J. Mt. Sci. (2010) 7: 167–175
DOI: 10.1007/s11629-010-1115-2

Alpine Taxa Exhibit Differing Responses to Climate Warming in the Snowy Mountains of Australia

K. GREEN

National Parks and Wildlife Service, Snowy Mountains Region, PO Box 2228, Jindabyne NSW 2627, Australia

E-mail: kenneth.green@environment.nsw.gov.au; Tel: +61 (0)2 6450 5538

Abstract: The phenologies of plants and animals in snow-covered landscapes are expected to accelerate with global warming. However, there are few studies that have examined a range of unrelated taxa in alpine environments to determine whether there is commonality in the proximate causes, synchrony in timing, or the direction of any changes. Records for five alpine animal species and two alpine plant species, chosen primarily for their visibility, were examined to determine their temporal response to regional climate warming. Over the 30-year period studied, they showed an array of different phenological responses. Plant flowering appeared linked to date of snow melt, whereas animal responses varied. Although having accelerated phenologies, two migratory bird species exhibited contrary changes; one to low-altitude warming regardless of snow conditions in the alpine zone (flame robin) and the other to state of the snowpack regardless of low-altitude temperatures (Richard's pipit). By contrast, the migratory bogong moth arrived significantly later over the years with no apparent explanatory climatic cause. Although bogong moths are not responding to earlier snow melt, insectivorous predators on the ground are. This could lead to a serious mismatch in timing at different trophic levels, putting pressure on endangered vertebrates. Emergence of locally wintering insect species, March flies and Macleay's swallowtails, were not significantly related to measured climatic parameters over the study period. A consequence of the disparate responses to climate warming recorded here is the questionable value of 'indicator species' to examine the impact of climate warming on alpine ecosystems.

Keywords: Bogong moth; Climate change; Migration; Mismatch; Phenology

Introduction

As a response to general regional climate warming over the second half of the 20th century, there has been a significant decrease in the depth and duration of snow in the Snowy Mountains of south-eastern Australia (Whetton 1998, Hennessy et al. 2003, Nicholls 2005, Green and Pickering 2009). However, there have been few biological studies aimed specifically at examining changes in the responses of biota over this time, although Gallagher et al. (2009) did attempt to examine changing phenology based on herbarium records. Compared to North America (Miller-Rushing and Primack 2008) and Europe (Sparks et al. 2000), there are few long-term data sets in the Southern Hemisphere from which to elucidate a fingerprint of global warming, particularly at higher altitudes (Gallagher et al. 2009). The expected responses of different species to climate warming is largely theoretical, however it is also largely unpredictable (Inouye et al. 2002). The earlier arrival of bird species and higher penetration of some mammals into the Snowy Mountains on a decadal scale was documented by Green and Pickering (2002). In

Received: 9 November 2009
Accepted: 28 February 2010

subsequent studies, Norment and Green (2004) found that the arrival of Richard's pipit (*Anthus novaeseelandiae*) was correlated with date of snow melt, and Green (2006) showed that migratory woodland birds were responding to presence or absence of snowpack.

Because few studies have examined more than one taxon, inferences concerning future ecosystem functioning derived from one group may not be valid if applied across interacting taxa. Where meta-analyses of phenological changes over time have taken place, reports of responses of birds, insects and plants to climate warming are couched in terms of earlier arrival/flowering by an average figure per decade, suggesting that the change in phenology is a directed continuum, (Parmesan and Yohe 2003, Root et al. 2003, Lehikoinen et al. 2004). However, there is no *a priori* reason to expect that all species will have phenologies shifting at the same rate (Visser et al. 2004), and differentially accelerated phenologies may have consequences for pollination and pollinators (Thórhallsdóttir 1998, Inouye et al. 2002, Dunne et al. 2003, Gallagher et al. 2009), and predators and prey (Visser et al. 2004).

Unlike in Europe and North America, there is not a long history in Australia of natural historians collecting data on phenology. Hence, there are few data specifically collected on the phenology of alpine plants, insects or birds in Australia and no accessible long term data sets with which to determine the relationship between time of flowering and various climatic factors (Gallagher et al. 2009). The present study, therefore, examined a collection of observations on animals and plants made during the conduct of a number of research projects in the Snowy Mountains, to determine whether all species showed a similar acceleration in phenology linked to the same cause or whether there was variation in responses among taxa.

1 Study area

This study was conducted in the area of the Snowy Mountains (36°27' S 148°16' E) around continental Australia's highest mountain, Mt Kosciuszko, 2228 m (Figure 1, Figure 2). The area is characterised by continuous snow cover for four to six months per year with six to eight months having minimum temperatures below freezing. Precipitation is in the range of 1800-3100 mm per year with about 60% of this falling as snow (Costin et al. 1979).

2 Materials and Methods

2.1 Climate data

Snow data were obtained from the Snowy Hydro snow course at Spencers Creek (1830 m asl Figure 2). This is the only regularly-monitored high altitude snow course in the Snowy Mountains, and snow depth has been measured there weekly through the winter since 1954. The date of snow melt was taken as the first date in spring when the snow course was recorded as being free of snow, or if this record was not available, one week after the last record of snow at the snow course. To reflect both depth and duration of snow cover, snow data were transformed into metre-days of snow by multiplying the depth of snow by the numbers of days at that depth and summing the weekly result to give a single figure of 'the amount of snow' for each year. For one early insect record (1922), data were not available from Spencers Creek so the thaw date was estimated from amount of snow modelled by Duus (1992).

2.2 The species

I have kept field notebooks of observations in the Snowy Mountains during a number of research projects since 1977. The field notebooks were searched to determine whether there were sufficient data on any species that might be useful in examining the impact of climate change across the 30+ year period. Species for consideration were based on three criteria: they had to be highly visible, recognisable from first acquaintance such that recording did not depend on increased familiarity over time, and the date I first recorded them each year had to be well represented among years in my field notebooks. The periods 1977-1983 and 1986-1987 were characterised by frequent field trips in spring to the Snowy Mountains with less frequent trips from 1984-1985 and 1988-1994. From 1995 to the present, trips have again been more frequent. The first record of each of the species was generally

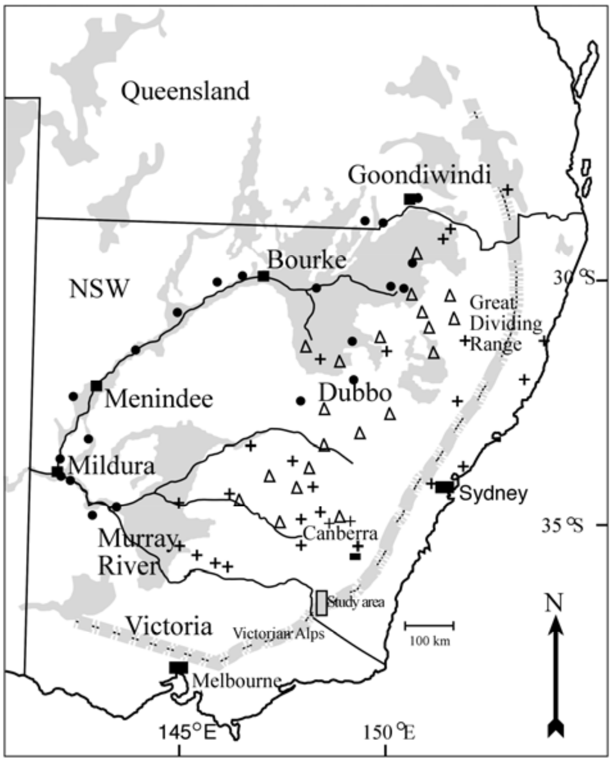

Figure 1 Map of south-eastern Australia showing the regional location of the study site. The shaded areas are the self mulching soils which are thought to be the important breeding areas for bogong moths (*Agrotis infusa*). Locations where larvae were collected by Froggatt (1900) (open triangles), Common (1954) (crosses), Green (2008) (closed circles) and the sites outside of the Snowy Mountains mentioned in the text. (After Common 1954)

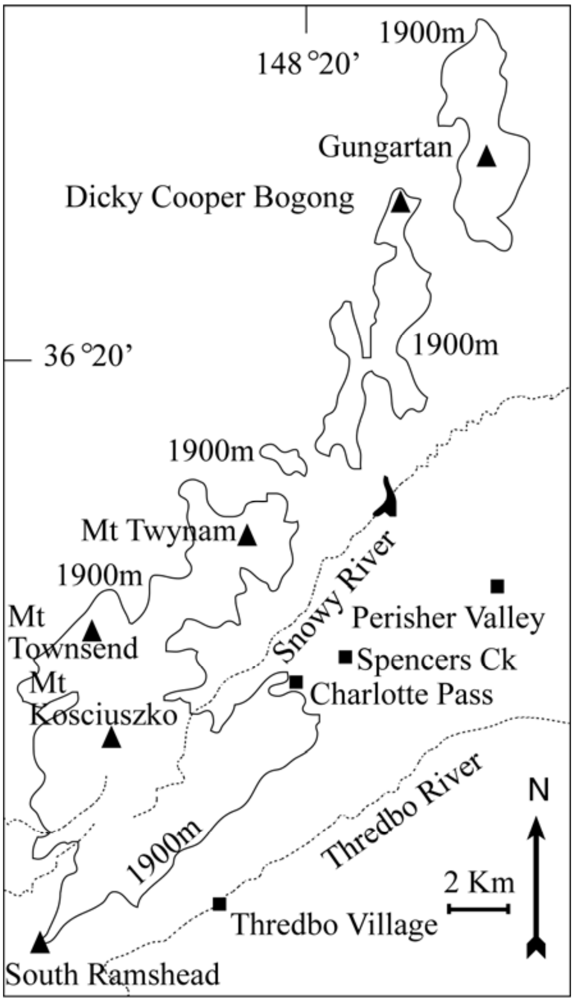

Figure 2 Map of the central alpine area of the Snowy Mountains from which all records were collected

discarded if the record was from my first day of arrival in the mountains, or if my spring visit was late and was preceded by a period of absence from the mountains that covered the expected appearance of the species.

The two selected plant species were the marsh marigold (*Caltha introloba*) and Mueller's snow-gentian (*Chionogentias muelleriana*). These were chosen because of their prominence and time of flowering; the marsh marigold flowers first and Mueller's snow-gentian is traditionally thought of as a harbinger of autumn (Costin et al. 2000, A. Costin personal communication 2009). Data from my own field notebooks were supplemented by records from the Kosciuszko National Park herbarium and for the marsh marigold by I. Wardlaw (personal communication 2009).

Five easily observed and identifiable animal species were chosen: three insect species and two birds. Insects comprised two resident forms: Macleays swallowtail (*Graphium macleayanum*) and March flies (*Scaptia* spp.) and one long-distance migrant, the noctuid bogong moth (*Agrotis infusa*). Macleays Swallowtail is the most common of the Papilionidae in the Snowy Mountains. They have a single generation in the high country and it is not known what breaks the pupal diapause (T. Edwards personal communication 2009). Data from two dates in 1922 and 1970 were obtained from the Australian National Insect Collection (Canberra) and probably reflect date of emergence, because dates on specimens tend to emphasize the beginning of the flight period when specimens are in good condition

(T. Edwards personal communication 2009). The predacious larvae of March flies (Tabanidae) live in moist soil and owing to the adult's bite make their presence felt early in the summer. The bogong moth is a multivoltine species with the cutworm larvae feeding on annual plants in the western plains of eastern Australia from the Darling Downs in Queensland, south to the north-western plains of Victoria (Figure 1). In the absence of their food plants over summer, the adults of the spring generation migrate to the Australian Alps where they fast whilst aestivating gregariously in rock crevices and caves (Common 1954). Records from other sources (Blakers 1980, L. Broome personal communication 2009) for years that coincided with my own records were also examined and all such records of first occurrence were later than my own. The two bird species were both altitudinal migrants that winter in the tablelands and agricultural areas as far away as the lower Murray River valley and move up in spring to breed at alpine and subalpine altitudes: Richard's pipit and flame robin (*Petroica phoenicea*) (Green and Osborne 1994).

2.3 Species-climate interactions

Marsh marigold has fully developed flowers beneath the snow that open in full sunlight within 1.5 h of snow removal (Wardlaw et al. 1989). Hence, simple linear regression was used to detect trends in Julian date of first flowering against date of snow melt. First flowering date for Mueller's snow-gentian and first sighting of all fauna species were regressed against date of snow melt and year. Because of the absence of quality mountain data for temperature, year was used as a proxy for general global warming as alpine regions of south-eastern Australia have warmed over the past 35 years at a rate of about 0.2°C per decade (Whetton 1998, Hennessy et al. 2003).

The Thredbo Valley (Figure 2) is a major migratory route for birds and insects (Gall and Longmore 1978, Green 1982), hence data for the migratory species, bogong moth, flame robin and Richard's pipit were also regressed against the average minimum temperature for September at Thredbo Village (1380 m asl Figure 2). To determine whether there was a proximate cause in the date of commencement of migration of bogong moths to the mountains, such as the end of the main growing seasons for plants, rainfall and evaporation data were used to calculate effective rainfall for four locations in the larval range (Figure 1). As a rule of thumb, the evaporation from an exposed soil surface is about one-third that from an evaporimeter, and effective rainfall is that which is greater than 2/3 the evaporation (NSW Department of Primary Industry). Time of arrival of bogong moths in the mountains was regressed against effective rainfall in July and August for each year available for Goondiwindi (217 m asl), Bourke (107 m asl), Menindee (64 m asl), and Mildura (50 m asl) (Figure 1).

3 Results

Although there has been much variation in the annual snow amount (metre-days), the general trend in the 55-year data set is an overall decline (Figure 3). There is a significant annual downward trend in the raw snow data (Figure 3; $F_{1\text{-}53} = 4.810$, $r^2 = 0.083$, $P = 0.033$) that is more evident in the five-year running mean ($F_{1,50} = 26.467$, $r^2 = 0.346$, $p < 0.0001$). The date of snow melt is correlated with snow amount ($r^2 = 0.6387$, $P < 0.0001$). There is a significant trend for earlier snow melt with year

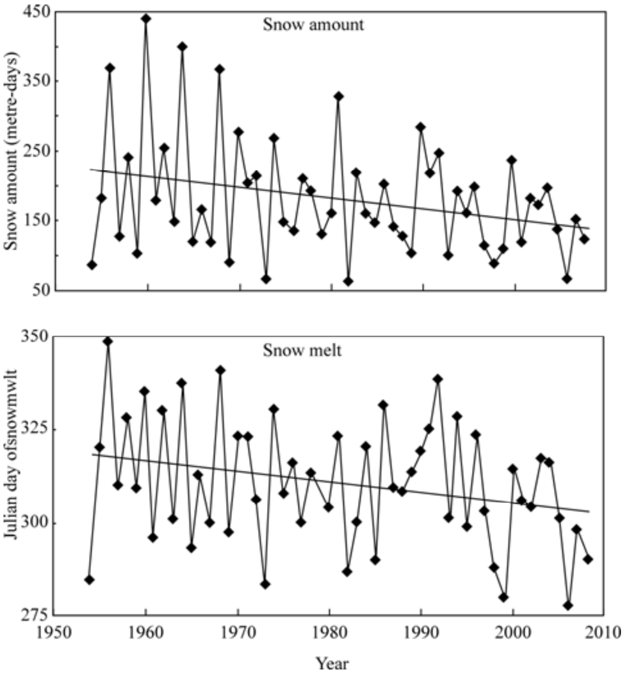

Figure 3 Trends in snow amount and date of snow melt at Spencers Creek from 1954 to 2008

based on raw data (F_{1-53} =4.810, r^2=0.075, P<0.05). Based on the five-year mean trendline (F_{1-49} =62.495, r^2=0. 310, P <0.0001), the snow melt has advanced by 2.75 days per decade.

The first flowering of marsh marigold was significantly correlated with date of snow melt (Figure 4; F_{1-6} =9.092, r^2=0.602, P< 0.05). Earliest flowering for Mueller's snow-gentian was also correlated with snow melt date (Figure 4; F_{1-13} =10.333, r^2=0.840, P< 0.01).

Among the five selected faunal species, there was high variation between the predictors of time of arrival or emergence, with no two species responding in the same way. Snow melt date was a significant predictor of first sighting of only one species, Richard's pipit (Figure 4; F_{1-15}=4.725, r^2=0.240, P=0.046). Although year was a significant predictor of first sighting of both bogong moth (F_{1-15}=5.293, r^2=0.261, P=0.036) and flame robin (F_{1-14}=6.790, r^2=0.327, P=0.021), bogong moth showed a positive relationship while flame robins showed a negative response (Figure 5). None of the climatic parameters was a significant predictor of first sighting of Macleays swallowtail nor March flies.

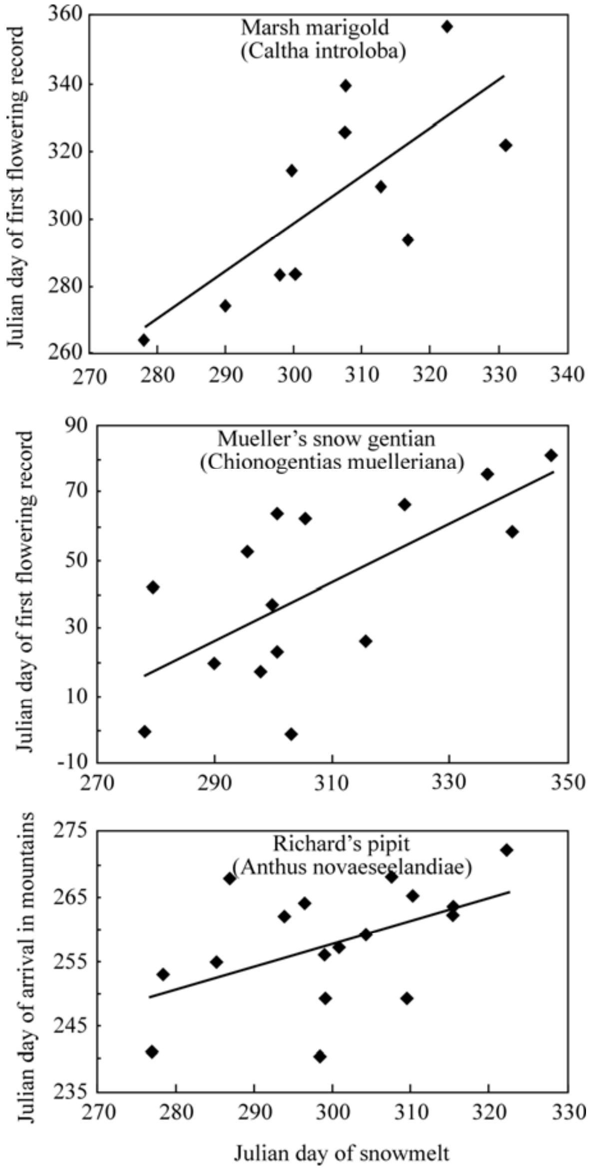

Figure 4 Relationship between day of snow melt at Spencers Creek and day of flowering for *Caltha introloba* and *Chionogentias muelleriana*, and arrival in the mountains of Richard's pipit (*Anthus novaeseelandiae*)

The two species whose time of arrival was correlated with year (bogong moth and flame robin) were both long-distance migrants and therefore may have been responding to climate in localities away from the mountains. Flame robin arrival was correlated negatively with year and also negatively (F_{1-13} =4.810, r^2=0.269, P= 0.047) with minimum temperature for September at Thredbo Valley (there was no significant correlation with maximum temperature). Time of first arrival of bogong moths had a significant positive correlation with year, but there was no significant correlation between time of first arrival and temperature at Thredbo (P=0.150), nor with effective rainfall in July and August combined, for Goondiwindi, Bourke, Menindee and Mildura individually or

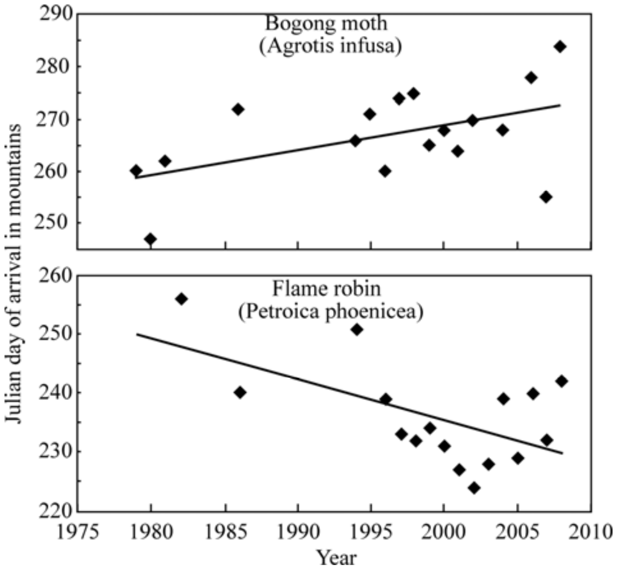

Figure 5 Relationship between day of arrival in the mountains and year for bogong moths (*Agrotis infusa*) and flame robins (*Petroica phoenicea*)

combined (*P*=0.718).

4 Discussion

In the Snowy Mountains, snow melt date at Spencers Creek is a good surrogate for date of snow melt throughout the mountains, being highly correlated with the thaw of snowpatches (Green and Pickering 2009) and with the date of ice breakup on the glacial lakes (Green unpublished data). Although there has been much variation, there is a significant downward trend in peak depth of snow at Spencers Creek that is associated with increasing temperature rather than reduced precipitation (Nicholls 2005). Reduced snow has led to an advance of the date of snow melt by 2.75 days per decade. As snow melt is a major cue for flowering in alpine areas (Inouye et al. 2002; Dunne et al. 2003), the response of the two plant species in the present study was an advance in the phenology of flowering. However, Hülber et al. (2006, 2010) found an overriding importance of temperature sum and not snow melt date for flowering in high alpine plant species in the European Central Alps. Floral initiation in marsh marigold occurs in mid summer, with flowers fully developed before late autumn and remaining closed under the snow until after the snow melt, although if the snow melt is very late it will flower beneath the snow (Wardlaw et al. 1989). Flowering was therefore expected to reflect the snow melt date, and as local snow melt initiates flowering, it frequently preceded the snow melt at Spencers Creek.

Flowering in Mueller's snow-gentian also advanced with the date of snow melt. Correlation of date of late flowering species with the date of snow melt was also found for sagebrush (*Artemesia tridentate*), one of the last species to flower in the Colorado Rocky Mountains (Inouye et al. 2000). Flowering in Mueller's snow-gentian also occurred earlier with year, probably as a result of higher spring/summer temperatures. In areas with warm summers and a steep gradient in temperature at the commencement of the growing season, the effects of date of snow melt and higher temperatures are difficult to separate (Thórhallsdóttir 1998). Similarly, early snow melt, lower snowfall and depth of snowpack are highly correlated and their effects are difficult to separate (Dunne et al. 2003). Regardless of which factor is the most important, the flowering of Mueller's snow-gentian, and hence the end of the flowering season, has advanced over the years, with flowering of this species now commencing in December or January, whereas Costin et al. (1979) recorded it as flowering ‘rather later in the season (February-March) than most other species’.

It is likely that the succession of alpine species coming into flower is generally the same among years (Molau et al. 2005). This was not necessarily the case in subalpine studies in the Snowy Mountains, nor the Victorian Alps (Pickering 1995, Jarrad et al. 2008), and flowering times may change with increasing temperature at different rates even for closely related species in the same area (Miller-Rushing and Primack 2008). However, in her alpine sites, Pickering (1995) found that flowering of five species of *Ranunculus* occurred in the same sequence between years. Preliminary evidence from a study over 2006-2009 has shown that, of 66 species monitored in each year, marsh marigold flowered first in all years and Mueller's snow-gentian near last (Green unpublished data). Between these, there was a similar sequence of plant species flowering. Hence the two species chosen as representing early and late flowering species were good indicators of the length and timing of the flowering season and therefore delineated the period of importance to pollinating insects.

The five animal species studied here, chosen primarily for their visibility and hence availability of records rather than any *a priori* assumption that they would vary in their responses, showed an array of different responses to the impacts of regional warming.

Only one species, Richard’s pipit, arrived earlier with an early snow melt. It differs from flame robin in that it is a ground nester as well as being a ground feeder (on insects), and therefore it is probably more responsive to the reduction in snow cover, as is the American pipit (*Anthus rubescens*) in alpine Wyoming (Hendricks 2003). Flame robin appeared to be the only species responding to increased warming *per se*. Its arrival in the snow country was independent of date of snow melt or year but appeared to be related to higher temperatures in the lower valleys. This is a similar response to the earlier arrival of American robins (*Turdus migratorius*) in the west Elk Mountains (Colorado), owing to advancing phenology at lower altitudes in overwintering sites (Inouye et al. 2000). Low-elevation migrants are adversely affected by earlier arrival on the breeding grounds before conditions become suitable (Hendricks 2003), and Inouye et al. (2000) predicted that if the disjunction between climate change at low and high altitude widens, then long-distance altitudinal migrants will encounter problems. It appears that there is an occasional mismatch in migration timing with flame robin appearing earlier and out of phase with weather conditions in the Snowy Mountains (Green 2006), whereas for Richard's pipit, which is waiting until the snow disappears this is not the case.

Among the insects examined here, none showed a significant response to climatic factors in the mountains. Although diptera are the most important pollinators of alpine plants in the Snowy Mountains (Inouye and Pyke 1988), March flies did not respond to earlier snow melt, with an almost unvarying emergence in mid December. This differs from emergence of bumblebees and tephritid flies in the Colorado Rocky Mountains, both of which respond to date of snow melt (Inouye 2008). If Australian alpine plants flower earlier, without the concomitant response by their pollinating flies, then this might decrease their chances of reproductive success as suggested by Kudo et al. (2008). Bogong moths, showed a contrary response, appearing significantly later as the snow melt occurred earlier. Animals migrating over long distances are likely dependent upon the environment in a number of different areas (Stenseth and Mysterud 2002). Bogong moths migrate because of lack of food over summer, however, the trigger for migration could not be found in the best indicator of plant growth (effective rainfall) in their dry western natal sites.

In the Colorado Rocky Mountains, where the phenology of insects and birds has been studied in addition to flowers, there is no evidence for a change in the timing of the disappearance of the winter snowpack and hence the commencement of the growing season (Inouye et al. 2000). This has led to the mismatch in timing with the snow melt for altitudinally migrating American robins and hibernating yellow-bellied marmots (*Marmota flaviventris*) (Inouye et al. 2000). Because the growing season in the Snowy Mountains occurs earlier as a result of earlier snow melt (Green and Pickering 2009) it might be expected that the chances of mismatch in timing are reduced. This, however, is not the case. Among the breeding birds, flame robin, Richard's pipit and ravens (*Corvus* spp.) have all been recorded feeding on bogong moths on spring snowbanks (Green personal observation). All are dependent on ready access to insect food that is otherwise limited in alpine areas in early spring (Green 1997). This spring food may, for example, be an important resource for egg production (Visser et al. 2004). This is an interesting contrast to the situation in Europe where moth caterpillar phenology is accelerating but arrival of their migratory avian predators is not, resulting in a mismatch (Both et al. 2006, Cresswell and McCleery 2003). In the Snowy Mountains, resident mammalian predators are also dependent upon a ready source of food in spring at a time of high energy demand (Green and Osborne 1994). At about the time of the bogong moth migration, mountain pygmy possums (*Burramys parvus*) are exiting hibernation. Concurrently dusky antechinus (*Antechinus swainsonii*) have their single chance at breeding (the males die off soon after) and females are raising newly born young. Bogong moths are therefore an important food at this time of the year for a number of vertebrate species. A key concern, therefore, with climate change and predicted earlier snow melt is the timing of the immigration of bogong moths, which is not correlated with the snow melt. This may lead to impacts on nesting success in birds and greater predation pressure, particularly on small mammals that themselves are stressed by lack of food.

5 Conclusions

Modelling of impacts of climate change frequently takes into account the response of individual or related taxa to changes in temperature. However, the responses of unrelated but frequently interacting species and the drivers of those responses may be uncertain. This means that greater attention will need to be focused in the future on interactions between species responding differently to climate change such that their interactions may outweigh the direct impacts of a changed climate. Gallagher et al. (2009) suggested that earlier flowering plants could be used as indicator species to show the effect of climate change in the alpine area of Australia. However, the results presented here suggest that, like in the Arctic (Danks 2004), alpine systems are more complex than we frequently appreciate. There may be no single indicator species or taxonomic group that is predictive of ecosystem response to climate change and we may have no alternative but to try and understand whole ecosystem processes.

Acknowledgements

I thank Snowy Hydro, previously the Snowy Mountains Hydro-electric Authority for access to snow course records. David Inouye, Catherine Pickering and Susanna Venn commented on the manuscript.

References

Blakers, R. 1980. Insects in the Alpine Zone. Honours Thesis, Australian National University, Canberra.

Both, C., Bouwhuis, S., Lessells ,C.M. and Visser, M.E. 2006. Climate Change and Population Declines in a Long-distance Migratory Bird. Nature **441**: 81-83.

Common, I.F.B. 1954. A Study of the Ecology of the Adult Bogong Moth *Agrotis infusa* (Boisd.) (Lepidoptera: Noctuidae), with Special Reference to its Behaviour During Migration and Aestivation. Australian Journal of Zoology **2**: 223-263.

Costin, A.B., Gray, M., Totterdell, C.J. and Wimbush, D.J. 1979. Kosciusko Alpine Flora. CSIRO Collins, Pp. 408.

Costin, A.B., Gray, M., Totterdell, C.J. and Wimbush, D.J. 2000. Kosciuszko Alpine Flora (2nd Edition*)* CSIRO Publishing, Pp. 398.

Cresswell, W. andMcCleery, R. 2003. How Great tits Maintain Synchronization of their Hatch Date with Food Supply in Response to Long-term Variability in Temperature. Journal of Animal Ecology **72**: 356-366.

Danks, H.V. 2004. Seasonal Adaptations in Arctic Insects. Integrative and Comparative Biology **44**: 85-94.

Dunne, J.A., Harte, J. and Taylor, K.J. 2003. Subalpine Meadow Flowering Phenology Responses to Climate Change: Integrating Experimental and Gradient Methods. Ecological Monographs **73**: 69-86.

Duus, A.l. 1992. Estimation and Analysis of Snow Cover in the Snowy Mountains between 1910 and 1991. Australian Meteorological Magazine **40**: 195-204.

Froggatt, W.W. 1900. Caterpillars: The Bugong Moth (*Agrotis infusa* Boisd.). Agricultural Gazette of NSW **10**: 1252-1256.

Gall, B.C. and Longmore, N.W. 1978. Avifauna of the Thredbo Valley, Kosciusko National Park. Emu **78**: 189-196.

Gallagher, R.V., Hughes, L. and Leishman, M.R. 2009. Phenological Trends among Australian Alpine Species; using Herbarium Records to Identify Climate-change Indicators. Australian Journal of Botany **57**: 1-9.

Green, K. 1982. Migration of an Ichneumonid Wasp over a Subalpine Pass. Victorian Naturalist **99**: 260.

Green, K. 1997. Inter-annual, Seasonal and Altitudinal Differences in Invertebrate Activity in the Snowy Mountains. Victorian Naturalist **114**: 222-229.

Green, K. 2006. The Effect of Variation in Snowpack on Timing of Bird Migration in the Snowy Mountains. Emu **106**: 187-192.

Green, K. 2008. Migratory Bogong Moths (*Agrotis infusa*) Transport Arsenic and Concentrate it to Lethal Effect by Gregariously Aestivating in Alpine Regions of the Snowy Mountains of Australia. Arctic Antarctic and Alpine Research **40**: 74-80.

Green, K. and Osborne, W.S. 1994. Wildlife of the Australian Snow-Country. Reed, Pp.200.

Green, K. and Pickering, C.M. 2002. A Scenario for Mammal and Bird Diversity in the Australian Snowy Mountains in Relation to Climate Change. In: Körner C. and Spehn E.M. (eds.), Mountain Biodiversity: a Global Assessment. Parthenon Publishing. Pp. 241-249.

Green, K. and Pickering, C.M. 2009. The Decline of Snowpatches in the Snowy Mountains of Australia: Importance of Climate Warming, Variable Snow and Wind. Arctic Antarctic and Alpine Research **41**: 212-218.

Hendricks, P. 2003. Spring Snow Conditions, Laying Date, and Clutch Size in an Alpine Population of American Pipits. Journal of Field Ornithology **74**: 423-429.

Hennessy, K., Whetton, P., Smith, I., Bathols, J., Hutchinson, M. and Sharples, J. 2003. The Impact of Climate Change on Snow Conditions in Mainland Australia. CSIRO Atmospheric Research, Pp.47.

Hülber, K., Gottfried, M., Pauli, H., Winkler, M. and Grabherr, G. 2006. Phenological Responses of Snowbed Species to Snow Removal Dates in the Central Alps: Implications for Climate Warming. Arctic Antarctic and Alpine Research **38**: 99-103.

Hülber, K., Winkler, M. and Grabherr, G. 2010. Intraseasonal Climate and Habitat-specific Variability Controls the Flowering Phenology of High Alpine Plant Species. Functional Ecology **24**: 245-252.

Inouye, D.W. 2008. Effects of Climate Change on Phenology, Frost Damage, and Floral Abundance of Montane Wildflowers. Ecology **89**: 353-362.

Inouye, D.W., Barr, B., Armitage, K.B. and Inouye, B.D. 2000. Climate Change is Affecting Altitudinal Migrants and Hibernating Species. Proceedings of the National Academy of Science USA **97**: 1630-1633.

Inouye, D.W., Morales, M.A. and Dodge, G.J. 2002. Variation in Timing and Abundance of Flowering by *Delphinium barbeyi* Huth (Ranunculaceae): The Roles of Snowpack, Frost, and La Niña, in the Context of Climate Change. Oecologia **130**: 543-550.

Inouye, D.W. and Pyke, G.H. 1988. Pollination Biology of the Snowy Mountains of Australia: Comparisons with Montane Colorado, USA. Australian Journal of Ecology **13**: 191-210.

Jarrad, F.C., Wahren, C., Williams, R.J. and Burgman M.A. 2008. Impacts of Experimental Warming and Fire on Phenology of Subalpine Open-heath Species. Australian Journal of Botany **56**: 617-629.

Kudo, G., Ida, T.Y. and Tani, T. 2008. Linkages between Phenology, Pollination, Photosynthesis, and Reproduction in Deciduous Forest Understory Plants. Ecology **89**:321-331.

Lehikoinen, E., Sparks, T. and Zalakevicius, M. 2004. Arrival and Departure Dates. Advances in Ecological Research **35**: 1-

31.

Miller-Rushing, A.J. and Primack, R.B. 2008. Global Warming and Flowering Times in Thoreau's Concord: a Community Perspective. Ecology **89**: 332-341.

Molau, U., Nordenhäll, U. and Eriksen, B. 2005. Onset of Flowering and Climate Variability in an Alpine Landscape: a 10-year Study from Swedish Lapland. American Journal of Botany **92**: 422-431.

New South Wales Department of Primary Industry http://www.agric.nsw.gov.au/reader/efarm-climate/rainfall-evap.htm Viewed 7 March 08.

Nicholls, N. 2005. Climate Variability, Climate Change and the Australian Snow Season. Australian Meteorological Magazine **54**: 177-185.

Norment, C.J. and Green, K. 2004. Breeding Ecology of Richard's Pipit (*Anthus novaeseelandiae*) in the Snowy Mountains. Emu **104**: 327-336.

Parmesan, C. and Yohe, G. 2003. A Globally Coherent Fingerprint of Climate Change Impacts across Natural Systems. Nature **421**: 37-42.

Pickering, C.M. 1995. Variation in Flowering Parameters within and among Five Species of Australian Alpine *Ranunculus*. Australian Journal of Botany **43**: 103-112.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. and Pounds, J.A. 2003. Fingerprints of Global Warming on Wild Animals and Plants. Nature **421**: 57-60.

Sparks, T.H., Jeffree, E.P. and Jeffree, C.E. 2000. An Examination of the Relationship between Flowering Times and Temperature at the National Scale using Long-term Phenological Records from the UK. International Journal of Biometeorology **44**: 82-87.

Stenseth, N.C. and Mysterud, A. 2002. Climate, Changing Phenology, and other Life History Traits: Nonlinearity and Match-mismatch to the Environment. Proceedings of the National Academy of Science USA **99**:13379-13381.

Thórhallsdóttir, T.E. 1998. Flowering Phenology in the Central Highland of Iceland and Implications for Climatic Warming in the Arctic, Oecologia **114**: 43-49.

Visser, M.E., Both, C. and Lambrechts, M.M. 2004. Global Climate Change Leads to Mistimed Avian Reproduction. Advances in Ecological Research **35**: 89-110.

Wardlaw, I.F., Moncur, M.W. and Totterdell, C.J. 1989. The Growth and Development of *Caltha introloba* F. Muell. I. The Pattern and Control of Flowering. Australian Journal of Botany **37**: 275-89.

Whetton, P.H. 1998. Climate Change Impacts on the Spatial extent of Snow-cover in the Australian Alps. In: Green K. (ed.), Snow: A Natural History; an Uncertain Future. Australian Alps Liaison Committee. Pp. 195-206.