

Effect of altitude on seasonal flight activity of *Rhagoletis cerasi* flies (Diptera: Tephritidae)

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Abstract

The effect of altitudinal variation on the seasonal flight activity of *Rhagoletis cerasi* (Linnaeus) flies was evaluated along an altitudinal gradient from 150 to 1170 m in Mount Uludag, northwestern Turkey. The predicted dates of fly emergence, flight duration and dates of 5%, 50% and 95% cumulative fly catches at various altitudes were estimated from a degree-day model. Degree-day predictions were compared with those obtained from observations made with yellow sticky traps. The observed and predicted dates of appearance of adults were delayed by 1.4 and 2.0 days for every 100 m increase in altitude, respectively. The delay in phenology events was less at high altitudes than postulated by Hopkins' bioclimatic law, whether observed or predicted. The average absolute difference in predicted and observed dates of cumulative percentage catch of adults was 4.9 and 3.0 days in 1997 and 1998, respectively, but these differences were not significant. Prolonged flight activity was predicted and observed at higher altitudes, but the flight period lasted significantly longer than predicted. The observed flight period varied from 29 to 43 days in 1997 and from 36 to 52 days in 1998 between the lowest and highest altitude on the transect. Altitudinal variation between geographically close locations should be taken into account to properly time monitoring activities and hence to manage *R. cerasi* populations more effectively.

Keywords: elevation, European cherry fruit fly, flight, phenology, yellow sticky traps

Introduction

Maintaining an adaptive seasonality, which often requires synchronous occurrence of specific life stages with host plant phenology, is a basic ecological requisite for many insect species (Powell & Logan, 2005). For example, emergence of *Rhagoletis cerasi* (Linnaeus) (Diptera: Tephritidae) flies must coincide with the ripening period of sweet cherries, when fruits start turning from a bright green to a straw-yellow, in order to be able to lay eggs. However, adult emergence dates may vary from one location to another because, although locations can be geographically close together, they may be subject to widely differing climatic

regimes (Randall, 1982). Therefore, it is difficult to provide specific emergence dates even for geographically close locations, as the timing of adult emergence can be affected by altitude, latitude, slope, and other environmental factors (Muller, 1970; Engel, 1976).

Altitude has long been known to have direct effects on both insect and plant phenology (Hopkins, 1919). Hopkins' bioclimatic law states that phenology events, such as bloom time or adult emergence, are usually delayed for four days for each increase of 122 m in altitude. In fact, insects are not affected by altitude *per se*, but by the associated climatic changes along the gradient (Mani, 1962). Temperature is the most important of these climatic changes, which decreases about 0.5–0.6°C with every 100 m increase in altitude (Coulson *et al.*, 1976).

As a consequence of the decrease in temperature at high altitudes, the phenology of events like the opening of buds,

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Table 1. The monthly average temperatures (°C) recorded at three meteorological stations at different altitudes from January to December in 1997 and 1998 in Mount Uludag, Bursa (Turkey).

Location	Altitude (m)	Year	Month											
			J	F	M	A	M	J	J	A	S	O	N	D
Doburca	150	1997	3.7	5.7	5.3	9.6	18.1	22.3	24.5	21.8	17.4	14.8	10.6	7.5
		1998	5.2	6.4	6.1	15.4	17.1	22.4	22.2	24.6	19.5	13.7	10.9	10.3
Yigitali	400	1997	2.1	2.6	3.6	8.4	16.8	20.1	21.2	20.0	16.8	14.0	9.1	6.6
		1998	2.7	3.0	5.3	12.2	15.5	19.8	21.4	22.2	18.3	11.5	8.7	7.9
Sogukpinar	1025	1997	0.3	0.9	2.4	7.8	14.0	17.5	19.4	19.2	15.7	12.5	8.7	4.7
		1998	1.1	1.7	3.6	10.4	13.9	18.2	20.8	19.9	16.2	9.7	6.6	3.8

or larval growth and development are delayed. In contrast, seasonal events in the autumn are correspondingly hastened in mountains (Alexander & Hilliard, 1969). According to the bioclimatic law, the season is thus shortened not only by a day at the beginning but also by a day at the end for each 30 m increase in altitude. Thus, a species with a wide altitudinal range appears later in the season at higher altitudes, and at these locations it must be adapted to a shorter season.

Rhagoletis cerasi is the most serious pest of sweet cherries *Prunus avium* (L.) (Fischer-Colbrie & Busch-Petersen, 1989). It is distributed over a wide range of altitudes up to 1200 m throughout Europe and in parts of temperate Asia (Leski, 1963; Engel, 1976; Leclercq, 1979). Boller & Bush (1974) reported that adult emergence patterns of *R. cerasi* changed significantly along a north-south transect. A prolonged emergence period on this transect was attributed to decreasing latitude. Nevertheless, the effect of increasing altitude on adult emergence patterns is unknown. Increasing altitude tends to mimic latitudinal gradients, with more variable and extreme climatic conditions (Smith *et al.*, 2000). In addition, the length of the photoperiod varies considerably along a latitudinal gradient but is not affected by altitude (Fielding *et al.*, 1999).

Because of the differences between the effects of altitude and latitude, studies of altitude should be made along an east-west altitudinal gradient in a relatively narrow band of latitude (Alexander & Hilliard, 1969). Such a gradient exists in Mount Uludag near Bursa, northwestern Turkey. Therefore, the present studies were concentrated in a band along the 40th parallel, north latitude in order to reduce latitudinal variation to a minimum.

The objectives of this study were to investigate the extent to which the seasonal flight activity of *R. cerasi* adults is influenced by altitude and to identify the differences in adult emergence patterns between geographically close sites at different altitudes in response to varying climatic gradients.

Materials and methods

Experimental sites

Studies were carried out in sweet cherry orchards around Mount Uludag, Bursa (40°19'N, 29°06'E), northwestern Turkey, from early May until mid-August in 1997 and 1998. Sweet cherry orchards were 1–30 km apart, and varied from small-scale backyard orchards to large-scale commercial orchards in forested areas. Orchards ranged in size from 0.5 to 3 ha and consisted of medium-ripening 'Bing' and late-ripening '0900 Ziraat' varieties. In 1997, low and high altitude sites were compared to detect if there were any

differences between adult emergence patterns. Based on the findings of 1997, the study area was enlarged to cover as much as possible of the regional variation in the phenology of adult flight at varying altitudes in 1998.

Monitoring

Rebell type yellow sticky traps (Swiss Federal Research Station, Wädenswil, Switzerland) consisting of two crossed panels, coated with a layer of Tangletrap adhesive (The Tanglefoot Company, Grand Rapids, Michigan, USA) were used to monitor the dynamics of adult flight in Bursa, northwestern Turkey in 1997 and 1998. Traps were set before the start of adult flight between 1–15 May depending on location. They were checked daily until the first sustained fly captures occurred and then adults were counted and removed from traps once a week. Traps were generally removed after three consecutive zero captures.

In 1997, eight traps were set in Mount Uludag (two in each of Cukurca, Doburca, Bagli, and Sogukpinar). In 1998, eight traps were set at the same locations as in 1997, and eight traps were set in new locations (two in each of Yigitali-1, Yigitali-2, Yigitali-3, and Kirazli).

Meteorological data

Meteorological data were obtained from 105 m at Hurriyet (40.18°N 29.00°E), at 400 m at Yigitali (40.30°N 28.88°E) and at 1025 m at Yenikonak (40.10°N 29.20°E). The three meteorological stations were located as far as 1–4 km from the monitoring sites. Monthly mean temperatures recorded at these stations are summarized in table 1. The daily mean temperatures for the three meteorological stations were regressed against altitude and the daily lapse-rate, the rate at which temperature decreases with altitude, was used to interpolate the daily mean temperature. The monthly mean of the lapse-rate of daily mean temperature varied considerably among months (fig. 1), with the steepest temperature lapse-rates occurring in February. In June and July when the larvae were developing, temperature declined by 0.5°C per 100 m increase in altitude. This resulted in a difference of 5.1°C in the mean temperatures between the lowest (150 m) and highest (1170 m) sampling site.

Management

Diazinon (Hezudin 20 EM, Hektas, Kocaeli, Turkey) was applied to control *R. cerasi* adults at 1.4 l in 1000 l of water per ha using an air-blast sprayer at all locations except for two untreated orchards (Yigitali-1 and Yigitali-2) in Yigitali in 1998. Both the timing and number of insecticide applications

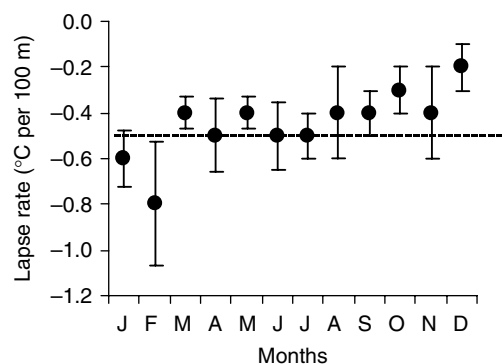


Fig. 1. The monthly change (\pm SEM) in lapse-rate of daily mean temperature with altitude in Mount Uludag transect ($n=3$), Bursa (Turkey). Data are for 1 January 1997 to 31 December 1998. The horizontal dashed line represents the annual mean lapse rate of 0.45°C per 100 m increase in altitude.

varied among locations. Cukurca orchard received the most intensive treatments with insecticides compared with other locations. At this location, three insecticide treatments were applied on 1, 10 and 20 June in 1997 and 23 May, 2 and 13 June in 1998, respectively. In Doburca, diazinon was applied twice per season on 7 and 20 June in 1997 and 30 May and 14 June in 1998. Only one diazinon application was made in Bagli orchard on 25 and 22 June in 1997 and 1998, respectively. Sogukpinar orchard was treated with two diazinon applications on 27 June and 7 July in each year of the study. Yigitali-3 and Kirazli orchards received a single application of insecticide on 12 and 15 June in 1998, respectively.

Data analysis

The predicted dates of adult appearance, flight duration and dates of 5%, 50% and 95% cumulative fly catches were estimated from the degree-day model of Leski (1963). Degree-days, which are accumulated heat units above a specified base temperature during a 24-h period, were calculated using the standard weather bureau formula, also known as the Means Method (Pruess, 1983; Fry, 1983):

$$\left[\frac{\text{Max. temperature} + \text{Min. temperature}}{2} - \text{base developmental temperature} \right]$$

This formula has been used successfully for other tephritid pests including the western cherry fruit fly *Rhagoletis indifferens* Curran and apple maggot *Rhagoletis pomonella* (Walsh) (Aliniaze, 1976; Reissig *et al.*, 1979). All temperature values were rounded to the nearest $^{\circ}\text{C}$ including the base developmental temperature, for which a value of 7°C was used starting from 1 January (Leski, 1963).

Observed dates of 5%, 50% and 95% cumulative fly catches were estimated at each location by linear interpolation based on the relationship between cumulative catches on successive dates when traps were checked (SAS Institute, 2001). Assuming that fly capture in yellow sticky traps is in direct relation to fly density, dates of 5%, 50% and 95% cumulative fly numbers were estimated, to the nearest day, from cumulative fly frequency.

Observed dates were regressed on predicted dates and the slopes (m) were tested for significance ($H_0: m=0$) as well as for deviation from unity ($H_0: m=1$). Linear regression

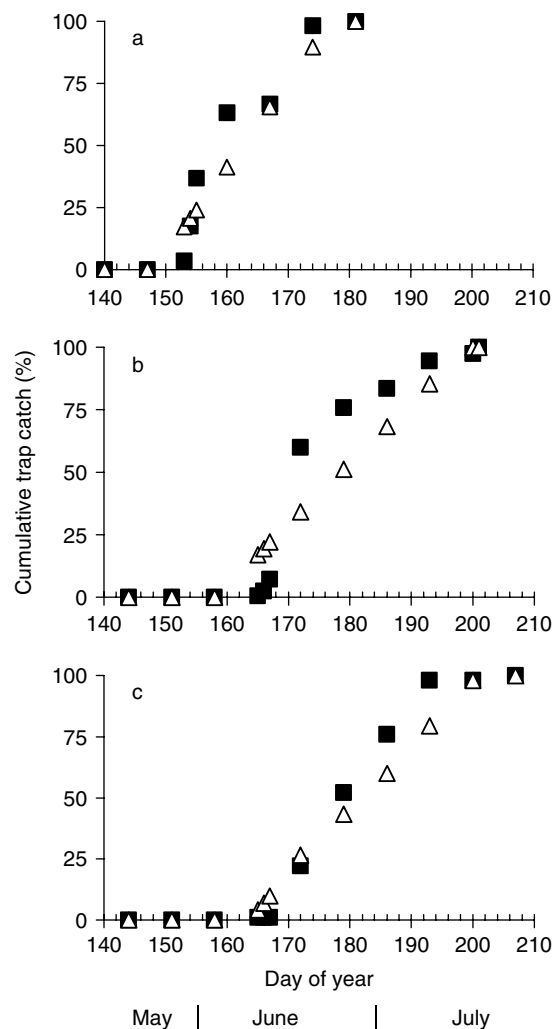


Fig. 2. Comparison of observed (\blacksquare) and predicted (\triangle) cumulative catch of *Rhagoletis cerasi* flies in Mount Uludag, Bursa (Turkey) in 1997: (a) Doburca, 150 m; (b) Bagli, 1070 m; (c) Sogukpinar, 1170 m.

analysis was used to determine relationships between dates of adult emergence, or 5%, 50%, 95% cumulative trap catch, and altitude. Duration of adult flight period was determined in terms of days and analysed in relation to altitude using linear regression analysis. Model bias (average difference) between predicted and observed dates of adult emergence, 5%, 50% and 95% cumulative catch, and the duration of adult flight period were calculated and tested for significance using t -tests.

Results

Adult emergence

Trap catches showed considerable differences in timing and intensity of adult *R. cerasi* emergence at varying altitudes in 1997 (fig. 2). The date of first adult emergence varied between 2 June (153rd day of year) and 14 June (165) at different altitudes in 1997, whereas adults were first caught between 24 May (143) and 6 June (157) depending on the altitude in 1998. There was a significant relationship

between altitude and dates of fly emergence, whether observed or predicted, in 1998 (fig. 3). No significant differences were found between predicted and observed dates of adult emergence ($t=0.40$; $P=0.89$). Slopes deviated significantly from zero in both cases ($F=12.58$; $df=1,5$; $P=0.02$ for observed; $F=101.20$; $df=1,5$; $P<0.01$ for predicted), but the differences between the slopes were not significant ($F=2.90$; $df=1,10$; $P=0.12$). The observed and predicted dates of appearance of adults was delayed by 1.4 and 2.0 days for every 100 m increase in altitude, respectively; a difference of 14–20 days between the lowest and highest altitude on the transect.

Percentage cumulative adult catch

A summary of the observed and predicted dates of 5%, 50% and 95% *R. cerasi* adult catch in 1997 and 1998 is given in table 2. Mean cumulative trap catches varied from 0 to 507 adults per trap among sites, which were under different management programmes. Predicted average dates of 5%, 50% and 95% *R. cerasi* adult catch were similar to those of actual observed catch. The average absolute difference in predicted and observed dates was 4.9 and 3.0 days in 1997 and 1998, respectively. Predicted dates of 5%, 50% and 95%

fly catch in 1997 were not significantly different from observed dates, which indicates that there was no significant bias in predicted dates of fly catch ($t=3.4$, $P=0.07$ for 5%; $t=3.3$, $P=0.08$ for 50%; $t=3.9$, $P=0.06$ for 95%). However, average predicted dates of 5% fly catch in 1998 were significantly earlier than observed (4.1 days; $t=8.2$; $P<0.01$). In contrast, later occurrence of 95% fly catch was predicted than those of observed (3.1 days; $t=3.3$; $P=0.02$). No significant differences were found between predicted and observed dates of 50% fly catch ($t=0.20$; $P=0.84$). Significant relationships were obtained between altitude and the dates of 5%, 50% and 95% trap catch in 1998 (fig. 4, table 3), but there were no significant slope differences between observed and predicted dates of 5%, 50% and 95% catch ($F=0.10$; $df=1,10$; $P=0.76$ for 5%; $F=0.04$; $df=1,10$; $P=0.85$ for 50%; $F=0.09$; $df=1,10$; $P=0.77$ for 95%).

Duration of adult flight period

With increasing altitude, the duration of adult flight period varied from 29 to 43 days in 1997. The last flies were captured at the lowest and highest altitude site on 30 June (181) and 26 July (207) in 1997, while last trap captures were recorded on 26 June (177) and 26 July (207) in 1998, respectively. In 1998, the relationship between altitude and dates of end of the flight period was statistically significant (table 3). Similarly, there was a significant relationship found between altitude and the observed and predicted duration of the flight period in terms of days ($F=42.24$; $df=1,5$; $P<0.01$; $R^2=0.90$ for observed; $F=85.43$; $df=1,5$; $P<0.01$; $R^2=0.95$ for predicted). Both the observed and predicted duration of the flight period in response to increasing altitude indicated that flight season tends to be prolonged in duration at higher altitudes. The observed flight period increased from 36 days in Doburca (150 m) to 52 days in Sogukpinar (1170 m). The observed and predicted duration of flight period was prolonged by 1.4 and 0.6 days for every 100 m increase in altitude, respectively (fig. 5); corresponding to a difference of 6–14 days between the lowest and highest altitude on the transect. However, there were significant differences between the slopes of observed and predicted values ($F=14.33$; $df=1,10$; $P<0.01$), which suggests that observed

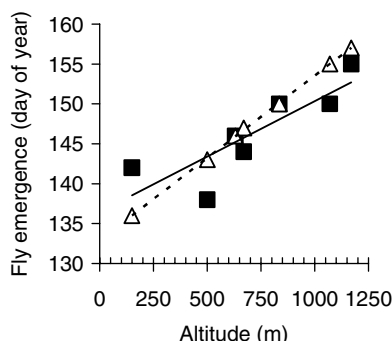


Fig. 3. Observed (■) and predicted (△) dates of appearance of adult *Rhagoletis cerasi* at different altitudes on Mount Uludag, Bursa (Turkey) in 1998.

Table 2. Dates of observed and predicted 5%, 50% and 95% cumulative trap catch of *Rhagoletis cerasi* adults in study sites under different management regimes at varying altitudes in 1997 and 1998.

Year/site	Altitude (m)	Management ^a	Total catch/trap	Observed dates			Predicted dates		
				5%	50%	95%	5%	50%	95%
1997									
Cukurca	105	+++	0	*	*	*	*	*	*
Doburca	150	++	29	154	159	173	150	163	176
Bagli	1070	+	369	166	172	193	160	180	201
Sogukpinar	1170	++	147	166	178	192	164	181	198
1998									
Cukurca	105	+++	1	*	*	*	*	*	*
Doburca	150	++	30	144	160	171	140	159	173
Yigitali-1	500	–	507	141	155	170	137	157	178
Yigitali-2	630	–	98	147	163	182	144	162	184
Yigitali-3	670	+	36	151	168	183	149	169	185
Kirazli	835	+	27	157	172	188	152	170	192
Bagli	1070	+	359	159	173	189	153	172	193
Sogukpinar	1170	++	211	164	176	200	159	179	200

^a –, no insecticide; +, one insecticide application.

* Could not be determined because of very low or zero trap catches.

dates were less dependent on altitude than predicted dates. The observed duration of flight period lasted significantly longer than predicted (5.1 days; $t = 3.8$; $P < 0.01$).

Discussion

The present results clearly showed that climatic changes along the altitudinal gradient affected the seasonal flight

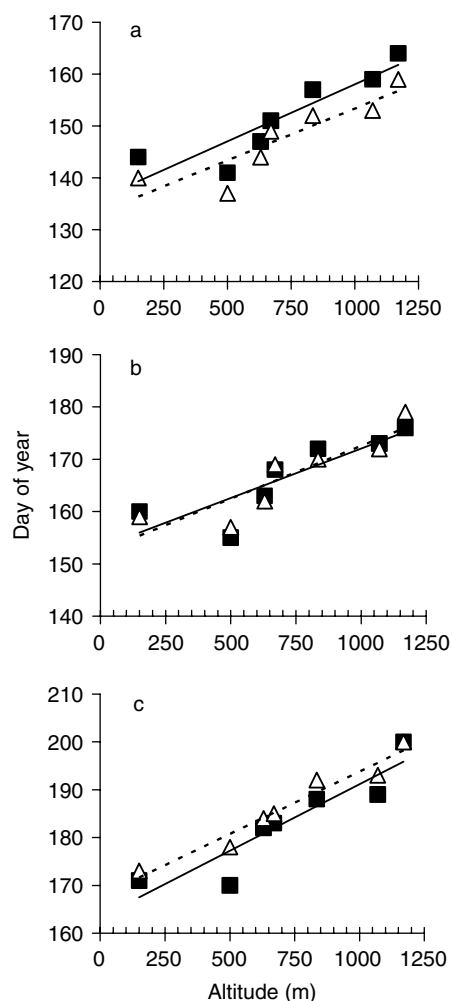


Fig. 4. Relationships between altitude and observed (■) or predicted (△) dates of 5% (a), 50% (b) and 95% (c) cumulative trap catch of *Rhagoletis cerasi* adults in Mount Uludag, Bursa (Turkey) in 1998.

activity of *R. cerasi* adults. Life-cycle stages appeared to be completed more rapidly under warmer conditions. Adults emerged 14–20 days earlier at lower than at higher altitudes. However, the delays with altitude are less than expected from the Hopkins' bioclimatic law, in which a 122 m increase in altitude corresponds to a four-day delay in phenology events. This suggests a local adaptation of timing and intensity of adult emergence at varying altitudes, either due to differences between development and physiology of low and high altitude populations or differences in elevational decrease in temperature among the early, mid- and late-season (Fielding *et al.*, 1999). In fact, the steepest temperature lapse-rates occurred in February and the lapse-rates declined as the season progressed. Although the elevational decrease in temperature appeared to be compensated by the increasing temperatures because of the advancement of the season, there was still a difference of 5.1°C in the mean temperatures between the lowest and highest sampling site during the larval growth period in June and July.

The later appearance of adults at high altitude may also be explained either by the differences in timing of diapause termination or by the differences in post-diapause development (Baker & Miller, 1978). *Rhagoletis cerasi* is univoltine and undergoes obligate pupal diapause, which stops development after about 6–9 months in general and more than a year in some cases (Vallo *et al.*, 1976). In temperate *Rhagoletis* species, pupal diapause is terminated by exposure to low temperature during the winter months (Fletcher, 1989). Van Kirk & Aliniaze (1982) showed that the period needed to complete pupal development of *Rhagoletis* spp. was negatively correlated with the length of winter cold period. In this case, the termination of diapause occurs earlier at low temperatures and later at higher temperatures

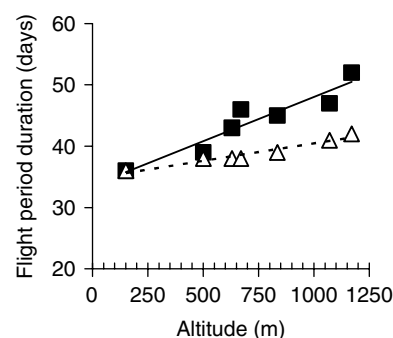


Fig. 5. Relationship between altitude and the observed (■) or predicted (△) duration of adult *Rhagoletis cerasi* flight period in Mount Uludag, Bursa (Turkey) in 1998.

Table 3. Comparison of mean observed and predicted dates of adult *Rhagoletis cerasi* flight activity averaged over sites in 1998 at Mount Uludag, Bursa (Turkey) together with data on the relationship between observed and predicted dates with altitude.

Adult flight activity	Observed dates				Predicted dates			
	Means	Intercept	Slope	R ²	Means	Intercept	Slope	R ²
Fly emergence	146.4 ± 2.2	136.4 ± 3.1	0.01 ± 0.003	0.72	147.7 ± 2.7	132.9 ± 0.2	0.02 ± 0.0002	0.99
Cumulative catch								
5%	151.9 ± 3.2	136.0 ± 3.7	0.02 ± 0.005	0.82	148.7 ± 2.9	133.4 ± 3.6	0.02 ± 0.005	0.80
50%	166.7 ± 2.9	153.1 ± 4.0	0.02 ± 0.005	0.74	166.9 ± 3.0	152.3 ± 3.6	0.02 ± 0.005	0.80
95%	183.3 ± 4.0	163.3 ± 4.2	0.03 ± 0.005	0.85	186.4 ± 3.5	167.7 ± 2.1	0.03 ± 0.003	0.95
End of flight	190.4 ± 4.0	170.1 ± 4.0	0.03 ± 0.005	0.86	186.6 ± 3.5	167.7 ± 0.4	0.03 ± 0.005	0.99

(Tauber *et al.*, 1986). Post-diapause development in *R. cerasi* then commences in response to spring temperature rise when average daily temperatures reach above a developmental threshold of 7°C (Leski, 1963). This usually corresponds to a period between February and March depending on the altitude (Feron, 1952). The later appearance of adults at high altitude is considered to be largely the consequence of low temperatures during the post-diapause development. Temperature has been shown to be the main cause of observed altitudinal variation in life-history patterns in many insect species including carabid beetles (Sparks *et al.*, 1995), dung flies (Baldwin & Dingle, 1986) and milkweed bugs (Blanckenhorn, 1997). However, it is important to note that temperature is not the only factor affecting emergence patterns and other factors including rainfall, amount of sunlight, soil type and the larval host should also be considered (Muller, 1970; Engel, 1976).

Predictions yielded similar results to the observed dates of adult *R. cerasi* flight recorded by yellow sticky traps over a large geographic area. The average absolute difference in predicted and observed dates of 5%, 50% and 95% adult catch was 4.9 and 3.0 days in 1997 and 1998, respectively. There were no significant slope differences between observed and predicted dates of adult catch, indicating that trap catches were largely dependent on altitude. It appears that flies originating at varying altitude do not mix with each other. This is in agreement with the findings of Katsoyannos *et al.* (1986) who reported that *R. cerasi* adults are weak fliers. However, they also observed slight dispersal of *R. cerasi* flies to surrounding vegetation when their host had no fruit, or was highly infested. In addition, sterile insect release studies showed that cherry fruit flies could travel at least 500 m from the point of release if oviposition substrates are lacking (Haisch, 1975).

The present results showed that flight season tends to increase in duration with increasing altitude. The fact that observed total flight period was less dependent on altitude than predicted dates indicates that there may be other factors affecting emergence patterns. Boller & Bush (1974) also found prolonged emergence curves for pupae from three out of 17 sites and suggested that these emergence curves may be associated with the uneven ripening of cherries in these areas. Whether host plant variety affects the developmental rate of *R. cerasi* larvae, and thus the time when they enter and complete diapause development is unknown. However, flight activity lasted 14–16 days longer at high altitude sites than at low altitude although all sites consisted of medium and late-ripening sweet cherry varieties in this study. In this case, it is suspected that the presence of an alternative host may be a contributor to the prolonged emergence pattern at high altitude sites. Sour cherries bear fruit later in the season than sweet cherry and fruit infestations can reach up to 33% in this area (Kovanci, 1998). Apparently, sour cherries provide an alternative oviposition site especially if sweet cherries are harvested or become highly infested and their ripening period can determine the range of the emergence time. In a heterogeneous environment, larval oligophagy together with the ability of local populations to adapt to the chemical quality and ripening period of the dominant host plant also makes the opportunistic use of low quality host species, in this case sour cherries, possible (Tikkanen, 2000).

In conclusion, evidence was found for the relationship between *R. cerasi* phenology and increasing altitude as postulated by Hopkins (1919) for insect species in temperate

North America, but phenology events occurred somewhat earlier than expected at high altitudes. This is consistent with earlier findings reported by Alexander & Hilliard (1969) that the delay in the life cycle of *Melanoplus dodgei* (Thomas) (Orthoptera: Acrididae) was less at high altitudes than projected in North America. The researchers attributed the shorter delay in *M. dodgei* phenology at high altitudes in Colorado to the duration of frost-free growing season, which lasted longer than calculated from Hopkins' bioclimatic law. According to the Hopkins' bioclimatic law, the growing season is shortened 10 days both in the spring and autumn with each 305 m increase in altitude. However, several studies have shown that spring and summer tended to occur earlier in Europe in recent decades, whereas autumn appears to be slightly delayed due to climate warming (Ahas *et al.*, 2002; Sparks & Menzel, 2002; Walther *et al.*, 2002). As a result of climate warming, the growing season lasts nearly 12 and 18 days longer than it did during the past two decades in North America and Eurasia, respectively (Zhou *et al.*, 2001). The extended growing season may account for the smaller delay in the life cycle of *R. cerasi* at high altitudes than the proposed delay of Hopkins' bioclimatic law. Another potential source of differences between the observed and projected delay may be the temporal variability of lapse rates of mean temperature during the growing season. In contrast to Hopkins' assumption of constant lapse rate, the present results indicated temporal differences in the magnitude of the lapse rate (fig. 1). The steepest lapse rates of mean temperature were recorded in the winter in this study as previously reported by Coulson *et al.* (1976) in Britain. These results raise the question of whether there is actually a hastened seasonal pattern at high altitudes as proposed by Hopkins (1919).

Clearly, altitudinal variation between geographically close locations should be taken into account to properly time monitoring activities and hence to manage *R. cerasi* populations more effectively. A better understanding of adaptation to short seasons of high altitudes could considerably improve our predictions. Additional information is needed to determine whether the adaptation to high altitudes in *R. cerasi* is regulated by an extended diapause in the pupa, by cooler temperatures during the post-diapause development or by an abbreviated life cycle. Potential reasons for delayed or prolonged emergence patterns of adults at high altitudes are unknown, but may be attributed to the elevational decrease in temperature, presence of alternative host plants, variation in diapause requirements, and/or a genetically linked trait. Further studies are required to examine all these assumptions.

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