

# Survival, movement, and resource use of the butterfly *Parnassius clodius*

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**Abstract.** 1. A mark–recapture study was conducted on the American Apollo butterfly *Parnassius clodius* Menetries during three field seasons (1998–2000) to examine its movement patterns over the course of a season within a sagebrush meadow in Grand Teton National Park, Wyoming, U.S.A. The study examined how resources affected butterfly distribution patterns and used mark–recapture data to gain insight into movement differences between sexes and over time.

2. The average straight-line movement of *P. clodius* was  $202 \text{ m day}^{-1}$ , adjusted for sampling effort at different distances. Movement estimates in all 3 years were highly correlated with the average distance between plots sampled.

3. Butterfly abundance was correlated positively with per cent cover of its host plant *Dicentra uniflora*, but this relationship decreased in importance during the peak of the flight period when individuals may be more interested in finding mates. There was a weak, positive correlation between butterfly abundance and the abundance of its primary nectar source, *Eriogonum umbellatum* in 1999, but no relationship in 2000.

4. Survival, recapture, and transition probabilities were estimated using open population, capture–recapture models. Survival and recapture probability decreased over the course of each season, while the probability of moving between plots increased. Recapture probability was significantly lower for females than for males among all 3 years, but there was no difference between the sexes in survival rate.

**Key words.** Butterflies, dispersal, mark–release–recapture, movement, *Parnassius clodius*.

## Introduction

The complex spatial arrangement of many natural populations has received much attention over the past 10 years and the metapopulation perspective has become well accepted for studying butterfly populations (Thomas & Harrison, 1992; Baguette & Nève, 1994; Hanski & Thomas, 1994; Hill *et al.*, 1996; Sutcliffe & Thomas, 1996; Sutcliff *et al.*, 1997; Brommer & Fred, 1999; Roland *et al.*, 2000). Understanding movement between habitat patches is key to understanding population processes in heterogeneous landscapes (Turchin, 1986; Wiens *et al.*, 1993; Diffendorfer *et al.*, 1995; Lima &

Zollner, 1996); however, understanding fine-scale, *within-patch* movement is also key to understanding transfer processes at a larger scale (Wiens *et al.*, 1993; Ims & Yoccoz, 1997). Some of the earlier studies of butterfly movement and population structure focused on within-patch movements (e.g. Brussard *et al.*, 1974); however, little recent effort has been devoted to estimating movement characteristics of butterflies within a single large patch (Thomas & Harrison, 1992; Hill *et al.*, 1996; Brommer & Fred, 1999; Roland *et al.*, 2000; but see Ries & Debinski, 2001).

Knowledge of movement patterns within a patch may aid in explaining events that are more difficult to predict, including even movement between patches of habitat. Studying within-patch behaviour also gives valuable insight into the potential for seasonal changes in movement patterns. Most metapopulation models assume that the habitat within the patches, and thus the distribution of organisms and their resources, is homogeneous and that the probability

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of movement between patches is constant over time. This may not be a realistic portrayal of the patch environment. The density and distribution of individuals within a patch is dependent on movements in response to resources and habitat structure (Crist & Wiens, 1995). Details of this resource distribution include mate location, nectar resources, and host-plant availability (Scott, 1986). Predator avoidance and puddling for minerals also play a role (Sculley & Boggs, 1996). The spatial distribution of butterflies is determined by the trade-offs and interactions in acquiring these resources. Mating strategy, sex, and time of day determine which resources are the most important for butterflies (Watanabe, 1978; Boggs, 1986; Odendaal *et al.*, 1988).

Further, a key difficulty in quantifying disappearance from a patch is separating mortality from dispersal. By focusing on *within-patch* resource distribution and butterfly behaviour, how individuals respond to their local environment and how life-history parameters affecting movement change over the course of the season can be examined more fully. Estimation of both movement and survival parameters from mark–recapture studies is a common practice, especially in studies of vertebrates. Yet butterfly studies typically only estimate population size and movements between habitat patches (e.g. Baguette & Nève, 1994; Roland *et al.*, 2000; but see Wahlberg *et al.*, 2002b). This is an under-utilisation of potentially valuable information about population dynamics (Schmidt & Anholt, 1999; Hanski *et al.*, 2000; Schtickzelle *et al.*, 2002). Recent developments in statistical theory facilitate in-depth hypothesis testing from mark–recapture data (Lebreton *et al.*, 1992, 1993). Hestbeck *et al.* (1991) developed models that explicitly separate transition probability, often called apparent survival ( $\phi$ ), into the component processes of survival ( $S$ ) and movement probability ( $P$ ). Movement probability can then be examined as a function of habitat condition, sex, or life stage. In this case, movement probability is a measure of the rate of movement between plots in a relatively homogeneous habitat patch. Associated programs, such as Mark, can be used to estimate recapture, survival, and movement probabilities and facilitate comparisons between sexes, times, or groups (White & Burnham, 1999).

A mark–recapture study was used to meet three objectives: (1) to examine the relationship between the butterfly *Parnassius clodius* and its host plant and nectar plant resources, (2) to estimate movement distances of *P. clodius* within a meadow, and (3) to model relationships among recapture, survival, and movement probability over the season. The arrangement and number of sampling plots were modified over three consecutive summers, enabling the effect of different sampling efforts on estimates of movement distance to be examined.

## Methods

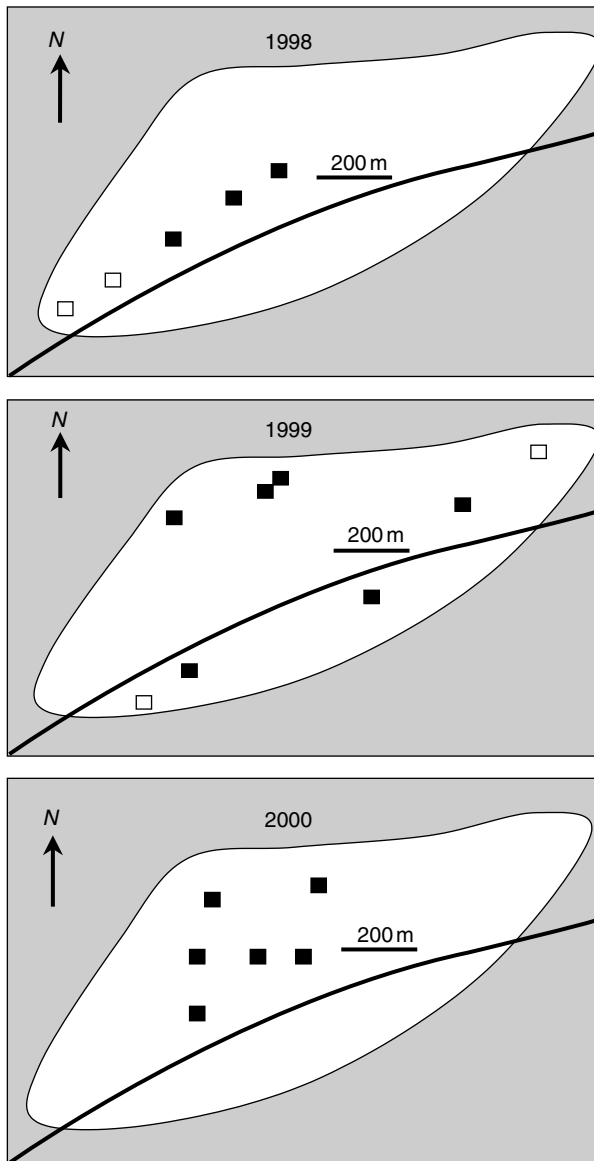
*Parnassius clodius* Menetries (Lepidoptera: Papilionidae) is a medium-sized, mostly white butterfly of western Canada

and the north-western U.S.A. It is found in open woods and meadows. In the study area, *P. clodius* was found at highest densities in dry, cobbly, sagebrush meadows where its host-plant species, *Dicentra uniflora* (Steershead) (Fumariaceae), is abundant (Scott, 1986). *Dicentra uniflora* is a small, spring ephemeral that contains poisonous alkaloids. *Parnassius clodius* is thought to be capable of sequestering these alkaloids, and all life stages are probably poisonous (Scott, 1986). *Parnassius clodius* females lay eggs on vegetation close to the host plant. *Parnassius clodius* overwinter as eggs, and the larvae emerge in early spring and feed on their host plant. Pupation occurs in the soil. *Parnassius clodius* has one flight per year, from late June to mid July. During copulation, the male attaches a sphragis to the female's abdomen, which prevents her from mating again (Scott, 1986).

The study was conducted during the summer (June to August) in Grand Teton National Park, north-western Wyoming from 1998 to 2000. The rugged topography of the Rocky Mountains creates a heterogeneous distribution of meadow and forest communities along altitudinal and moisture gradients. The meadow communities range from wet marshy areas (Kindscher *et al.*, 1998) to dry sagebrush meadows (Jakubauskas *et al.*, 1998). The cobbly sagebrush meadows preferred by *P. clodius* in Grand Teton National Park tend to occur near waterways and are typically surrounded by forests. The study site was a relatively homogeneous sagebrush meadow at 110°35'10"W, 43°54'70"N. The topography is flat with an elevation of 2100 m. The meadow is 1500 × 300 m in size.

Mark–recapture methods were used to study a population of *P. clodius* during three annual flight periods (1998–2000). A preliminary mark–recapture study was conducted from 30 June to 9 July 1998, using three 75 × 75 m plots separated by 100 and 225 m (Fig. 1). Two people captured all butterfly species in each plot for 35 min between 10.00 and 17.00 hours. Butterflies were held in glassine envelopes until the end of the survey. Each captured butterfly was marked with a permanent marker on both of its hindwings, indicating the day and plot in which it was caught. All butterflies were released from the centre of the plot. Mated females were identified by the presence of a sphragis. Surveys were limited to times when the temperature was above 21 °C, wind was <16 km h<sup>-1</sup>, and the sun was not obscured by clouds. Plots were surveyed in a random order each day. All three plots were visited for 10 consecutive days (30 June to 9 July). On 8–10 July, two additional plots were monitored for *P. clodius* only. They were separated by 100 and 225 m (Fig. 1).

During 1999 and 2000, 50 × 50 m plots were surveyed for 20 min, and only *P. clodius* was captured. The smaller plots and shortened survey time enabled a larger area of the meadow to be sampled. If weather prevented the plots to be sampled for a whole day, the rotation was completed on the following day. The surveying of the plots was started a few days after the beginning of the flight period and continued until fewer than five butterflies per plot were being caught during the survey period. An individual number was



**Fig. 1.** Sampling plot arrangements 1998–2000. Plots are represented by squares. Plots sampled regularly are black. Plots with lower sampling effort are outlined in black. Plots were  $75 \times 75$  m in 1998, and  $50 \times 50$  m in 1999 and 2000. The meadow is white, the forest is grey, and a road runs through the study area.

drawn with a permanent marker on both hindwings of each captured butterfly. The sex of each butterfly and mating condition of females were recorded based on morphological differences and the presence or absence of a spermatheca.

From 28 June to 15 July 1999, butterflies were captured and marked in eight plots placed randomly throughout the meadow (Fig. 1). Six plots were monitored consistently through the flight period. Two additional plots were monitored during the peak of the flight period in order to increase the sample size and survey a larger portion of the meadow. From 17 June to 2 July 2000, butterflies were

captured and marked in six  $50 \times 50$  m plots placed randomly in the eastern half of the meadow (Fig. 1). Plot placement in 2000 was restricted spatially to increase the number of recaptures.

#### *Host and nectar plants*

During late May 1999, the per cent cover of *P. clodius*'s host plant, *D. uniflora*, was estimated in each butterfly survey plot. These surveys were conducted prior to the butterfly sampling because the plants senesce and are very difficult to find later in the season. Transects were placed every 5 m within the  $50 \times 50$  m plot, and the per cent cover was estimated along each transect at 5-m intervals using a  $0.25\text{-m}^2$  quadrat. During May 2000, no host plants were present in the study area, so the same measurements could not be repeated. Nectar plant abundance in 1999 was estimated between 7 and 10 July, just after the peak of the flight season. Three transects were placed evenly within each  $50 \times 50$  m plot, and the number of inflorescences of each flowering species was estimated in  $0.5\text{-m}^2$  quadrats spaced at 2-m intervals along the transect. During 2000, all nectar plant data were collected on 24 June, just after the peak of the flight season. Sampling effort was reduced during 2000 and measurements were taken every fifth metre. Buckwheat, *Eriogonum umbellatum*, was the predominant nectar plant source in the study area during the sampling in both years, it was the only flower species that was not senescing during the count, and it was the preferred source of nectar for *P. clodius* (J.N. Auckland, pers. obs.). Thus, only *E. umbellatum* was used in nectar plant analyses. The total number of *P. clodius* caught in each plot on the days immediately surrounding the nectar plant sampling was used in the analyses. *Parnassius clodius* numbers on 9, 10, 12, and 13 July 1999 and between 22 and 26 June 2000 were compared with the mean number of inflorescences of *E. umbellatum* per  $\text{m}^2$  in each plot during the respective years. The relationship between butterfly abundance and *E. umbellatum* abundance was analysed using general linear models (PROC GLM SAS v. 6.12, SAS Institute Inc., 1990).

#### *Movement distance*

Butterfly movement data were adjusted for capture effort at different distances (Porter & Dooley, 1993; C. Ray, pers. comm.) and for time between captures. The number of butterflies marked in each plot was multiplied by the number of subsequent days of recapture effort to obtain the number of *butterfly days* available in each plot. Recaptures were only possible at discrete distances from any capture point because sampling was done in plots. Therefore, the number of butterflies available for resight at each distance and time were calculated from the *butterfly days* adjustment. The relative probability of resighting butterflies (the proportion of total *butterfly days*) at each time and distance was then calculated by dividing the available number of

butterflies recaptured at each distance and time by the total number of butterflies recaptured.

These data were then corrected for catch effort because as distance from a release plot increases, the area sampled decreases (area sampled = plot width  $2\pi \times$  radius). For example, at 0 m from the  $50 \times 50$  m release plot, 100% of the area is sampled, but 100 m away from the release point, only 8% of the perimeter is sampled.

#### Survival and movement probability

Open-population, capture–recapture models were used to estimate recapture ( $p$ ), apparent survival ( $\phi$ ), and movement ( $P$ ) probabilities (Hestbeck *et al.*, 1991). Recapture probability is the probability that a marked individual is recaptured, given that it is alive. Survival probability is the probability that an individual survives from day to day. Movement probability is the probability of moving between plots during a sampling interval given that a butterfly survived (Hestbeck *et al.*, 1991; Lebreton *et al.*, 1992). All of these estimates represent daily probabilities.

Program Mark (White & Burnham, 1999) was used for all of the mark–recapture data analyses. Program Mark estimates recapture, survival, and movement probabilities using numerical maximum likelihood techniques, and computes bias-corrected versions of Akaike's information criterion (AIC) values for each model, which enabled models to be fitted and hypotheses to be tested objectively (Akaike, 1973; Pollock *et al.*, 1990; Burnham *et al.*, 1995). Changes in recapture, survival, and movement probability over time were analysed in two ways. The first analysis was done using Program Mark to test for temporal trends in the data. Program Mark estimated an intercept and a time-dependent slope for each parameter. The fit of these models was then compared with the fit of models with and without time effects using AIC values (Akaike, 1973). A second analysis was performed by grouping sexes together and dividing the capture–recapture period in each year into four discrete, approximately equal (3–4 days), time intervals. Thus, separate estimates were calculated for each time interval. Trends over time were analysed using a linear regression. Comparisons of survival and recapture probability differences between males and females over all 3 years were made using a paired Z-test, weighted with standard error (Hedges *et al.*, 1999).

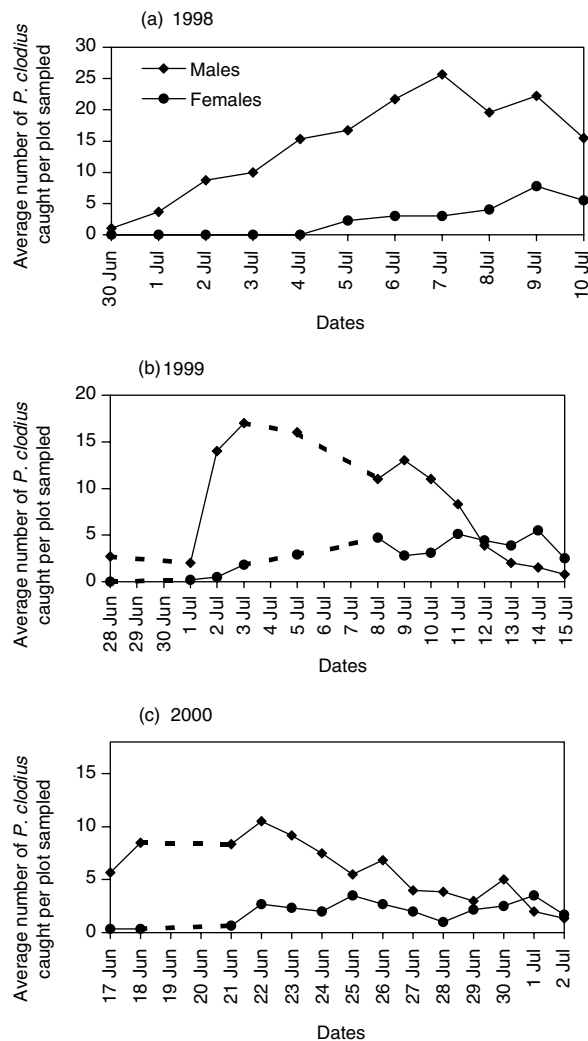
## Results

### Emergence

During all 3 years, males emerged first and were captured more frequently than females (Fig. 2). In 1998, butterflies were surveyed from the beginning of the flight period until the population started to decline (Fig. 2a). During 1999, the entire flight period of *P. clodius* was covered, although it

was only possible to sample one day between 4 and 8 July because of cloudy weather (Fig. 2b). Adult *P. clodius* emerged 2 weeks earlier in 2000 than in 1998 or 1999. They were first observed on 15 June; however, low temperatures and cloudy weather prevented surveying during the first few days of the flight (Fig. 2c).

In 1998, a total of 500 *P. clodius* were marked and 119 (24%) individuals were recaptured a total of 139 times during the 11-day mark–release–recapture period (Table 1). Seventy-seven (55%) recaptures occurred in the plots where the butterflies were originally captured. Two hundred and fifty-six other butterflies of multiple species were also marked and 18 (7%) were recaptured. The analyses was limited to *P. clodius*.



**Fig. 2.** Average number of *Parnassius clodius* caught per plot censused on each date. Dates when no plots were censused are indicated by a dashed line. In 1998, plots were  $75 \times 75$  m and censused for 35 min. In 1999 and 2000, plots were  $50 \times 50$  m and censused for 20 min.

**Table 1.** The number of *Parnassius clodius* captured and recaptured in all plots during surveys 1998–2000.

		Males	Females	Total
1998	Captured	404	96	500
	Recaptured	107	12	119
	% Recaptured	26	13	24
1999	Captured	552	223	775
	Recaptured	55	6	61
	% Recaptured	10	3	8
2000	Captured	343	145	488
	Recaptured	77	8	85
	% Recaptured	22	6	17

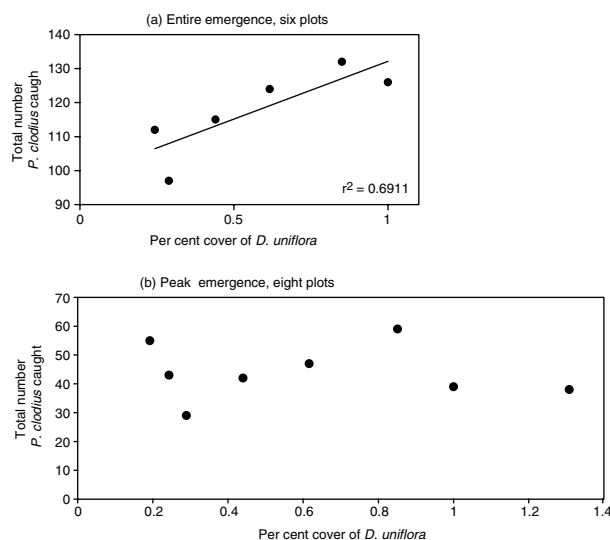
During 1999, 775 *P. clodius* were marked and 61 (8%) individuals were recaptured (Table 1). There was a total of 65 recapture events because four butterflies were recaptured twice. Twenty-seven (42%) of the recaptures occurred in the plot where the butterfly was captured previously.

During 2000, 488 *P. clodius* were marked and 85 (17%) individuals were recaptured (Table 1). There was a total of 100 recapture events because 20 butterflies were recaptured twice, one was recaptured three times, and one was recaptured four times. Twenty-seven (25%) of the recaptures occurred in the plot where the butterfly was captured previously.

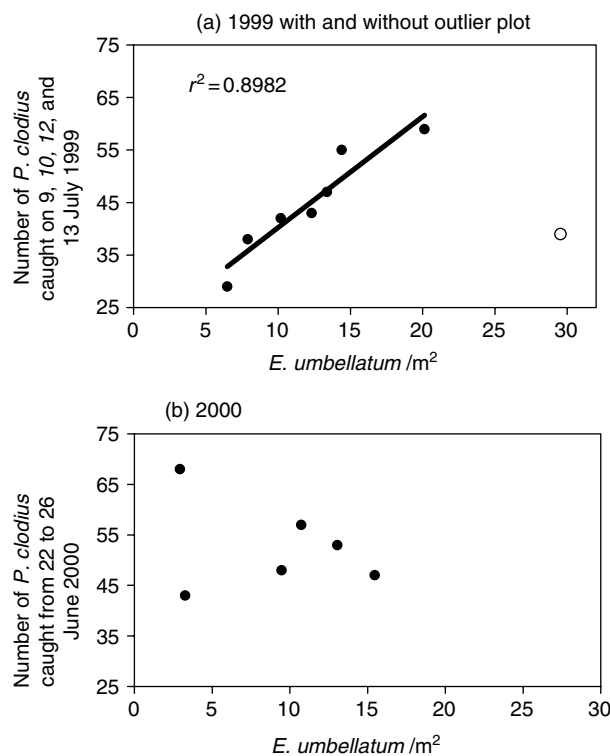
#### Host and nectar plants

There was no significant interaction between sex and host-plant cover, so sexes were analysed together. *Parnassius clodius* abundance (in the six plots surveyed equally over the entire flight period) was correlated positively with per cent cover of the host plant *D. uniflora* ( $r^2=0.69$ ,  $P<0.05$ ) (Fig. 3a). *Parnassius clodius* abundance during the peak of the flight period (all eight plots surveyed equally 9, 10, 12, and 13 July) was not correlated significantly with host-plant coverage ( $r^2=0.00$ ,  $P=NS$ ) (Fig. 3b).

The 1999 data showed a non-significant relationship between nectar plants and butterfly abundance (Fig. 4a). The assumption of equal variance of nectar plant abundance between plots was not met by the 1999 data and could not be corrected by transforming the data. One plot had a very high amount of nectar plants but relatively few butterflies. When it was omitted from the analysis, the assumption of equal variance was met and the relationship between butterfly abundance and nectar plants was significant (Fig. 4a). There was no significant interaction between sex and nectar plants ( $P=NS$ ); however, when analysed separately males had a significant response to nectar plants ( $r^2=0.61$ ,  $P<0.05$ ) while females did not ( $r^2=0.12$ ,  $P=NS$ ). The 2000 nectar plant data showed a non-significant relationship between *P. clodius* and *E. umbellatum* (Fig. 4b). There was a significant interaction between sex and nectar plants ( $P<0.05$ ). Males had a non-significant



**Fig. 3.** Regression of number of *Parnassius clodius* caught against host plant *Dicentra uniflora* per cent cover (a) for the six main plots in 1999 monitored throughout the flight period ( $F=8.95$ , d.f. = 5,  $P<0.05$ ), (b) for the eight plots monitored only during the peak emergence in 1999 ( $F=0.02$ , d.f. = 7,  $P=NS$ ).



**Fig. 4.** Regressions of numbers of *Parnassius clodius* against number of inflorescences per  $m^2$  of the primary nectar source, *Eriogonum umbellatum*, during the peak flight period. (a) There was no significant relationship between *P. clodius* and *E. umbellatum* in 1999.  $F=0.84$ , d.f. = 7,  $P=NS$ ; however, if one outlier plot (open circle) was removed, there was a significant positive correlation. The trend line fits these data.  $F=44.13$ , d.f. = 6,  $P<0.01$ . (b) For year 2000,  $F=0.38$ , d.f. = 5,  $P=NS$ .

**Table 2.** The mean distance ( $m$ ) moved by *Parnassius clodius* between recaptures ( $m/move$ ), the mean distance moved per day (mean/day), the mean distance moved per day corrected for effort at different distances (corrected  $m/day$ ), and the mean distance between plots (effort).

Year	$m/move$	Mean/day	Corrected $m/day$	Effort
1998	122	77	187	236
1999	334	112	287	491
2000	146	91	132	190
Mean	201	93	202	306

negative relationship with *E. umbellatum* abundance ( $r^2 = 0.15$ ,  $P = NS$ ) while females had a non-significant positive relationship ( $r^2 = 0.00$ ,  $P = NS$ ). Again, the assumption of equal variance of nectar plant abundance between plots was not met and the data could not be corrected by transformation. There was no significant relationship between butterfly abundance and nectar plant abundance when data were combined for the 2 years.

#### Movement distance

The mean distance moved per day by *P. clodius* was 200 m when averaged among the 3 years. The corrected means for daily movement were much higher than the raw means in 1998 and 1999 (Table 2). In all years, both the raw and corrected movement distances were correlated with the mean distance between plots. Movements were recorded at the farthest distances possible in all 3 years. One marked male in 2000 was captured 12 km from the study area.

#### Survival and movement probability

Model fitting began with fully time-specific parameters of apparent survival and recapture probability and model selection was based on AIC values. In each year one of the two best models had either constant or linear trends in apparent survival, recapture probability, or both (Table 3). In all years the fit of these competing differed by  $< 2$  AIC units, which

indicates that both models have some weight in explaining the observed variation in apparent survival and recapture (Lebreton *et al.*, 1992). In 1998, a trend model showed an increase in movement probability over time (Fig. 5).

Sex-specific rates of recapture, apparent survival, and movement probability were estimated using simple models with constant parameters (Table 4). Male apparent survival rate estimates were higher than female apparent survival rate estimates in 1999 and 2000; however, there was not a statistically significant difference between average male and female survival pooled across all 3 years. The pooled mean difference in survival, weighted by standard error, was 0.068 ( $SE_D = 0.1030$ ,  $Z = 0.654$ ,  $P > 0.05$ ). Male recapture probability was higher than female recapture probability in 1998 and 2000 (Table 4). The Z-test, weighted by standard error, showed that male recapture probability across all 3 years was significantly higher than female recapture probability with a difference of 0.1090 ( $SE_D = 0.0274$ ,  $Z = 3.978$ ,  $P < 0.05$ ).

Detection of a difference in movement probabilities between the sexes was only possible in 2000 because too few females were recaptured in 1998 and 1999 to estimate movement probabilities accurately (Table 4). During 2000, female movement probability was almost double the movement probability of males (Table 4). This was a significant difference ( $SE_D = 0.1010$ ,  $Z = 2.679$ ,  $P < 0.05$ ).

Recapture, survival, and movement probabilities varied with time in all three summers (Fig. 5). Survival and recapture probability decreased over time during each of the 3 years, whereas movement probability increased (Fig. 5). Regression analyses of these trends were significant for survival ( $P < 0.05$ ) and recapture probability ( $P < 0.05$ ) in 1999, and recapture probability in 1998 ( $P = 0.05$ ).

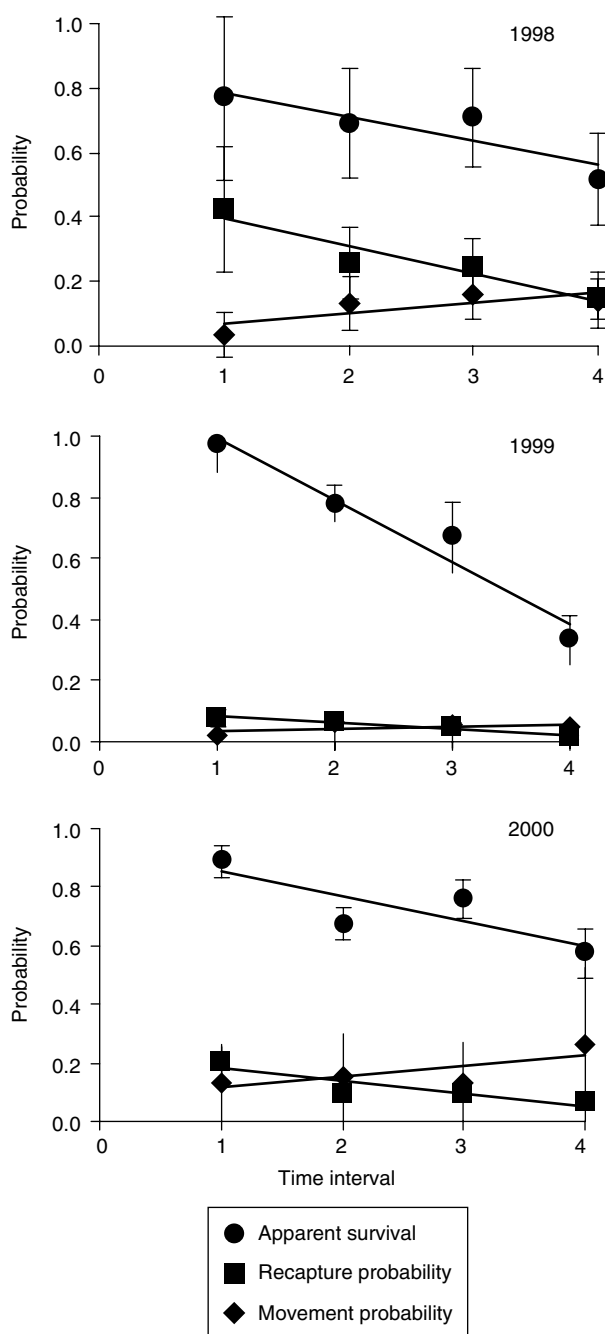
## Discussion

#### Mark–recapture

The mark–recapture studies were timed to maximise the probability of capturing individuals during the entire emer-

**Table 3.** Daily survival rate ( $\phi$ ), recapture probabilities ( $p$ ), and transition probabilities ( $P$ ) for male and female *Parnassius clodius* estimated using Program Mark (White & Burnham, 1999).

Year	Males			Females		
	Estimate	SE	95% CI	Estimate	SE	95% CI
<b>Recapture probability</b>						
1998	0.242	0.036	0.171–0.576	0.143	0.088	–0.029–0.315
1999	0.054	0.012	0.030–0.113	0.081	0.062	–0.039–0.202
2000	0.168	0.024	0.121–0.406	0.022	0.015	–0.008–0.052
<b>Survival</b>						
1998	0.658	0.047	0.565–0.750	0.895	0.245	0.415–1.374
1999	0.751	0.046	0.662–0.841	0.359	0.165	0.036–0.682
2000	0.820	0.029	0.762–0.878	0.569	0.148	0.280–0.859
<b>Transition probability</b>						
1998	0.142	0.023	0.103–0.193	0.033	0.033	–0.032–0.098
1999	0.514	0.010	0.035–0.075	0.033	0.022	0.009–0.114
2000	0.129	0.020	0.095–0.174	0.230	0.032	0.173–0.298



**Fig. 5.** Program Mark temporal models. Parameter estimates for recapture, survival, and movement probabilities are estimated over equal time intervals. Trend lines are shown for illustrative purposes only.

gence period. The experimental design differed between years because there was a trade-off between spreading plots out to improve estimates of movement distance and placing plots close together to increase the number of recaptures. Plots were closest together in 1998 and 2000, so the largest percentage of individuals in those years were recaptured and more accurate estimates of demographic

parameters from the mark–recapture data were made. In 1999, plots were spaced farthest apart and there were few recaptures, but estimates of movement were obtained over a broader range of distances. The emergence patterns of adults followed the typical pattern for butterflies in which males emerge first and their population peaks slightly before that of females (Scott, 1986). Typically, the males emerge first and wait near the site where the females will emerge. Butterflies have evolved this staggered emergence to maximise the chance of finding a mate (Thornhill & Alcock, 1983; Scott, 1986).

#### *Host and nectar plants*

There was a strong positive relationship between host-plant cover and *P. clodius* abundance in 1999 when examined over the entire flight period (Fig. 3a). This relationship was driven by the males. Interestingly, this relationship does not hold during the peak of the flight period (Fig. 3b) for either males or females. This result suggests that at different times of the flight period, different resources are more important. Host-plant density has been found to be a good predictor of presence, but not always the density of butterflies. Wahlberg *et al.* (2002a) found that the most important variables explaining the presence of *Euphydryas aurinia* in Finland were patch area and the density of host plants. Matter *et al.* (2003), however, found that butterfly density decreased with increasing area primarily because butterfly density decreased with increasing host-plant abundance. Gilbert and Singer (1973), when examining adult dispersal tendencies in *Euphydryas editha* in California, found that adult movement and distribution patterns could vary significantly with local or regional situations, and even among individuals that some of these differences were at least partly genetically based.

During 2000, almost no host plants were observed. Because adults emerged in near normal numbers, it was suspected that the caterpillars emerged early in response to the early snow melt and ate most of the host plants earlier than in 1999. The winter snow melted 2 weeks earlier in 2000 (15 April) than in 1998 (28 April) or 1999 (2 May). Emergence of *P. clodius* adults seems to be correlated most tightly with snow melt (J.N. Auckland, pers. obs.). Early larval emergence following snow melt could explain both the absence of host plants in May 2000 and the subsequent early emergence of adults the same year.

There was a significant relationship between *P. clodius* abundance and the nectar plant *E. umbellatum* in 1999 if one outlier plot was removed from the analysis (Fig. 4a). This plot had more nectar plants than any of the other plots, but it was located 10 m from the forest edge, which may have resulted in lower usage of the area. Although there was a significant effect of nectar plant abundance on *P. clodius*, when the sexes were analysed separately, this effect was insignificant for females. Similarly, Matter and Roland (2002) observed that flower abundance significantly affected the abundance of male *Parnassius smintheus*, but

**Table 4.** Apparent survival rate ( $\phi$ ), recapture probabilities ( $p$ ), and movement probabilities (P) for male and female *Parnassius clodius* estimated using Program Mark (White & Burnham, 1999).

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1999	0.514	0.010	0.035–0.075	0.033	0.022	0.009–0.114
2000	0.129	0.020	0.095–0.174	0.230	0.032	0.173–0.298

not females. There was no significant relationship in 2000 between butterfly and nectar plant abundance. It is impossible to determine whether the apparent trend in 1999 is typical or whether there is usually no relationship for these two species. Weather during 2000 was warmer and drier than in 1999, so different factors may have influenced *P. clodius* distribution in each year. Distribution of butterflies may not always be explained by the variables that would be expected because males and females may experience different levels of attraction to host plant and nectar resources (Matter & Roland, 2002). Furthermore, males may be attracted to areas with high numbers of females even if nectar resources are low, while females may avoid areas with high densities of males even when host plants are abundant (Baguette *et al.*, 1996). Therefore, behaviours that have evolved as a result of intraspecific mate-searching competition strategies may result in what appear to be non-adaptive butterfly distributions (Thornhill & Alcock, 1983; Baguette *et al.*, 1996).

#### Movement distance

Average distances moved by *Parnassius clodius* were similar to movements estimated for *P. apollo* (200 and 230 m respectively) (Brommer & Fred, 1999). Scott (1975) estimated that mean *P. smintheus* movements were almost 200 m, while Roland *et al.* (2000) found that they moved 145 m in alpine meadows. Determining the appropriate sampling scale and correcting for effort is critical in estimating dispersal; however, there is an inevitable trade-off between increasing the area sampled and decreasing the numbers of recaptures. Changing scale in each year of the study enabled better estimates of demographic parameters in 1998 and 2000 to be calculated, but provided the best estimate of movement in 1999 (Table 2).

Sampling effort and observed movement distance were correlated over the 3 years of the research (Table 2),

providing further evidence that estimates of movement distance are biased by the distance over which sampling occurs (Porter & Dooley, 1993; Koenig *et al.*, 2000; Schneider, 2003). Correcting for sampling effort improved movement estimates (Table 2). Obtaining measurements of maximum dispersal distances is virtually impossible because long-distance dispersers are probably missed by most studies (Koenig *et al.*, 2000). Recent genetic studies corroborate field studies that have found butterflies capable of dispersing much greater distances than are typically observed in mark–recapture studies (Peterson, 1996; Roland *et al.*, 2000).

While distance alone might not limit butterfly movement in large butterflies such as *Parnassius* at a scale of 1500 m or less, changes in habitat type may present substantial barriers to movement. In all 3 years of the study, individuals were recaptured at the maximum distances sampled and one marked male was captured 12 km outside the study area, a distance comparable to a dispersal distance observed for *Boloria aquilonaris* (Baguette, 2003). Forest edges probably have a greater effect on limiting dispersal than distance. When *P. clodius* were observed encountering forest edges, they either turned back or followed along the edge over 50% of the time (J. N. Auckland, pers. obs.). Edge avoidance by butterflies has also been observed by Sutcliffe and Thomas (1996), Haddad (1999), Roland *et al.* (2000), and Ries and Debinski (2001). Behavioural observations and a mark–recapture study of the ringlet butterfly (*Aphantopus hyperantus*) found that they avoided flying into the forests and were more likely to move between forest glades if glades were connected by open corridors (Sutcliffe & Thomas, 1996). Likewise, Ries and Debinski (2001) observed that the prairie specialist regal fritillary (*Speyeria idalia*) avoided crossing treeline edges 92% of the time whereas monarch butterflies (*Danaus plexippus*), which are much more habitat generalists, avoided crossing them 76% of the time. Haddad (1999) observed that two Coliadinae species avoided forest edges, but the swallowtail, *Papilio troilus*, crossed edges readily. Roland *et al.* (2000) found that forests were twice as resistant to movement of *Parnassius smintheus* as

open meadow habitat. This could be a result of butterflies either moving more slowly through forest or avoiding forest habitat.

Habitat edges, especially strong edges such as those found between grasslands and forest, seem to prevent real barriers to many species of butterflies. Stamps *et al.* (1987) developed computer simulations of emigration and found that edge permeability and geometry of a patch are the most important factors affecting emigration from a patch. Kuussaari *et al.* (1996) conducted field experiments on factors affecting immigration and emigration in the Glanville fritillary butterfly *Melitaea cinxia* and found that high densities of butterflies, great abundance of flowers, and large patch area decreased the rate of emigration while large open areas adjacent to the patch increased the emigration rate. Conradt *et al.* (2000) found that when meadow brown butterflies (*Maniola jurtina*) were released within the range of their normal dispersal in a non-habitat, they did not move at random, but rather oriented towards their suitable habitat. When released at larger distances from their habitat, they used a systematic search strategy. Further, butterflies returned to specific familiar patches when given a choice. Similarly, Ries and Debinski (2001) found that the prairie habitat specialist, *Speyeria idalia*, responded strongly to edges, turning to avoid crossing them and returning to the plot if they had crossed an edge. Thus, reluctance of individuals to cross edges may be the mechanism decreasing movement between patches rather than reduced movement after crossing into matrix habitat.

#### *Survival and movement probability*

Survival probability did not differ significantly between females and males; however, female recapture probability was significantly lower than male recapture probability (Table 1). Many studies of butterflies have observed lower return probabilities of females than of males (Scott, 1986; Sculley & Boggs, 1996; Brommer & Fred, 1999; Gutiérrez & Thomas, 2000; Roland *et al.*, 2000), but Petit *et al.* (2001) found higher mortality in males than in females within habitat patches. Because return probability is a function of both survival and recapture probability, correct analyses of these parameters are critical for understanding population biology and life-history parameters (Lebreton *et al.*, 1992; Schmidt & Anholt, 1999). Multiple capture events are needed to be able to separate the contributions of survival and recapture probability to return probability. The interdependence of these two estimates can easily be ignored in analyses reporting lower return probabilities for females. The analyses demonstrate clearly that for *P. clodius*, recapture probability is lower for females independently of survival rates.

Survival and recapture probability decreased over time in all years. Movement probability trends were confounded by the strong effect of distance, but there was a statistically non-significant increase over time in all years. This pattern probably reflects the fact that early in the emergence the population is composed predominantly of males that stay

close to areas with the best habitat. Multiple factors probably interact to increase movement as the flight season progresses. Later in the season, most females have emerged, mated, and are ranging widely in search of host plants. As the population ages, the probability of a male finding an unmated female in the meadow decreases. Simultaneously, nectar resources in the dry sagebrush meadow begin to senesce towards the end of the flight period while nectar lasts longer in more mesic adjacent habitats. Therefore, decreased mating probability and increased need for nectar may combine to increase the likelihood that males will leave the meadow. Butterflies are increasingly likely to emigrate as nectar decreases (Kuussaari *et al.*, 1996; Ries & Debinski, 2001) and Petit *et al.* (2001) found that females, which make up a larger percentage of the population as the population ages, tended to be more mobile than males, spending more time outside of their natal patch. Increasing movement of both sexes combined with an increasing proportion of females in the population results in recapture probability decreasing over time. Survival probability decreases as the entire population ages. Analysis of temporal variation can explain some of the variance in data and can be used to gain insight into life-history strategies of organisms (Gould & Nichols, 1998).

#### *Summary*

Individual movements between sub-populations and/or habitat patches within a metapopulation are the key to maintaining genetic diversity, recolonisation of areas where existing populations have gone extinct, and colonisation of new habitats that become available due to disturbance or succession. Understanding responses to resources, population processes, and seasonal changes *within a patch* is key to understanding emigration stimuli and the cues used to immigrate to a new habitat. *Parnassius clodius* seems to be responding to host plant and nectar plant resources differently based on sex and over time within the flight period. Estimates of movement suggest that they are not limited by distance in open habitat at the scale of hundreds of metres, but that their probable avoidance of edges may limit emigration and, thus, dispersal.

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