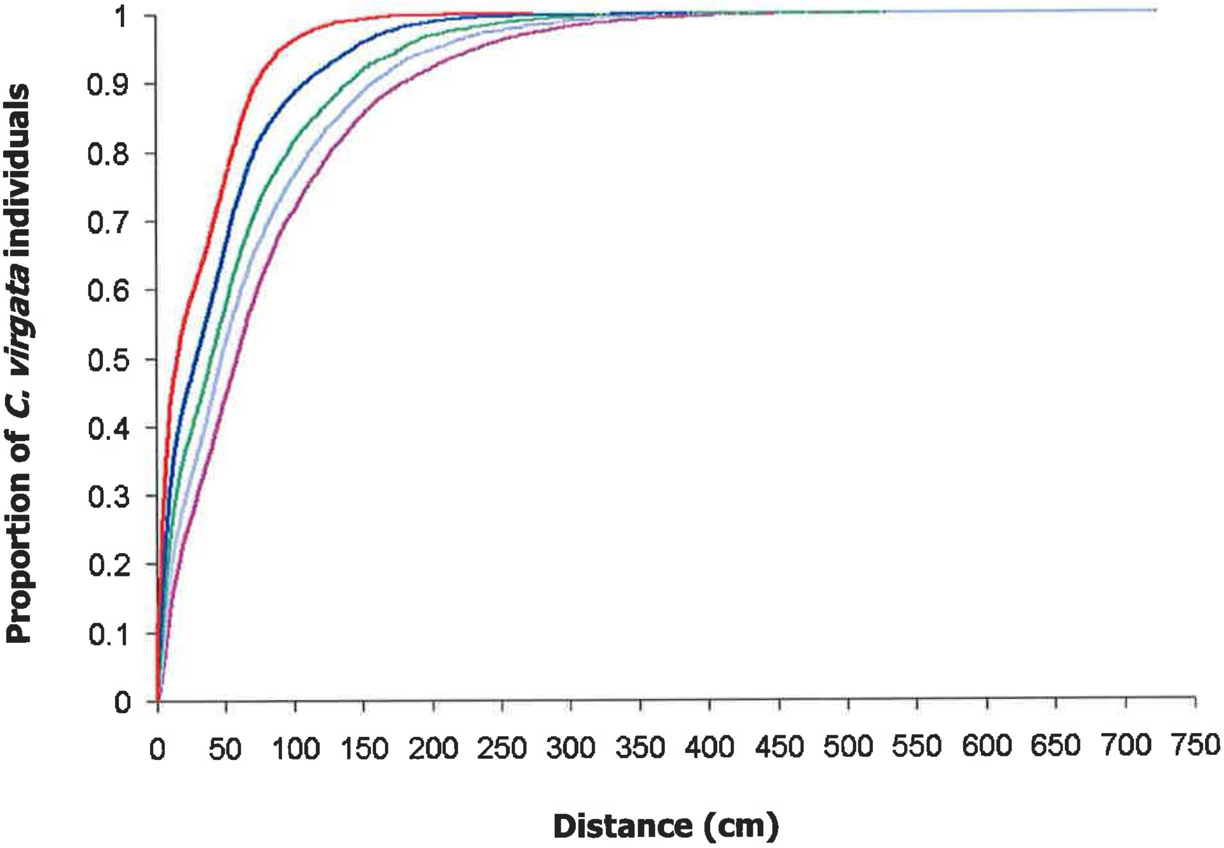

Figure 6.2. Forecasted proportion of individual adult *C. virgata* in barley, within a given distance at day 1 ▬ day 2 ▬ day 3 ▬ day 4 ▬ and day 5 ▬. n = 10 000.

Table 6.11. Forecasted proportion of adult *C. virgata* in barley, forecasted to be within given distances from origin. n = 10 000.

Distance moved (cm)	Proportion of total individuals				
	Day 1	Day 2	Day 3	Day 4	Day 5
5	29.16	19.13	13.77	9.39	6.23
10	43.63	31.63	24.24	18.82	13.96
20	54.96	43.47	35.76	28.82	23.49
30	61.59	50.78	42.79	36.22	30.49
40	68.75	58.24	50.32	43.93	36.95
50	76.03	66.33	57.47	52.35	44.40
60	83.01	73.48	64.39	58.76	51.14
70	88.87	79.24	70.24	64.78	57.97
80	92.26	83.31	74.84	69.17	63.31
90	94.73	86.10	78.19	72.88	68.22
100	96.19	88.44	81.48	76.36	71.35
150	99.30	95.90	91.82	88.67	85.15
200	99.84	98.92	96.9	94.75	92.13
250	99.97	99.65	98.69	97.55	96.12
300	.	99.86	99.50	98.98	98.18
350	.	99.94	99.81	99.55	99.60
400	.	.	99.91	99.87	99.65
450	.	.	99.99	99.94	99.90
500	.	.	.	99.96	99.95

The forecast mean displacement for adult *C. virgata* in barley increased with each consecutive day (Table 6.12). Kurtosis values greater than 1.223 indicate that a distribution has more concentration around the mean and / or the 'tails' far from the mean (Zar, 1999), as was the case for the predicted mean displacement of adult *C. virgata* released in barley. For each day, the simulation model forecasts that a proportion of snails would be found at the release point. This is because the curve was truncated, as the model set all movement lengths to greater than, or equal to zero to prevent negative movement lengths occurring. However, the maximum displacement increased with each consecutive day. The median value was lower than the mean, therefore only a few snails dispersed over greater distances.

Table 6.12. Descriptive statistics for the forecasted displacement for adult *C. virgata* in barley over five days obtained from simulation model.

	Day 1	Day 2	Day 3	Day 4	Day 5
Mean (cm)	29.2124	43.3354	56.8442	67.0383	78.6539
Median (cm)	15.2494	28.9137	39.6492	46.9038	58.3593
Standard deviation	32.9366	47.6135	59.7155	67.4296	75.0934
Kurtosis	3.6893	4.7193	3.8911	4.4679	3.7690
Minimum (cm)	0	0	0	0	0
Maximum (cm)	272.61	387.56	522.45	721.01	722.15

To determine whether this model could be used to forecast displacement of adult *C. virgata* in barley, empirical data of displacement on day five were plotted against forecasted data for day five. The distribution of forecasted displacement at day five was greater than that measured in June (Figure 6.3), however, the actual distribution of adult *C. virgata* in barley in September was greater than the forecast. The actual and forecasted distribution of displacement for *C. virgata* in July were similar (Figure 6.3). This variation may be explained by temperature and rainfall differences over the season relating to movement of *C. virgata*. Actual June temperature data were lower than that given in the model, as the model used the average over the season. However, in September, temperatures were higher than the average for the season, which may explain the greater distribution of displacement observed.

As the parameters of the simulation model were based on the average over the season, actual displacement data for these snails for June, July and September were combined, and plotted against forecasted data for day five (Figure 6.4). This then resulted in the forecasted distribution of displacement fitting the empirical data for day five. However, the maximum forecast displacement at day five was greater than the observed displacement at day five over each of the releases, indicating that the frequency of turning angles in the field differed from that forecast by the model. It is important to remember however, that only a few individuals reached the maximum distances, and the forecasted distribution is perhaps more informative than the dispersion of a few individual snails.

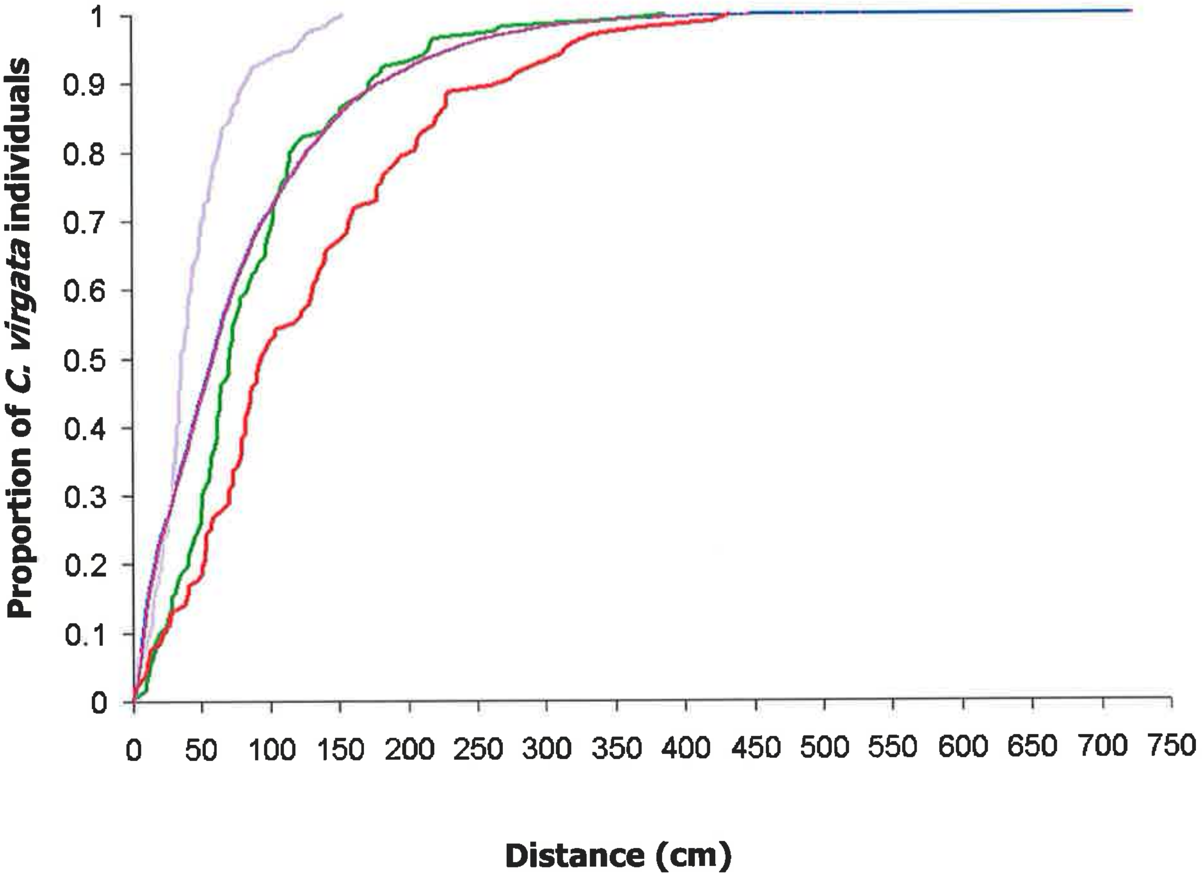

Figure 6.3. Forecasted proportion of observed displacement in June 2002 —; July —; and September 2002 —; and forecast — individual adult *C. virgata* in barley, at day 5.

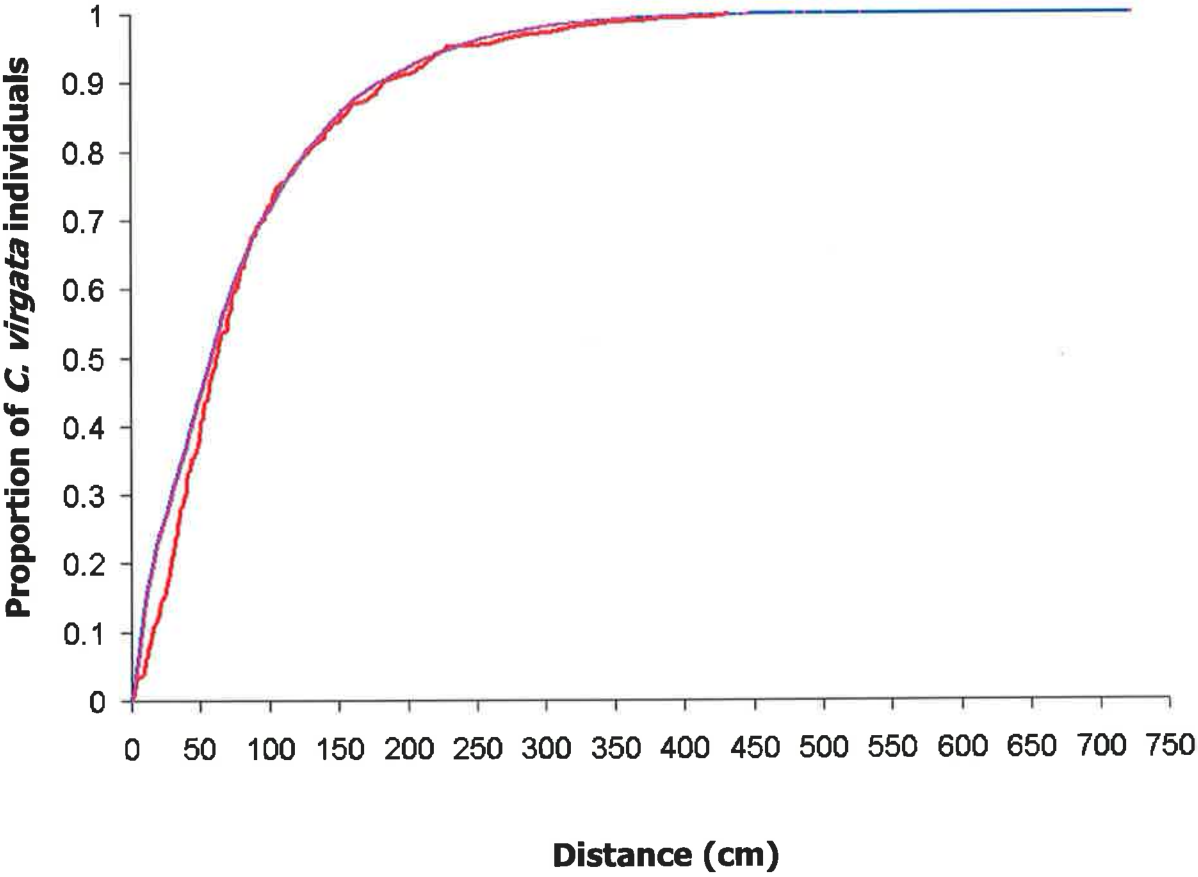

Figure 6.4. Forecasted proportion of observed 🟥 and forecast 🟦 individual adult *C. virgata* in barley, at day 5. Observed data from June, July and September 2002 releases combined.

6.4 DISCUSSION

6.4.1 Factors that are associated with dispersal

It is difficult to define precisely the environmental factors that explain land snail distribution (Labaune and Magnin, 2001). In general, factors identified as determinant in snail movement are climate (temperature, rainfall, humidity; Cameron 1970a, b, c; Jaremovic and Rollo, 1979; Labaune and Magnin, 2001), vegetation and soil (pH, calcium content and texture; Labaune and Magnin, 2001), and photoperiod (Cameron, 1970a, b, c). Terrestrial mollusc behaviour is tightly controlled by environmental conditions (Waite, 1987), and given their reliance on maintaining water balance, it is not surprising that in this study, temperature and rainfall were associated with snail movement.

The plant habitat, barley or medic, into which the snails were released, was associated with the movement length of adult and juvenile *C. virgata* and *C. acuta*. Plant habitat has been shown to exert considerable effect on the dispersal of the land snails *Sitala jenyns* (Kasigwa, 1999a, b), *Cepea nemoralis* (Tilling, 1985a, b) and *T. pisana* (Johnson, 1981). In the case of *S. jenyns*, this was attributed to feeding preferences and the edibility of the plants (Kasigwa, 1991). Additionally, the rates of snail dispersal were reduced in shrub habitats, because in such vegetation the snails covered long distances three-dimensionally, however, dispersal was enhanced in short grasses (Kasigwa, 1999a, b). The effects of temperature, rainfall and humidity are also likely to vary according to plant habitat. Soil moisture, and relative humidity may be better retained in a barely crop than in grazed medic.

Dispersion was measured daily, so it is likely that actual movement between measurements would have been greater than that recorded. If an individual snail dispersed in one continuous direction from their previous position, then its net displacement would be greater than if it turned several times during the day between measured 'steps' around their previous point. Over five days, the variables that were associated with individual snail movement on a finer scale were not investigated, and therefore variables that initiate movement are not part of the statistical model. However, the aim was to measure dispersal on a daily basis, so that those variables that were associated with movement on a daily basis could be used as parameters in a simulation model. From this, farmers can forecast population displacement over a season, and plan control measures based on the forecasted displacement of the population.

Some general patterns emerged when examining the variables that related to movement length of adult and juvenile *C. virgata* and *C. acuta* in barley and medic. Minimum air temperature and rainfall, either individually or as part of an interaction were the climatic variables that were associated with snail movement across the species, age-classes and habitat types. Minimum temperature was positively associated with adult *C. virgata* but was negatively associated with *C. acuta.* Minimum temperature did not explain juvenile *C. virgata* and *C. acuta* movement. Rainfall on its own was associated only with adult *C. virgata*. However, when combined with minimum temperature or previous movement length, was significantly associated with snail movement length. Snail behaviour differed significantly between species, age and plant type. Therefore, the timing and application of different control measures must be adjusted to target individual snail populations. The climatic variables that were associated with movement length of juvenile *C. virgata* in medic were different from those that explained movement length in *C. acuta* or adult *C.*

virgata. Movement length was associated with mean air temperature and mean soil temperature. In addition, the non-climatic variables that were associated with movement length of juvenile *C. virgata* in medic were previous movement length and previous turning angle. This shows that juvenile *C. virgata* in medic may be driven by different stimuli than for adult *C. virgata*, *C. virgata* in barley, and *C. acuta*.

Previous studies have indicated that weather factors affect the nocturnal cycle of snail activity (Barnes and Weil, 1945; Pomeroy, 1967). Minimum temperature was found to be a limiting factor in movement for some snail species (Labaune and Magnin, 2001). Over winter in England, falling temperatures stimulate the movement of slugs including *Deroceras reticulatus* (Dainton, 1954a, b) and *Arion ater* (Karlin, 1961; Lewis, 1969a; b; Dainton and Write, 1985). Falling temperatures in winter in England can induce hibernation of *Helix aspersa* (Bailey, 1981) and thus limits movement. Conversely, slug activity has been found to be greatest on warmer nights (Barnes and Weil, 1945; White, 1959).

Moderate to heavy rainfall has been shown to affect snail dispersion rates (Cameron, 1970a, b), and snails are more likely to be active and move greater distances on rainy nights than dry nights (Murphy, 2002). Dry weather, through its generally high evaporative potentials, causes the snails to become quiescent rather than remain active (Cameron, 1970a, b). Thus, as *C. virgata* is nocturnal (Pomeroy, 1967; 1969) it would be expected that it would be more active on a rainy night than on a dry night. The activity of *T. pisana* increased with rainfall, and these snails may be active during the day if there is sufficient rainfall at this time (Nevo and Bar, 1976). Additionally, the Australian land snail *Hedleyella falconeri* was more active and moved further in wet weather than in dry weather (Murphy, 2002). While the amount of rainfall in this present study was not found to be a good indicator of snail movement, classifying rainfall as heavy, moderate or light might be relevant in further models. This measure of classification however is rather subjective, and it is more likely that it is soil moisture, which is dependent on rainfall, that was associated with snail movement, and the distance moved by snails. Similarly, slug activity is highly dependent on sufficient soil moisture (Speiser and Hochstrasser, 1998).

Statistical models showed that the interaction between and within climatic and non-climatic variables were associated with movement length of adult and juvenile *C. virgata*. This interaction was not surprising given that variables are often interrelated (Goodfriend, 1992). In the case of adult *C. virgata* in barley, for which the simulation model was written, the variables were not only interrelated, but also were correlated with each other. *C. virgata* moved further when minimum temperatures were warmer (e.g. 8°C compared to 4°C) and there was rainfall. Additionally, if the weather in the model was set at 8°C and there was no rainfall, then the movement was negatively affected. Cameron (1970a, b, c) found that the locomotary activity of the land snail, *Arianta arbustorum* occurred only under particular physical conditions. Decreased activity of three species of land snails, *Cepea nemoralis*, *C. hortensis* and *Arianta arbustorum* have been shown to be correlated with increasing temperature (Cameron, 1970a). Similar results were found with the activity of slugs including *D. reticulatus* (Dainton, 1954a) and *Arion ater* (Lewis, 1969b). Welby, (1964) demonstrated that slug activity was correlated with night air temperature, rainfall and wind speed, but not relative humidity. However, Kasigwa (1999a) found that there was a positive correlation between land snail dispersal and humidity.

Turning angles, directions of heading and previous movement length have rarely been included in models that forecasts movement. This is surprising, as the statistical models in this study showed that turning angles and previous movement lengths were important variables that were associated with movement length of the snails. Previous movement length, as a predictor of snail dispersal, may indicate the tendency for particular snails to move further than other snails. While knowing previous movement length assists in improving the accuracy of the simulation model, it is not a useful indicator for the farmer or agronomist, who are concerned with population spread more than individual spread.

6.4.2 The simulation model

Simulation modelling of pest populations can be a powerful tool in investigating the management of pest species, and has been used for a variety of pests including the almond moth *Cadra cautella* (Thorne et al, 1998), the bostrichid *Prostephanus truncatus* (Meikle et al 1998), the strawberry bud beetle *Anthonomus signatus* (Bostanian et al, 1999), and the field slug *Deroceras reticulatum* (Shirley et al, 2001).

An essential part of developing a model is testing the model against empirical data (Englund and Moen, 2003). The observed displacement at day five of adult *C. virgata* in barley closely fitted the forecasted curve when all data were combined. This shows that the simulation model developed in this chapter is a good indicator of average adult *C. virgata* movement in barley on the Yorke Peninsula. The fact that this model fits the observed data confirms that the mechanisms included in this model were sufficient to explain the observed displacement. However, as the model was compared to the data that was used to parameterise it, this model could not necessarily be used to predict other populations.

Further validation of this model would include testing the present model against the mass-mark release study conducted in 2001. The environmental simulation model generated a set of weather parameters appropriate to the location on the Yorke Peninsula, and the average climatic conditions over the season. However, when comparing empirical data from each release separately, the distribution of displacement of adult *C. virgata* in barley differed between releases. This suggested that a farmer or agronomist wishing to forecast movement over a shorter period of time, for example over six weeks, could end up with either an over-estimation or under-estimation of the displacement of adult *C. virgata*. However, longer-term predictions of *C. virgata* movement, such as their displacement at the end of their active season with respect to their aestivation sites at the beginning of their active season, indicate that the model could be used to accurately forecast movement (April-September). Similar models could be developed to predict the displacement of adult *C. virgata* in medic, juvenile *C. virgata* in barley and medic, and (of) adult and juvenile *C. acuta* in barley and medic.

Simulation models have a number of problems associated with them. 'Models are constructions of knowledge and caricatures of reality' (Beissinger and Westphal, 1998). The representation and accuracy of background information and assumptions need to be assessed. In the present model each weather variable was based on the average for the season, and not varied according to the changes within the breeding season. Obviously temperature and rainfall vary between autumn, winter and spring. Additionally, there was no consideration for control measures or land use practices, which would obviously influence movement. The model did not consider reproduction, disease or mortality, nor changes in life stages of *C. virgata*. Moreover, some basic facts about movement on a finer scale are not known. However, the model developed in this study should approximate dispersal of field populations of *C. virgata* within an order of magnitude or less.

6.4.3 Wider implications

Invertebrates impact on humans in part, through their effects on crops and diseases. Therefore, predicting pest activity in crops is one of the most practical means of management (Shirley et al, 2001). The ability to make quantitative predictions based on the interdependence of two variables is a central theme in ecology (Scharf et al, 1998). There is no disputing that diffusion approximations can effectively describe the redistribution of populations that arises as a result of animal movement (Okubo and Levin, 2002). However, to forecast the displacement of adult *C. virgata* in a barley crop, a more complex simulation model was required.

Forecasting pest abundance and its timing is considered central to aspects of integrated pest management (Dent, 1991). The results from the mixed models and the simulation models showed that temperature and rainfall are important stimulants of movement. Farmers can use this model to determine the risk of a snail population moving certain distances into a crop. Based on this information, they can then apply more strategic control measures to decrease the risk of contamination. In addition, information from the models can be used to ascertain longer-term snail dispersal, such as whether or not a population will disperse into an adjacent field (see below), which could aid in the development of more optimal control strategies against these populations.

The forecasted distribution of adult *C. virgata* in barley over five days can give rise to information on forecasted displacement at larger time intervals. While the mean net displacement increased with each consecutive day, the standard deviation was very large for each day. The kurtosis and skewness for the curves for each day were very similar, suggesting that the distribution of the snails did not change greatly over the five days. Forecast displacement based on the regression analysis from the model output showed that the mean displacement was greater than the median displacement (Table 6.13). Therefore, while the mean displacement for adult *C. virgata* in barley after one month (≈ 30 days) is 3.86 metres, half of the snails would have displaced within 2.15 meters. However, a farmer would need to take into consideration the maximum displacement of 13.88 meters. Implications of this might mean that a farmer could forecast that while half of the snails would move 2.15 meters in a month, individual snails could move over 13 meters. If only a few snails made it this far, and were not breeding, then this would not be an issue. However, if these snails were breeding, they could produce many eggs (up to 400 eggs per snail (V. Carne unpublished results)) and thus pose a serious threat to crops either at the end of the season, or in the following season.

To look at the longer-term consequences of displacement, it is realistic to compare displacement at the beginning and end of their active season (Table 6.13). It is reasonable to assume that a large population of snails will have the same origin at the beginning of the breeding season, as they aggregate on posts and trees (on perimeters of paddocks) during their aestivation immediately prior to breeding season. As an example: if a population (of several hundred) of snails are on a fence post at day zero, a farmer could use this model to forecast that by harvest, at time 120 days, half of the adult *C. virgata* would have moved 12.57 meters, but average displacement of the population would be 14.89 meters. The farmer should also take into consideration that the outliers could move up to 149.45 meters, well into a crop, and thus pose the greatest threat at harvest. This model does not take into account any driving stimulus that may drive movement in a more directional way than is included in the model. That is to say, that the snails may move faster and more directionally towards the crops from the origin, and then, once inside the habitat, move in the way the model forecasts. This is because the model was developed based upon data obtained from movement of adult *C. virgata* already in a barley crop.

Table 6.13. Forecasted mean, median and maximum displacement of adult *C. virgata* in barley at days 10, 20, 30, 60, 90 and 120. Forecasts based on a regression analysis from the descriptive statistics derived from the simulation model.

Day	Mean (cm) $y = 12.259x + 18.241$	Median (cm) $y = 10.421x + 6.5521$	Maximum (cm) $y = 123.25x + 155.4$
10	141	59	1388
20	263	111	2620
30	386	215	3853
60	754	319	7550
90	1122	632	11248
120	1489	1257	14945

This model highlights the non-normal distribution of snail displacement over each day, and confirms what was observed with the real data in that movement length does not follow a normal distribution. There are often other species present in the same fields at the same time, which may have different responses to environmental factors, and therefore complicate decisions about the timing of snail control. There has been considerable interest in attempting to identify the most effective time to apply control measures to obtain the maximum reduction in the snail populations. The model developed here may have some utility in planning control strategies. The application of molluscicides requires careful timing and at times, strategic application. At 5 kg / hectare, based upon bait size and active ingredient, 10-12 bait points are recommended per square meter (M. Leyson, pers. comm.). Therefore, these bait pellets should be applied when snails will be active such that they move far enough that they will encounter a bait pellet. Baits degrade at varying rates depending on bait type, size and climatic conditions. Thus, if snails are not active when baits are applied, then the baits may be less effective when snails are stimulated into activity and encounter a bait pellet. Furthermore, the model could be used to determine whether strategic baiting, ie, baiting around populations; or broadacre baiting would be more effective given the forecasted population distribution.

There are relatively narrow windows of opportunity for snail control. This is when adults are active, but they should be targeted before they lay eggs for optimal control. Additionally, baiting must be applied at least six weeks before harvest in order to prevent contamination (G. Baker and D. Hopkins, pers. comm.). For most farmers this means identifying the seasons or stages in the cropping cycle when control will be most effective. Models that predict slug activity in the short term (Young et al, 1991) have shown that molluscicidal usage can be reduced by using such models to optimise control methods (Young et al, 1993). The results from the simulation models developed in the present study can also be used to aid farmers to strategically bait snail populations early in their active season when snails are more aggregated at fence lines or roadsides. From the point of view of pest management, timing needs to be linked to optimal phases in the population cycle of the pest (Shirley et al, 2001).

Simulation models of snail dispersal, a result of cumulative daily movement, could serve as an aid to farmers in making management decisions (Byrne et al, 2002). By using information derived from Table 6.13, it can be ascertained how far half of the snails will have moved over a given time, and also the maximum distance that *C. virgata* in barley would be expected to have moved. Strategic baiting early in the snail's active season, when snails are aggregated at fence lines and roadside, or after a catastrophic control measure, such as a hot burn, could decrease the risk of snails dispersing into fields and thus, the risk of contamination.

CHAPTER VII

GENERAL DISCUSSION AND FUTURE RESEARCH

7.1 INTRODUCTION

Gastropod mollusc species currently constitute some of the most significant and intractable threats to sustainable agriculture (Barker, 2002). Their pest status has increased in temperate regions, as a result of cultivation of new crops, intensification of agricultural production systems, and spread through human activities (Barker, 2002).

The main aim of this study was to gain a better understanding of the behaviour and ecology of Mediterranean snails in southern Australia in order to provide input into developing optimal control measures against these pests. This was done in three stages: *firstly*, the factors that may affect the population ecology of the snails were examined (Chapter 3); *secondly*, the breeding behaviour of *C. virgata* under different soil type and soil moisture conditions was investigated (Chapter 4); and *thirdly*, the dispersal and factors that affect movement of adult and juvenile *C. virgata* and *C. acuta* were studied throughout their active season (April through October) (Chapters 5 and 6). In this general discussion, I will summarise the key findings of the research and discuss their implications in a broader context.

7.2 PROJECT OVERVIEW

Stage 1 Population ecology of *Cernuella virgata, Cochlicella acuta* and *Theba pisana*

Forecasting pest abundance can assist in the implementation of effective integrated pest management (Dent, 1991). Statistical models can provide a useful tool in predicting pest population pressure. If successful, they can highlight the factors that influence snail populations, and farmers can implement control measures based on predicted densities. However, if the predictors of population densities are inconsistent or contrary across sites, as was the case for the populations that were monitored on the Yorke Peninsula (Chapter 3), then they are of little practical use to farmers.

Twenty years of population data provided a unique opportunity to study the population dynamics of Mediterranean snails on the Yorke Peninsula, however, the data were not collected with this purpose in mind, and therefore, there were several limitations with the data set. Even at a local level the models developed in chapter 3 are unlikely to be accurate predictors of snail population densities as they may not be consistent for the particular sites. That is, would the results have been different had snail population densities been measured some time later or if the data from some years was excluded? Land management practices should also be incorporated into these models, however, this could be difficult to achieve as these systems are constantly evolving, and often reflect a reaction to a pest problem. Furthermore, this information was not available to incorporate into the statistical models.

Different snail- and crop- age classes would alter snail population densities included in the counts with variation between sites being dependent on habitat and location. While temperature may remain relatively similar across sites, rainfall and soil moisture can vary over very short distances. Habitat, slope-aspect and latitude all have an effect on soil moisture, which influences breeding and egg-laying (Baker, 1989; Carter and Baker, 1997a, b). Snails are likely to breed earlier at sites where there is an earlier onset of rainfall than at sites with lower or a later onset of rainfall (Chapter 4). Thus, as the snail counts were all conducted within a day of each other, it is probable that a population at one site may have been comprised predominantly of larger individuals (> 6 mm), while populations at the other site could have been comprised predominantly smaller individuals, which therefore would be excluded from the counts. Additionally, mortality may be greater where snails are exposed to longer hours of sunlight where moisture is lower.

Migration is another factor that must be considered when examining snail population densities between seasons and years. Snails move from a pasture into a crop in spring and from fence lines and road edges into the field after the opening rains (Baker, 1989; 2002). Furthermore, a population of adult *C. virgata* in a barley crop disperses an average net distance of 7.5 meters over a two-month period (Chapter 6); however, this study has shown that individuals can disperse up to ten times this distance. Therefore, not only is the habitat on which the snails were counted important, but also the adjacent habitats. A field that is adjacent to a roadside or pasture is likely to have different density fluctuations than those that are adjacent to cropping fields.

Stage 2 Breeding behaviour of *Cernuella virgata*

Soil type and moisture play an important role in the breeding behaviour of *C. virgata*. The incidence of egg-laying was greater in the non-calcareous soil than in the calcareous soil. This is intriguing as the snails were collected from a soil type similar to the calcareous soil and the distribution of *C. virgata* in southern Australia is closely related to available calcium (Pomeroy, 1967). The effects of the physical characteristics of the soil on egg-laying should also be considered (Baker and Hawke, 1990), such as pore and particle size of the soil. K. Davies and S. Charwat (pers. comm.) showed the importance of the quality of organic matter for oviposition, with *C. virgata* laying eggs in soil that had not been heat sterilised, but not on soil that had. The number of egg-clusters laid by *C. virgata* was greater in moist soils than in dry soils. Additionally, egg-laying started earlier in the moist soils, therefore, those sites that have higher rainfall, or those habitats that have higher soil moisture retention are likely to have larger snail numbers.

The effects of weather on snail breeding behaviour can have important consequences for grain farmers. The risk of grain contamination in spring is predicted to be greater following a relatively wet autumn and spring. However, late rains may lead to snails breeding later in the season, and thus, juveniles arising from later breeding are likely to be smaller at the time of the harvest, and thus, present a greater contamination risk. Juvenile snails are harder to separate from grain heads than are adults, therefore they pose a greater threat of grain contamination at harvest.

Stage 3 Dispersal

Directed movement has been observed in many land snail species (Edelstam and Palmer, 1950; Wolda, 1963; Pollard, 1975; Peake, 1978; Johnson, 1981; Livshits, 1985; Baur and Gosteli, 1986, Baker, 1988b; Baker and Vogelzang, 1988). Dispersal studies showed that movement of adult *C. virgata* and *C. acuta* populations was biased, however, the direction of movement on a given day varied between species and habitats (Chapter 5). Furthermore, direction of heading varied within species between days and releases. It was apparent that external factors were driving these movements, but the nature of these factors remains unknown. The concentration of organic matter, and applied chemicals, and the orientation and compaction of rows, and the interaction of these variables with climatic variables such as rainfall, and temperature are likely to affect the dispersal of *C. virgata* and *C. acuta,* and should be investigated further.

It has been suggested that snails sometimes move towards a particular landmark, such as a fence post, or an aestivation site (Baker, 2002). Peake (1978) suggested that gastropods can move towards shapes such as trees and shrubs that are silhouetted against the sky at night, and Zanforlin (1976) showed that *T. pisana* moved towards large objects in the laboratory. However, these factors were unlikely to have been a particular large-scale landscape feature since the biased directional movements of *C. virgata* and *C. acuta* were not persistent. The habitat in which snails were released, particularly the tall canola and barley, precluded visual orientation to landmarks, so it is unlikely that snails would have been able to see past their habitat whilst on the ground. It is likely that small-scale environmental structure, that is, the alignment of crops, and the results of this influence the biased movements of these snails (Chapter 5).

The investigation of how and why juvenile *C. virgata* and *C. acuta* disperse addressed an important gap in Mediterranean snail ecology (Chapter 5). Juvenile snails moved greater distances than adults in September, which is consistent with obvservations for *C. virgata* by Pomeroy (1967). However, other studies have found that juvenile snails are less efficient than adults in locating different attractants or food sources, which has been attributed to a lower velocity of smaller snails (Madsen, 1992; Abd El-Hamid, 1996). Therefore, juvenile snails need to be carefully and strategically monitored and managed to decrease the risk and severity of crop contamination.

Climatic factors have been found to drive movement in other land molluscs, in particular, temperature (White, 1959; Welby, 1964; Reichardt et al, 1985) and moisture (Barnes and Weil, 1944; Rollo, 1991; Murphy, 2002). The study of individual movement highlighted the factors that drive adult and juvenile *C. virgata* and *C. acuta* dispersal. Separate factors or different thresholds were driving the movement of *C. virgata* and *C. acuta.* These factors were extrinsic, particularly temperature and rainfall, and intrinsic, including previous movement distances and turning angles.

It is important for a farmer to be able to forecast net displacement of a snail population over a given time so that he / she can strategically manage these populations. These forecasts are particularly relevant at the beginning of the season when snails are aggregated on fence posts, on roadside weeds, or along field margins. Integrating information on breeding behaviour (Chapter 4) and dispersal (Chapters 5 and 6) provides the farmer an opportunity to evaluate the risk of contamination that they may face at harvest. Increased rainfall will lead to higher soil moister. Therefore, it would be predicted that in a wet autumn / winter, egg laying by these Mediterranean snails will be greater, and therefore increase contamination risk. Furthermore, a farmer may be able to ascertain the dispersal of populations of snails, and implement strategic control against the snails at key times in the season saving both time and money.

Based on the results of the statistical models (Chapter 6) that highlight factors that influence dispersal of adult and juvenile *C. virgata* and *C. acuta*, further simulation models could be developed. Simulation models with different structures could aim to look at movement under different control measures, such as baiting regimes to investigate the chance of encountering a bait pellet. Additionally, a simulation model that incorporated the dispersal of adult and juvenile snails at the appropriate times of the year would provide a clearer idea as to how populations of snails move over the season.

7.3 FUTURE RESEARCH

As with most research, in the process of answering the questions posed at the beginning of this thesis, many more questions have been uncovered. Some of the many future issues that can be addressed are discussed.

Forecasting the population dynamics of snails on the southern Yorke Peninsula is a worthwhile goal, despite the inherent problems that were encountered in this analysis. To determine factors that drive population ecology of the Mediterranean snails, more frequent sampling of the snails at each site would provide greater insight into the population ecology of these snails. Further information at the time of collection should differentiate size and age classes of snails. Additionally, the inclusion of land management practices into the statistical models could highlight their effects on snail populations. Such practices may include snail control, tillage, rotation, and the use of insecticides or herbicides either in the longer-or shorter-term. Movement from roadsides and pastures into crops should be considered. Furthermore, conducting long-term snail counts in a standardised cropping system, with consistent management practices, would eliminate much of the variation in the results.

The timing of the counts, relative to opening rains, harvest / sewing or a land management event will affect population counts. For example, harvesting of crops will collect many of the snails in the sample, but will also crush many snails that would then be not included in the counts. If the timing of the counts relative to opening rains and harvest, and other biological meaningful times of the year were consistent between years, then there would be no indication of the potential threat that a population of snails may pose at harvest time. The times of the year in which the counts were done, i.e. autumn and spring counts, are important. The autumn population is the potential breeding population, whereas the spring population includes the potential contaminants at harvest.

Predictions of autumn and spring snail population densities would be useful in determining appropriate control measures. Furthermore, an understanding of the drivers of population dynamics is required to determine the appropriate timing of snail counts such that they were conducted at a biologically meaningful time. Additionally, bait manufactures and suppliers, and farmers could use these predictors to determine how much bait to manufacture / stock, and buy as baits have a shelf life, and thus unused bait is an economic loss to the manufacturer / supplier and farmer.

Current control measures against snails in southern Australia are not always satisfactory (Baker 1986; 1988b; Baker and Hawke, 1990a, b; Hopkins and Baker, 1993). Statistical models could be used to determine the effect that the timing and integration of different control methods have on the snail's population dynamics. Unfortunately, the statistical models to determine predictors of population dynamics were inconsistent, and only one population of *C. acuta* was monitored.

Demonstrating competition is notoriously difficult. Research on inter- and intra-specific competition, focusing on growth rates at different food availability levels, the effect of mucus trails, and densities of these trails would add further to our knowledge of how these pests behave and disperse in the field. In many fields across the Yorke Peninsula, two or more of the Mediterranean snail species co-exist. Studies of the population dynamics of *C. virgata*, *C. acuta* and *T. pisana* (Chapter 3) showed that the abundance of each of these species is influenced by one or more of the other species. If one of these species is controlled, what will happen to the other species? Will one control strategy be effective on one or both of the other species, or will controlling one species lead to an increase in abundance of another? Information on inter- specific competition will lead to more optimal control measures against these pests at both population and species levels.

Further to the results of *C. virgata* breeding behaviour (Chapter 4), investigations into the characteristics of the non-calcareous Mid-North soil could help to answer why some fields have large populations whilst others have very little or none. Furthermore, the survival, growth and fecundity of hatchlings in the soils would show whether the egg-laying preference is related to the survival of hatchlings. Comparing a greater variety of soil types, perhaps with different moisture retention capacities, will further highlight which soil characteristics are important for egg laying by these snails.

Additional research on the breeding behaviour of these snails could involve the effects of a range of temperature, particularly extreme cold. *C. virgata* and *C. acuta* react differently to rainfall and temperatures (Chapter 6). The interaction between rainfall and temperature is associated with movement, and these factors could be investigated by varying temperature and rainfall to determine the optimal conditions for breeding. Additionally, two or more species could be put in the same enclosure, and their breeding behaviour compared when in isolation, and when in competition. This would then highlight whether there was inter- or intra-specific competition among species that naturally occur in the field. From this, it could be established whether the suppression of a population in a field could result in an explosion of another.

Incorporating dispersal data with information on snail behaviour towards baits can lead to more optimal spatial distribution of baits. Additionally, juvenile Mediterranean snails in southern Australia do not seem to be affected by broadacre baits, and it was suggested that they were not dispersing far enough in order to encounter a bait pellet (S. Charwat, pers comm). Dispersal studies in this present study have shown however, that juvenile *C. virgata* and *C. acuta* move further than adults of their own species. It is therefore likely that while the juvenile snails may be encountering bait, there are other factors that prevent or limit juvenile consumption of baits. Reasons might be that the mouthparts of juvenile snails are not large enough to consume the bait (Kpikpi and Thomas, 1992). The nature of the feeding behaviour or metabolism of juvenile snails, and differences among species may influence bait uptake (Abd El-Hamid, 1996). Information as to why juvenile snails are not affected by baits is important (to know), in order to develop baits that will target these snails more effectively.

Dispersal data generated in this study provided information on the movement of snails on a daily basis. However, snails do not move in continuous straight lines. Therefore, to examine movement on a finer scale, time-lapse video films using infra-red lighting were conducted examining the movement of *C. virgata* and *C. acuta* in small outdoor arenas (data not shown). However, due to technical problems no useful results were obtained from this study. Small arenas were required due to limited resolution of the video equipment. The aim was to correlate movement with air and soil temperature, relative humidity and rainfall. Time-lapse video films have been used to examine movement of the slug *Deroceras reticulatum* (Bailey, 1989; Howling 1991; Howling and Port, 1989). From the video films, information on the reaction of snails to the mucus trails of other snails can be determined. Additionally, snail's reaction to baits, whether or not they are attracted to them, how far the bait pellets need to be placed from one another and how long it takes for the snail to die could be established using time-lapse filming.

Baits may affect movements of organisms in a variety of ways including directed attraction (Howling, 1991; Turchin, 1997). Baits attract different species to different extents (Crawford-Sidebothom, 1970). Mature slugs are caught more readily than immature slugs and many slugs that are initially poisoned recover (Crawford-Sidebothom, 1972). Information derived from the use of time-lapse video studies could incorporate the attractiveness of different baits to different snails species, and additionally, to their age-classes. Further, the length of time baits take to kill a certain proportion of snails could be determined. Information on how long it takes for snails to die after consuming different baits is vital when determining the efficacy of the bait. The slug *Deroceras reticulatum* dies quicker after consuming baits containing metaldehyde than those with methiocarb (Howling and Port, 1989). This could further be investigated by using Mediterranean snails in southern Australian conditions.

The simulation model in Chapter 6 could be extended to help target future investigations into snail population dynamics. This could be achieved by identifying processes that have significant effects on the life histories of snails (Wotton and Bell, 1992). The effect of available water on snail mortality has not been investigated, but has been shown to be a key factor in driving snail population dynamics (Shirley et al, 2001). The simulation model presented in Chapter 6 could be modified to forecast displacement of adult *C. virgata* in medic, adult *C. acuta* in medic and barley as well as movement of juvenile *C. virgata* and *C. acuta* in barley and medic. As juveniles are most common in spring, the model forecasting juvenile movement would need to be developed for a shorter time scale. Ideally, a model that represented all snail species and age classes, regardless of habitat could be developed, however, as has been identified, *C. virgata* and *C. acuta* behave differently depending on habitat, age and climatic conditions. Therefore, this needs to be considered when implementing control strategies, and predicting the risk of contamination in a crop or pasture. The model could be further expanded, with the initiation point of the snails being randomly spread around 'the field' rather than just a point, and let the snails diffuse into the field. By scattering bait pellets randomly according to suggested rates, and knowing how far away from these pellets that snails can respond to the bait, and the probability of it encountering it, would provide a management scenario model. In addition, the model could examine the value of not harvesting a certain margin around the edge of the crop, allowing the farmer to weigh up the benefits of cleaner grains to lost income of not harvesting that margin.

7.3 CHALLENGES OF SNAIL MANAGEMENT

Attempts to remove or reduce the density of an exotic species are challenging (Myers et al, 2000). Historically, most pest control efforts have sought to find a single simple, direct intervention that quickly reduces the pest populations below an acceptable level (Hill et al, 1999). However Mediterranean snails on the Yorke Peninsula cannot be controlled simply or quickly. The study of the breeding behaviour of *C. virgata* showed that soil type and soil moisture are important factors for egg laying. These results help to predict that egg-laying during breeding seasons will be higher in wetter seasons, and therefore the risk of crop contamination in spring that follows will be greater than in drier seasons. To further complicate snail management, the dispersal behaviour of *C. virgata* and *C. acuta* differs significantly between species, age-classes and habitats. This may be that they are responding to different stimuli, or that one species is more sensitive to certain stimuli than the other. This must all be taken into consideration when considering managing these pests.

In general, it is difficult to eradicate established populations of alien species (Cowie, 2002) such as *C. virgata*, *C. acuta*, *T. pisana* and *C. barbara*. Use of molluscicides over large areas is expensive and often is inappropriate from human safety and environmental perspectives. Biological control agents can, at best, reduce pest numbers to acceptable levels (Cowie, 2002). Equally important is the awareness of long-term and global implications of current practices (Parker et al, 1993; Hill et al, 1999). Unfortunately, as agricultural practices steer towards improving soil conservation, snail populations increase. However, by increasing knowledge on the breeding behaviour of these snails and how far and why they are moving, the implementation of control strategies can be optimised, thereby reducing the time and economic loss to farmers. Most importantly, farmers can now strive to strategically control populations rather than treating all snails as equal, thus enabling more effective control. The research presented in this thesis has added to our understanding of factors that influence the spread and population growth of the Mediterranean snails in southern Australia.

APPENDIX 1. Descriptive statistics of climatic and non-climatic variables, which relate to the population densities of *C. virgata* over 20 years at Balgowan South Australia. Climatic data from Maitland, South Australia (Commonwealth Bureau of Meteorology). N = 'Number of days'.

Variable	Mean	Standard deviation	Minimum value	Maximum value
Previous spring snail count	84.01	161.58	0.48	645.28
Mean annual rainfall	40.86	8.48	30.17	68.73
Previous years total rainfall	40.83	8.46	30.17	68.73
February rainfall	17.88	26.64	0.00	108.40
March rainfall	19.49	15.44	0.00	57.60
Summer + Autumn rainfall	161.07	56.34	69.40	295.60
Mean minimum autumn temperature	12.24	0.74	10.26	13.32
N. in spring where maximum temperature 15-25°C	61.94	4.70	54.00	73.00
N. in winter where maximum temperature 10-15°C	47.78	11.69	25.00	76.00
January SOI	-2.47	12.80	-30.60	15.60
March SOI	-6.33	12.09	-28.50	9.40
July SOI	-1.01	9.52	-18.60	14.60

APPENDIX 2. Descriptive statistics of climatic and non-climatic variables that affect the population densities of *C. virgata* over 20 years at Weetulta, South Australia. Climatic data from Maitland, South Australia (Commonwealth Bureau of Meteorology). N = 'Number of days'.

Variable	Mean	Standard deviation	Minimum value	Maximum value
Previous spring counts	13.63	28.67	0.80	117.90
April rain	26.48	23.01	2.40	79.00
N in summer with no rain	74.83	5.77	61.00	81.00
N in summer where minimum temperature < 20°C	3.83	3.01	0.00	10.00
N in autumn where maximum temperature > 30°C	9.39	4.89	0.00	16.00
N in winter where minimum temperature < 10 °C	70.06	7.15	53.00	77.00
Feb SOI	-3.29	12.41	-33.30	13.30
Mar SOI	-6.33	12.09	-28.50	9.40

APPENDIX 3. Descriptive statistics of climatic and non-climatic variables that affect the population densities of *C. virgata*, *T. pisana and C. acuta* over 20 years at Hardwicke Bay. Climatic data from Warooka, South Australia (Commonwealth Bureau of Meteorology). N = 'Number of days'.

Variable	Mean	Standard deviation	Minimum value	Maximum value
Previous year's total rainfall	38.22	8.62	26.95	66.47
February rainfall	13.82	14.48	0.20	47.40
March rainfall	20.62	24.03	0.00	76.00
April rainfall	26.42	23.25	0.60	83.00
June rainfall	67.77	25.89	16.40	103.60
July rainfall	67.33	28.68	25.00	136.80
September rainfall	53.16	24.97	9.60	110.80
Autumn rain	95.69	44.75	41.60	220.60
Summer +Autumn rainfall	146.53	49.13	85.00	251.80
Winter + Summer rainfall	303.65	71.75	132.80	472.40
N in summer with no rain	74.17	4.81	62.00	81.00
N in summer where minimum temperature < 20°C	4.67	5.40	0.00	23.00
N in autumn where maximum temperature > 30°C	20.28	6.99	3.00	31.00
N in summer where minimum temperature < 15°C	49.33	12.30	27.00	76.00
N in autumn where minimum temperature < 15°C	1.11	1.02	0.00	3.00

APPENDIX 3. (Cont)

Variable	Mean	Standard deviation	Minimum value	Maximum value
N in autumn where maximum temperature > 30°C	5.78	3.10	0.00	11.00
N. in winter where maximum temperature 10-15°C	33.39	11.04	17.00	60.00
March SOI	-6.33	12.09	-28.50	9.40
May SOI	-2.59	11.19	-22.40	14.70
December SOI	-1.09	8.91	-16.70	13.30
Population density of *C. virgata*	9.91	20.19	0.08	87.84
Population density of *C. acuta*	17.13	46.52	0.00	194.80
Population density of *T. pisana*	17.13	46.52	0.00	194.80

APPENDIX 4. Climatic data measured at the release site (Minlaton, South Australia) for each release in the 2001 (2 day release) and 2002 (5 day release) field seasons.

Climatic data measured at the Minlaton field trial site for June 21 – June 22, 2001. Rainfall on the release day was 0.4 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (°C)	13.6 +/- 1.7	11.5	17.7
	Soil temperature (°C)	12.7 +/- 1.8	10.1	16.5
	Relative humidity (%)	96.3 +/-5.1	81	100
	Rainfall (mm)			3.3
Day 2	Air temperature (°C)	13.5 +/-1.1	11.7	15.1
	Soil temperature (°C)	12.3 +/- 1.1	11.2	18
	Relative humidity (%)	85.0 +/- 7.5	73	100.
	Rainfall (mm)			0.2

Continued

Climatic data measured at the Minlaton field trial site for July 18 – July 20, 2001. Rainfall on the day of the release was 2.7 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (^{o}C)	9.8 +/- 2.6	5.1	14.8
	Soil temperature (^{o}C)	10.1 +/- 3.1	6.4	16.8
	Relative humidity (%)	91.9 +/- 11.3	64.8	100
	Rainfall (mm)			0.2
Day 2	Air temperature (^{o}C)	11.7 +/- 4.3	3.9	19.2
	Soil temperature (^{o}C)	12.0 +/- 5.0	5.4	21.8
	Relative humidity (%)	77.0 +/- 26.2	0.3	100
	Rainfall (mm)			0.0

Continued

Climatic data measured at the Minlaton field trial site for September 05 – September 07, 2001. Rainfall on the release day was 0.2 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (°C)	9.7 +/- 5.1	2.3	17.1
	Soil temperature (°C)	10.8 +/- 2.7	7.2	15.4
	Relative humidity (%)	85.6 +/- 15.6	56.8	100
	Rainfall (mm)			12.0
Day 2	Air temperature (°C)	13.5 +/- 3.8	7.5	19.9
	Soil temperature (°C)	12.5 +/- 2.7	9.0	17.4
	Relative humidity (%)	79.7 +/- 12.7	44.9	100
	Rainfall (mm)			4.7

Continued

Climatic data measured at the Minlaton field trial site for October 27 – October 28, 2001.

Rainfall on the release day was 2.9 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (°C)	12.9 +/- 6.8	1.6	22.7
	Soil temperature (°C)	16.7 +/- 5.8	8.5	26.5
	Relative humidity (%)	70.4 +/- 25.0	20.5	100
	Rainfall (mm)			1.6
Day 2	Air temperature (°C)	15.5 +/- 5.0	3.1	23.1
	Soil temperature (°C)	18.7 +/- 5.4	10.6	29.8
	Relative humidity (%)	64.5 +/- 21.9	33.6	100
	Rainfall (mm)			0.0

Continued

Climatic data measured at the Minlaton field trial site for June 28 – July 02, 2002. Rainfall on the release day was 0.2 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (°C)	8.7 +/- 1.4	4.1	13.7
	Soil temperature (°C)	7.79 +/- 1.1	5.4	10.9
	Relative humidity (%)	76.9 +/- 10.3	52.2	95.5
	Rainfall (mm)			3.3
Day 2	Air temperature (°C)	8.7 +/- 2.4	3.4	13.1
	Soil temperature (°C)	8.7 +/- 2.1	5.6	12.6
	Relative humidity (%)	74.8 +/- 18.2	49.9	96.6
	Rainfall (mm)			1.0
Day 3	Air temperature (°C)	7.4 +/- 1.8	2.6	14.5
	Soil temperature (°C)	7.0 +/- 1.4	3.9	11.7
	Relative humidity (%)	78.7 +/- 21.2	51.2	100
	Rainfall (mm)			0.3
Day 4	Air temperature (°C)	8.5 +/- 2.1	3.9	15.4
	Soil temperature (°C)	7.1 +/- 1.1	4.1	12.0
	Relative humidity (%)	68.8 +/- 15.7	36.2	94.4
	Rainfall (mm)			0
Day 5	Air temperature (°C)	14.3 +/- 3.5	5.7	25.8
	Soil temperature (°C)	13.1 +/- 3.1	5.7	27.6
	Relative humidity (%)	58.15+/- 25.1	24.9	100
	Rainfall (mm)			6.47

Continued

Climatic data measured at the Minlaton field trial site for July 29 – August 02, 2002. Rainfall on the release day was 0.7 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (°C)	11.2 +/- 1.3	8.0	16.2
	Soil temperature (°C)	10.6 +/- 2.1	8.8	14.0
	Relative humidity (%)	77.8 +/- 19.2	47.6	100
	Rainfall (mm)			17.8
Day 2	Air temperature (°C)	13.8 +/- 3.6	9.8	20.5
	Soil temperature (°C)	11.4 +/- 1.3	9.6	14.0
	Relative humidity (%)	66.5 +/- 13.2	38.3	88.3
	Rainfall (mm)			0.4
Day 3	Air temperature (°C)	11.9 +/- 1.2	8.0	16.0
	Soil temperature (°C)	11.4 +/- 0.6	9.6	14.0
	Relative humidity (%)	83.4 +/- 12.1	69.0	98.9
	Rainfall (mm)			02
Day 4	Air temperature (°C)	10.0 +/- 2.5	5.4	15.1
	Soil temperature (°C)	10.2 +/- 1.0	7.1	12.8
	Relative humidity (%)	89.7 +/- 16.2	61.1	100
	Rainfall (mm)			0.4
Day 5	Air temperature (°C)	13.0 +/- 1.1	9.3	18.3
	Soil temperature (°C)	13.1 +/- 1.2	9.0	18.9
	Relative humidity (%)	77.1 +/- 2.4	54.0	91.0
	Rainfall (mm)			1.8

Continued

Climatic data measured at the Minlaton field trial site for September 28 – October 03, 2002. Rainfall on the release day was 1.9 mm

		Mean +/- Standard deviation	Minimum	Maximum
Day 1	Air temperature (°C)	15.5 +/- 1.6	10.6	22.7
	Soil temperature (°C)	16.0 +/- 2.4	12.6	21.1
	Relative humidity (%)	78.2 +/- 23.1	50.3	97.2
	Rainfall (mm)			0.5
Day 2	Air temperature (°C)	12.7 +/- 1.4	10.6	16.8
	Soil temperature (°C)	16.0 +/- 1.1	14.2	18.6
	Relative humidity (%)	76.7 +/- 21.8	56.4	93.8
	Rainfall (mm)			0.0
Day 3	Air temperature (°C)	13.9+/- 4.1	6.4	22.0
	Soil temperature (°C)	16.1 +/- 1.7	12.3	20.8
	Relative humidity (%)	72.6 +/- 24.2	44.4	100
	Rainfall (mm)			4.0
Day 4	Air temperature (°C)	13.6 +/- 1.8	9.6	18.3
	Soil temperature (°C)	16.1 +/- 1.1	14.0	19.9
	Relative humidity (%)	78.8 +/- 19.8	45.8	99.9
	Rainfall (mm)			4.3
Day 5	Air temperature (°C)	14.3 +/- 1.0	10.4	18
	Soil temperature (°C)	15.4 +/- 0.9	13.1	18
	Relative humidity (%)	79.7 +/- 17.8	55.4	100
	Rainfall (mm)			5.4

APPENDIX 5. Descriptive statistics of dispersal over two days for adult *C. virgata* and *C. acuta* in 2001 relating to chapter 5.

Descriptive statistics for day one and day two for the density dependent and mass-mark-release-recapture field trials. Following from this, the data are presented according to month, then species, with results for *C. virgata* presented before those for *C. acuta.* Headings of 90° are north, and 270° are south. Headings of 180° indicate a western directions and 0° indicate a eastern direction.

Descriptive statistics for the dispersal of three *C. virgata* populations (8 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	117.8	155.0	75.9	189.4	215.5	255.1
Standard deviation (cm)	94.7	111.0	105.0	201.3	139.8	162.2
Mean angle (degrees)	61	102	109	80	129	135
Angular variance (degrees)	74	62	38	46	27	26
Angular deviation (degrees)	65	59	47	51	40	39
Rayleigh's *z*	1.01	1.71	3.58	2.86	4.64	4.73

Descriptive statistics for the dispersal of three *C. virgata* populations (16 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	106.7	90.5	163.7	104.8	161.2	202.4
Standard deviation (cm)	131.0	47.5	123.7	133.8	138.1	158.9
Mean angle (degrees)	50	112	112	58	80	104
Angular variance (degrees)	52	64	39	58	55	52
Angular deviation (degrees)	54	60	47	58	56	55
Rayleigh's *z*	4.81	3.09	6.90	3.90	4.34	4.76

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	105.5	94.3	107.4	127.8	160.4	163.4
Standard deviation (cm)	63.4	101.6	139.2	77.5	158.3	207.9
Mean angle (degrees)	102	110	98	125	114	97
Circular variance (degrees)	20.0	14.0	17.2	22.0	17.5	15.0
Angular variance (degrees)	39.9	28.1	34.4	44.1	35.0	29.9
Angular deviation (degrees)	47.8	40.1	44.4	50.2	44.8	41.4
Rayleigh's *z*	17.00	22.80	19.57	12.36	19.30	21.83

Descriptive statistics for the dispersal of three *C. virgata* populations (100 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	170.8	155.7	200.2	248.4	203.0	217.2
Standard deviation (cm)	121.9	95.5	94.1	111.5	126.3	150.0
Mean angle (degrees)	70	83	86	84	91	93
Angular variance (degrees)	49	32	24	49	32	22
Angular deviation (degrees)	53	43	37	53	43	36
Rayleigh's *z*	33.12	51	62.68	33.14	51.56	65.27

Descriptive statistics for the dispersal of three *C. acuta* populations (8 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	55.9	45.4	96.6	107.1	52.4	79.6
Standard deviation (cm)	36.6	33.8	60.4	52.3	31.8	65.4
Mean angle (degrees)	142	174	128	140	142	299
Angular variance (degrees)	38	94	70	26	96	87
Angular deviation (degrees)	46	73	63	39	74	71
Rayleigh's *z*	3.62	0.26	1.23	4.75	0.21	0.46

Descriptive statistics for the dispersal of three *C. acuta* populations (16 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	70.5	41.9	44.2	89.5	48.4	72.7
Standard deviation (cm)	55.7	26.6	54.8	84.5	25.6	73.0
Mean angle (degrees)	113	186	117	135	252	148
Angular variance (degrees)	57	77	26	39	69	43
Angular deviation (degrees)	57	67	39	47	63	49
Rayleigh's *z*	4.07	1.69	9.51	6.91	2.56	6.33

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	73.6	59.8	99.1	85.4	95.1	119.8
Standard deviation (cm)	86.7	56.5	74.1	80.9	73.2	80.1
Mean angle (degrees)	117	130	102	97	130	136
Circular variance (degrees)	36.0	21.9	44.6	41.7	32.4	33.2
Angular variance (degrees)	72.1	43.8	89.1	83.4	64.9	66.3
Angular deviation (degrees)	64.3	50.1	71.5	69.1	61.0	61.6
Rayleigh's *z*	5.50	15.29	1.98	2.96	7.53	7.02

Descriptive statistics for the dispersal of three *C. acuta* populations (100 snails each) released in canola on unburnt soil in June 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	41.9	169.8	100.4	67.0	196.9	114.9
Standard deviation (cm)	55.2	89.9	51.9	62.6	102.7	58.2
Mean angle (degrees)	124	117	128	139	124	126
Angular variance (degrees)	68	17	55	63	16	57
Angular deviation (degrees)	62	31	56	60	30	57
Rayleigh's *z*	16.19	72.18	26.7	20.08	74.31	25.58

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in barley on burnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	39.3	56.5	53.3	75.5	92.7	105.3
Standard deviation (cm)	36.6	69.5	65.1	77.6	127.9	164.7
Mean angle (degrees)	177	178	196	157	177	196
Circular variance (degrees)	28.6	25.1	35.1	21.3	18.1	33.8
Angular variance (degrees)	57.1	50.1	70.3	42.6	36.2	67.6
Angular deviation (degrees)	57.2	53.6	63.5	49.5	45.5	62.3
Rayleigh's *z*	9.05	12.05	5.53	14.59	19.19	6.72

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in barley on unburnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	40.5	35.6	41.6	51.3	39.2	64.0
Standard deviation (cm)	32.5	26.9	23.3	45.7	24.6	38.4
Mean angle (degrees)	167	154	184	160	143	181
Circular variance (degrees)	30.2	37.7	20.5	37.7	31.7	17.8
Angular variance (degrees)	60.4	75.5	41.0	75.4	63.4	35.5
Angular deviation (degrees)	58.8	65.8	48.5	65.7	60.3	45.1
Rayleigh's *z*	8.73	4.78	14.68	4.54	7.79	19.05

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on burnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	34.3	52.2	34.0	45.6	53.5	44.2
Standard deviation (cm)	20.4	41.5	33.1	25.5	42.8	40.0
Mean angle (degrees)* †	172	114	177	166	119	183
Circular variance (degrees)	18.0	26.4	24.3	16.3	29.5	28.6
Angular variance (degrees)	35.9	52.8	48.6	32.6	59.0	57.1
Angular deviation (degrees)	45.4	55.0	52.8	43.2	58.1	57.2
Rayleigh's *z*	17.90	11.65	12.60	18.93	9.18	9.81

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on unburnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	19.1	22.1	19.9	23.0	26.5	28.2
Standard deviation (cm)	11.2	13.6	8.5	12.3	18.2	12.7
Mean angle (degrees) * †	225	195	89	241	184	113
Circular variance (degrees)	26.6	45.1	37.5	34.6	42.6	36.4
Angular variance (degrees)	53.3	90.3	75.0	69.1	85.3	72.8
Angular deviation (degrees)	55.3	71.9	65.6	62.9	69.9	64.6
Rayleigh's z	11.17	1.76	4.77	6.30	2.49	5.45

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in medic in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	37.9	25.8	23.2	60.8	40.9	24.6
Standard deviation (cm)	41.4	25.8	24.7	63.5	30.1	27.5
Mean angle (degrees) †	176	189	187	181	197	223
Circular variance (degrees)	18.4	27.0	13.2	14.8	28.8	37.1
Angular variance (degrees)	36.7	54.0	26.4	29.6	57.5	74.1
Angular deviation (degrees)	45.9	55.6	38.9	41.2	57.4	65.2
Rayleigh's z	18.46	11.18	23.08	20.93	9.92	4.61

† Significant difference among replicates on day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in barley on burnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	26.4	37.3	32.5	65.6	55.6	40.5
Standard deviation (cm)	10.8	27.3	32.6	149.6	36.2	53.7
Mean angle (degrees)* †	156	127	191	154	159	190
Circular variance (degrees)	26.5	29.7	25.1	29.2	56.0	28.4
Angular variance (degrees)	53.1	59.4	50.3	58.4	111.9	56.8
Angular deviation (degrees)	55.2	58.3	53.7	57.9	80.1	57.1
Rayleigh's *z*	11.52	8.54	10.08	8.90	0.02	8.65

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in barley on unburnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	35.5	35.2	18.4	40.4	45.8	24.6
Standard deviation (cm)	24.1	26.6	10.2	19.9	27.3	13.3
Mean angle (degrees)*	206	237	176	175	175	217
Circular variance (degrees)	42.0	33.6	30.7	26.1	32.5	15.6
Angular variance (degrees)	83.9	67.2	61.4	52.2	65.0	31.2
Angular deviation (degrees)	69.3	62.1	59.3	54.7	61.0	42.3
Rayleigh's *z*	2.73	5.64	7.75	10.68	7.50	18.03

* Significant difference among replicates on day 1.

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on burnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	43.9	42.4	43.0	56.3	49.4	50.4
Standard deviation (cm)	24.3	18.0	17.3	45.4	23.7	27.8
Mean angle (degrees)* †	195	139	247	200	157	284
Circular variance (degrees)	31.9	48.7	39.5	33.7	38.5	34.9
Angular variance (degrees)	63.8	97.5	78.9	67.5	76.9	69.8
Angular deviation (degrees)	60.5	74.7	67.2	62.2	66.4	63.2
Rayleigh's *z*	7.46	0.83	3.30	6.43	4.11	5.36

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on unburnt soil in July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	32.4	22.8	19.6	33.8	25.8	22.5
Standard deviation (cm)	17.2	10.8	17.9	16.8	12.8	11.0
Mean angle (degrees) * †	259	12	129	193	31	1
Circular variance (degrees)	54.0	23.7	35.5	42.0	20.8	42.2
Angular variance (degrees)	108.1	47.4	71.1	83.9	41.6	84.3
Angular deviation (degrees)	78.7	52.1	63.8	83.9	41.6	84.3
Rayleigh's *z*	0.12	13.77	4.91	2.73	15.44	2.71

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in medic July 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	13.2	18.8	14.7	23.4	26.1	17.7
Standard deviation (cm)	12.9	11.8	9.2	17.2	13.6	11.6
Mean angle (degrees)* †	162	182	125	209	196	84
Circular variance (degrees)	28.4	24.0	49.6	37.9	36.2	46.6
Angular variance (degrees)	56.9	48.1	99.3	75.9	72.4	93.2
Angular deviation (degrees)	57.1	52.5	75.4	65.9	64.4	73.1
Rayleigh's *z*	10.15	12.13	0.65	4.11	5.28	1.32

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in barley on burnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	22.8	15.2	15.1	36.8	28.9	31.8
Standard deviation (cm)	12.9	9.7	10.9	22.1	21.6	24.8
Mean angle (degrees) * †	248	184	184	278	148	67
Circular variance (degrees)	27.3	23.7	45.1	25.3	26.3	36.0
Angular variance (degrees)	54.6	47.3	90.3	50.6	52.5	72.0
Angular deviation (degrees)	55.9	52.1	71.9	53.9	54.9	64.2
Rayleigh's *z*	10.69	13.80	1.85	12.16	10.56	5.12

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in barley on unburnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	31.5	34.4	17.3	38.0	50.5	26.3
Standard deviation (cm)	16.0	27.7	12.6	22.2	35.4	28.7
Mean angle (degrees)* †	62	221	334	152	273	69
Circular variance (degrees)	47.5	45.9	19.3	46.7	34.8	46.8
Angular variance (degrees)	95.0	91.7	38.5	93.4	69.7	93.5
Angular deviation (degrees)	73.8	73.0	47.0	73.1	63.2	73.2
Rayleigh's *z*	1.17	1.60	17.63	1.20	5.84	1.36

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on burnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	19.9	24.6	14.1	26.5	39.7	20.6
Standard deviation (cm)	10.1	13.7	8.1	12.5	23.6	16.6
Mean angle (degrees) * †	217	250	233	353	303	233
Circular variance (degrees)	33.0	37.4	41.0	43.0	29.1	25.2
Angular variance (degrees)	65.9	74.8	82.0	85.9	58.2	50.5
Angular deviation (degrees)	61.5	65.5	68.5	70.2	57.8	53.8
Rayleigh's *z*	7.20	4.70	3.16	2.37	9.44	12.21

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on unburnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	22.6	24.1	9.8	31.9	32.5	14.3
Standard deviation (cm)	11.4	15.4	6.2	15.9	25.1	10.4
Mean angle (degrees) * †	141	233.	210	66	201	280
Circular variance (degrees)	28.1	42.4	33.7	42.2	34.8	23.7
Angular variance (degrees)	56.1	84.8	67.4	42.2	34.8	23.7
Angular deviation (degrees)	56.7	69.7	62.1	69.6	63.1	52.1
Rayleigh's *z*	10.42	2.71	6.63	2.77	6.04	113.11

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in medic in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	12.8	23.8	13.8	14.3	42.3	22.2
Standard deviation (cm)	6.3	19.2	19.6	6.6	35.5	27.8
Mean angle (degrees) * †	220	193	7.2	229	215	308
Circular variance (degrees)	15.3	32.1	49.8	11.5	49.9	43.8
Angular variance (degrees)	30.5	64.1	99.7	22.9	99.8	87.6
Angular deviation (degrees)	41.8	60.6	75.6	36.2	75.6	70.8
Rayleigh's *z*	21.53	7.18	0.67	25.61	0.66	2.17

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in barley on burnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	26.4	13.7	15.4	43.1	23.7	26.9
Standard deviation (cm)	18.4	9.5	10.7	23.2	14.5	14.4
Mean angle (degrees) * †	226	149	242	256	81	314
Circular variance (degrees)	28.4	34.4	42.0	39.7	39.9	33.5
Angular variance (degrees)	56.8	68.8	84.0	79.4	79.7	66.9
Angular deviation (degrees)	57.1	62.8	69.4	67.5	67.6	61.9
Rayleigh's *z*	10.16	6.39	2.85	3.77	3.43	6.41

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in barley on unburnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	17.3	14.0	11.4	27.9	17.6	25.6
Standard deviation (cm)	12.0	6.8	4.5	13.8	12.1	19.8
Mean angle (degrees) * †	243	357	257	0	194	267
Circular variance (degrees)	37.2	30.6	27.5	43.3	45.6	31.7
Angular variance (degrees)	74.4	61.2	54.9	86.6	91.1	63.3
Angular deviation (degrees)	65.3	59.2	56.1	70.4	72.3	60.2
Rayleigh's *z*	4.31	8.68	10.86	2.15	1.68	7.41

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on burnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	17.2	18.0	17.3	23.6	23.3	20.4
Standard deviation (cm)	10.0	13.5	13.6	15.5	16.1	14.9
Mean angle (degrees) * †	2	262	327	329	81	308
Circular variance (degrees)	38.1	34.2	12.7	40.6	37.8	47.2
Angular variance (degrees)	76.2	68.4	25.4	81.2	75.5	94.4
Angular deviation (degrees)	66.1	62.6	38.1	68.2	65.8	73.6
Rayleigh's *z*	4.37	6.34	23.04	3.40	4.65	1.24

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on unburnt soil in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	12.6	11.9	14.5	16.6	13.9	15.7
Standard deviation (cm)	8.8	8.2	7.9	10.3	9.2	9.1
Mean angle (degrees) * †	188	338	247	77	191	252
Circular variance (degrees)	35.6	44.6	15.8	32.3	22.5	27.1
Angular variance (degrees)	71.1	89.2	31.7	64.6	45.1	54.2
Angular deviation (degrees)	63.8	71.5	42.6	60.9	50.8	55.8
Rayleigh's *z*	5.76	1.97	20.94	7.61	14.73	10.26

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in medic in September 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	13.4	8.8	13.0	13.9	11.2	14.5
Standard deviation (cm)	11.4	4.6	5.9	6.5	7.2	10.2
Mean angle (degrees) †	217	185	205	183	240	251
Circular variance (degrees)	24.8	29.1	22.1	34.7	34.6	40.3
Angular variance (degrees)	49.7	58.3	44.2	69.3	69.3	80.6
Angular deviation (degrees)	53.4	57.8	50.3	63.0	63.0	68.0
Rayleigh's *z*	12.84	9.67	15.08	5.77	6.26	3.26

†Significant difference among replicates on day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in barley on burnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	29.7	25.13	23.6	59.6	43.2	32.2
Standard deviation (cm)	15.1	9.1	11.6	40.0	27.2	15.3
Mean angle (degrees) * †	280	119	128	194	101	300
Circular variance (degrees)	30.3	44.6	47.3	41.3	33.9	41.3
Angular variance (degrees)	60.5	89.2	94.6	82.6	67.9	82.7
Angular deviation (degrees)	58.9	71.5	73.6	68.8	62.4	68.8
Rayleigh's *z*	8.90	1.47	1.22	2.97	6.49	3.02

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in barley on unburnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	41.6	40.5	34.9	53.3	62.4	37.3
Standard deviation (cm)	23.1	21.4	19.3	20.2	38.6	21.8
Mean angle (degrees) * †	271	16	310	238	18	256
Circular variance (degrees)	33.0	40.0	31.7	32.8	30.5	54.1
Angular variance (degrees)	66.0	80.0	63.5	65.5	61.0	108.2
Angular deviation (degrees)	61.5	67.7	60.3	61.3	59.1	78.7
Rayleigh's *z*	6.83	3.55	7.57	6.42	7.2	0.10

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on burnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	30.8	32.9	31.5	49.9	47.8	32.1
Standard deviation (cm)	13.4	16.4	15.6	27.4	18.8	18.5
Mean angle (degrees) * †	158	216	322	176	161	261
Circular variance (degrees)	46.4	55.9	47.5	46.4	44.0	45.7
Angular variance (degrees)	92.9	111.8	95.0	92.9	88.0	91.4
Angular deviation (degrees)	73.0	80.0	73.8	73.0	71.0	72.4
Rayleigh's *z*	1.47	0.02	1.16	1.36	2.10	1.51

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in canola on unburnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	37.1	43.1	55.3	82.3	80.3	31.8
Standard deviation (cm)	20.2	26.9	13.9	47.4	39.6	12.5
Mean angle (degrees) * †	292	12	25	228	4	223
Circular variance (degrees)	42.7	49.8	43.1	33.0	50.2	47.2
Angular variance (degrees)	85.4	99.7	86.1	66.1	100.3	94.4
Angular deviation (degrees)	70.0	75.6	70.2	61.5	75.8	73.5
Rayleigh's *z*	2.60	0.54	2.10	5.38	0.52	1.06

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. virgata* populations (40 snails each) released in medic October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	25.2	32.0	23.9	57.7	50.2	41.9
Standard deviation (cm)	19.7	16.1	17.9	44.8	37.9	38.7
Mean angle (degrees) * †	216	180	255	76	206	200
Circular variance (degrees)	48.1	36.2	40.0	41.8	36.4	46.7
Angular variance (degrees)	96.1	72.5	80.0	83.5	72.7	93.4
Angular deviation (degrees)	74.2	64.4	67.7	69.2	64.6	73.1
Rayleigh's *z*	0.99	5.27	3.56	2.50	4.54	1.13

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in barley on burnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	18.7	24.0	27.7	21.0	22.1	23.1
Standard deviation (cm)	8.4	10.9	10.9	11.9	15.3	16.2
Mean angle (degrees) * †	237	341	35	283	55	89
Circular variance (degrees)	21.9	15.9	22.5	41.0	42.7	24.5
Angular variance (degrees)	43.7	31.7	45.1	81.9	85.4	49.0
Angular deviation (degrees)	50.1	42.6	50.8	68.5	70.0	53.0
Rayleigh's *z*	15.30	21.96	14.72	3.33	2.59	12.79

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in barley on unburnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	19.3	26.9	27.5	31.3	33.1	33.0
Standard deviation (cm)	7.3	13.7	16.2	16.5	19.4	18.6
Mean angle (degrees) * †	251	302	90	326	60	107
Circular variance (degrees)	47.9	50.3	50.1	45.2	44.8	37.6
Angular variance (degrees)	95.9	100.7	100.3	91.6	89.6	75.2
Angular deviation (degrees)	74.1	75.9	75.8	72.5	71.6	65.7
Rayleigh's *z*	0.94	0.56	0.61	1.53	1.86	3.90

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on burnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	17.8	19.2	18.2	31.3	31.5	21.8
Standard deviation (cm)	12.7	13.1	12.5	15.0	18.6	10.9
Mean angle (degrees) * †	225	142	261	199	205	286
Circular variance (degrees)	50.9	57.0	54.0	52.1	50.3	52.0
Angular variance (degrees)	101.7	114.0	108.0	104.2	100.5	104.0
Angular deviation (degrees)	76.3	80.8	78.7	77.3	75.9	77.2
Rayleigh's *z*	0.51	0.00	0.13	0.34	0.57	0.34

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in canola on unburnt soil in October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	19.8	15.7	23.2	55.9	33.1	29.2
Standard deviation (cm)	10.5	8.3	17.0	32.6	16.1	12.4
Mean angle (degrees) * †	63	167	291	346	188.5	238
Circular variance (degrees)	51.7	52.5	41.0	44.9	51.8	38.8
Angular variance (degrees)	103.4	105.1	82.0	89.9	103.6	77.7
Angular deviation (degrees)	77.0	77.6	68.6	71.8	77.0	66.7
Rayleigh's *z*	0.36	0.26	3.15	1.53	0.33	3.64

* Significant difference among replicates on day 1 and; on † day 2

Descriptive statistics for the dispersal of three *C. acuta* populations (40 snails each) released in medic October 2001.

	Day 1			Day 2		
Replicate	1	2	3	1	2	3
Mean distance (cm)	21.9	19.9	18.0	23.4	23.3	23.1
Standard deviation (cm)	7.1	8.4	7.6	10.4	13.3	11.1
Mean angle (degrees) * †	68	145	163	74	190	64
Circular variance (degrees)	18.3	48.4	37.4	29.1	33.9	45.9
Angular variance (degrees)	36.6	96.8	74.8	58.1	67.7	91.8
Angular deviation (degrees)	45.8	74.5	65.5	57.7	62.3	72.5
Rayleigh's *z*	19.44	0.96	4.47	9.71	6.36	1.50

* Significant difference among replicates on day 1 and; on † day 2

APPENDIX 6.: Descriptive statistics for headings and turning angles of individual adult and juvenile *C. virgata* and *C. acuta* in 2002. Dispersal data shown in this section are for individual snails on each given day. That is, a description of movement from day to day, rather than describing net displacement from the origin as in the previous section. Data are presented according to month, then species, with results for *C. virgata* presented before those for *C. acuta*. Headings of 90° are north, and 270° are south. Headings of 180° indicate a western directions and 0° indicate a eastern direction.

Descriptive statistics for individual dispersal of three populations of adult *C. virgata* (40 snails each) released in barley June 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	20.7	28.0	38.4			
	Standard deviation (cm)	17.3	31.9	36.7			
	Mean angle (degrees) † *	95	62	185			
	Angular variance (degrees)	101.2	96.4	102.8			
	Angular deviation (degrees)	76.1	74.3	76.7			
	Rayleigh's *z*	0.55	1.01	0.42			
Day 2	Mean distance (cm)	20.6	25.9	22.0			
	Standard deviation (cm)	24.3	58.2	21.3			
	Mean angle (degrees) † *	297	203	33	254	81	269
	Angular variance (degrees)	102.5	98.6	95.2	86.9	83.2	80.7
	Angular deviation (degrees)	76.6	75.2	73.8	70.6	69.0	68.0
	Rayleigh's *z*	0.45	0.78	1.15	2.33	3.01	3.50
Day 3	Mean distance (cm)	15.6	22.8	17.8			
	Standard deviation (cm)	15.2	45.8	17.9			
	Mean angle (degrees) † *	334	307	190	245	323	86
	Angular variance (degrees)	98.4	87.9	93.7	91.7	103.4	89.1
	Angular deviation (degrees)	75.1	71.0	73.3	72.5	77.0	71.4
	Rayleigh's *z*	0.79	2.17	1.33	1.59	0.37	1.98

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	13.7	12.0	15.7			
	Standard deviation (cm)	13.4	9.3	11.8			
	Mean angle (degrees) † *	245	330	49	317	243	149
	Angular variance (degrees)	89.9	105.0	95.4	98.9	64.5	94.7
	Angular deviation (degrees)	71.8	77.6	73.9	75.3	60.8	73.7
	Rayleigh's *z*	1.86	0.28	1.13	0.75	7.64	1.21
Day 5	Mean distance (cm)	7.5	10.0	13.3			
	Standard deviation (cm)	7.3	16.2	8.2			
	Mean angle (degrees) †	189	253	299	193	226	142
	Angular variance (degrees)	78.8	87.6	54.2	67.6	38.8	54.7
	Angular deviation (degrees)	67.2	70.8	55.7	62.3	47.1	56.0
	Rayleigh's *z*	3.89	2.17	11.12	6.71	17.51	10.94

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. virgata* (40 snails each) released in medic, June 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	11.5	35.3	19.5			
	Standard deviation (cm)	13.8	41.9	20.6			
	Mean angle (degrees) † *	136	195	198			
	Angular variance (degrees)	96.5	100.6	101.7			
	Angular deviation (degrees)	74.3	75.9	76.3			
	Rayleigh's *z*	1.00	0.60	0.51			
Day 2	Mean distance (cm)	10.7	25.6	15.1			
	Standard deviation (cm)	10.7	27.9	20.6			
	Mean angle (degrees) *	326	355	357	196	110	210
	Angular variance (degrees)	104.0	92.1	105.8	86.4	105.8	93.3
	Angular deviation (degrees)	77.2	75.7	77.9	70.4	77.8	73.1
	Rayleigh's *z*	0.34	1.50	0.24	2.36	0.24	1.39
Day 3	Mean distance (cm)	12.0	15.4	19.8			
	Standard deviation (cm)	11.0	13.2	19.8			
	Mean angle (degrees) †*	76	75	173	131	104	199
	Angular variance (degrees)	88.3	86.7	77.7	94.4	103.1	107.5
	Angular deviation (degrees)	71.1	70.5	66.7	73.6	76.9	78.5
	Rayleigh's *z*	2.01	2.31	4.14	1.21	0.39	0.15

Descriptive statistics for individual dispersal of three populations of adult *C. acuta* (40 snails each) released in barley June 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	25.9	32.6	26.1			
	Standard deviation (cm)	17.9	25.1	25.6			
	Mean angle (degrees) *	73	10	78			
	Angular variance (degrees)	83.3	59.9	95.2			
	Angular deviation (degrees)	69.1	58.6	73.9			
	Rayleigh's *z*	2.99	9.13	1.15			
Day 2	Mean distance (cm)	8.1	16.7	12.4			
	Standard deviation (cm)	5.9	10.9	10.6			
	Mean angle (degrees) †	168	52	16	317	227	66
	Angular variance (degrees)	79.4	94.0	71.3	97.9	107.6	102.8
	Angular deviation (degrees)	67.4	73.4	63.9	74.9	78.5	76.8
	Rayleigh's *z*	3.69	1.26	5.71	0.84	0.14	0.42
Day 3	Mean distance (cm)	8.6	17.4	13.0			
	Standard deviation (cm)	5.2	15.8	20.9			
	Mean angle (degrees) † *	21	233	137	110	156	140
	Angular variance (degrees)	88.8	48.8	105.8	56.6	56.4	100.4
	Angular deviation (degrees)	71.3	52.9	77.9	56.9	56.8	75.8
	Rayleigh's *z*	2.03	12.51	0.23	10.00	9.55	0.59

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	8.7	23.8	18.9			
	Standard deviation (cm)	11.0	17.9	26.7			
	Mean angle (degrees) †	26	200	278	263	49	228
	Angular variance (degrees)	99.7	72.0	69.0	70.5	61.4	92.2
	Angular deviation (degrees)	75.6	64.2	62.9	63.5	59.3	72.7
	Rayleigh's *z*	0.68	5.11	6.03	5.48	7.98	1.49
Day 5	Mean distance (cm)	13.0	10.9	13.3			
	Standard deviation (cm)	19.3	15.5	21.5			
	Mean angle (degrees) †	213	330	202	180	123	187
	Angular variance (degrees)	78.6	82.4	82.4	23.0	11.78	75.9
	Angular deviation (degrees)	67.1	68.7	68.7	36.3	26.0	66.0
	Rayleigh's *z*	3.95	2.75	2.91	25.57	29.78	4.33

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. acuta* (40 snails each) released in medic, June 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	36.3	24.9	26.2			
	Standard deviation (cm)	25.4	21.4	28.2			
	Mean angle (degrees) † *	235	140	185			
	Angular variance (degrees)	82.4	99.6	95.3			
	Angular deviation (degrees)	68.7	75.5	73.9			
	Rayleigh's *z*	3.16	0.68	1.13			
Day 2	Mean distance (cm)	17.6	27.0	18.3			
	Standard deviation (cm)	18.9	30.8	16.6			
	Mean angle (degrees) † *	188	332	137	82	132	129
	Angular variance (degrees)	74.6	83.9	101.8	79.8	96.8	78.2
	Angular deviation (degrees)	65.4	69.3	76.4	67.6	74.5	66.9
	Rayleigh's *z*	4.51	2.72	0.48	3.41	0.89	3.73
Day 3	Mean distance (cm)	13.5	26.2	15.3			
	Standard deviation (cm)	16.9	33.1	16.7			
	Mean angle (degrees) † *	233	316	211	354	96	208
	Angular variance (degrees)	86.2	94.6	61.4	105.4	99.8	68.8
	Angular deviation (degrees)	70.3	73.6	59.3	77.7	75.6	62.8
	Rayleigh's *z*	2.15	1.10	7.54	0.23	4.91	6.08

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	13.7	27.7	19.3			
	Standard deviation (cm)	22.3	28.7	19.4			
	Mean angle (degrees) † *	154	146	327	61	56	220
	Angular variance (degrees)	96.3	101.3	87.0	95.1	106.0	53.5
	Angular deviation (degrees)	74.3	76.2	70.6	73.8	77.9	55.3
	Rayleigh's *z*	0.92	0.50	2.15	1.01	0.19	9.67
Day 5	Mean distance (cm)	11.0	23.6	10.8			
	Standard deviation (cm)	21.7	24.4	14.0			
	Mean angle (degrees) †	230	212	327	145	133	230
	Angular variance (degrees)	98.1	51.0	91.9	60.9	58.8	36.4
	Angular deviation (degrees)	75.0	54.1	72.6	59.1	58.0	45.7
	Rayleigh's *z*	0.77	11.38	1.57	7.92	8.78	17.23

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. virgata* (40 snails each) released in barley July 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	42.2	40.7	30.4			
	Standard deviation (cm)	32.4	37.5	18.7			
	Mean angle (degrees) † *	70	38	146			
	Angular variance (degrees)	80.0	90.0	84.8			
	Angular deviation (degrees)	67.7	71.8	69.7			
	Rayleigh's *z*	3.64	8.58	2.70			
Day 2	Mean distance (cm)	17.7	14.5	13.6			
	Standard deviation (cm)	35.0	12.6	13.5			
	Mean angle (degrees) † *	258	178	276	149	142	262
	Angular variance (degrees)	76.8	64.1	77.5	74.3	79.3	47.4
	Angular deviation (degrees)	66.3	60.6	66.6	65.2	67.4	52.1
	Rayleigh's *z*	4.36	7.77	4.20	4.95	3.79	13.76
Day 3	Mean distance (cm)	6.8	11.9	8.6			
	Standard deviation (cm)	5.6	8.5	7.6			
	Mean angle (degrees) † *	145	16	115	207	149	5
	Angular variance (degrees)	94.6	66.6	80.0	84.6	80.1	85.9
	Angular deviation (degrees)	73.6	61.8	67.7	69.6	67.7	70.2
	Rayleigh's *z*	1.15	7.00	3.65	2.67	3.63	2.44

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	49.9	33.0	59.0			
	Standard deviation (cm)	39.4	27.4	43.0			
	Mean angle (degrees) †	65	3	84	81	188	302
	Angular variance (degrees)	59.7	106.0	103.7	88.0	89.8	104.7
	Angular deviation (degrees)	58.5	77.9	77.1	71.0	71.7	77.5
	Rayleigh's *z*	8.94	0.22	0.35	2.04	1.88	0.29
Day 5	Mean distance (cm)	46.3	69.4	50.9			
	Standard deviation (cm)	33.3	61.7	47.8			
	Mean angle (degrees) †	94	137	61	183	172	194
	Angular variance (degrees)	78.0	85.4	84.2	39.5	39.0	22.3
	Angular deviation (degrees)	66.8	70.0	69.5	47.6	47.3	35.7
	Rayleigh's *z*	4.09	2.59	2.67	16.75	17.41	25.32

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. virgata* (40 snails each) released in medic July 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	50.5	51.5	50.8			
	Standard deviation (cm)	37.9	35.7	37.7			
	Mean angle (degrees) † *	91	91	158			
	Angular variance (degrees)	84.9	86.5	97.5			
	Angular deviation (degrees)	69.7	70.4	74.7			
	Rayleigh's *z*	2.68	2.34	0.85			
Day 2	Mean distance (cm)	49.5	48.2	37.7			
	Standard deviation (cm)	52.1	45.8	29.4			
	Mean angle (degrees) † *	197	20	177	238	62	246
	Angular variance (degrees)	90.2	89.1	96.4	83.2	104.4	94.4
	Angular deviation (degrees)	71.9	71.5	74.3	69.0	77.3	73.6
	Rayleigh's *z*	1.81	1.92	0.96	2.78	0.30	1.17
Day 3	Mean distance (cm)	29.0	28.3	23.9			
	Standard deviation (cm)	38.1	33.7	34.2			
	Mean angle (degrees) † *	167	192	278	277	183	105
	Angular variance (degrees)	82.7	87.0	68.3	96.8	75.0	111.3
	Angular deviation (degrees)	68.8	70.6	62.5	74.5	65.6	79.9
	Rayleigh's *z*	2.94	2.20	6.37	0.87	4.30	0.03

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	107.8	114.3	133.5			
	Standard deviation (cm)	86.2	77.3	87.3			
	Mean angle (degrees)	242	177	171	218	299	103
	Angular variance (degrees)	61.9	50.2	51.2	83.3	107.2	100.5
	Angular deviation (degrees)	59.6	53.6	54.2	69.1	78.4	75.9
	Rayleigh's *z*	7.19	11.38	11.93	2.54	0.16	0.59
Day 5	Mean distance (cm)	53.5	101.7	63.3			
	Standard deviation (cm)	50.2	72.1	49.8			
	Mean angle (degrees) †	179	67	74	186	189	175
	Angular variance (degrees)	91.7	87.6	69.1	38.8	16.5	29.8
	Angular deviation (degrees)	72.5	70.8	62.9	47.2	30.8	41.3
	Rayleigh's *z*	1.36	2.00	6.14	14.87	26.38	21.36

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. virgata* (40 snails each) released in barley September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	36.6	49.4	41.8			
	Standard deviation (cm)	21.4	26.4	29.8			
	Mean angle (degrees) †	211	230	45			
	Angular variance (degrees)	95.3	90.8	88.1			
	Angular deviation (degrees)	73.9	72.1	71.1			
	Rayleigh's *z*	0.99	7.68	1.92			
Day 2	Mean distance (cm)	9.9	17.3	20.5			
	Standard deviation (cm)	5.8	19.4	19.5			
	Mean angle (degrees)	167	188	225	203	220	205
	Angular variance (degrees)	70.0	103.0	106.0	97.0	94.6	83.0
	Angular deviation (degrees)	63.3	76.8	77.9	74.5	73.6	69.0
	Rayleigh's *z*	5.29	0.39	0.20	0.80	1.12	2.88
Day 3	Mean distance (cm)	13.9	17.4	25.6			
	Standard deviation (cm)	16.4	14.7	24.1			
	Mean angle (degrees) † *	182	316	225	160	175	147
	Angular variance (degrees)	77.9	101.0	104.5	72.9	103.9	79.4
	Angular deviation (degrees)	66.8	76.1	77.4	64.4	77.2	67.5
	Rayleigh's *z*	3.58	0.44	0.26	4.64	0.33	3.49

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	33.8	51.7	51.2			
	Standard deviation (cm)	30.3	37.6	50.2			
	Mean angle (degrees) †	177	200	29	183	285	144
	Angular variance (degrees)	49.7	45.8	107.7	83.6	96.2	87.8
	Angular deviation (degrees)	53.4	51.2	78.6	69.2	74.3	70.9
	Rayleigh's *z*	11.87	13.71	0.13	2.56	0.79	1.96
Day 5	Mean distance (cm)	90.9	89.8	85.2			
	Standard deviation (cm)	107.5	53.3	60.0			
	Mean angle (degrees) †	176	188	23	178	194	179
	Angular variance (degrees)	39.4	133.3	100.2	52.4	32.5	41.9
	Angular deviation (degrees)	47.5	43.7	75.8	54.8	43.2	19.0
	Rayleigh's *z*	12.49	16.08	0.44	10.30	19.48	15.28

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. virgata* (40 snails each) released in medic September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	45.1	31.7	87.7			
	Standard deviation (cm)	34.2	29.8	28.1			
	Mean angle (degrees) † *	94	136	7			
	Angular variance (degrees)	93.7	100.2	106.9			
	Angular deviation (degrees)	73.3	71.9	78.3			
	Rayleigh's *z*	1.30	1.47	0.12			
Day 2	Mean distance (cm)	25.5	18.6	16.8			
	Standard deviation (cm)	41.7	12.8	21.0			
	Mean angle (degrees) † *	193	143	8	231	199	300
	Angular variance (degrees)	103.6	99.8	106.7	113.1	109.3	101.8
	Angular deviation (degrees)	77.0	78.2	78.2	80.5	79.1	76.4
	Rayleigh's *z*	0.34	0.38	0.11	0.01	0.07	0.40
Day 3	Mean distance (cm)	31.1	41.8	12.9			
	Standard deviation (cm)	35.0	37.8	11.4			
	Mean angle (degrees) † *	112	221	217	168	102	337
	Angular variance (degrees)	86.1	98.8	87.8	103.6	99.1	107.4
	Angular deviation (degrees)	70.2	72.6	70.9	77.1	75.3	78.5
	Rayleigh's *z*	2.29	2.11	1.15	0.34	0.61	1.68

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	50.5	87.9	23.8			
	Standard deviation (cm)	41.2	86.3	18.7			
	Mean angle (degrees) †	156	237	203	232	100	175
	Angular variance (degrees)	33.3	103.6	89.1	97.2	96.2	85.0
	Angular deviation (degrees)	43.7	47.3	71.4	74.6	74.2	69.8
	Rayleigh's *z*	18.12	16.71	1.24	0.85	0.93	1.73
Day 5	Mean distance (cm)	103.7	113.9	33.6			
	Standard deviation (cm)	71.8	86.4	27.8			
	Mean angle (degrees) †	153	91	197	179	185	127
	Angular variance (degrees)	25.2	110.7	89.3	47.3	45.5	93.2
	Angular deviation (degrees)	38.0	39.8	71.5	52.0	51.1	73.1
	Rayleigh's *z*	15.81	16.41	0.73	10.36	14.16	0.70

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. acuta* (40 snails each) released in barley September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	20.8	23.5	25.1			
	Standard deviation (cm)	23.0	15.7	22.8			
	Mean angle (degrees) *	72	105	90			
	Angular variance (degrees)	65.4	68.6	48.4			
	Angular deviation (degrees)	61.2	62.7	52.7			
	Rayleigh's *z*	7.37	5.65	11.01			
Day 2	Mean distance (cm)	12.4	14.9	15.4			
	Standard deviation (cm)	12.8	10.2	8.9			
	Mean angle (degrees) † *	95	285	177	388	164	88
	Angular variance (degrees)	86.5	108.8	89.7	91.0	101.2	102.2
	Angular deviation (degrees)	70.4	78.9	71.7	72.2	76.1	76.5
	Rayleigh's *z*	1.02	0.09	1.23	0.21	4.09	3.77
Day 3	Mean distance (cm)	24.7	26.4	23.7			
	Standard deviation (cm)	23.4	12.2	14.4			
	Mean angle (degrees) † *	254	90	259	261	83	117
	Angular variance (degrees)	102.3	91.9	98.2	98.4	101.4	75.4
	Angular deviation (degrees)	76.6	72.6	75.0	75.1	76.2	65.7
	Rayleigh's *z*	0.26	1.33	0.71	0.34	4.14	4.20

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	38.4	35.6	36.0			
	Standard deviation (cm)	27.0	25.6	24.1			
	Mean angle (degrees)	192	199	170	129	270	108
	Angular variance (degrees)	48.7	68.5	54.1	111.0	106.1	104.7
	Angular deviation (degrees)	52.8	62.6	55.7	79.8	78.0	77.5
	Rayleigh's *z*	7.28	14.89	6.70	0.03	0.19	0.26
Day 5	Mean distance (cm)	63.9	76.4	89.4			
	Standard deviation (cm)	71.0	71.0	63.6			
	Mean angle (degrees)	85	90	129	210	180	182
	Angular variance (degrees)	60.3	59.7	61.2	61.8	62.5	68.3
	Angular deviation (degrees)	49.7	58.5	51.3	59.5	59.8	62.6
	Rayleigh's *z*	2.14	2.76	2.11	6.57	6.41	5.05

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of adult *C. acuta* (40 snails each) released in medic September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	20.5	19.6	14.7			
	Standard deviation (cm)	21.3	17.0	19.5			
	Mean angle (degrees) † *	105	85	230			
	Angular variance (degrees)	32.5	71.9	20.2			
	Angular deviation (degrees)	43.1	64.2	34.1			
	Rayleigh's *z*	13.87	3.47	16.27			
Day 2	Mean distance (cm)	10.5	12.5	13.9			
	Standard deviation (cm)	6.4	9.6	19.2			
	Mean angle (degrees) † *	172	224	61	233	279	140
	Angular variance (degrees)	97.7	57.1	87.6	89.8	95.5	45.0
	Angular deviation (degrees)	74.8	57.2	70.9	71.7	74.0	50.7
	Rayleigh's *z*	3.84	5.04	1.38	1.78	0.89	9.97
Day 3	Mean distance (cm)	14.9	23.5	8.3			
	Standard deviation (cm)	16.6	13.5	7.4			
	Mean angle (degrees) *	199	246	265	250	220	293
	Angular variance (degrees)	108.0	109.2	69.6	76.1	82.2	81.9
	Angular deviation (degrees)	78.7	79.1	63.2	66.0	68.6	68.5
	Rayleigh's *z*	0.09	0.89	4.31	3.72	2.93	2.03

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	37.5	44.4	47.6			
	Standard deviation (cm)	26.6	37.8	26.6			
	Mean angle (degrees)	155	175	172	259	96	96
	Angular variance (degrees)	49.3	47.7	21.4	87.3	85.4	76.8
	Angular deviation (degrees)	53.2	52.3	35.0	70.7	70.0	66.3
	Rayleigh's *z*	8.43	7.15	17.87	1.82	1.88	3.37
Day 5	Mean distance (cm)	39.7	42.9	44.1			
	Standard deviation (cm)	28.1	22.3	14.9			
	Mean angle (degrees) †	161	194	225	206	178	194
	Angular variance (degrees)	61.9	63.3	40.2	59.6	58.6	37.6
	Angular deviation (degrees)	57.8	58.6	48.0	58.4	57.9	46.4
	Rayleigh's *z*	4.39	5.94	0.84	7.14	5.97	14.88

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of juvenile *C. virgata* (40 snails each) released in barley September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	29.1	32.6	31.9			
	Standard deviation (cm)	19.2	16.7	22.4			
	Mean angle (degrees) † *	89	91	6			
	Angular variance (degrees)	71.2	63.8	95.4			
	Angular deviation (degrees)	65.3	60.5	73.9			
	Rayleigh's *z*	3.19	5.30	0.70			
Day 2	Mean distance (cm)	10.2	14.8	32.0			
	Standard deviation (cm)	10.2	14.9	27.9			
	Mean angle (degrees)	141	87	204	358	247	44
	Angular variance (degrees)	93.1	91.7	91.1	77.4	112.1	88.2
	Angular deviation (degrees)	71.8	72.5	72.2	66.6	80.2	71.1
	Rayleigh's *z*	0.84	1.00	0.76	3.38	0.01	1.33
Day 3	Mean distance (cm)	24.8	24.5	40.5			
	Standard deviation (cm)	15.8	16.1	30.3			
	Mean angle (degrees) *	136	114	148	246	272	117
	Angular variance (degrees)	94.1	86.7	107.8	105.7	92.2	82.1
	Angular deviation (degrees)	73.8	70.5	78.6	77.8	72.7	68.6
	Rayleigh's *z*	1.09	1.83	0.07	0.23	1.26	2.10

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	35.8	28.7	45.7			
	Standard deviation (cm)	18.6	20.9	39.9			
	Mean angle (degrees)	192	187	193	177	164	106
	Angular variance (degrees)	53.6	79.7	45.1	110.0	103.3	99.2
	Angular deviation (degrees)	57.2	67.6	50.9	79.4	77.0	75.4
	Rayleigh's *z*	4.93	2.68	8.08	0.05	0.32	0.48
Day 5	Mean distance (cm)	39.2	39.3	89.6			
	Standard deviation (cm)	23.8	33.9	59.0			
	Mean angle (degrees)	193	215	187	174	134	191
	Angular variance (degrees)	59.1	70.3	35.3	61.7	74.4	58.7
	Angular deviation (degrees)	51.4	63.5	44.9	59.4	65.3	58.0
	Rayleigh's *z*	2.93	2.39	3.83	5.97	3.93	5.95

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of juvenile *C. virgata* (40 snails each) released in medic September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	58.5	23.1	109.6			
	Standard deviation (cm)	16.5	16.3	36.3			
	Mean angle (degrees) *	94	28	44			
	Angular variance (degrees)	99.6	73.5	74.3			
	Angular deviation (degrees)	75.5	64.9	65.3			
	Rayleigh's *z*	0.34	3.08	2.96			
Day 2	Mean distance (cm)	21.1	13.2	35.2			
	Standard deviation (cm)	18.5	17.5	41.1			
	Mean angle (degrees) † *	222	219	312	267	45	358
	Angular variance (degrees)	76.4	73.7	102.6	77.4	102.1	85.9
	Angular deviation (degrees)	66.2	65.0	76.7	66.6	76.5	70.1
	Rayleigh's *z*	1.67	3.05	0.19	4.22	0.29	1.51
Day 3	Mean distance (cm)	41.9	32.2	52.9			
	Standard deviation (cm)	48.9	21.8	30.6			
	Mean angle (degrees) *	101	122	125	201	156	68
	Angular variance (degrees)	99.9	62.5	88.7	92.9	86.8	100.7
	Angular deviation (degrees)	75.7	59.9	71.3	73	70.5	76.0
	Rayleigh's *z*	0.30	4.75	0.97	0.75	1.94	0.38

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	38.9	38.7	60.7			
	Standard deviation (cm)	21.6	27.6	47.5			
	Mean angle (degrees)	171	181	217	329	180	161
	Angular variance (degrees)	101.2	49.6	82.8	108.2	87.8	102.6
	Angular deviation (degrees)	76.2	53.3	68.9	78.7	70.9	76.7
	Rayleigh's *z*	0.15	5.15	1.15	0.08	1.31	0.28
Day 5	Mean distance (cm)	152.8	61.6	109.2			
	Standard deviation (cm)	0.1	33.6	84.1			
	Mean angle (degrees)	159	178	120	235	210	188
	Angular variance (degrees)	36.8	39.7	65.6	72.4	73.6	97.9
	Angular deviation (degrees)	45.9	47.7	61.3	64.4	64.9	74.9
	Rayleigh's *z*	1.38	2.99	1.64	1.49	3.33	0.49

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of juvenile *C. acuta* (40 snails each) released in barley September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	15.9	14.5	21.4			
	Standard deviation (cm)	7.8	11.8	8.3			
	Mean angle (degrees) † *	240	133	136			
	Angular variance (degrees)	84.3	35.0	75.5			
	Angular deviation (degrees)	69.5	44.8	65.8			
	Rayleigh's *z*	2.10	14.95	1.98			
Day 2	Mean distance (cm)	9.4	6.1	11.6			
	Standard deviation (cm)	14.9	7.0	7.54			
	Mean angle (degrees) †*	281	233	305	133	158	183
	Angular variance (degrees)	83.3	86.7	112.5	92.7	55.9	86.3
	Angular deviation (degrees)	69.1	70.5	80.3	72.9	56.6	70.3
	Rayleigh's *z*	1.79	1.90	0.00	1.10	8.12	1.03
Day 3	Mean distance (cm)	12.1	7.4	14.6			
	Standard deviation (cm)	18.8	8.5	16.4			
	Mean angle (degrees)	153	207	147	78	105	297
	Angular variance (degrees)	80.6	93.1	81.3	90.4	56.9	112.8
	Angular deviation (degrees)	68.0	73.0	68.3	72.0	57.1	80.4
	Rayleigh's *z*	1.76	1.12	1.35	1.21	9.13	0.00

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	11.2	13.2	23.3			
	Standard deviation (cm)	9.3	15.2	9.6			
	Mean angle (degrees)	206	200	171	112	164	127
	Angular variance (degrees)	87.0	61.3	39.8	43.0	95.2	79.6
	Angular deviation (degrees)	70.6	59.3	47.8	49.6	73.9	67.5
	Rayleigh's *z*	1.16	6.91	6.82	8.60	0.94	1.96
Day 5	Mean distance (cm)	25.0	27.9	30.7			
	Standard deviation (cm)	19.3	27.1	17.6			
	Mean angle (degrees)	179	160	173	124	174	164
	Angular variance (degrees)	88.7	50.8	54.2	70.8	61.3	62.9
	Angular deviation (degrees)	71.3	53.9	55.7	63.7	59.2	60.0
	Rayleigh's *z*	0.56	6.21	3.05	3.80	7.36	4.07

† Significant difference in distribution of headings and * turning angles.

Descriptive statistics for individual dispersal of three populations of juvenile *C. acuta* (40 snails each) released in barley September 2002. n = 40.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 1	Mean distance (cm)	17.7	11.9	122.2			
	Standard deviation (cm)	8.5	16.9	36.0			
	Mean angle (degrees) † *	63	96	188			
	Angular variance (degrees)	75.1	74.4	77.3			
	Angular deviation (degrees)	65.6	65.3	66.6			
	Rayleigh's *z*	3.32	4.07	2.22			
Day 2	Mean distance (cm)	9.4	13.0	90.5			
	Standard deviation (cm)	7.8	16.6	92.7			
	Mean angle (degrees) *	190	227	206	64	109	139
	Angular variance (degrees)	88.1	83.7	80.6	78.7	102.4	65.4
	Angular deviation (degrees)	71.1	69.2	68.0	67.2	76.6	61.2
	Rayleigh's *z*	1.60	2.47	1.58	3.14	0.42	3.86
Day 3	Mean distance (cm)	12.6	10.4	69.9			
	Standard deviation (cm)	10.1	7.7	74.0			
	Mean angle (degrees) † *	202	305	164	120	124	211
	Angular variance (degrees)	94.7	105.6	101.7	67.6	76.6	95.8
	Angular deviation (degrees)	73.6	77.8	76.3	62.2	66.2	74.1
	Rayleigh's *z*	5.57	0.21	0.37	5.55	3.75	0.92

Continued.

		Direction of heading			Turning angle		
	Replicate	1	2	3	1	2	3
Day 4	Mean distance (cm)	11.0	26.0	110.1			
	Standard deviation (cm)	7.3	18.8	85.6			
	Mean angle (degrees) † *	259	124	188	137	286	179
	Angular variance (degrees)	92.0	85.9	76.3	91.5	96.5	102.2
	Angular deviation (degrees)	72.6	70.2	66.1	72.4	74.4	76.5
	Rayleigh's *z*	1.09	1.32	3.02	1.43	0.92	0.34
Day 5	Mean distance (cm)	35.3	Insufficient data	98.8			
	Standard deviation (cm)	28.4		60.4			
	Mean angle (degrees)	201		207	297	115	166
	Angular variance (degrees)	47.5		58.8	106.6	76.6	75.4
	Angular deviation (degrees)	52.2		58.0	78.1	66.2	65.7
	Rayleigh's *z*	4.46		1.19	0.15	2.31	3.15

† Significant difference in distribution of headings and * turning angles.

APPENDIX 7. MATLAB Code defining functions used in calculating the extinction time cumulative distribution function and its confidence limits. From Box 3.3 (Morris and Doak, 2003). pp 80.

```
function phi=stdnormcdf(z)
%stdnormcdf(z) calculates the standard normal cumulative
%distribution function, using the built-in MATLAB error funciton
%erf;
phi=0.5*(1+(erf(z/sqrt(2))));
```

APPENDIX 8. A MATLAB m-file defining the function stretchbetaval which returns stretched beta-distributed values. Note that this procedures uses betaval, defined in Appendix 7. From Box 8.5 (Morris and Doak, 2003). pp 283.

```
function bb=stretchbetaval(mn,sd,minb,maxb,fx)
%STBetaval(mean,sd,minb,maxb,fx)
%this routine generates a stretched beta number with
%mean mn, standard deviation sd, minimum and maximum
%values (minb, maxb), and CDF value (fx).
%This function calls the function betaval.m

if sd==0; bb=mn; %with no variation, then the value=mean
else
   %convert the stretched beata parameters to corresponding
   %ones for a {0,1} beta
   mnbeta=(mn-minb)/(maxb-minb);
   sdbeta=sd/(maxb-minb);
   % next,check for undoable parameter combos
   if sdbeta<(mnbeta*(1-mnbeta))^0.5
      bvalue=betaval(mnbeta,sdbeta,fx); %find beta value
      bb=bvalue*(maxb-minb)+minb; %convert to stretched value
   else
      disp('the sd is too high for the mean');
      disp ('for a vital rate with the following')
      disp('mean, sd, and min and max values')
      disp([mn,sd,minb,maxb])
      disp ('the maximum sd possible is:')
      maxsd=((mnbeta*(1-mnbeta))^0.5)*(maxb-minb);
      disp(maxsd);
```

```
        disp('you should abort the program (control C)')
        disp('and reset the limits or the sd of this rate');
        pause;
        bb=NaN;
    end; %else
end; %else
```

APPENDIX 9. A second MATLAB function to make beta-distributed random numbers (See Appendix 7). 'betaval' returns a beta-distributed value with the specified CDF (cumulative distribution function) value. The program BetaDemo is also included, showing the use of betaval. From Box 8.3 (Morris and Doak, 2003). pp 277.

```
function bb = betaval(mn,sd,fx)
%BETAVAL(mean, sd, Fx)
% This function calculates a random number
% from a beta distribution with mean mn, standard deviation
% sd, and cum. distr. function fx.
% This function uses the MATLAB function betainc(x, vv,ww),
% where x is the value of beta, v,w are beta parameters
% that are called a and b in the text.
if sd == 0; bb = mn;
else
 toler = 0.0001; % this is tolerance of answer: how close
 % the CDF value of the answer must be to the input value (Fx)
 var = sd^2;
 if var >=(1-mn)*mn disp('sd too high for beta'), pause, end;
 % this checks that the input mean and st. deviation
 % are possible for a beta.

 vv = mn*((mn.*(1-mn)/(var))-1); % calculate the beta parameters
 ww = (1-mn).*((mn.*(1-mn)/(var))-1);

 upval = 1; lowval = 0; x = 0.5+ 0.02*rand;
 % start with a beginning guess x; the use of rand
 % adds wiggle to the search start to avoid pathologies
 i = betainc(x,vv,ww); % find the CDF value for x
```

```
% the following while loop searches for ever better
% values of x, until the value has a CDF within the
% toler of Fx (unless the value
% is very close to 0 or 1, which will also terminate
% the search)
 while ( (toler < abs(i-fx))&(x >1e-6)&((1-x)>1e-6) )
       if fx > i
          lowval = x; x = (upval+lowval)/2;
       else
          upval = x; x = (upval+lowval)/2;
        end; %if
       i = betainc(x,vv,ww);
 end; % while

% This makes values of x somewhat random to eliminate
% pathologies when variance is very small or large.
% It also truncates values of x, with the
% smallest values equal to toler and the biggest
% equal to 1 - toler.
bbb = x + toler*0.1*(0.5-rand);
if bbb < toler; bbb = toler; end;
if bbb > 1; bbb = 1- toler; end;

bb=bbb;
end; %else
```

REFERENCES

Abd El-Hamid A. 1996. Attraction of *Biomphalaria alexandrina* snails to different carbohydrates. *Egyptian Journal of Bilharziasos* **18:** 39-54.

Adamo S, and Chase R. 1987. Courtship and copulation in the terrestrial snail *Helix aspersa*. *Canadian Journal of Zoology* **66:** 1446-1453.

Akaike H. 1969. Fitting autoregressive models for prediction. *Annals of the Institute of Statistical Mathematics* **21:** 243 -247.

Akaike H. 1974. A new look at the statistical model identification. *IEEE Transaction on Automatic Control, AC* **19**.

Akçakaya R, and Baur B. 1996. Effects of population subdivision and catastrophes on the persistence of a land snail metapopulation. *Oecologia* **105:** 475-483.

Allan R, Lindesay J, and Parker D. 1996. *El Nino Southern Oscillation and climatic variability*. CSIRO, Melbourne.

Arad Z. 1990. Resistance to desiccation and distribution patterns in bush-dwelling land snails. *Journal of Zoology, London* **221:** 113-124.

Arad Z, Goldenberg S, Aviv T, and Heller J. 1993. Intraspecific variation in resistance to desiccation in the land snail *Theba pisana*. *International Journal of Biometeorology* **37:** 183-189.

Arad Z, and Avivi T. 1998. Ontogeny of resistance to desiccation in the bush dwelling snail *Theba pisana* (Helicidae). *Journal of Zoology, London* **244:** 515-526.

Arnaud J, Maldec L, Bellido A, and Guiller A. 1999. Microspatial genetic structure in the land snail *Helix aspersa* (Gastropoda: Helicidae). *Heredity* **83:** 110-119.

Asami T. 1993a. Interspecific differences in desiccation tolerance of juvenile land snails. *Functional Ecology* **7:** 571-577.

Asami T. 1993b. Divergence of activity patterns in coexisting species of land snails. *Malacologia* **35:** 399-406.

Atkins W, and Leebour M. 1923. The hydrogen ion concentration of the soil and natural water in relation to the distribution of snails. *Scientific Proceedings R.D.S* **17:** 234-240.

Aubertin D, Ellis A, and Robson G. 1930. The natural history and variation of the pointed snail *Cochlicella acuta. Proceedings of the Zoological Society. London* **1930:** 1027-1055.

Avidov Z, and Harpaz I. 1969. *Plant Pests of Israel.* Israel University Press. Jerusalem.

Bailey S. 1975. The seasonal and daily patterns of locomotor activity in the snail *Helix aspersa* Müller, and their relation to environmental variables. *Proceedings of the Malacological Society. London* **41:** 415-428.

Bailey S. 1981. Circannual and circadian rhythms in the snail *Helix aspersa* Müller and the photoperiodic control of annual activity and reproduction. *Journal of Comparative Physiology A Sensory Neural and Behavioural Physiology* **142:** 89-94.

Bailey S. 1989. Foraging behaviour of terrestrial gastropods: integrating field and laboratory studies. *Journal of Molluscan Studies* **55:** 263-272.

Bailey S. 2002. Molluscicidal baits for control of terrestrial gastropods. In: Barker G, ed. *Molluscs as Crop Pests*. Oxon, UK: CABI Publishing.**pp**.33-54.

Bailey S, and Lazaridou-Dimitriadou M. 1986. Circadian components in the daily activity of *Helix lucorum* L. from northern Greece. *Journal of Molluscan Studies* **52:** 190-192.

Bailey S, and Wedgwood M. 1991. Complementary video and acoustic recordings of foraging by two pest species of slugs on non-toxic and molluscicidal baits. *Annals of Applied Biology* **119:** 163-176.

Baker G. 1986. *The biology and control of white snails (Mollusca: Helicidae), Introduced pests in Australia.* Commonwealth Scientific and Industrial Research Organisation, Australia. Technical Report No. 25.

Baker G. 1988a. Population dynamics of the white snail, *Cernuella virgata* (Mollusca Helicidae), in a pasture-cereal rotation in South Australia. Fifth Australasian Conference on Grassland Invertebrate Ecology. University of Melbourne, Victoria, **pp.** 177-183.

Baker G. 1988b. The life history, population dynamics and polymorphism of *Cernuella virgata* (Mollusca Helicidae). *Australian Journal of Zoology* **36:** 497-512.

Baker G. 1988c. Dispersal of *Theba pisana* (Mollusca: Helicidae). *Journal of Applied Ecology* **25:** 889-900.

Baker G. 1988d. The dispersal of *Cernuella virgata* (Mollusca: Helicidae). *Australian Journal of Zoology* **36:** 513-520.

Baker G. 1989. Damage, population dynamics, movement and control of pest Helicid snails in Southern Australia. In Henderson, IF ed. BCPC MONO Symposium Proceedings *Slug and Snail Pests in Agriculture*, No. 41. Thornton Heath. **pp**. 175-183.

Baker G. 1992. Movement of introduced white snails between pastures and cereal crops in South Australia. In: Delfosse ES, ed. *Pests of Pastures: Weed, Invertebrate and Disease Pests of Australian Sheep Pastures*. Melbourne, Australia: Commonwealth Scientific and Industrial Research Organisation Information Services. **pp.** 115-120.

Baker G. 1996. Population dynamics of the Mediterranean snail, *Cernuella virgata,* in pasture-cereal rotation in South Australia. In. Henderson, IF ed BCPC Symposium Proceedings *Slug and Snail Pests in Agriculture*, Farnham. No. 66. **pp.**, 117-124.

Baker G. 1998. Recognising and responding to the influences of agricultural and other land use practices on soil fauna in Australia. *Applied Soil Ecology* **9:** 303-310.

Baker G. 2002. Helicid and Hygromiid Snails in Cereal Crops and Pastures in Southern Australia. In: Barker G, ed. *Terrestrial Molluscs as Crop Pests*. UK: CABI Publishing. **pp**.193-216.

Baker G, and Vogelzang B. 1988. Life history, population dynamics and polymorphism of *Theba pisana* (Mollusca: Helicidae) in Australia. *Journal of Applied Ecology* **25:** 867-887.

Baker G, and Hawke B. 1990a. Life history, population dynamics and polymorphism of *Theba pisana* (Mollusca: Helicidae) in Australia. *Journal of Applied Ecology* **25:** 867-887.

Baker G, and Hawke B. 1990b. Life history and population dynamics of *Theba pisana* (Mollusca: Helicidae) in a cereal-pasture rotation. *Journal of Applied Ecology* **27:** 16-29.

Baker G. 1991. Production of eggs and young snails by adult *Theba pisana* (Müller) and *Cernuella virgata* (da Costa) (Mollusca: Helicidae) in laboratory cultures. *Australian Journal of Zoology* **39:** 673-679.

Baker G, and Hawke B. 1991. Fecundity of *Cochlicella acuta* (Mollusca: Helicidae) in laboratory cultures. *Invertebrate Reproduction and Development* **20:** 243-247.

Baker G, Hawke B, and Vogelzang B. 1991. Life History and population dynamics of *Cochlicella acuta* (Müller) (Gastropoda: Helicidae) in a pasture-cereal rotation. *Journal of Molluscan Studies* **57:** 259-266.

Baker H. 1958. Land snail dispersal. *Nautilus* **71:** 141-148.

Bar Z. 1977. Human consumption of the land snails in Israel. *Basteria* **41:** 53-58.

Bar Z, and Nevo E. 1976. Natural selection of shell banding polymorphism in *Theba pisana* (Mollusca) along climatic gradients. *Israel Journal of Zoology* **25:** 214-215.

Barker G. 1990. Pasture renovation: interactions of vegetation control with slug and insect infestations. *Journal of Agricultural Science, Cambridge* **115:** 195-202.

Barker G. 2002. Preface. In: Barker G, ed. *Molluscs as Crop Pests*. Oxon, UK: CABI Publishing.

Barnes D, and Weil J. 1944. Slugs in gardens: their numbers, activities and distribution. Part 1. *Journal of Animal Ecology* **13:** 140-175.

Barnes H, and Weil J. 1945. Slugs in gardens: their numbers, activities, and distribution Part 2. *Journal of Animal Ecology* **14:** 71-105.

Basinger A. 1923. The white snail *(Helix pisana)* at La Jolla, California. *Journal of Economical Entomology* **16:** 522-526.

Basinger A. 1927. The eradication campaign against the white snail (*Helix pisana*) at La Jolla, California. *Monthly Bulletin Department of Agriculture. State of California* **26:** 51-76.

Baur A, and Baur B. 1988. Individual movement patterns of the minute land snail *Punctum pygmaeum* (Draparnaud) (Pulmonata: Endodontidae). *The Veliger* **30:** 372-376.

Baur A, and Baur. B. 1990. Are roads barriers to dispersal in the land snail *Arianta arbustorum*. *Canadian Journal of Zoology* **68.:** 613-617.

Baur A, and Baur B. 1993. Daily movement patterns and dispersal in the land snail *Arianta arbistorum*. *Malacologia* **35:** 89-98.

Baur A, Baur B, and Froberg L. 1994. Herbivory on calcicolous lichens: different food preferences and growth rates in two co-existing land snails. *Oecologia* **98:** 313-319.

Baur B. 1984. Early maturity and breeding in *Arianta arbustorum* (L.) (Pulmonata: Helicidae). *Journal of Molluscan Studies* **50:** 241-242.

Baur B. 1988a. Do the risks of egg cannibalism and desiccation influence the choice of oviposition sites in the land snail *Arianta arbustorum*? *Journal of Zoology, London* **216:** 495-502.

Baur B. 1988b. Population regulation in the land snail *Arianta arbustorum*: density effects on adult size, clutch size and incidence of egg cannibalism. *Oecologia* **77:** 390-394.

Baur B. 1988c. Egg-species recognition in cannibalistic hatchlings of the land snails *Arianta arbustorum* and *Helix pomatia*. *Experientia* **44:** 276-277.

Baur B. 1992. Random mating by size in the simultaneously hermaphroditic land snail *Arianta arbustorum*: experiments and explanation. *Animal Behaviour* **43:** 511-518.

Baur B, and Baur A. 1986. Proximate factors influencing egg cannibalism in the land snail *Arianta arbustorum* (Pulmonata: Helicidae). *Oecologia* **70:** 283-287.

Baur B, and Gosteli. 1986. Between and within population differences in geotactic response in the land snail *Arianta arbistorum* (L.) (Helicidae). *Behaviour* **97:** 147-160.

Baur B, and Baur A. 1993. Climatic warming due to thermal radiation from an urban area as possible cause for the local extinction of a land snail. *Journal of Applied Ecology* **30:** 333-340.

Bayne C. 1969. Survival of the embryos of the grey field slug *Agriolimax reticulatus*, following desiccation of the egg. *Malacologia* **9:** 391-401.

Bayomy M, and Joosse J. 1987. Effects of temperature and photoperiod on egg laying, body growth and survival of *Bulinus truncatus*. *Proceedings of the Koninklijke Nederlandse Akadmie van Wetenschappen Series C Biological and Medical Sciences* **90:** 243-256.

Beissinger S, and Westphal M. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* **62:** 821-841.

Berg C. 1953. Sciomyzid larvae (Diptera) that feed on snails. *Journal of Parasitology* **39:** 630-636.

Berg C, and Knutson L. 1978. Biology and systematics of the Sciomyzidae. *Annual Review of Entomology* **23:** 239-258.

Biannic M, Coillot J, and Daguzan J. 1994. Heart rate in relation to dehydration in the snail *Helix aspersa* Müller (Gastropoda, Pulmonata). *Comparative Biochemistry and Physiology A Comparative Physiology* **108:** 65-67.

Biannic M, Coillot J, and Daguzan J. 1995. Circadian cardiac rhythm in relation to environmental variables in the snail *Helix aspersa* Müller. *Journal of Molluscan Studies* **61:** 289-292.

Bishop M. 1977. Approaches to the qualitative description of terrestrial mollusc populations and habitats. *Malacologia* **16:** 61-66.

Block G, Geusz M, Khalsa S, Manivannan K, Michel S, and Whitmore D. 1994. Unwinding the snail's clock: cellular analysis of a retinal circadian pacemaker. *Netherlands Journal of Zoology* **44:** 550-562.

Boag D. 1982. Overcoming sampling bias in studies of terrestrial gastropods. *Canadian Journal of Zoology* **60:** 1289-1292.

Boag D. 1985. Micro distribution of three genera of small terrestrial snails (Stylommatophorea: Pulmonata). *Canadian Journal of Zoology* **63:** 1089-1095.

Bostanian N, Binns M, Kovach J, Racette G, and Mailoux G. 1999. Predictive model for strawberry bud weevil (Coleoptera: Curculionidae) adults in a strawberry field. *Environmental Entomology* **28:** 398-406.

Bourne N, Jones G, and Bowen I. 1988. Slug feeding behaviour in relation to control with molluscicidal baits. *Journal of Molluscan Studies* **54:** 327-338.

Bowen I, and Antoine S. 1996. Reformulation studies with Methiocarb. In Henderson IF ed BCPC Symposium Proceedings *Slug and Snail Pests in Agriculture,* No. 66. Farnham **pp.** 397-404.

Boycott A. 1943. The habitats of land molluscs in Britain. *Journal of Ecology* **22:** 1-38.

Bride M, and Gomot L. 1989. L'escargot ou les difficultes de l'hermaphrodisme. *Invertebrate Reproduction and Development* **16:** 75-85.

Bull C, Baker G, Lawson L, and Steed M. 1992. Investigation of the role of mucus and faeces in interspecific interactions of two land snails (Gastropoda: Pulmonata). *Journal of Molluscan Studies* **58:** 433-441.

Burch J. 1956. Distribution of the land snails in plant associations in eastern Virginia. *Nautilus* **70:** 60-64.

Burch J. 1960. Some snails and slugs of quarantine significance to the United States. *U.S. Department of Agriculture. Agricultural. Research Services. ARS* **82:** 1-73.

Butcher A, Talbot G, Norton R, Kirk M, Cribb T, Forsyth J, Knight B, and Cameron A. 1996. Locally acquired *Brachylaima spp* (Digenea: Brachylaimidae) intestinal fluke infection in two South Australian infants. *Medical Journal of Australia* **164:** 475-478.

Butcher A, Parasuramar P, Thompson C, and Grove D. 1998. First report of the isolation of an adult worm of the genus *Brachylaima* (Digena: Brachylaimidae), from the gastrointestinal tract of a human. *International Journal for Parasitology* **28:** 697-610.

Butler A. 1972. The food of the terrestrial snail *Helicella virgata*(da Costa) in South Australia PhD Thesis. *Crop Protection.* Adelaide, South Australia: University of Adelaide.

Butler A. 1976. A shortage of food for the terrestrial snail *Helicella virgata* in South Australia. *Oecologia* **25:** 349-371.

Butler A, and Murphy C. 1977. Distribution of introduced land snails on Yorke Peninsula, South Australia. *Transactions of the Royal Society of South Australia* **101:** 91-98.

Byers J. 2001. Correlated random walk equations of animal dispersal resolved by simulation. *Ecology* **82:** 1680-1690.

Byrne D, Issaacs R, and Veenstra J. 2002. Local dispersal and migration by insect pests and their importance in IPM strategies: University of Minnesota. Electronic Resource. http://ipmworld.umn.edu/chapters/byrne. Access date: April 25, 2002.

Cabaret J. 1983. The polymorphism of shell ornamentation of three helicids and susceptibility to protostrongly infection. *Journal of Molluscan Studies* **Supplement, 12A:** 6-9.

Cabaret J. 1987. Regulation of infection by a nematode (*Müllerius capillaris*) in the snail *Theba pisana. Journal of Invertebrate Pathology* **49:** 242-245.

Caberet J, and Vendroux P. 1986. The response of four terrestrial molluscs to the presence of herbivore faeces: its influence on infection by protostrongylids. *Canadian Journal of Zoology* **64:** 850-854.

Cain A. 1984. Genetics of some morphs in the land snail *Theba pisana. Malacologia* **25:** 381-412.

Cain A. 1977. Variation in the spire index of some coiled gastropod shells, and its evolutionary significance. *Philosophical Transactions of the Royal Society of London B* **277:** 377-428.

Cain A, and Currey J. 1968. Studies on *Cepaea* III. Ecogenetics of a population of *Cepaea nemoralis* (L). subject to strong area effects. *Transactions of the Royal Society of London B* **253:** 447-482.

Cain A, and Cowie R. 1978. Activity of different species of land snail on surfaces of different inclinations. *Journal of Conchology* **29:** 267-272.

Calow P. 1977. Ecology, evolution and energetics: a study in metabolic adaptation. *Advances in Ecological Research* **10:** 1-62.

Cameron A, Down K, and Pannett D. 1980a. Historical and environmental influences on hedgerow snail faunas. *Journal of Linnean Society* **13:** 75-87.

Cameron R. 1970a. The effect of temperature on the activity of three species of Helicid snail (Mollusca: Gastropoda). *Journal of Zoology, London* **162:** 303-315.

Cameron R. 1970b. The survival, weight loss and behaviour of three species of land snail in conditions of low humidity. *Journal of Zoology. London* **160:** 143-157.

Cameron R. 1970c. Differences in the distribution of three species of helicid snail in limestone district of Derbyshire. *Proceedings of the Royal Society of London B* **176:** 131-159.

Cameron R. 1973. Some woodland mollusc faunas from Southern England. *Malacologia* **14:** 355-370.

Cameron R. 1978. Differences in the sites of activity of coexisting species of land mollusca. *Journal of Conchology* **29:** 273-278.

Cameron R. 1981. Functional aspects of shell geometry in some British land snails. *Biological Journal Linnean Society* **16:** 157-168.

Cameron R, and Williamson P. 1977. Estimating migration and the effects of disturbance in mark-recapture studies on the snail *Cepaea nemoralis* L. *Journal of Animal Ecology* **46:** 173-179.

Cameron R, and Carter M. 1979. Intra- and interspecific effects of population density on growth and activity in some helicid land snails (Gastropoda: Pulmonata). *Journal of Animal Ecology* **48:** 237-246.

Cameron R, Down K, and Pannett D. 1980b. Historical and environmental influences on hedgerow snail faunas. *Journal of Linnean Society* **13:** 75-87.

Carson, R. 1962. Silent Spring. Hamilton. London

Carter P, and Baker G. 1997a. Biological control of white and conical snails. *Farming Systems Developments*. Waite Campus, University of Adelaide, **pp.** 113-114.

Carter P, and Baker G. 1997b. Parasitic flies to reduce snail contamination. *Farming Ahead* **69:** 59.

Charwat S, and Davies KA. 1999. Laboratory screening of nematodes isolated from South Australia for potential as biological control agents of helicid snails. *Journal of Invertebrate Pathology* **74:** 55-61.

Charwat S, Hopkins D, and Baker G. 1999. Life cycle of white and conical snails in southern Australia. Fact Sheet, SARDI, South Australia.

Charwat S, Davies K, and Hunt C. 2000. Impact of a Rhabditid Nematode on survival and fecundity of *Cernuella virgata* (Mollusca: Helicidae). *Biocontrol Science and Technology* **10:** 147-155.

Charwat S, and Davies K. 2001. Nematodes - Biocontrol agents of Helicid snails: Rural Industries Research and Development Corporation. RIRDC Publication No 01/03.

Chase R, Croll R, and Zeichner L. 1980. Aggregation in snails, *Achatina falica. Behaviour and Neurobiology* **30:** 218-230.

Chase R, and Croll R. 1981. Tentacular function in snail olfactory orientation. *Journal of Comparative Physiology* **143:** 357-362.

Clark J. 1998. Why trees migrate so fast: confronting theory with dispersal record and the Paleorecord. *The American Naturalist* **152:** 204-224.

Clark J, Lewis M, and Horvath L. 2001. Invasion by extremes: Population spread with variation in dispersal and reproduction. *The American Naturalist* **157:** 537-554.

Commonwealth Bureau of Meteorology. 2002, Adelaide, Australia.

Cook A. 1979. Homing in gastropods. *Malacologia* **18:** 315-318.

Cook A. 1980. Field studies of homing in the pulmonate slug *Limax pseudoflavus* (Evans). *Journal of Molluscan Studies* **46:** 100-105.

Cook A. 1981. Huddling and the control of water loss by the slug *Limax pseudoflavus* Evans. *Animal Behaviour* **29:** 289-298.

Cory J, and Myers J. 2000. Direct and indirect ecological effects of biological control. *TRENDS in Ecology and Evolution* **15:** 137-139.

Cottam D. 1985. Frequency-dependent grazing by slugs and grasshoppers. *Journal of Ecology* **73:** 925-933.

Cotton BC. 1937. Records of snails and slugs introduced to South Australia. *South Australian Naturalist* **16:** 58-60.

Coupland J. 1996a. The biological control of helicid snail pests in Australia: surveys, screening and potential agents. In Henderson, IF ed. BCPC MONO, *Slug and Snail Pests in Agriculture* No. 66 Farnham, **pp.** 255-261.

Coupland J. 1996b. The efficacy of metaldehyde formulations against helicid snails: the effect of concentration, formulation and species. In Henderson, IF ed. BCPC MONO, *Slug and Snail Pests in Agriculture* No. 66 Farnham, **pp.** 151-156.

Coupland J, and Baker G. 1994. Host distribution, larviposition behaviour and generation time of *Sarcophaga penicillata* (Diptera: Sarcphagidae), a parasitoid of conical snails. *Bulletin of Entomological Research* **84:** 185-189.

Coupland J, Espiau A, and Baker G. 1994. Seasonality, longevity, host choice and infection efficiency of *Salticella fasciata* (Diptera: Sciomyzidae), a candidate for the biological control of helicid snails. *Biological Control* **4:** 32-37.

Coupland J, and Baker G. 1995. The potential of several species of terrestrial Sciomyzidae as biological control agents of pest helicid snails in Australia. *Crop Protection* **14:** 573-576.

Cowie R. 1980a. Observations on the dispersal of two species of British land snail. *Journal of Conchology* **30:** 201-208.

Cowie R. 1980b. Precocious breeding of *Theba pisana* (Müller) (Pulmanata: Helicidae). *Journal of Conchology* **30:** 238.

Cowie R. 1984a. The life-cycle and productivity of the land snail *Theba pisana* (Mollusca: Helicidae). *Journal of Animal Ecology* **53:** 311-325.

Cowie R. 1984b. Ecogenetics of *Theba pisana* (Pulmanata: Helicidae) at the northern edge of its range. *Malacologia* **25:** 361-380.

Cowie R. 1984c. Density, dispersal and neighbourhood size in the land snail *Theba pisana*. *Heredity* **52:** 391-401.

Cowie R. 1984d. Shell thickness in the land snail *Theba pisana* (Pulmanata: Helicidae). *Biological Journal of the Linnean Society* **21:** 423-429.

Cowie R. 1984e. Genetics of some morphs in the land snail *Theba pisana*. *Malacologia* **25:** 381-411.

Cowie R. 1985. Microhabitat choice and high temperature tolerance in the land snail *Theba pisana* (Mollusca: Gastropoda). *Journal of Zoology, London* **207:** 201-211.

Cowie R. 1990. Climatic selection on body colour in the land snail *Theba pisana* (Pulmonata: Helicidae). *Heredity* **65:** 123-126.

Cowie R. 1992. Shell pattern polymorphism in a 13-year study of the land snail *Theba pisana* (Müller) (Pulmanata: Helicidae). *Malacologia* **34:** 87-97.

Cowie R. 1995. Identity, distribution and impacts of introduced Ampullariidae and Viviparidae in the Hawaiian Islands. *Journal of Medical and Applied Malacology* **5:** 61-67.

Cowie R. 2002. Apple snails (Ampullariidae) as agricultural pests: their biology, impacts and management. In: Barker G, ed. *Molluscs as Crop Pests*. Oxon, UK: CABI Publishing. **pp.** 145-192.

Cragg J, and Vincent M. 1952. The action of metaldehyde on the slug *Agriolinax reticulateus* (Müller). *Annals of Applied Biology* **39:** 392-406.

Crawford-Sidebotham T. 1970. Differential susceptibility of species of slugs to metaldehyde/ bran and to methiocarb baits. *Oecologia (Berl.)* **5:** 303-324.

Crawford-Sidebotham T. 1972. The influence of weather upon the activity of slugs. *Oecologia* **9:** 141-154.

Croll R, and Chase R. 1977. A long-term memory for food odours in the land snail, *Achatina fulica. Behavioural Biology* **19:** 261-268.

Croll R, and Chase R. 1980. Plasticity of olfactory orientation to foods in the snail *Achatina fulica. Journal of Comparative Physiology* **136:** 267-277.

Cronin M, Hyland K, and Abrahamson W. 2001. The pattern, rate and range of within-patch movement of a stem-galling fly. *Ecological Entomology* **26:** 16-24.

Crowell H. 1977. *Chemical control of terrestrial slugs and snails.* Oregon State University. Station Bulletin Agriculture Experimental Station. **628. pp.** 69.

Dainton B. 1954a. The activity of slugs. I. The induction of activity by changing temperatures. *Journal of Experimental Biology* **31:** 165-187.

Dainton B. 1954b. The activity of slugs. II. The effect of light and air currents. *Journal of Experimental Biology* **31:** 188-198.

Dainton B, and Write J. 1985. Falling temperature stimulates activity in the slug *Arion ater. Journal of Experimental Biology* **118:** 439-443.

Dan N, and Bailey S. 1982. Growth, mortality, and feeding rates of the snail *Helix aspersa* at different population densities in the laboratory, and the depression of activity of helicid snails by other individuals, or their mucus. *Journal of Molluscan Studies* **48:** 257-265.

Datta G, and Smith D. 2003. On propriety of posterior distributions of variance components in small area estimation. *Journal of Statistical Planning and Inference* **112:** 175-183.

Davies M, Hawkins S, and Jones H. 1990. Mucus production and physiological energetics in *Patella vulgata* L. *Journal of Molluscan Studies* **56:** 499-503.

Davis P, Van Schagen J, Widmer M, and Craven T. 1996. Assessment of molluscicidal activity of a copper complex compound. In Henderson IF ed. BCPC MONO, *Slug and Snail Pests in Agriculture* No. 66, Farnham. **pp.** 53-62.

Dawson G, Henderson I, Martin A, and Pye B. 1996. Phyiochemical barriers as plant protectants against slugs (Gastropoda: Pulmonata). In Henderson IF ed. BCPC MONO, *Slug and Snail Pests in Agriculture* No. 66, Farnham. **pp.** 439-444.

DeAngelis D. 1988. Strategies and difficulties of applying models to aquatic populations. *Ecological Modelling* **43:** 57-73.

Denny M. 1980a. Locomotion: the cost of gastropod crawling. *Science* **208:** 1288-1290.

Denny M. 1980b. The role of gastropod pedal mucus in locomotion. *Nature* **285:** 160-161.

Dent D. 1991. *Insect pest management.* CAB International. Wallingford.

Doak D, Marino P, and Kareiva P. 1992. Spatial scale mediates in the influence of habitat fragmentation on dispersal success: Implications for conservation. *Theoretical Population Biology* **41:** 315-336.

Doak P. 2000a. Habitat patchiness and the distribution, abundance and population dynamics of an insect herbivore. *Ecology* **81:** 1842-1857.

Doak P. 2000b. Population consequences of restricted dispersal for an insect herbivore in a subdivided habitat. *Ecology* **81:** 1828-1841.

Edelstam C, and Palmer C. 1950. Homing behaviour in gastropods. *Oikos* **2:** 259-270.

Enee J, Bonnefoy-Claudet R, and Gomot L. 1982. General Biology. The effect of artificial photoperiod on reproduction in the snail *Helix aspersa* Müller. *Comptes Rendus des Seances de l'Academie des Sciences Serie III Sciences de la Vie* **294:** 357-360.

Englund G, and Cooper S. 2002. Scale effects and extra-polation in ecological experiments. *Advances in Ecological Research* **33:** 161-213.

Englund G, and Moen R. 2003. Testing models of trophic dynamics: the problem of translating from model to nature. *Austral Ecology* **28:** 61-69.

Eversole JW. 1971. Mortalities of *Cochlicella barbara* and *Theba pisana* land snails exposed to low temperatures in Morocco. *Journal of Economic Entomology* **64:** 667-670.

Fagan W. 1997. Introducing a 'boundary-flux' approach to quantifying insect diffusion rates. *Ecology* **78:** 579-587.

Farkas S, and Shorey H. 1976. Anemotaxis and odour-trail following by the terrestrial snail *Helix aspersa*. *Animal Behaviour* **24:** 686-689.

Fearnley R. 1996. Heterogenic copulatory behaviour produces non-random mating in laboratory trials in the land snail *Helix aspersa* Müller. *Journal of Molluscan Studies* **62:** 159-164.

Gaines S, and Denny M. 1993. The largest, smallest, highest, lowest, longest and shortest: extremes in ecology. *Ecology* **74:** 1677-1692.

Garthwaite D, and Thomas M. 1996. The usage of molluscicides in agriculture and horticulture in Great Britain over the last 30 years. In Henderson IF ed. BCPC MONO, *Slug and Snail Pests in Agriculture* No. 66, Farnham. **pp.** 39-46.

Gaugler R, Lewis E, and Stuart R. 1997. Ecology in the service of biological control: the case of the entomopathogenic nematodes. *Oecologia* **109:** 483-489.

Geiger R. 1965. *The climate near the ground.* Harvard University Press. Cambridge Mass

Gleich J, and Gilbert F. 1976. A survey of terrestrial gastropods from central Maine. *Canadian Journal of Zoology* **54:** 620-627.

Glen D, and Orsman I. 1986. Comparison of molluscicides based on metaldehyde, methiocarb or aluminium sulphate. *Crop Protection* **5:** 371-375.

Glen D, Wiltshire C, and Butler R. 1991. Slug population changes following molluscicide treatment in relation to distance from edge of treated area. *Crop Protection* **10:** 408-412.

Godan D. 1983. *Pest slugs and snails*. Springer-Verlag, Berlin.

Gomot A, Gomot L, Boukraa S, and Bruckert S. 1989a. Influence of soil on the growth of the land snail *Helix aspersa*. An experimental study of the absorption route for the stimulating factors. *Journal of Molluscan Studies* **55:** 1-8.

Gomot P, Gomot L, and Griffond B. 1989b. Evidence for a light compensation of the inhibition of reproduction by low temperatures in the snail *Helix aspersa*. Ovotestis and albumen gland responsiveness to different conditions of photoperiods and temperatures. *Biology of Reproduction* **40:** 1237-1245.

Goodfriend G. 1983. Anemotaxis and its relation to migration in the land snail *Cepaea nemoralis*. *American Midland Naturalist* **109:** 414-415.

Goodfriend G. 1992. Rapid racemization of aspartic acid in mollusc shells and potential for dating over recent centuries. *Nature (London)*. **357:** 399-401.

Goodhart C. 1962. Variation in a colony of the snail *Cepaea nemoralis* (L.). *Journal of Animal Ecology* **31:** 207-237.

Goodwin B, and Fahrig L. 2002. Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*. *Canadian Journal of Zoology* **80:** 24-35.

Graveland J, and van der Wal R. 1996. Decline in snail abundance due to soil acidification causes eggshell defects in forest passerines. *Oecologia* **105:** 351-360.

Greenwood J. 1974. Effective population numbers in the snail *Cepaea neomoralis. Evolution* **28:** 513-526.

Grevstad F. 1999. Factors influencing the chance of population establishment: implications for release strategies in biocontrol. *Ecological Applications* **9:** 1439-1447.

Grime J, Macpherson-Stewart S, and Dearman R. 1968. An investigation of leaf palatability using the snail *Cepea nemoralis* L. *Journal of Ecology* **56:** 405-420.

Hagler J, and Jackson C. 2001. Methods for marking insects: Current techniques and future prospects. *Annual Review of Entomology* **46:** 511-543.

Hamilton W, and Wellington W. 1981. The effects of food and density on the movement of *Arion ater* and *Ariolimax columbianus* (Pulmonata: Stylommatophora) between habitats. *Residential Population Ecology. Kyoto University* **23:** 299-308.

Hamilton W, Woodruff D, and Jamieson A. 1991. Role of computer-based decision aids in farm decision making and in agricultural extension. In Muchow R and Bellamy J, eds. Models and management for the semiarid tropics and subtropics. 1. Tropical regions and subtropical areas. Agriculture. Brisbane, QLD Australia: CAB International, UK, **pp.** 411-4423.

Hammer G, KcKeon G, Clewitt J, and Woodruff D. 1991. Usefulness of seasonal climate forecasts in crop and pasture management. Proceedings: Conference on Agricultural Meteorology. Melbourne, Australia: Bureau of Meteorology, **pp.** 15-23.

Hanley M, Fenner M, and Edwards P. 1995. An experimental field study of the effects of mollusc grazing on seedling recruitment and survival in grassland. *Journal of Ecology* **83:** 621-627.

Harpaz I, and Oseri Y. 1961. Crop damaging snails in Israel and their control *Hebrew University Faculty of Agriculture*. Tel Aviv: Report and citrus marketing board. **44.**

Harrison S. 1991. Local extinction in metapopulation context: an empirical evaluation. *Biological Journal Linnean Society* **42:** 73-88.

Hawthorne J, Holden K, and Zimmerman D. 1984. White Snails: a pest in SA. *Fact Sheet, Department of Agriculture, SA.* **November**.

Hazel W, and Johnson M. 1990. Microhabitat choice and polymorphism in the land snail *Theba pisana* (Müller). *Heredity* **65:** 449-454.

Heim I. 2000. Metaldehyde: New understanding of the mode of action and efficiency under wet and cold conditions. *Meta News* **10**.

Heller J. 1981. Visual versus climatic selection of shell banding in the land snail *Theba pisana* in Israel. *Journal of Zoology, London* **194:** 85-101.

Heller J. 1982. Natural history of *Theba pisana* in Israel (Pulmanata: Helicidae). *Journal of Zoology* **196:** 475-487.

Heller J, and Gadot M. 1984. Shell polymorphism of *Theba pisana* - the effects of rodent distribution. *Malacologia* **25:** 349-354.

Hermida J, Ondina P, and Outeiro A. 1995. Influence of soil characteristics on the distribution of terrestrial gastropods on northwest Spain. *European Journal of Soil Biology* **31:** 29-38.

Hill R, Vincent M, and Chouinard G. 1999. Evolving ecosystems approaches to fruit insect pest management. *Agriculture, Ecosystems and Environment* **73:** 107-110.

Hillborn R, and Mangle M. 1997. *The Ecological Detective. Confronting models with data.* Princeton University Press, Princeton.

Hollingsworth R, Armstrong J, and Campbell E. 2002. Caffeine as a repellent for slugs and snails. *Nature* **417:** 915-916.

Hommay G, Lorvelec O, and Jacky F. 1998. Daily activity rhythm and use of shelter in the slugs *Deroceras reticulatum* and *Arion Distinctus* under laboratory conditions. *Annals of Applied Biology* **132:** 167-185.

Hopkins D. 1990a. Snail contamination of Barley *South Australian Cereal Farming Systems: Collected Papers*. Adelaide, South Australia, Australia. Department of Agriculture. 11.11-11.13.

Hopkins D. 1990b. Snails - pests of crops and pastures in South Australia. *Agriculture Fact Sheet, Department of Agriculture, South Australia.* **pp. 29/81**.

Hopkins D. 1996. Biological control of snails and weeds. Workshop papers - Farming Systems Developments. Waite Institute, South Australia.

Hopkins D. 2000. Snails, a quarantine concern for export citrus to the USA. Adelaide: Entomology Unit, SARDI.

Hopkins D, and Baker G. 1993. Biological control of white and conical snails. In: Corey SA, Dall, D. J. and Bulne, W. M., ed. *Pest Control and Sustainable Agriculture.* Canberra, Australia: CSIRO. Division of Entomology. **pp.** 246-249.

Howling G, and Port G. 1989. Time-lapse video assessment of molluscicide baits. In Henderson, IF ed. BCPC MONO, *Slugs and Snails in World Agriculture* No. 41, Thornton, Heath. **pp.** 161-166.

Howling G. 1991. Slug foraging behaviour: Attraction to food items from a distance. *Annals of Applied Biology* **119:** 147-153.

Ims R, and Yoccoz N. 1997. Studying transfer processes in metapopulations: emigration, migration and colonisation. In: Hanski I and Gilpin M, eds. *Metapopulation biology: ecology, genetics and evolution*. London, UK: Academic Press. **pp.** 247-265.

Jaremovic R, and Rollo C. 1979. Tree climbing by the snail *Cepaea nemoralis* (L.): a possible method for regulating temperature and hydration. *Canadian Journal of Zoology* **57:** 1010-1014.

Jess S, and Marks R. 1998. Effect of temperature and photoperiod on growth and reproduction of *Helix aspersa* var. *maxima. Journal of Agricultural Science, Cambridge* **130:** 367-372.

Johnson M. 1980. Association of shell banding and habitat in a colony of the land snail *Theba pisana. Heredity* **45:** 7-14.

Johnson M. 1981. Effects of migration and habitat choice on shell banding frequencies in *Theba pisana* at a habitat boundary. *Heredity* **47:** 121-133.

Jones R, Gilbert N, Guppy N, and Nealis V. 1980. Long-distance movement of *Peiris rapae. Journal of Animal Ecology* **49:** 629-642.

Jorne J, and Safriel U. 1979. Linear and non-linear diffusion models applied to the behaviour of a population of an intertidal snail. *Journal of Theoretical Biology* **79:** 367-380.

Joubert C, and Walters S. 1951. The control of snails and slugs. *Farming in South Africa* **26:** 379-380.

Judge G, Griffiths W, Hill R, and Lee T. 1980. *The Theory and Practice of Econometrics*. John Wiley & Sons, Inc, New York.

Kareiva P. 1982. Experimental and mathematical analysis of herbivore movement: quantifying the influence of plant spacing and quality on foraging discrimination. *Ecological Monographs* **52:** 261-282.

Kareiva P. 1989. Renewing the dialogue between theory and experiments in population ecology. In: Roughgarden J, RM May and SA Levin, eds. *Perspectives in Ecological Theory*. Princeton: Princeton University Press. 68-88.

Kareiva P. 1990. Population dynamics in spatially complex environments: theory and data. *Philosophical Transactions of the Royal Society of London B* **330:** 175-190.

Kareiva P, and Shigesada N. 1983. Analysing insect movement as a correlated random walk. *Oecologia* **56:** 234-238.

Karlin E. 1961. Temperature and light as factors affecting the locomotor activity of slugs. *Nautilus* **74:** 125-130.

Kasigwa P. 1991. Diet and its ecological implications in the East African arboreal snail *Sitala jenynsi*. *Journal of African Zoology* **105:** 81-91.

Kasigwa P. 1999a. Dispersion factors in the arboreal snail *Sitala jenynsi* (Gastropoda: Ariophantidae). *South African Journal of Zoology* **34:** 145-152.

Kasigwa P. 1999b. Snail arboreality: the microdistribution of *Sitala jenynsi* (Gastropoda: Ariophantidae). *South African Journal of Zoology* **34:** 154-162.

Kawata M. 1993. Reletive importance of direct and indirect interaction among individual snails. *Res. Population Ecology* **35:** 69-77.

Kelly J, and Martin T. 1989. Twenty one years experience with methiocarb bait. In Henderson IF ed. BCPC MONO. *Slugs and Snails in World Agriculture,* No. 41. Thornton, Heath. **pp.** 131-145.

Kerney M, and Cameron R. 1979. *A field guide to the land snails of Britain and north-west Europe*. Collins, London, UK.

Kidd C. 1995. White snail pests in Australia. *Australian Grain* **June-July:** 20-23.

Kleewein D. 1999. Population size, density and spatial distribution and dispersal in an Austrian population of the land snail *Arianta arbistorum styriaca* (Gastropoda: Helicidae). *Journal of Molluscan Studies* **65:** 303-315.

Klute A. 1986. *Methods of soil analysis Part 1 - Physical and mineralogical methods*: 2nd edition. American Society of Agronomy Inc.

Kowalchuk R, and Keselman H. 2001. Mixed model pairwise multiple comparisons of repeated measured means. *Physiological Methods* **6:** 282-296.

Kpikpi J, and Thomas J. 1992. A study of the sugar chemoreception niches of two bulinid snail hosts of schistosomiasis. *Annuals of Tropical Medical Parasitology* **86:** 181.

Kupfermann I, and Carew T. 1974. Behaviour patterns of *Aplysia californica* in its natural environment. *Behavioural Biology* **12:** 317-337.

Kuussaari M, Nieminen M, and Hanski I. 1996. An experimental study of migration in the Glanvilee fritillary butterfly *Melitaea cinxia*. *Journal of Animal Ecology* **65:** 791-801.

Labaune C, and Magnin F. 2001. Land snail communities in Mediterranean upland grasslands: the relative importance of four sets of environmental and spatial variables. *Journal of Molluscan Studies* **67:** 463-474.

Leeper G, and Uren N. 1995. *Soil Science; an introduction. Fifth edition.* Melbourne University press. Melbourne, Australia.

Letourneau D, and Goldstein B. 2001. Pest damage and arthropod community structure in organic vs conventional tomato production in California. *Journal of Applied Ecology* **38:** 557-570.

Levy M, Tunis M, and Isseroff H. 1973. Population control in snails by natural inhibitors. *Nature* **241:** 65-66.

Lewis G. 1975. Shell polymorphism in the snail *Cochlicella acuta* (Müller) and some data on its genetics. *Biological Journal of the Linnean Society* **7:** 147-160.

Lewis G. 1977. Polymorphism and the selection of *Cochlicella acuta. Philosophical Transactions of the Royal Society of London B* **276:** 399-451.

Lewis R. 1969a. Studies on the locomotor activity of the slug *Arion ater* (Linnaeus). I. Humidity, temperature and light reactions. *Malacologia* **7:** 295-306.

Lewis R. 1969b. Studies on the locomotor activity of the slug *Arion ater* (Linnaeus). II. Locomotor activity rhythms. *Malacologia* **7:** 307-312.

Leyson M, Hopkins D, and Charwat S. 2003. Release and establishment of *Sarcophaga penicillata* in South Australia (Diptera: Sarcophagidae), a biological control agent for *Cochlicella acuta* (Mollusca: Hygromiidae). In *Slugs and Snails Agricultural, Veterinary and Environmental Perspectives*. Canterbury, Kent, UK. *In Press*.

Lim Y, and Jenkins R. 1972. The white Italian snail *Theba pisana* (Müller) in South Australia with particular reference to the distribution in the south east of South Australia. *Experimental Records of the Department of Agriculture of South Australia* **6:** 23-25.

Livshits G. 1985. Ecology of the terrestrial snail *Brephulopsis bidens* (Pulmonata: Enidae) mortality, burrowing and migratory activity. *Malacologia* **26:** 313-323.

Locher R, and Baur B. 2000a. Mating frequency and resource allocation to male and female function in the simultaneous hermaphrodite land snail *Arianta arbustorum*. *Journal of Evolutionary Biology* **13:** 607-614.

Locher R, and Baur B. 2000b. Sperm delivery and egg production of the simultaneously hermaphroditic land snail *Arianta arbustorum* exposed to an increased sperm competition risk. *Invertebrate Reproduction and Development* **38:** 53-60.

Lovei G, Stringer I, Devine C, and Cartellieri M. 1997. Harmonic radar - a method using inexpensive tags to study invertebrate movement on land. *New Zealand Journal of Ecology* **21:** 187-193.

Loxdale H, Hardie J, Halbert S, Foottit R, Kidd N, and Carter C. 1993. The relative importance of short- and long- range movement of flying aphids. *Biological Review* **1:** 291-311.

Lüsis O. 1966. Changes induced in the reproductive system of *Arion ater rufus* L. by varying environmental conditions. *Proceedings of the Malacological Society. London* **37:** 19-26.

Macintosh R. 2002. Mangrove rehabilitation and intertidal biodiversity: A study in the Ranong mangrove ecosystem, Thailand. *Estuarine Coastal and Shelf Science* **55:** 331-345.

Madsen H. 1992. A comparative study on the food-locating ability of *Helisoma duryi, Biomphalaria camerunensis* and *Bulinus truncatus* (Pulmonate: Planorbidae). *Journal of Applied Ecology* **29:** 70-83.

Maelzer D, and Zalucki M. 2000. Long range forecasts of the numbers of *Helicoverpa punctigera* and *H. armigera* (Lepidoptera: Noctuidae) in Australia using the Southern Oscillation Index and the Sea Surface Temperature. *Bulletin of Entomological Research* **90:** 133-146.

Marin S, Grant W, and Dronen N. 1998. Simulation of population dynamics of *Haematolecus coloradenis* in its three host species: effects of environmental temperature and precipitation. *Ecological Modelling* **105:** 185-211.

Martin A. 1991. Molluscs as agricultural pests. *Outlook Agriculture* **20:** 167-174.

Mazumdar S, Begley A, Houck P, Yang Y, Reynolds C, and Kupfer D. 1999. Residual analysis in random regressions using SAS and S-PLUS. *Computer Methods and Programs in Biomedicine* **58:** 281-282.

McBride J, and Nicholls N. 1983. Season relationship between Australian and the Southern Oscillation. *Monthly Weather Review* **111:** 1998-2004.

McCann E, Sullivan S, Ericson D, and DeYoung R. 1997. Environmental awareness, economic orientation, and farming practices: comparisons of organic and conventional farmers. *Environmental Management* **21:** 747-758.

McEvoy P, and Coombs E. 2000. Why things bite back: unintended consequences of biological weed control. In: Follett PA and Duan JJ, eds. *Non-target effects of biological control.* Kluwer- Academic Publishers. Boston, U.S.A. **pp.** 166-194.

McIntosh R. 1999. Technique for labelling individual *Pissodes strobi* (Coleptera: Curculonidae) for mark-release studies. *Canadian Entomologist* **131:** 131-136.

McQuaid C, Branch G, and Frost P. 1979. Aestivation behaviour and thermal relations of the pulmonate *Theba pisana* in a semi-arid environment. *Journal of Thermal Biology* **4:** 47-55.

Meikle W, Holst N, Scholz D, and Markham D. 1998. Simulation model of *Prostephanus truncates* (Coleoptera: Bostrichidae) in rural maize stores in the Republic of Benin. *Environmental Entomology* **27:** 59-69.

Miller E, Swails S, Swails D, Olsen F, and Staten R. 1988. White garden snail *Theba pisana* (Müller): Efficacy of selected bait and sprayable molluscicides. *Journal of Agricultural Entomology* **5:** 189-197.

Mills J, McCrohan C, Bailey S, and Wedgewood M. 1990. Effects of metaldehyde and acetaldehyde on feeding responses and neuronal activity in the snail, *Lymnaea stagnalis. Pesticide Science* **28:** 89-99.

Moran S. 1989. Weather-and population density-induced infantilism in the land snail *Theba pisana* in a semi-arid climate. *International Journal of Biometeorology* **33:** 101-108.

Morris W, and Doak D. 2002. *Quantitative Conservation Biology: theory and practice of population viability analysis*. Sinauer Associates, Southerland Massatusses, USA.

Murdoch W, McCauley E, Nesbit R, Gurney W, and deRoos A. 1992. Individual based models: combining testability and generality. In: DeAngelis, DA and Gross JL, ed. *Individual based models and approaches in ecology: populations, communities and Ecosystems*. Chapman and Hall. New York. **pp.** 18-35.

Murphy M. 2002. Observations on the behaviour of the Australian land snail *Hedleyella falconeri* (Grey, 1834) (Pulmonata: Caryodidae) using the spool-and-line tracking technique. *Molluscan Research* **22:** 149-164.

Mutze G, and Hubbard D. 2000. Effects of molluscicide baits on field populations of house mice. *Agriculture, Ecosystems and Environment* **80:** 205-211.

Myers J, Simberloff D, Kuris A, and Carey J. 2000. Eradication revisited: dealing with exotic species. *TRENDS in Ecology and Evolution* **15:** 316-320.

Nahal I. 1981. The Mediterranean climate from a biological view point. In: Di Castri F, Goodall, W., Specht, RL., ed. *Ecosystems of the world 11. Mediterranean type shrub lands*: Elsevier Scientific Publishing Co. Amsterdam. **pp.** 63-72.

Nathan R. 2001. The challenges of studying dispersal. *TRENDS in Ecology and Evolution* **16:** 481-483.

Nevo E, and Bar Z. 1976. Natural selection of genetic polymorphisms along climatic gradients. In: Karlin S and Nevo, E., ed. *Population Genetics and Ecology* 159-184.

Nicholls N. 1986. A method for predicting Murray Valley encephalitis in southeast Australia using the Southern Oscillation. *Australian Journal of Biological and Medical Sciences* **64:** 587-594.

Nicholls N, Lavary B, Frederiksen C, Drosdowski W, and Torak S. 1996. Recent apparent changes in relationships between the El Nino Southern Oscillation and Australian rainfall and temperature. *Geophysical Research Letters* **23:** 3357-3360.

Oggier P, Zschokke S, and Baur B. 1998. A comparison of three methods for assessing the gastropod community in dry grassland. *Pedobiologia* **42:** 348-357.

Okubo A. 1980. *Diffusion and ecological problems: mathematical models*. Springer-Verlag, Heidelberg, Germany.

Okubo A. and Levin, 2002 *Diffusion and ecological problems: Modern Perspective.* 2nd edition. Springer. New York, USA.

Ondina P, Mato S, Hermida J, and Outeiro A. 1998. Importance of soil exchangeable cations and aluminium content on land snail distribution. *Applied Soil Ecology* **9:** 229-232.

Oosterhoff L. 1977. Variation in growth rate as an ecological factor in the land snail *Cepaea nemoralis* (L.). *Netherlands Journal of Zoology* **27.:** 1-132.

Outeiro A, Agüera D, and Parejo C. 1993. Use of ecological profiles and canonical correspondence analysis in a study of the relationships of terrestrial gastropods and environmental factors. *Journal of Conchology* **34:** 365-374.

Parker G. 1983. Mate quality and mating decisions. In: Bateson P, ed. *Mate Choice*: Cambridge University Press. Cambridge. **pp.** 141-166.

Parker I, Simberloff D, Lonsdale W, Goodell K, Wonham M, Kareiva P, Williamson M, Holle B, Moyle P, Beyers J, and Goldswasser L. 1993. Impact: Toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1:** 3-9.

Paul C. 1978. The ecology of Mollusca in ancient woodland. 2. Analysis of distribution and experiments in Hayley Wood, Cambridgeshire. *Journal of Conchology, London* **29:** 281-294.

Peake J. 1978. Distribution and ecology of *Stylommatophora Pulmates. Systematics and Ecology*: Academic Press, London. **pp.** 429-526.

Perrett S, and Whitfield P. 1996. Currently available molluscicides. *Parasitology Today* **12:** 156-159.

Peters R. 1991. *A Critique for Ecology.* Cambridge University Press, Cambridge.

Pfister G, El-Naggar M, and Bahadir M. 1994. Evaluation of controlled release molluscicide formulations with improved environmental acceptance. *Chemosphere* **28:** 305-312.

Pollard E. 1975. Aspects of the ecology of *Helix pomatia* L. *Journal of Animal Ecology* **44:** 305-329.

Pomeroy D. 1966. The Ecology of *Helicella virgata* and related species of snails in South Australia. *Department of Zoology.* PhD thesis. University of Adelaide. South Australia.

Pomeroy D. 1967. The influence of environment on two species of land snails in South Australia. *Australian Journal of Zoology* **17:** 495-514.

Pomeroy D. 1968. Dormancy in the land snail *Helix virgata* (Pulmonata: Helicidae). *Australian Journal of Zoology* **16:** 857-869.

Pomeroy D. 1969. Some aspects of the ecology of the land snail, *Helicella virgata,* in South Australia. *Australian Journal of Zoology* **17:** 495-514.

Pomeroy D, and Laws H. 1967. The distribution of introduced land snails in South Australia. *Records of South Australian Museum* **15:** 483-494.

Pomiankowski A, and Reguera P. 2001. The point of love. *Trends in Ecology and Evolution* **16:** 533-534.

Potts D. 1975. Persistence and extinction of local populations of the garden snail *Helix aspersa* in unfavourable environments. *Oecologia* **21:** 313-334.

Price C. 1979. Physical factors and neurosecretion in the control of reproduction in *Melampus* (Mollusca: Pulmonata). *Journal of Experimental Biology* **207:** 269-282.

Quick H. 1952. Emigrant British Snails. *Proceedings of the Malacological Society, London* **29:** 181-189.

Rees M, and Brown V. 1992. Interactions between invertebrate herbivores and plant competition. *Journal of Ecology* **80:** 353-360.

Reeve J. 1990. Stability, variability and persistence in host-parasitoid systems. *Ecology* **71:** 422-426.

Reganold J. 1989. Farming's organic future. *New Scientist* **122:** 49-52.

Reichardt A, Rabound C, Burla H, and Baur B. 1985. Causes of death and possible regulatory processes in *Arianta arbustorum* (L. 1758) (Pulmonata: Helicidae). *Basteria* **49:** 37-49.

Reidenbach J, Vala J, and Ghamizi M. 1989. The slug-killing *Sciomyzidae* (Diptera): potential agents in the biological control of crop pest molluscs. In Henderson IF ed. BCPC MONO, *Slugs and Snails in World Agriculture* No. 41, 273-280.

Rimes G. 1968. Snail investigations - a progress report. *Journal of Agriculture of Western Australia* **9:** 584-587.

Rollo C. 1989. Experimental and analytical methodologies for studying molluscan activity. In Henderson IF ed. BCPC MONO *Slugs and Snails in World Agriculture*, No. 41, Thornton, Heath. **pp.** 343-348.

Rollo C. 1991. Endogenous and exogenous regulation of activity in *Deroceras reticulatum*, a weather-sensitive terrestrial slug. *Malacologia* **33:** 199-220.

Rollo C, and Wellington W. 1981. Environmental orientation by terrestrial Mollusca with particular reference to homing behaviour. *Canadian Journal of Zoology* **59:** 225-239.

Rosenberg N, Blad B, and Verma S. 1983. Atmospheric humidity and due. In: Rosenberg N, Blad B and Verma S, eds. *Microclime: The Biological Environment*. 2nd ed. John Wiley and Son. New York. **pp.** 167-189.

Roth B, Hertz C, and Cerutti R. 1987. White snails (Helicidae) in San Diego County, California. *Festivus* **16:** 84-88.

Rudd N, and McEvoy P. 1996. Local dispersal by the Cinnabar Moth, *Tyria jacobaeae*. *Ecological Applications* **6:** 285-297.

Runham N. 1983. 12. Mollusca. In: Adiyodi KG and Adiyodi, RG ed. *Reproductive biology of invertebrates, Volume 5 Sexual differentiation and Behaviour*. John Wiley and Sons. Toronto, **pp.** 193-228.

SAS Institute S. 1991. *SAS Users Guide: Statistics*. SAS Institute, Cary, North Carolina. USA

SAS Institute Inc. 2001. 5.0.2195ed. Cary, North Carolina. USA

Scharf F, Juanes F, and Michael S. 1998. Inferring ecological relationships from the edges of scatter diagrams: comparison of regression techniques. *Ecology* **79:** 448-460.

Scheidel U, and Bruelheide H. 1999. Selective slug grazing on montane meadow plants. *Journal of Ecology* **87:** 823-838.

Schilthuizen M, and Lombaerts M. 1994. Population structure and levels of gene flow in the Mediterranean land snail *Albinaria corrugata* (Pulmonata: Clausiliidae). *Evolution* **48:** 577-586.

Schmitz O. 2001. From interesting detail to dynamical relevance: To more effective use of empirical insights into theory construction. *Oikos* **94:** 39-50.

Schrag S, and Read A. 1992. Temperature determination of male outcrossing ability in simultaneous hermaphrodite. *Evolution* **46:** 1698-1707.

Schrag S, Mooers A, Ndifon G, and Read A. 1994a. Ecological correlates of male outcrossing ability in a simultaneous hermaphroditic snail. *The American Naturalist* **143:** 636-655.

Schrag S, Ndifon G, and Read A. 1994b. Temperature-determined outcrossing ability in wild populations of a simultaneous hermaphrodite snail. *Ecology* **75:** 2066-2077.

Shirley M, Rushton S, Young A, and Port G. 2001. Simulating the long-term dynamics of slug populations: based on a process-based modelling approach for pest control. *Journal of Applied Ecology* **38:** 401-411.

Simberloff D. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecological Systems* **19:** 473-511.

Skellam J ed. 1973. *The mathematical theory of the dynamics of biological populations.* London: Academic Press.

Smallridge M, and Kirby G. 1988. Competitive interactions between the land snails *Theba pisana* (Müller) and *Cernuella virgata*(Da Costa) from South Australia. *Journal of Molluscan Studies* **54:** 251-258.

Smith B. 1981. Introduced non-marine molluscs in Australia. *Victorian Naturalist* **98:** 24-27.

Smith B. 1989. Travelling snails. *Journal of Medical and Applied Malacology* **1:** 195-204.

Smith B, and Kershaw R. 1979. *Field guide to the non-marine molluscs of south-eastern Australia.* Griffin Press Limited, South Australia.

Sokolove P, Melrose G, Gordon T, and O'Neil M. 1983. Stimulation of spermatogonial DNA synthesis in slug gonad by a factor released from cerebral ganglia under the influence of long days. *General Comparative Endocrinology* **50:** 95-104.

South A. 1982. A comparison of the life cycles of *D. reticulatum* (Müller) and *A. intermedius* Normand (Pulmonata: Stylommatophora) at different temperatures under laboratory conditions. *Journal of Molluscan Studies* **48:** 233-244.

Southwood T. 1977a. Habitat. The templet for ecological strategies? *Journal of Animal Ecology* **46:** 337-365.

Speiser B, and Hochstrasser M. 1998. Slug damage in relation to watering regime. *Agriculture, Ecosystems and Environment* **70:** 273-275.

Stacey P, Johnson V, and Taper M. 1997. Migration within metapopulations: the impact upon local population dynamics. In: Hanski I, and Gilpin M, eds. *Metapopulation biology: ecology, genetics and evolution.*: Academic Press. London, UK, **pp.** 267-291.

Staikou A, Lazaridou-Dimitriadou M, and Kattoulas M. 1989. Behavioural patterns of the edible snail *Helix lucorum* L. in the different seasons of the year in the field. *Haliotis* **19:** 129-136.

Stanley R, Farkas R, and Shorey H. 1976. Anemotaxis and odour-trail following by the terrestrial snail *Helix aspersa. Animal Behaviour* **24:** 686-689.

Steinberg E, and Kareiva P. 1996. Challenges and opportunities for empirical evaluation of spatial theory. In: Tilman D, and Kareiva P, ed. *Spatial Ecology*. Princeton University Press. Princeton, New Jersey, USA. **pp.** 318-332.

Stephens C, and Stephens G. 1966. Photoperiodic simulation of egg-laying in the land snail *Helix aspersa. Nature* **212:** 1582.

Sternberg M. 2000. Terrestrial gastropods and experimental change: A field study in a calcareous grassland. *Ecological Research* **15:** 73-81.

Suzuki S, and Sheu C-F. 1999. Using Proc-mixed in Hierarchical linear models: Examples from two and three level school-effect analysis, and meta-analysis research.

Szlavecz K. 1986. Food selection and nocturnal behaviour of the land *Monadenia hillebrandi mariposa* AG Smith (Pulmonata: Helminthoglyptidae). *Veliger* **29:** 183-190.

Tattersfield P. 1981. Density and environmental effects on shell size in some sand dune snail populations. *Biological Journal of the Linnean Society* **16:** 71-81.

Tattersfield P. 1989. Variation in foot size and shape in some British land snails and its functional significance. *Biological Journal of the Linnean Society* **36:** 365-376.

Taylor. 1912. Monograph of British land and freshwater Mollusca. **pp.** 140-160.

Taylor A. 1990. Metapopulations, dispersal and predator-prey dynamics: an overview. *Ecology* **71:** 429-433.

Ter Matt A, Lodder J, Veenstra J, and Goldschmeding J. 1982. Suppression of egg laying during starvation in the snail *Lymnaea stagnalis* by inhibition of the ovulation hormone producing caudo-dorsal cells. *Brain Research* **239:** 535-542.

Thiébaut R, Jacqmin-Gadda H, Chêne G, Leport C, and Commenges D. 2002. Bivariate linear mixed models using SAS proc-MIXED. *Computer Methods and Programs in Biomedicine* **69:** 249-256.

Thomas J, Goldsworthy G, and Aram R. 1975. Studies in the chemical ecology of snails: the effect of chemical conditioning by adult snails on the growth of juvenile snails. *Journal of Animal Ecology* **44:** 1-28.

Thorne J, Hagstrum D, and Nawrot J. 1998. Computer model for simulating almond moth (Lepidoptera: Pyralidae) population dynamics. *Environmental Entomology* **27:** 334-354.

Tilling S. 1985a. The effects of density and interspecific interactions on mortality in experimental populations of adult *Cepea nemoralis*. *Biological Journal of Linnean Society* **24:** 61-70.

Tilling S. 1985b. The effect of interspecific interaction on spatial distribution patterns in experimental populations of *Cepaca nemoralis* (L) and *C. hortensis* (Müller). *Biological Journal of the Linnean Society* **24:** 71-81.

Topp G, Galganov Y, Ball B, and Carter M. 1993. Soil Water Desorption Curves. In: Carter M, ed. *Soil Sampling and Methods of Analysis*: Canadian Society of Soil Science. Lewis Publishers. **pp.** 569-579.

Tow P. 1991. *Dryland farming : a systems approach : an analysis of dryland agriculture in Australia*. Sydney University Press, in association with Oxford University Press. Sydney, Australia.

Turchin P. 1991. Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72:** 1253-1266.

Turchin P. 1997. The role of aggregation in the response of the Mexican bean beetles to host-plant density. *Oecologia* **71:** 577-582.

Turchin P. 1998. *Quantitative Analysis of Movement: Measuring and modelling population redistribution in animal and plants.* Sinauer Associates, Inc Publishers, MA. USA.

Turchin P, and Thoeny W. 1993. Quantifying dispersal of southern pine beetles with mark-recapture experiments and a diffusion model. *Ecological Applications* **3:** 187-198.

Turner M, Arthaud G, Engstrom R, Hejl S, Liu J, Leob S, and McKelvey K. 1995. Usefulness of spatially explicit animal models in land management. *Ecological Applications* **5:** 12-16.

Vorhaben J, Klotz A, and Campbell J. 1984. Activity and oxidative metabolism of the land snail *Helix aspersa. Physiological Zoology* **57:** 357-365.

Voss M. 2000. Neurophysiological and behavioural responses to olfactory stimuli in the snail *Helix pomatia* L. *Physiological Research* **49:** 463-469.

Voss M, Hoppe H, and Ulber B. 1998a. Estimation of slug activity and slug abundance. *Journal of Plant Diseases and Protection* **105:** 314-321.

Voss M, Ulber B, and Hoppe H. 1998b. Impact of reduced and zero tillage on activity and abundance of slugs in winter oilseed rape. *Journal of Plant Diseases and Protection* **105:** 632-640.

Vyn T, and Hooker D. 2002. Assessment of multiple and single-factor stress impacts on corn. *Field Crops Research* **75:** 123-137.

Waite T. 1987. Behavioural control of water loss in the terrestrial slug *Deroceras reiculatum* (Müller): body size constraints. *Veliger* **30:** 134-137.

Wolda H. 1963. Natural populations of the polymorphic land snail *Cepaea nemoralis* (L.). Factors affecting their size and their genetic constitution. *Archives Neerlandaisies de Zoologie* **15:** 381-471.

Wolda H, and Kreulen D. 1973. Ecology of some experimental populations of the land snail *Cepaea nemoralis* (L.). II Production and survival of eggs and juveniles. *Netherlands Journal of Zoology* **23:** 168-188.

Wäreborn I. 1970. Environmental factors influencing the distribution of land molluscs of an oligotrophic area in southern Sweden. *Oikos* **21**.

Welby D. 1964. Slug activity in relation to weather. *Annals of Applied Biology* **53:** 407-414.

White A. 1959. Observations on slug activity in a Northumberland garden. *Plant Pathology* **8:** 62-63.

Wiens J, Crist T, and Milne B. 1993a. On quantifying insect movements. *Environmental Entomologist* **22:** 709-715.

Wiens J, Stenseth N, Van Horne B, and Ims R. 1993b. Ecological mechanisms and landscape ecology. *Oikos* **66:** 369-380.

Williamson M. 1976. Size-weight relationship and field growth rates of the land snail Cepea nemoralis L. *Journal of Animal Ecology* **45:** 875-885.

Williamson P, Cameron R, and Carter M. 1977. Population dynamics of the land snail *Cepea nemoralis* L.: a six-year study. *Journal of Animal Ecology* **46:** 181-194.

Wolfinger R, and Change M. 2003. Comparing the SAS GLM and MIXED procedures for repeated measures.: SAS Institute Inc., Cary, NC.

Woodruff, D, and Gould, S 1980. Geographic Differentiation and Speciation in Cerion: A Preliminary Discussion of Patterns and Processes. *Biological Journal of the Linnean Society* **14:** 389-416.

Wotton J, and Bell D. 1992. A metapopulation model of the peregrine falcon in California: viability and management strategies. *Ecological Applications* **2:** 307-321.

Yom-Tov Y. 1970. The effects of predation on population density of some desert snails. *Ecology* **51:** 907-911.

Yom-Tov Y. 1983. Life history tactics in two species of desert snails. *Journal of Arid Environments* **6:** 39-41.

Young A, Port G, Emmett B, and Green D. 1991. Development of a forecast of slug activity: models to relate slug activity to meteorological conditions. *Crop Protection* **10:** 413-415.

Young A, Port G, and Green D. 1993. Development of a forecast of slug activity: validation of models to predict slug activity from meteorological studies. *Crop Protection* **12:** 232-236.

Young C. 1996a. Metal chelates as stomach poison molluscicides for introduced pests, *Helix aspersa, Theba pisana, Cernuella virgata* and *Derocera reticulatum* in Australia. In Henderson, IF ed. BCPC Symposium Proceedings: *Slug and Snails Pests in Agriculture.* No. 66. Farnham. **pp.** 237-243.

Young C. 1996b. Kill the slugs and snails, but watch the dog! *Chemistry in Australia*: 494-496.

Zanforlin M. 1976. Observations on the visual perception of the snail *Eupariphа pisana* (Müller). *Bollettino di Zoologia* **43:** 303-315.

Zar J. 1999. *Biostatistical Analysis*. Prentice-Hall Inc, New Jersey, USA.