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The Australian Bogong moth *Agrotis infusa* (Lepidoptera: Noctuidae), 1951-2020: Decline and crash

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Keywords:	migration, drought, climate change, historical record, population decline, alpine ecosystem, mountains, Bogong moth, <i>Agrotis infusa</i> , pesticides
Abstract:	The Bogong moth <i>Agrotis infusa</i> is well known for its remarkable long-distance migration – a return journey from the plains of southeast Australia to the Australian Alps – as well as for its cultural significance for Indigenous Australians. Each Spring, as many as 4 billion moths are estimated to arrive in the Australian Alps to aestivate in cool mountain caves and in boulder fields, bringing with them a massive annual influx of energy and nutrients critical for the health of the alpine ecosystem. However, a massive decline in moths present at their aestivation sites has occurred over the past three years, with only a few individuals present where hundreds of thousands could earlier be found. In order to understand the possible sources of decline, we analysed historical records of Bogong moth numbers at aestivation sites in the Australian Alps, including observations on Mt. Gingera (NSW) in the early 1950s, observations from 1980 onwards in the Snowy Mountains (NSW), and an almost-unbroken series of observations each summer over the past 53 years in three caves at different elevations on Mt. Buffalo (Victoria). This analysis shows that moth numbers were probably steady from 1951 until about 1980, fluctuated and slowly fell from then until 2016 and dramatically crashed in 2017. In the Murray–Darling Basin, the main winter breeding ground of Bogong moths, changes in farming practices, such as increasing land clearing for crops (which has removed around a quarter of a billion moths annually from the mountains compared to pre-European levels) has probably driven some of the decline in Bogong

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	<p>moth numbers observed from 1980 to 2016. The impact of insecticide remains unclear and is in urgent need of further study. Even though we found little evidence that increasing global temperatures per se are responsible for the Bogong moth decline, the Australian climate has nonetheless become drier and warmer over past decades, possibly hampering the survival of immature stages in the breeding areas and confining adult aestivation to gradually higher elevations. The crash in moth numbers from 2017 is most likely due to the recent severe drought in the moth's breeding grounds.</p>

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3 **The Australian Bogong moth *Agrotis infusa* (Lepidoptera:**
4 **Noctuidae), 1951-2020: Decline and crash**
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37 **Running title:** Population decline in Bogong moths
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Abstract

The Bogong moth *Agrotis infusa* is well known for its remarkable long-distance migration – a return journey from the plains of southeast Australia to the Australian Alps – as well as for its cultural significance for Indigenous Australians. Each Spring, as many as 4 billion moths are estimated to arrive in the Australian Alps to aestivate in cool mountain caves and in boulder fields, bringing with them a massive annual influx of energy and nutrients critical for the health of the alpine ecosystem. However, a massive decline in moths present at their aestivation sites has occurred over the past three years, with only a few individuals present where hundreds of thousands could earlier be found. In order to understand the possible sources of decline, we analysed historical records of Bogong moth numbers at aestivation sites in the Australian Alps, including observations on Mt. Gingera (NSW) in the early 1950s, observations from 1980 onwards in the Snowy Mountains (NSW), and an almost-unbroken series of observations each summer over the past 53 years in three caves at different elevations on Mt. Buffalo (Victoria). This analysis shows that moth numbers were probably steady from 1951 until about 1980, fluctuated and slowly fell from then until 2016 and dramatically crashed in 2017. In the Murray–Darling Basin, the main winter breeding ground of Bogong moths, changes in farming practices, such as increasing land clearing for crops (which has removed around a quarter of a billion moths annually from the mountains compared to pre-European levels) has probably driven some of the decline in Bogong moth numbers observed from 1980 to 2016. The impact of insecticide remains unclear and is in urgent need of further study. Even though we found little evidence that increasing global temperatures *per se* are responsible for the Bogong moth decline, the Australian climate has nonetheless become drier and warmer over past decades, possibly hampering the survival of immature stages in the breeding areas and confining adult aestivation to gradually higher elevations. The crash in moth numbers from 2017 is most likely due to the recent severe drought in the moth's breeding grounds.

Key words: Bogong moth, *Agrotis infusa*, alpine ecosystem, climate change, drought, historical record, migration, pesticide, population decline.

INTRODUCTION

The Bogong moth *Agrotis infusa* is well known for its remarkable long-distance migration (Common 1952, 1954; Warrant *et al.* 2016; Dreyer *et al.* 2018) and its cultural significance for Indigenous Australians (Flood 1980, 1996). Newly emerged Bogong moths escape the increasing heat of the breeding grounds in western and north-western New South Wales (NSW), southern Queensland, western Victoria and South Australia, by migrating during spring to the mountain regions of south-eastern Australia, a journey of up to 1000 km. Once at high elevation in the mountains, moths eventually seek out the shelter of cool caves, and the deep hollows and crevices of boulder fields, where they aestivate in vast numbers until autumn (aestivation is a state of dormancy similar to hibernation but instead occurring in summer). Bogong moths – which tile the cave walls at a density of around 17,000 individuals per square metre – are capable of aestivating for up to four months (Common 1954). Following this period, the same individuals that arrived months earlier return to the breeding grounds where they mate, lay their eggs and die (Common 1952, 1954; Warrant *et al.* 2016). The larvae then develop during the coming winter, being found in soils across a variety of land types, where they feed on the stems of broad-leafed plants at ground level. Pupation occurs in late winter, about 2-3 cm underground, with eclosion occurring during the following spring (Common, 1981; Warrant *et al.* 2016).

Bogong moth aggregations in the mountains were first reported in NSW by Bennet (1834) and later by Scott *et al.* (1872) but no satisfactory explanation for the moth assemblages was offered until that by Common (1952). In this and his later paper (Common 1954), Common argues that the reason for migration, and subsequent aestivation, is the increasingly unfavourable conditions of the breeding grounds. Before Bogong moths begin to congregate at high elevations in the mountains to aestivate over the summer, a number of lower sites are usually occupied temporarily (Common 1954), most often at lower sub-alpine elevations in the mountains. However, in some years, these lower sites can also occur at a great distance from the mountain aestivation sites, for instance in houses, Parliament House in Canberra or other similar locations (such as sports grounds) where large bright lights attract them. These are ‘accidental’ sites, however, and away from lights Bogong moths may use a variety of ground-based sites such as dead trees. Moths have even been observed to congregate in small animal traps that have been used in dietary studies of mammals. The dates of the first Bogong moth arrivals at these lower sites can vary depending on the year and the location.

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3 Bogong moths eventually cease feeding and ascend to the caves to aestivate. The moth's aestivation
4 sites include a variety of granitic locations in the Brindabella Ranges of the Australian Capital
5 Territory (ACT) and NSW, and in the Bogong Peaks and Snowy Mountains of NSW, and at a
6 number of granitic sites in Victoria, including Mt. Buffalo and the Jaithmathangs. These mountains
7 are characterised by granitic outcrops and boulder fields (Common 1954), and include the highest
8 sites where Bogong moths can aestivate and be observed throughout the summer. The basalt
9 boulder fields of Victoria (e.g. on the Bogong and Hotham High Plains) also provide aestivation
10 sites (Mansergh 1988; Mansergh and Heinze 2019).
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18 The first 30 years of Bogong moth research (1950-1980) established the numbers of Bogong moths
19 at a time when climate change was becoming an issue of concern, with the global mean surface
20 temperature having now been established relative to the 1951–1980 mean (ASA Goddard Institute
21 for Space Studies). In 60 years of recorded measurements from the central Snowy Mountains, there
22 has been a steady decrease in the maximum depth of the snowpack, and a shortening of the mean
23 duration of the snowpack, by 18.5 days. These changes have resulted from a mean temperature
24 increase of 0.36°C per decade (Sánchez-Bayo and Green 2013), which may have also impacted
25 Bogong moth numbers.
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33 Although there has been some suspicion that moth numbers at aestivation sites have declined over
34 the years (Flood 1980; but see a discussion in Blakers 1980), records of Bogong moth abundance
35 collated and/or collected by the authors over nearly 70 years (detailed below) indicate that we have
36 now experienced a sudden and major decline (see also Mansergh and Heinze 2019). This occurred
37 in the summer of 2017-18, the worst summer ever recorded for Bogong moth numbers, with very
38 few moths seen in a continuously monitored cave on an unnamed peak above Dead Horse Gap
39 near Thredbo (2020 m), a boulder outcrop near South Ramshead in the Kosciuszko Main Range
40 of NSW (which we, the first author's co-authors, in recognition of his long history of visits to the
41 site, have dubbed "Ken Green Bogong"). In January 2019, no moths at all were found in this cave.
42 This situation was mirrored in caves at a number of other mountain locations that had been studied
43 over many years: Mt. Gingera (NSW/ACT), Mt. Morgan (NSW), Mt. Buffalo (Vic.) and the
44 Bogong and Hotham High Plains (Vic.) (Mansergh and Heinze 2019). Increases in moth numbers
45 were observed in the NSW and ACT caves during the summer of 2019-20, but the population was
46 still depleted. This rapid decline probably had a tremendous impact on the health of the alpine
47 ecosystem of south-eastern Australia as the massive influx of energy and nutrients that Bogong
48 moths provide via their summer migration to the mountains (Green 2011) had evaporated. The
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3 aim of this review is to examine the timing and causes of the dramatic decline in Bogong moth
4 numbers in the Australian Alps.
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8 To examine this decline, we re-examined data collected in the early 1950s by Ian Common from
9 Mt. Gingera, on the border between NSW and the ACT (Common 1952, 1954), and analysed our
10 own data collected from a number of locations over the past 53 years. These data include notes on
11 Bogong moth arrivals and moth activity over four decades in 13 regularly surveyed aestivation sites
12 across the Snowy Mountains of NSW (KG: personal field notebooks and PhD data), data from
13 over four decades of studies of the diet of foxes in the Snowy Mountains (KG: biannual 6 km
14 transects), Bogong moth activity on Mt. Gingera (PC: 37 separate aestivation sites, observed
15 approximately bi-weekly from September to May since 2014, excluding the summers of 2016-17
16 and 2017-18), records of Bogong moth numbers from aestivation sites at three elevations on Mt.
17 Buffalo in Victoria over the past 53 years (MB), and moth collections from the Snowy Mountains,
18 the Brindabella Ranges and the Mt. Kaputar National Park (northern NSW) for studies of Bogong
19 moth migration (EW, DD and JW: each year during spring and autumn since 2010).
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31 **OBSERVATIONS OF BOGONG MOTH NUMBERS IN SOUTHEAST AUSTRALIA**

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35 **Larvae in the breeding grounds**

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39 Even though Bogong moths can be recorded elsewhere, regions of inland south-eastern Australia
40 that possess grey cracking clays are the most common breeding grounds (Common 1954). We
41 measured these areas in NSW and Queensland to obtain an approximate area of 101,180 km².
42 Bogong moth larvae were surveyed from 29 sites in 2001, primarily in locations with grey cracking
43 clays (Green 2008 – see Fig. 1). This resulted in a calculated density of 0.78 Bogong moth larvae
44 per 10 m², (or 78,000 larvae km⁻²) giving a total of around 7.9 billion larvae within the region of
45 grey cracking clays of NSW and Queensland. Adult Bogong moth numbers were also calculated
46 for the Snowy Mountains, based on calculations of predation and other sources of mortality (Green
47 2010b) together with a percentage survival from Blakers (1980), to give a total number of 2.2 billion
48 adult Bogong moths. According to the Interim Biogeographic Regionalisation for
49 Australia (IBRA), developed by the Australian Government, the Australian Alps consists of two
50 subregions: the Snowy Mountains (IBRA code AUA01: area 713,114 Ha) and the Victorian Alps
51 (IBRA code AUA02: area 519,866 Ha). The areas of these two subregions indicate that the
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3 Victorian Alps cover around 73% of the area of the Snowy Mountains (see the white alpine regions
4 shown in Fig. 1). If we assume that moths are evenly spread over both alpine regions, this would
5 imply that around 1.6 billion adults moths are present in Victoria, giving a total of 3.8 billion
6 Bogong moths overall in the Australian Alps. If the figures above (7.9 and 3.8 billion) are reliable,
7 this would suggest an attrition of ~50% from Bogong moth larvae to post-migration adults. There
8 are occasional records of Bogong moth adults occurring far from the Australian Alps during the
9 summer (and at other times of the year), but these moths are in low numbers and none of them
10 have been recorded aestivating in any other cave system outside the Australian Alps, either in NSW
11 or Victoria. These moths may represent individuals from small non-migratory populations
12 (Common 1954; Warrant *et al.* 2016).
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22 **Adults during migration**

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25 During migration, Bogong moths are apparently not attracted to caves along the route, and in areas
26 where moth migration is commonly recorded, for example on Mt. Kaputar (EW), no evidence of
27 Bogong moth aestivation was found in the bat-free caves around the summit (at 1510 m). However,
28 some of these caves housed other species of moths, such as the Granny's Cloak moth *Speiredonia*
29 *spectans* (investigations in caves near the summit by KG in October 2015: Warrant *et al.* 2016).
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35 As part of studies of the Bogong moth migration, adult moths were collected at light traps during
36 spring on Mt. Kaputar in northern NSW. These moths were flying south-southwest (Dreyer *et al.*
37 2018) so had most likely originated in south-eastern Queensland (see Fig. 1). Moths were captured
38 every third night with hundreds being caught during most trapping sessions from 2011 to 2015. In
39 2017, trapping re-commenced at Mt. Kaputar and in the first 10 days of November only 70 moths
40 were caught. In 2018 around 100 moths were caught over a two-week period in October. Trapping
41 of adult moths – when moths were presumably at the beginning of their migration – was also
42 undertaken at various locations along the Darling River in western NSW in mid-October 2016,
43 with 41 moths taken over 2 nights with a light trap near Wentworth and 42 moths on a single night
44 at Wilcannia. Some nights had adverse weather conditions (very low temperatures and/or rain) and
45 on these nights no moths were trapped. The winter and spring of 2016 were very wet across NSW
46 with major flooding occurring in several regions of the central west – the grasslands of western
47 NSW were dense and lush during that particular spring.
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3 In the following year – 2017, the first year of the recent current extreme drought – light trapping
4 of adults was again undertaken on the Western Plains during the last two weeks of October – at
5 Hay, Wentworth, Wilcannia and Bourke. Of the 44 Bogong moths caught over that two-week
6 period, 42 of them were caught over several nights at Hay. Trapping was again undertaken for the
7 entire month of October in 2018 near Hay, Wentworth, and west of the Grampians in Victoria,
8 with even lower numbers than the previous year – around 30 moths in almost as many nights.
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15 Thus, although light-trapping observations of adult migrants, many hundreds of kilometres from
16 the Australian Alps, have only been made since 2010, Bogong moths were highly abundant from
17 2010 until 2016 but suffered a dramatic drop in their numbers from 2017 to 2020. This implies
18 that the crash in Bogong moth numbers observed in the Australian Alps over the same period was
19 primarily due to losses in their breeding grounds, and not to conditions prevailing at their high
20 elevation aestivation sites (albeit some further losses may also have occurred in the mountains).
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27 **Arrival in the mountains**

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30 As Bogong moths arrive in the vicinity of the caves in the Australian Alps, they first arrive at lower
31 elevations where they shelter and feed until conditions improve sufficiently at higher elevations to
32 ascend to their aestivation caves (Common 1954; Warrant *et al.* 2016). In the Brindabella Ranges,
33 ‘temporary camps’ are occupied at lower elevations between 1220 and 1580 m (Common 1954).
34 They have also been observed in spring at lower elevations in northern parts of the Snowy
35 Mountains, notably at Happy Jacks (1240 m) and Snow Ridge (1495 m) (Gibson *et al.* 2018).
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42 During weekly surveys of several aestivation sites on Mt. Gingera, during two summers (2014-2015
43 and 2015-2016), Caley and Welvaert (2018) found that moths arrived approximately one month
44 earlier (in the first week of October) and left one month earlier (during early March) than they did
45 during the surveys conducted by Ian Common during the early 1950s (arrival in mid-November,
46 and departure during early April: Common 1954). This is consistent with the recent decades of
47 warmer climate, but further surveys are needed to confirm this trend.
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54 When the Bogong moths arrive at these lower elevations, it is likely that snow still blocks the
55 entrances to their aestivation caves at higher elevations. However, Bogong moths can shelter at
56 higher sites without snow blockage, even where sub-zero temperatures have been recorded using
57 temperature loggers (e.g. in a subalpine tree stump at 1860 m on 14 October 2001 and in an alpine
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3 cave at 1940 m on 10 November 2001). Most moths, however, are likely to be elsewhere, feeding
4 or waiting at lower elevations to move up hill to the aestivation sites. The lack of suitable sites at
5 these elevations makes it difficult to obtain data on these locations. However, predators such as
6 mountain pygmy possums and foxes provide a suitable source of data. The diet of foxes was studied
7 along a transect from 1500-1800 m elevation at Schlink Pass in the Kosciuszko National Park
8 (Green and Osborne 1981), with fox scats collected monthly from December 1978 to February
9 1980 (although these were not studied according to elevation). Of the 1159 scats collected and
10 analysed, 151 contained only Bogong moth remains (Green and Osborne 1981). The number of
11 Bogong moths present in scats increased from October to peak in December-January, both in 1978
12 and 1979, and declined to zero in May 1979 (Green and Osborne 1981). This indicates that moth
13 numbers rose early post snow-thaw below the elevation of Schlink Pass (1800 m). As moth
14 numbers fell in scats from the 1500-1800 m elevation band after their December peak, foxes were
15 probably still feeding on moths at elevations above 1800 m – at aestivating sites such as that at
16 Dicky Cooper Bogong (1985 m, above Schlink Pass) – possibly defecating up there rather than at
17 lower elevations where scats were being studied.
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29 Fox diet was also studied at well separated alpine and subalpine study sites (Green 2010b). This
30 showed that Bogong moth numbers in scats at subalpine sites again peaked in December-January,
31 declining rapidly from January with low numbers thereafter (Green 2010b). By contrast, at alpine
32 sites, numbers remained high and in fact increased (Green 2010b) (Fig. 2). The year 1996-97
33 showed a later arrival than in 1997-1998 but received more Bogong moth arrivals later in the season
34 (Fig. 2). This indicates that Bogong moths were moving to higher elevations as summer progressed,
35 and the same pattern can be observed from studies of the scats of the Mountain pygmy-possum *B.*
36 *parvus* (Gibson *et al.* 2018, Table 1).
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45 The first arrivals of Bogong moths above the snowline have been recorded by one of us (KG) by
46 ski surveys occurring on an almost daily basis from August until October since 1979 (Fig. 3). The
47 earliest arrival ever recorded was in 1980 on 3 September. There is a considerable spread in arrival
48 days across years, certainly due to yearly differences in weather conditions (e.g. harshness of
49 winter). The latest arrival was recorded in 2008 – on 10 October – although for the years before
50 and after, Bogong moths arrived almost a month earlier.
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Ascent and occupation of aestivation caves

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5 When conditions become less favourable at lower elevations, for instance due to rising
6 temperatures, Bogong moths ascend to their aestivation caves in the alpine zone above the tree-
7 line. Temperature is probably a major factor setting the lowest elevation where aestivation is
8 possible, and this is likely to be related to summer temperatures within the caves, although
9 significant variation in this temperature occurs depending on the location (Table 2).
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15 ***Numbers of aestivating moths 1951-2017: the decline***

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18 Qualitative observations of Bogong moth numbers at four main locations in the Australian Alps
19 have been made continuously or sporadically by a number of individuals (including the authors)
20 over the past 70 years (Table 4). A number of aestivation sites at each location were typically
21 sampled. The locations were Mt. Gingera in the Brindabella Ranges, on the border of the ACT and
22 NSW, Ken Green Bogong on the Main Range in the Snowy Mountains in NSW and Mt. Buffalo
23 and Mt. Higginbotham in the Victorian alps.
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30 Mt. Gingera is the site where Ian Common first described the aestivation and natural history of
31 Bogong moths in the early 1950s (Common 1954). Common's counts revealed as many as 17,000
32 aestivating moths tiled onto every square metre of cave wall (subsequent estimates from the three-
33 dimensional spaces provided by a boulder field suggest $>50,000$ moths/m³: Mansergh and Heinze
34 2019). Common made at least one visit to Mt. Gingera every summer at the peak of the aestivation
35 from 1951 until 1980, but made no mention of declining numbers over this period in his final paper
36 on Bogong moths in the early 1980s (Common 1981), suggesting that moth numbers probably
37 changed little. Records were not kept or available from Mt. Gingera from about 1980 until 2014.
38 However, since 2014, one of us (PC) has made weekly or fortnightly surveys of 37 aestivation sites
39 around the summit of Mt. Gingera. As mentioned above, during the summers of 2014-2015 and
40 2015-2016, Caley and Welvaert (2018) found that although Bogong moth numbers were high (Fig.
41 4), most had arrived, and also departed, one month earlier than observed by Common in the early
42 1950s (Common 1954). Their early arrival, as well as their early departure, long before the expected
43 end of the complete aestivation period, suggests that moths were departing because conditions
44 (possibly temperature and humidity) were no longer suitable for aestivation, a shift consistent with
45 recent decades of climate warming.
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3 Long-term records of Bogong moth numbers from caves on Mt. Buffalo (1600-1723 m) in Victoria
4 (started in the mid-1960s) and caves at different elevations at Ken Green Bogong (1860-2020 m)
5 in the Kosciuszko Main Range of NSW (started in the mid-1970s), also reveal interesting trends
6 (Table 4). At both locations, moth numbers were high and stable until the early 1980s. For all
7 summers between 1966-1967 and 1981-1982 (with the exception of 1968-1969), Bogong moths
8 were found regularly at the lowest site on 'The Horn' on Mt. Buffalo, at an elevation of around
9 1600 m, even during the drought period of 1979 to 1983 which revealed little impact on Bogong
10 moth numbers either here or at Ken Green Bogong (Table 4). During the final summer of this
11 drought (1982-1983), moths declined at Ken Green Bogong and possibly also at Mt. Buffalo (Table
12 4). This summer experienced the arrival of heavy deposits of red soil from drought-impacted lands
13 in the west of NSW (KG pers. obs., 20 November 1982).
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23 From the early 1980s, moth numbers at Ken Green Bogong began to fluctuate significantly from
24 year to year, and on average began to decline (Table 4). Similar fluctuations were also noted within
25 the basalt boulder fields of the Bogong and Hotham High Plains in Victoria's alpine region
26 (Mansergh and Heinze 2019). At Mt. Buffalo, moths continued to occupy one or both of the two
27 lower sites (at similar elevations) until at least the summer of 1992-1993; however, observations
28 over the following 20 years do not reveal whether moths continued this trend or whether during
29 some years they could only occupy the highest (coolest) caves.
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37 ***Numbers of aestivating moths 2017–2020: the crash***

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40 From the summer of 2017-2018, the numbers of aestivating Bogong moths we encountered in the
41 Australian Alps fell dramatically (Table 4). In addition to the aestivation sites listed in Table 4, two
42 others have also been regularly visited since 2013 (in conjunction with studies of the sensory basis
43 of the Bogong moth migration, based at Lund University: Warrant *et al.* 2016; Dreyer *et al.* 2018):
44 Mt. Morgan (1852 m) and Mt. Tingaringy (1434 m) in the northern and eastern Snowy Mountains
45 respectively.
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52 In the summer of 2017-2018 moths were absent from Mt. Morgan and Mt. Gingera (observations
53 were made on 7 and 8 January, respectively, and again on 4 and 2 February, respectively). At the
54 summit of Ken Green Bogong, which was visited on 10 January and 5 February 2018, the walls of
55 the main cave were empty, with moths only found in deep crevices. This was the lowest number
56 of Bogong moths ever recorded for this location (KG), with a similar report from Mount Buffalo
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3 for 18 and 19 January 2018 (MB).
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6 During the following summer season of 2018-2019, Mt. Buffalo was investigated on 16 December
7 2018 and no moths were found (KG). The following day, moths were observed in three deep
8 locations of the major upper cave on Ken Green Bogong (2020 m). Three other caves at lower
9 elevations near Ken Green Bogong were empty, apart from three moths inside one cave (KG). At
10 the same time on Mt. Gingera very few moths were observed (Fig. 4). On 7 January 2019 only one
11 live Bogong moth was found on Mt. Morgan and three were found on Mt. Gingera. On 9 January,
12 seven moths were observed at Ken Green Bogong. At higher elevations on the Kosciuszko Main
13 Range, larger numbers of moths were however found at two locations (KG): Club Lake (1950 m)
14 on 10 February and Mt. Kosciuszko (2100 m) on 21 February 2019. Further south in Victoria, in
15 early January 2018, the only Bogong moths observed on Mt. Buffalo were a handful of moths in
16 the upper cave under 'The Horn' (1723 m), while in January the following year (2019) moths were
17 entirely absent (MB). This almost complete absence of Bogong moths in previously richly
18 populated caves, both in NSW and Victoria, had never previously been observed in over half a
19 century of observations.
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31 During the spring of 2019, unexpectedly high numbers of Bogong moths flew into the Snowy
32 Mountains and the Victorian Alps, despite little relief in the drought. Why or how this was possible
33 is not clear. There were localised heavy falls of rainfall in areas of southwest Queensland from
34 February to April 2019, leading to flooding in some areas of southern Queensland that extended
35 into northern NSW. These weather patterns also led to reasonable falls in localised areas of western
36 NSW that may have promoted Bogong moth reproduction and survival. However, no matter what
37 the cause, the increased numbers of moths entering the mountains during the spring of 2019
38 translated into considerably larger aestivating cave populations than seen in the previous two
39 summers (but nowhere near as high as before the drought), although apparently only at higher
40 elevations. On Mt. Gingera (Fig. 4), a lower elevation site, the number of aestivation sites occupied
41 were many fewer than during previous recent summers (with the exception of the 2018-2019
42 summer when the numbers of occupied sites were even fewer). Following the devastating sub-
43 alpine fires of early January 2020, few Bogong moths remained at these high elevation aestivation
44 sites after mid-February, either having succumbed to smoke, or having been washed out of the
45 caves by heavy rains in the first half of February or having departed for the breeding grounds earlier
46 than normal.
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DISCUSSION

Our results, taken together with observations by Ian Common in the early 1950s, suggest that the Bogong moth population was stable until the early 1980s but since then has fluctuated, and on average slowly declined, until crashing over the last 2-3 years. This rapid decline has probably had a deleterious impact on the health of the alpine ecosystems of south-eastern Australia which depend on the massive influx of energy and nutrients that Bogong moths provide via their summer migration to the mountains (4929 GJ of energy, 7.2 tons of nitrogen and 0.97 tons of phosphorus: Green 2011).

The years 1951-1980 can probably be considered a baseline for 'normal' post-European population numbers of Bogong moths (Common 1954, 1981). In winter 1980, there was an extensive outbreak of caterpillars in south-western NSW, with Bogong moths being particularly numerous (Drake and Farrow 1985). This winter outbreak also coincided with the earliest records of Bogong moth arrivals above the snowline of the Snowy Mountains (Fig. 3), and that summer moth numbers were not only high in the Snowy Mountains but also in the Victorian Alps, at Mt. Buffalo (Mansergh pers. com. 2019). Moth numbers subsequently began to decline in Victoria (Table 4) although there is no data for Mt. Gingera (Ian Common last wrote of Bogong moths on Mt. Gingera in 1981), nor for the Snowy Mountains (between 1983-1994 only one record is available: from 1988 – KG pers. obs.). From the mid-1990s moth numbers started to fall in the Snowy Mountains and likely also on Mt. Buffalo (Table 4).

Admittedly the data we present here are necessarily sketchy. Until very recently, data on moth numbers were collected either for scientific reasons (to answer completely different questions from those presented here), or as a result of curiosity and interest (e.g., the long-term records of MB from Mt. Buffalo). In the past, few could have predicted that Bogong moths, usually common and plentiful in the Australian Alps, could now become so threatened, thus motivating the type of extensive population monitoring that would have strengthened the conclusions of this review (and which are likely warranted in the future). Thus our data only represent a handful of aestivation sites – fewer than 70 – although these are spread across their full latitudinal range and at a number of elevations. But this admittedly fragmented data – complemented by analyses of the faeces of Bogong moth predators – show that Bogong moth numbers are worryingly in decline.

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3 There are several possible causes of this decline, including agricultural practices (e.g., habitat loss
4 and insecticides), climate change (particularly drought), and other factors (e.g., foxes, pigs,
5 traditional hunting, urban light pollution). These factors have been implicated in the recent
6 dramatic declines of insects across the globe, both in terms of population loss and species
7 extinctions (with Lepidoptera prominent: Hallmann *et al.* 2017; Sánchez-Bayo and Wyckhuy 2019;
8 Goulson 2019; Wagner 2020). We discuss each of these factors in turn.
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14 15 **Agricultural practices** 16

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18 Agricultural practices in the landscape are very likely to have had an impact on Bogong moths.
19 Unfortunately, there is no consistent data on whether Bogong moth numbers have declined in the
20 breeding areas of western NSW (and hence in the mountains). If, after 1980, farming practices
21 gradually reduced the number of Bogong moths in the breeding areas over the following 35 years,
22 it is still difficult to disentangle agricultural impacts (e.g., habitat loss and pesticide use) from
23 impacts arising from the increasing temperatures that have resulted from climate change.
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30 To address the possible impacts of pesticides, Bogong moths were collected in 2001 from a cave
31 at Ken Green Bogong (1940 m) and were analysed by the New South Wales Department of
32 Agriculture for sub-lethal levels of 59 chemicals currently used in agriculture. These analyses
33 revealed no traces of these agricultural chemicals. Bogong moths killed by spraying in Parliament
34 House in Canberra were collected in spring 2003 and were analysed for 139 different chemicals by
35 the Australian Environmental Protection Authority. The pesticide used – Deltamethrin
36 (USEPA/OPP Pesticide Code: 097805) – was recorded at a rate of 0.95 mg kg⁻¹. Deltamethrin is
37 a pyrethroid ester insecticide and the main constituent of Cislin 10, one of the most popular
38 insecticides in the world. Apart from Deltamethrin, the moths collected at Parliament House
39 contained only trace concentrations of other pesticides (Hansard 2003).
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48 When deltamethrin enters the soil, it binds tightly to soil particles (National Pesticide Information
49 Centre 2010). Deltamethrin is commonly used against Lepidoptera and kills on contact, or by larval
50 consumption in the soil (EXTOXNET 1996). It does not persist in soil, with degradation occurring
51 within 1-2 weeks (EXTOXNET 1995). This suggests that Deltamethrin would generally kill
52 Bogong moths. The recent use of neonicotinoids (which has a persistence in plants of 1-2 years)
53 has also very likely impacted the survival rate of Bogong moth larvae in the breeding areas where
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3 applied. New chemical analyses of Bogong moths are urgently needed to check whether
4 neonicotinoids are present in their tissues.
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8 Chemical spraying of pesticides at Bogong moth breeding sites occurs mainly on broadacre
9 farmland in areas of grain production that lie in the central-east and southern regions of NSW and
10 extend into southern Queensland (Fig. 1). The biggest farming change in this area has been the
11 southward shift of cotton growing, taking in large areas along the Murrumbidgee River (Michael
12 Nash, pers. com.). The pesticides now used (and their quantities: Zalucki *et al.* 2009) may well have
13 changed since Bogong moths were collected and analysed in 2001 and 2003 (Green 2008). Indeed,
14 the introduction of neonicotinoids in the late 1990s to broadacre farming regions of southeast
15 Australia (Nash *et al.* 2019) may now be having an impact on Bogong moth populations. These
16 insecticides are currently under heavy scrutiny for their adverse effects on economically beneficial
17 insects such as bees and were partially banned in Europe in 2013. Even though the specific effects
18 of neonicotinoids on lepidopterans is currently unknown, various species of moths (and
19 particularly noctuids) are considered agricultural pests and are no doubt a target of these
20 insecticides.
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31 Little insecticide was used on arable dryland country in the Murray-Darling Basin (Fig. 1) over the
32 'last couple of years' due to drought conditions (Michael Nash, pers. com.). Further west, in rough
33 grazing and native vegetation country (Fig. 1), traditional pastoral lease holders would have used
34 even lower amounts of pesticides. Thus, the extent to which neonicotinoids and other types of
35 insecticides may have contributed to the Bogong moth decline is presently unknown.
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41 Two agriculture activities made possible by the availability of irrigation water – the production of
42 rice and cotton – may also adversely affect Bogong moth numbers. In Australia, rice is grown in
43 irrigated fields which exclude Bogong moths (since the larval and pupal stages are subterranean).
44 On average, the annual production area of rice is between 65,000–90,000 hectares (most of which
45 is in the Murrumbidgee and Murray valleys – Plant Health Australia 2020). Since Bogong moth
46 density in these areas is estimated at 0.78 moths per 10 m² (Green 2008, see above), the loss of
47 moths due to habitat loss would be 50.7–70.2 million moths annually, compared to pre-European
48 conditions.
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56 Cotton plantings may have also impacted Bogong moth numbers. Disregarding any impacts by
57 spraying, which has decreased since the 1996 introduction of genetically modified cotton (which
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3 expresses a *bt* toxin gene: Zalucki *et al.* 2009, Zalucki 2015), cotton fields are monocultures without
4 any grass between the cotton plants – hence resulting in no suitable food plants for Bogong moth
5 larvae. Although some cotton has been grown in Australia since the 1820s, by 1951 an established
6 cotton industry was still essentially non-existent. Using water from newly constructed dams, cotton
7 production increased to 435,000 bales per annum by 1980, and by 1985 it had more than doubled
8 to 1.1 million bales per annum. A further doubling occurred by 1992, and by 2011-2012 production
9 was 5.3 million bales per annum (de Garis 2013). Even though the combined area of cotton fields
10 that have successfully produced cotton has fluctuated significantly over the last two decades due
11 to drought (Zalucki 2015), the area of cotton fields themselves (productive or otherwise) has
12 grown. For Bogong moth areas in NSW and southern Queensland cotton fields cover an area of
13 483,890 hectares. Whether productive or not, these cotton fields remain fallow and empty over
14 winter and are thus highly unsuitable as Bogong moth breeding grounds. Again, assuming 0.78
15 Bogong moths per 10 m², and assuming cotton growing areas do not support Bogong moths, this
16 means the loss of a further 377.4 million moths annually, compared to pre-European conditions.
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28 Thus, cotton and rice cultivation in the grey cracking clays natal areas has resulted in a current-day
29 reduction of almost half a billion moths from the Bogong moth population annually. Of these,
30 around half would likely have arrived in the mountains (where close to 4 billion are thought to
31 arrive annually in regular years: Green 2010b, and see above). This loss – currently around 1/16 of
32 total moth arrivals – gradually grew from 1980.
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38 Thus, habitat loss via rice and cotton farming have almost certainly contributed to the slow long-
39 term decline of the Bogong moth. The role of synthetic pesticides is much less clear, and longer-
40 term monitoring studies, particularly to determine the impact of neonicotinoids and other
41 commonly used insecticides on Bogong moth decline, are urgently required to quantify these roles
42 more precisely.
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48 **Climate change**

49 *Effects of temperature*

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52 **Bogong moth arrivals in the mountains.** Increasing temperatures through climate change
53 appears to have had no impact on the arrival date of Bogong moths in the Snowy Mountains as
54 arrivals have been highly variable (Fig. 3). However, the arrival date of Bogong moths does have
55 an impact on alpine fauna because for many species they provide the only available food
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3 immediately after the snowmelt. Animals dependent upon winter snow cover are becoming active
4 earlier because of a decreasing snow mass and an increasingly earlier snowmelt (on average, about
5 2.75 days earlier per decade since the early 1950s: Green 2010a). With little else as a food source,
6 an earlier arrival date for Bogong moths thus becomes critical. However, there is no evidence for
7 this as arrival dates are highly variable (Fig. 3, Green 2010a). For instance in 1952, a good moth
8 year, Bogong moths were recorded arriving in the Brindabella Ranges in early September, nearly a
9 month earlier than in 1951 (Common 1954). A similar difference in first arrival dates (37 days,
10 from 4 September to 11 October) occurred in the Snowy Mountains during 40 years of
11 observations (Fig. 3). As with Common's 1952 record, the earliest arrival date recorded in these
12 later observations (Fig. 3) was in 1980, which was also a "good" moth year. However, an early
13 arrival date is not necessarily associated with a "good" moth year – the early arrival years of 2007
14 and 2009 were years with low numbers of moths, as appears to be the case for the third earliest
15 arrival in 2019, while the late arrival years of 2012 and 2016 were years with high numbers of moths.
16 These observations suggest that some other factor, rather than the snow duration in the mountains,
17 determines either the arrival date in the mountains or the date of departure from the breeding areas.
18 Indeed, factors along the migratory route – such as weather conditions or the availability of food
19 from flowering plants such as eucalypts – may affect the length and/or duration of the migratory
20 journey and thus the arrival time in the mountains.
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35 **Aestivation.** Despite differences in arrival date, the movement of Bogong moths into the
36 aestivation caves is more likely to be affected by the climate in the mountains themselves. In both
37 1951 and 1952 on Mt. Gingera, Common (1954) first recorded Bogong moths in the 'chief
38 observational cave' (an aestivation cave) on 20 November in 1951 and 26 November in 1952.
39 However, the arrival of moths in their aestivation sites in 2014 and 2015 was approximately six
40 weeks earlier (Fig. 4, Caley and Welvaert 2018). Moreover, Caley and Welvaert (2018) noted that
41 the greatest numbers of moths occurred on 1 November 2014 and 5 November 2015 and that
42 moth numbers had already declined before the date that Common recorded the maximum moth
43 number in the same cave in 1951 and 1952 (1 January). This suggests that Mt. Gingera is no longer
44 a preferred aestivation site, but rather has become a temporary camp before ascent to caves at
45 higher elevations. Indeed, even as early as 1954, Common had hypothesised that Bogong moths
46 might use Mt. Gingera as merely a stopover during their migration route between it and higher
47 elevations in the Snowy Mountains, both in the autumnal migration and possibly in the summer,
48 as in the hot summer of January-February 1952 (Table 5).
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3 The fact that moth declines are becoming noticeable at lower elevations, such as those close to the
4 summit Mt. Gingera (ca. 1840 m), can be explained by either of two possible (non-mutually
5 exclusive) scenarios: (1) lower elevation aestivation sites are becoming less suitable due to climate
6 change, or (2) higher elevation aestivation sites have always been preferred by the moths, but when
7 high numbers of moths filled the higher sites, additional moths were forced to aestivate at the lower
8 (and less-preferred) sites, so that when moth numbers began to decline, these lower sites emptied
9 first.

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11 Both of these scenarios are supported by the long-term moth declines observed at lower elevations
12 in the Australian Alps. The lower cave on Ken Green Bogong has almost always had a high number
13 of moths in early spring-summer, but numbers decline to zero in mid-summer as moths move
14 higher. This situation could well have been mirrored on Mt. Gingera during the summers of 2014-
15 2015, 2015-16 and 2019-2020 when Bogong moth numbers first rose and then declined (up to two
16 months earlier than they did during the summer of 1953-1954: Common 1954; Caley and Welvaert
17 2018; Fig. 4). Based on the January 2019 mean maximum temperature of 15.7°C in the lower (1860
18 m) cave at Ken Green Bogong (Table 5), the mean maximum temperature of the upper cave (2020
19 m) would have been 15.0°C (Green 2014). This temperature, higher than that measured by
20 Common (1954) in the cave near the summit of Mt. Gingera (ca. 1840 m) during the hot summer
21 of 1951-1952, suggests that Ken Green Bogong may have been unsuitable for Bogong moths and
22 that they might have migrated further up hill. Indeed, during the summer of 2018-2019, Bogong
23 moths appeared to be in good numbers only in locations just below the summit of Mt.
24 Kosciuszko where cave temperatures would have been around 13.0°C (Green 2014). Thus, during
25 this summer the upper cave at Ken Green Bogong was either too warm (at 15.0°C) for aestivation
26 (scenario 1), and/or the lower numbers of moths in the mountains were entirely accommodated
27 within the highest (and preferred) aestivation sites, leaving the lower sites (like those at Ken Green
28 Bogong) empty (scenario 2).

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30 The first scenario – that lower aestivation sites are becoming less suitable due to climate change –
31 would require that these sites have acquired average maximum temperatures that exceed the
32 maximum for which aestivation is permitted. However, this maximum temperature has never been
33 determined scientifically.

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35 What might this maximum temperature (and lowest elevation) be? The lowest definitely known
36 and regularly frequented whole-summer aestivation elevation is 1600 m at Mt. Buffalo – equivalent
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3 to 1700 m at Mt. Gingera when one accounts for Mt. Buffalo's 1.15° more southerly latitude. This
4 is only slightly lower than the lowest known aestivation sites below the summit of Mt. Gingera
5 (which are located at 1760 m: Table 2). In the northern Snowy Mountains, alpine pygmy possums
6 have been recorded eating Bogong moths in January at Boltons Hill (1581 m, above Happy Jacks
7 Valley; Linda Broome, pers. comm.), suggesting whole-summer aestivation at that location. In
8 contrast, almost 100 m lower at nearby Snow Ridge (1495 m), pygmy possums are found to
9 consume Bogong moths almost exclusively in Spring (as revealed by scat analyses in 2011: Gibson
10 *et al.* 2018) – presumably the moths do not remain here but instead migrate to higher elevations in
11 the early summer. In the eastern Snowy Mountains, moths have also been observed in good
12 numbers until at least 2015 at Mt. Tingaringy (1440 m), although it is not certain that they are there
13 for the entire summer (Table 2, note e), or if they move to higher elevations in January (the more
14 likely scenario).

25 Thus, the lowest elevation for regularly frequented whole-summer Bogong moth aestivation sites
26 is likely to be around 1600 m, both in New South Wales (Boltons Hill) and Victoria (Mt. Buffalo).
27 What do these elevations suggest about the maximum permissible aestivation temperature? Data
28 given in Table 5 reveal that between 2006 and 2020, the average maximum temperature measured
29 from a cave at Ken Green Bogong (1940 m) during January was 12.7°C. Using a lapse rate for the
30 Snowy Mountains of 9.1°C per kilometre of elevation (Green 2014), one can calculate that during
31 the same period the average maximum temperature from the lowest suspected aestivation site on
32 Boltons Hill (1581 m) would have been 16.0°C. We suggest that this is likely to be close to the
33 highest temperature that permits aestivation. Supporting this notion is an unusual observation
34 made by Ian Common during the summer of 1951-52 on Mt. Little Ginini in the ACT (1525 m,
35 and close to Mt. Gingera). Common noted that Bogong moths aestivated on Mt. Little Ginini for
36 the entire summer when the average January-February maximum temperature was projected to be
37 14.8°C (Table 3; Common 1954). This suggests that aestivation is permitted at temperatures at least
38 as high as 14.8°C, only 1.2°C lower than our predicted maximum. Thus 16°C seems to be a
39 reasonable estimate for the maximum temperature that permits aestivation.

52 From the turn of this century, Bogong moths at aestivation sites on Mt. Gingera have declined
53 during a 0.7°C temperature increase (i.e. 0.36°C per decade: Sánchez-Bayo and Green 2013). The
54 mean maximum January temperature in the currently preferred aestivation site (at around 1840 m)
55 was 16.2°C during 2020 (Table 4) – at or above our estimated maximum permissible temperature
56 for aestivation. These aestivation sites, together with those on Mt. Buffalo, are among the lowest
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3 aestivation sites known. There is no question that if climate change advances and global
4 temperatures continue to rise, aestivation will become more and more restricted to sites at higher
5 elevations. To determine the actual maximum temperature where aestivation is permitted, the
6 temperatures of caves at different elevations where moths aestivate need to be monitored using
7 temperature loggers. Such measurements will allow us to forecast the impact of climate change on
8 the Bogong moth population in the mountains and allow us to predict the impacts that changes in
9 this population will have on the alpine ecosystem.
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15 16 ***Effects of drought*** 17

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20 From 2017 to 2019 much of the agricultural lands of the Murray–Darling Basin in western New
21 South Wales and southern Queensland were affected by extreme drought, the most severe in the
22 recorded history of the Murray–Darling Basin. This drought has had a major impact on the Bogong
23 moth population, whose main breeding areas occur in this region. The Bogong moth crash seen in
24 the Australian Alps over the summer of 2017-2018 was sudden, widespread across all mountain
25 areas, and continued into the summers of 2018-2019 and to a lesser extent 2019-2020.
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32 There is no doubt that the major cause of the recent Bogong moth crash is the latest drought,
33 which may have affected moths in a number of ways. Firstly, a lack of food for the larvae in the
34 breeding areas would have been a major problem, coupled with unfavourable soil temperatures
35 and moisture levels. We do not know the direct effect of temperature on the larvae, but
36 temperatures were higher than normal, and coupled with a considerably drier soil and a lack of
37 food, there were probably very few larvae that survived the dry winter of 2017, and thus very few
38 adults that emerged and flew to the mountains in spring. Of course, even fewer of those that
39 migrated to the caves would have survived to return in autumn for the winter breeding season of
40 2018. Those few that did return would have encountered the same drought-stricken landscape that
41 they had experienced the previous year, leading to even fewer of their offspring surviving to
42 adulthood. Because the winters of 2018 and 2019 were equally dry (Fig. 5), it is not difficult to
43 understand how Bogong moth numbers plummeted.
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54 The effect of drought on Bogong moths numbers prior to 2017 is less clear, although significant
55 fluctuations are apparent (as has also been noted in Victorian alpine areas: Mansergh and Heinze
56 2019). Almost all of eastern Australia was affected by major droughts in 1958-1968 and 1979-1983,
57 with the 1982-1983 El Niño that developed from June to August creating severe conditions in
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3 terms of lack of rainfall and extreme heat. There was no noticeable impact of these droughts on
4 Bogong moth numbers at Mt. Buffalo apart from the significant temporary reduction experienced
5 in summer 1968-1969. However, by the summer of 1969-1970 Bogong moth numbers were back
6 to 'normal' (Table 4). In the summer of 1972-1973 the Bogong Peaks were reported as the only
7 site in NSW with Bogong moths in any quantity (Flood 1980). However, it is not clear whether any
8 other major aestivation sites in NSW were checked by Flood (1980 – see Blakers 1980). Initially,
9 the drought from 1979 to 1982 made no difference to Bogong moth numbers on Mt. Buffalo, in
10 the Snowy Mountains or during the one summer recorded at Mt. Gingera. Moth numbers in the
11 Snowy Mountains and on Mt. Buffalo declined in the summer of 1982-1983, and remained lower
12 at Mt. Buffalo but there are no records available elsewhere.
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21 The Millennium Drought in southeast Australia (2001–2009) was particularly severe and badly
22 affected the Murray-Darling Basin and virtually all of the southern cropping zones (Australian
23 Bureau of Meteorology 2015). Bogong moths continued to be found at lower levels on Mt. Buffalo
24 but the drought had major impacts on moth numbers in the Snowy Mountains during the summers
25 of 2006-2007 and 2008-2009 (Table 4). However, the successive La Niña events during the
26 summers of 2010-11 and 2011-12 were associated with record rainfall over much of Australia
27 (Australian Bureau of Meteorology) and resulted in good years for Bogong moth numbers in the
28 Australian Alps. At this point it was obvious that there had been a long-term decline in overall
29 numbers of Bogong moths, with declines that followed the drought of 1981-1983 and further
30 declines that commenced in 1993-1995 that pre-empted the Millennium drought (Table 4). The
31 decline in numbers from 2014-2015 on Mt. Higginbotham, coupled to the progressive movement
32 of Bogong moths to higher elevations, suggest that when numbers are low, Bogong moths on Mt.
33 Buffalo move to higher, cooler locations. This also appears to be occurring further north in NSW
34 on Mt. Gingera (35.58°S), where the lowest aestivation sites lie at 1760 m and continue upwards
35 to just below the summit at 1857 m. This is essentially the same elevation band for aestivation sites
36 a little further south at Charlotte Pass (36.43°S): 1755 to 1837 m. Bogong moths found here are
37 generally spring arrivals that migrate to higher elevations as summer develops (see above). The
38 latest drought began in NSW in mid-2017, with Bogong moth numbers crashing within the
39 breeding areas. Since then, there was no reprieve in the drought until well in to 2020 – NSW was
40 declared to be 100% in drought by August 2018 and Queensland 65.2% by May 2019 (NSW
41 Department of Primary Industries 2019). By July 2019 the drought was officially recorded as the
42 worst on record in the Murray–Darling Basin (Farm Online National 2019), exceeding the
43 Millennium drought, Federation Drought (1895–1903) and the World War II drought (1937-45).
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3 By the end of March 2019 rainfall deficiencies in the Murray–Darling Basin were the third lowest
4 on record. Temperatures were extremely high, with the nearest equivalent temperatures, according
5 to paleo-climatic data, being a hot period that occurred 2-3 million years BP (Dr. David Jones:
6 Australian Bureau of Meteorology). Together, these conditions suggest that the recent drought,
7 mediated by climate change, is sufficient in itself to have caused the Bogong moth collapse.
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13 **Other factors**

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17 In addition to agricultural practices and climate change, annual declines of Bogong moth numbers
18 may have occurred for the following reasons: (1) attrition as larvae in soil that is too dry and/or
19 too warm (as likely occurred during winter 2017 and 2018), or attrition during adult migration as a
20 result of (2) introduced predators, (3) environmental factors (such as increasing light pollution) or
21 (4) because of attrition once the moths reach the mountains (e.g. due to climatic factors, and
22 introduced predators and parasites). Obtaining a measure of the numbers of moths existing as
23 larvae (see Green 2008), or as adults during migration, is difficult, particularly if relying on light
24 traps. Local and synoptic weather systems can both affect the moth catch in light traps due to
25 thunderstorms and the passage of cold fronts or depressions. The wind speed, air temperature and
26 levels of moonlight may also have an affect (Gregg *et al.* 1994). The aestivating population of
27 Bogong moths, from their arrival at their caves in December until the beginning of their departure
28 in early March, is the part of the lifecycle where numbers of moths can be most accurately
29 measured.
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40 Ten years ago, a total number of 2.2 billion aestivating Bogong moths was estimated to exist in the
41 Snowy Mountains over the summer (Green 2011). This number suggested that observed losses of
42 moths in cities such as Canberra – where in occasional years migrating moths have been lured by
43 city lights after presumably being blown off course by unusually strong winds – may not have had
44 an overwhelming impact on overall numbers in the mountains as most moths eventually leave their
45 city refuges and continue their journeys. These losses from light pollution were probably
46 comparatively small (although the loss of moths by any cause is now becoming important). Apart
47 from light pollution, another major change since European settlement is the arrival of feral
48 predators such as foxes (arriving in the Snowy Mountains around 1900, after the first capture of a
49 fox in NSW in 1893: Rolls 1969). Fox predation now accounts for a loss of 55 imperial tons of
50 Bogong moths annually in the Snowy Mountains (Green 2011). However, fox baiting from 1999
51 onwards (which still continues annually above the treeline) had an immediate impact on fox
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3 numbers, with a decline of about 80% based on three criteria: fox scat counts, fox tracks found on
4 snow transects, and numbers of foxes counted at Charlotte Pass (K. Green, unpublished data). A
5 recent report indicates that wild pigs have also become significant predators of Bogong moths,
6 following the introduction of these feral animals to the Snowy Mountains in 1959 (Caley and
7 Welvaert 2018). Before European settlement a major impact on Bogong moths was hunting by
8 Aboriginal people, and there are estimates that this would have taken several tons of moths (Jardine
9 1901). However, without the actual figures, the impact of these hunting activities on moth numbers
10 cannot be calculated.
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18 CONCLUSIONS

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21 Records of Bogong moths collected over the past 70 years from around 50 to 60 aestivation sites,
22 and more recently along the migratory route, coupled with the analysis of Bogong moth remains
23 in mammalian predator faeces, reveal noticeable patterns in the numbers of moths present over
24 summer in the Australian Alps. Even though the data (our own and that of others) are admittedly
25 fragmentary, this analysis has revealed that Bogong moth numbers were fairly stable from 1950
26 until around 1980, apart from temporary falls in numbers due to occasional drought. From 1980
27 until 2016 Bogong moth numbers in the mountains began to fluctuate, with some years having
28 very high numbers of moths, while others had many fewer. Even though overall numbers remained
29 high, these years showed evidence of a slow decline. From 2017-2020 a sudden and worrying crash
30 in Bogong moth numbers occurred.
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40 Although the causes for the decline and recent crash in Bogong moth numbers remain uncertain,
41 one or more factors may be responsible. We currently have little evidence to suggest that increasing
42 global temperatures *per se* are responsible for the decline in Bogong moths seen across the
43 mountains, however the Australian climate has nonetheless become continuously drier and warmer
44 over past decades. This change in climate has possibly had a serious impact on the ability of Bogong
45 moth eggs, larvae and pupae to survive the winter in their breeding grounds, which in turn may
46 have slowly been reducing the number of moths entering the mountains. Moreover, our analysis
47 also suggests that the maximum temperature for aestivation may be around 16°C, and that a
48 warming climate is thus likely restricting aestivation to higher and higher elevations. These possible
49 effects of climate change, added to known changes in farming practices, such as increasing land
50 clearing for crops and an elevated use of insecticides, may account for the gradual decline in moth
51 numbers observed from about 1980 until 2016. These declines were followed by the catastrophic
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3 Bogong moth summers of 2017-2018 and 2018-2019 (and to a lesser extent 2019-2020) for which
4 only drought can be seen as the cause. This drought is very likely to have severely impacted the
5 survival of Bogong moth immature stages in their breeding grounds, a speculation supported by
6 the sudden disappearance of Bogong moths that we observed along their migratory routes during
7 Spring. The latest drought – the worst in recorded history in the Murray–Darling Basin – is almost
8 certainly the result of climate change (CSIRO 2018).
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15 Finally, as with the alarming worldwide decline of insects in general (Wagner 2020), the decline of
16 Bogong moths in the Australian Alps should be seen as a worrying development. The delicate
17 alpine environment is already severely threatened by climate change and the massive annual influx
18 of energy and nutrients provided by Bogong moths is of major importance for the health of this
19 ecosystem (Green 2011; Mansergh and Heinze 2019). Just a few years ago it would have been
20 difficult to believe that such an abundant and iconic insect – with 17,000 aestivating individuals
21 crowding onto each square metre of alpine cave wall, in untold numbers of caves and boulder fields
22 across the great expanse of the Australian Alps – could ever be threatened. But our analysis has
23 revealed that Bogong moths have been slowly declining for the last 40 years, and the latest drought
24 has made it glaringly obvious that in highly unfavourable conditions the Bogong moth population
25 can actually crash. Hopefully their numbers will rise again as conditions improve, but our analysis,
26 as well as that of Mansergh and Heinze (2019), suggest that further research is urgently needed.
27 Regular quantitative monitoring of Bogong moths during their migration (e.g. using light-trapping,
28 vertical radar and lidar methods), during aestivation in alpine caves and during development in
29 their breeding areas, coupled with long-term and frequent temperature and air/soil humidity
30 readings in these locations, is greatly warranted. Moreover, the currently unknown effects of
31 neonicotinoid insecticides on the health of Bogong moth breeding populations should be urgently
32 investigated.
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47 The Bogong moth is an iconic and culturally significant Australian insect whose remarkable highly-
48 directed migration (Warrant *et al.* 2016), and its use of stellar and magnetic compass cues for
49 nocturnal navigation (Dreyer *et al.* 2018; Adden *et al.*, in preparation), places it on-par with its better-
50 known diurnal counterpart in North America, the Monarch butterfly *Danaus plexippus* (Reppert and
51 de Roode 2018). This, in addition to its importance for the health of the alpine ecosystem (Green
52 2011; Mansergh and Heinze 2019), and its significance as a food source for critically endangered
53 alpine marsupials such as the Mountain pygmy possum (Gibson *et al.* 2018; Mansergh and Heinze
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2019), makes the Bogong moth both unique and exceptional among Australian insects, and worthy of every effort to ensure its long-term survival and protection.

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FIGURE CAPTIONS

Figure 1. Map of south-eastern Australia showing the locations where larvae have been collected by Froggatt (1900, *yellow circles*), Common (1954, *red circles*) and Green (2008, *white circles*). Also shown are the names of the major rivers in NSW, and the locations of various towns and mountain peaks mentioned in the text. The area of broadacre cropping farms across south eastern Australia during 2014-2015 is delineated by the *red line* (from ‘The Conversation’ 2017), while areas of grey cracking clays are shown in *grey*. Bogong moths fly towards the Australian Alps (*white areas*, elevations > 1500 m) from various regions of southeast Australia, from as far distant as eastern South Australia, western Victoria, western and northwest New South Wales and southern and southeast Queensland (*blue arrows*). Adapted from Warrant *et al.* (2016), after Green (2008). **Inset:** The Australian Bogong moth *Agrotis infusa* (Boisduval, 1832). Scale bar = 5 mm. Reproduced with the kind permission of the photographer; Ajay Narendra, Macquarie University, Australia.

Figure 2. Mean proportion of individual fox scats consisting of Bogong moth remains at subalpine (*orange lines and symbols*) and alpine altitudes (*blue lines and symbols*) over two summer seasons: 1996-1997 (*diamonds*) and 1997-1998 (*circles*). Redrawn from Green (2010b).

Figure 3. Date of first arrival of the Bogong moths above the snowline in the Snowy Mountains from 1979 until the present. *Regression line* has the following equation: $D = 0.19Y - 114$ ($R^2 = 0.050$) where D is the day of the year for the first moth arrival, and Y is the year.

Figure 4. Seasonal changes in site occupancy of aestivating Bogong moths around the summit of Mount Gingera in the Brindabella Ranges (on the NSW and ACT border), based on 37 sites surveyed by Caley & Welvaert (2018) during 2014–2016 (reproduced with permission), and during the recent extreme drought.

Figure 5. Australian rainfall deciles (1 January 2017 – 31 December 2019). Source: Bureau of Meteorology, Australian Government. Distribution based on gridded data.

Table 1. Maximal shade temperatures T in boulder fields on the Main Range of the Snowy Mountains at four elevations during the snow-free season^a, together with proportion of Bogong moths in Mountain pygmy possum (*Burramys parvus*) scats recorded over 17 years in different seasons^b and frequency of occurrence of Bogong moths in scats of Dusky antechinus (*Antechinus swainsonii*) in 1981-1987^{c,d}.

Location	Mean T (°C)	Late Spring	Late Summer
Charlotte Pass, 1755m	12.3±2.9	30% ^b	≈1% ^b
South Ramshead, 2000 m	10.7±3.5	62% ^{c,d}	2% ^{c,d}
Mt. Townsend, 2209 m	9.5±3.1	40% ^b	40% ^b
Mt. Kosciuszko, 2228 m	8.6±2.5	32% ^b	49% ^b

Notes

- a. The average maximum temperature over the period November 2009-March 2010, measured using a temperature logger placed in a shaded place within the boulder field at each location (Green 2010a). Temperatures measured at Charlotte Pass from a Bureau of Meteorology Stevenson Screen over the same time period ($12.3^{\circ}\text{C} \pm 3.5^{\circ}\text{C}$) was not significantly different to that measured by the logger placed in the nearby boulder field.
- b. Data from Mountain pygmy possum (Gibson *et al.* 2018)
- c. Data from Dusky antechinus
- d. See Table 2, Note d.

Table 2. The lowest elevations (m) at which aestivation of Bogong moths takes place at different locations in the Australian Alps (with notes)

Location	Latitude	Lowest elevation (m)
Mt. Gingera, NSW/ACT	35.583° S	1760 ^a
Bogong Mountains Big Plain/Mt. Jounama, NSW	35.576° S	1680/1710 ^b
Charlotte Pass, NSW	36.427° S	1755 ^c
Unnamed peak “Ken Green Bogong”, NSW	36.517° S	1860 ^d
Mt. Tingaringy, NSW	36.998° S	<1440 ^e
Mt. Higginbotham, Victoria	36.987° S	1720 ^f
Mt. Buffalo (The Horn), Victoria	36.736° S	1600 ^g

Notes

- a. The lowest ‘camp’ used as an aestivation cave was on nearby Little Ginini was at 1525-1585 m but in 1952-1953 it was only used as a ‘temporary camp’ in spring and early summer (Common 1954, p229). Apart from that record, in current years the lowest major aestivation site has been at 1760 m, below the peak of Mt. Gingera (which is at 1857 m).
- b. On 23 February 1999 Bogong moth remains were found in fox scats on the Bogong Peaks and Bogong moths were seen flying around camp from about 7 pm (KG, pers. obs.). Moths flying at this time usually do so for approximately an hour before returning to the caves. Even though the reason for this flight is unknown, it may possibly be to drink, to gauge atmospheric conditions in preparation for their return migration, or for some other purpose. The location of the lowest cave used as an aestivation site is not known. At one site on Big Plain, Bogong moths were found on 26th January 2015 but not in large agglomerations (Ben Keaney, pers.com). The higher site on Mt. Jounama has not been examined.
- c. At Charlotte Pass, the Mountain pygmy possum *Burramys parvus* was recorded with a diet consisting of 30% Bogong moths in spring, falling to ~1% in summer (Table 1, Gibson *et al.* 2018). This contrasted with higher elevation sites, where in summer the proportion of Bogong moths in the pygmy possum diet at Mount Townsend (2209 m) remained about the same as it was in Spring, while at Mount Kosciuszko the proportion increased throughout summer (Gibson *et al.* 2018). This suggests that Charlotte Pass was not a summer aestivation site and that the local lower limit for aestivation was thus at or above 1755 m.
- d. Bogong moths occurred in high numbers in pitfall traps and sheltered areas in the study sites of the Dusky antechinus *Antechinus swainsonii* at 1860 m and 1940 m (PhD data, KG). This mainly occurred in spring over the 1981-1987 seasons. Lepidopterans, mainly Bogong moths, were the most common food through the spring in the diet of *A. swainsonii*, but this declined through summer (Green 1989). Frequency of occurrence of Bogong moths in scats of *A. swainsonii* was 75% in a high sub-alpine site in spring and 62.5% in a low alpine site (Green 1989). Numbers then appeared to decline over summer (see Table 3 in Green 1989). However, this is a result of using “season” rather than month in the published study, and when the data were re-examined by month, the decline was found to occur in February with scats generally gone by March (PhD data, KG). In January at high subalpine sites, Bogong moth frequency of occurrence was 58.3% in *A. swainsonii* while in low alpine sites it was 66.7% (PhD data, KG). In contrast, this had fallen to 11% and 2% respectively in February and 1% and 0% respectively in March, indicating that as summer became warmer (or moth numbers declined) the moths moved higher (PhD data, KG).
- e. On 13th October 2001, Bogong moths were captured in their thousands whilst flying around the summit of Mt. Tingaringy. These moths smelled strongly of nectar and were being preyed upon by White-throated needletails (a type of swift) as well as unidentified bats. On 15th October, moths were lined up inside a cave on the north-west face of Mt. Tingaringy, with Quoll scats outside (which had been feeding on them). On 16th October “The Ampitheatre” was found, a crack in the mountain estimated to be an 80 m length of accessible cave, with dead moths 8-10 cm deep on the floor (KG and Tony Stubbs). A big catch of moths was also collected on 5th and 6th January 2013, with a smaller catch on 7th Jan 2016 (KG, EW). Although many moths use the site, there is no record of occupation later than 7th January, so despite its size, there is currently no data to prove that Mt. Tingaringy is an aestivation site.
- f. Aestivation sites up to a maximum of 1720m (Ian Mansergh, pers. com.)
- g. For all summers from 1966-1967 and 1981-1982 (with the exception of 1968-69), a cave (at 1600m) on ‘The Horn’ on Mt. Buffalo was the lowest site used by Bogong moths to aestivate (MB).

Table 3. Mean daily maximum temperature T from January to February at aestivation sites on Mt. Gingera^a and Mt. Little Ginini (1952-1953)^a, in the Snowy Mountains (2010), and on Mt. Buffalo (1967)

Location	Elevation (m)	Mean T (°C)
Mt. Gingera 1952	1840	12.7 ^b
Mt. Gingera 1953	1840	10.6
Mt. Gingera 2020	1840	14.7
Mt. Little Ginini 1952	1525	14.8 ^c
Mt. Little Ginini 1953	1525	12.7 ^c
Charlotte Pass	1755	13.8
Unnamed peak “Ken Green Bogong”	1860	11.8
Unnamed peak “Ken Green Bogong”	1940	11.9
Unnamed peak “Ken Green Bogong”	2020	11.5
Mt. Ramshead North	2140	11.7
Mt. Twynam	2150	8.9
Mt. Townsend	2150	10.4
Mt. Kosciuszko	2200	10.2
Mt. Buffalo (Vic)	1600	13.2

Notes

- a. Common 1954. The cave monitored by Common on Mt. Gingera was at about 1840 m, just below the summit at 1857 m. This was also the cave where temperatures were measured in 2020.
- b. In 1952, it appears that temperatures were measured in a location that may not have been fully shaded (Common 1954, p 254). If we assume that January temperatures did not exceed those at Kiandra, and set Mt. Gingera’s January temperature at 13.0°C, the corrected 1952 January-February mean temperature would then be 12.7°C.
- c. Extrapolated from temperatures measured at the summit of Mt. Gingera.

Table 4. Records of Bogong moth occurrence and relative abundance at aestivation sites on four mountains in the Australian Alps^a. Numbers 1-4 refer to relative abundance of moths at their aestivation sites, as follows: (1) good, (2) normal to poor, (3) bad, or (4) absent. For Mt. Buffalo, three cave sites were checked on one peak known as The Horn: two separated lower elevation sites (A and B at 1600 m), and several higher caves in close vicinity (C) ranging from 1680 m to the summit of The Horn at 1723 m – all sites may have been visited, but in certain years if site A had Bogong moths the other sites (B and C) were not visited. A single letter indicates the lowest cave that moths were found in (e.g. C); A or B indicates that moths were found in one or both of these cave sites (and were thus also found at cave site C), but no exact record was kept. P indicates that moths were present in one or more of these cave sites, but no exact record was kept.

Summer	Mt. Gingera	Ken Green Bogong	Mt. Buffalo	Mt. Higginbotham
1951-52	1			
1952-53	1			
1953-54	1			
1954-55	1			
1955-56	1			
1956-57	1			
1957-58	1			
1958-59	1			
1959-60	1			
1960-61	1			
1961-62	1			
1962-63	1			
1963-64	1			
1964-65	1			
1965-66	1			
1966-67	1		A	
1967-68	1		A	
1968-69	1		C	
1969-70	1			
1970-71	1			
1971-72	1			
1972-73	1			
1973-74	1			
1974-75	1		A	
1975-76	1		A	
1976-77	1	1	A	
1977-78	1	1	A	
1978-79	1	1	A ^b	1
1979-80	1	1	A ^b	1
1980-81		1	A	
1981-82		1	A	
1982-83		2	A or B ^b	1
1983-84			A or B	
1984-85			A or B	
1985-86			A or B	1

1					
2					
3	1986-87		2	A or B	1
4	1987-88		1	A or B	
5	1988-89			A or B	
6	1989-90	1		A or B	
7	1990-91				
8	1991-92			A or B	
9	1992-93			A or B	
10	1993-94		3	P	
11	1994-95		3	P	
12	1995-96		1	P	
13	1996-97		2	P	
14	1997-98		2	P	
15	1998-99		2	P	
16	1999-00			P	
17	2000-01		1	P	
18	2001-02		1	P	
19	2002-03		2	P	
20	2003-04			P	
21	2004-05		1	P	
22	2005-06		1	P	
23	2006-07		3		
24	2007-08		2	P	
25	2008-09		3	P	
26	2009-10		2	P	
27	2010-11		1	A	
28	2011-12	1	1	P	
29	2012-13	1	2	P ^e	
30	2013-14	1	2	A ^{b,c}	1
31	2014-15	3 ^f	1	A	3
32	2015-16	3 ^f	1	C ^{c,d}	3
33	2016-17		1	C ^{c,d}	3
34	2017-18	4	4	C ^{c,d,e}	4
35	2018-19	4	4	4 ^c	4

Notes

- a. Data was collected on (1) Mt. Gingera, NSW/ACT: 1952-1979 data from Common (1954, 1980) and pers. com.), 1979 and 1989 KG, 2011-2014 EW, 2015-2019 PC, (2) The unnamed peak “Ken Green Bogong”, close to South Ramshead in the Kosciuszko Main Range, NSW: 1977-2019 KG, (3) granite boulder fields around Mt. Higginbotham, Victoria: data from Mansergh and Heinze (2019), (4) Mt. Buffalo, Victoria: 1966-2019 (as A, B and C) MB, with other Victorian Records 1988-1989 Ian Mansergh - during 2013-2014 Dean Heinze reported that Bogong moth numbers were high, but did not appear to occupy either the low or medium cave sites.
- b. This was considered a good moth year on Mt. Buffalo
- c. Visit made in January
- d. Bogong moths were only present in the summit cave on The Horn (1723 m)
- e. Only a handful of Bogong moths were present
- f. There is a possibility that Bogong moths were in good numbers during these years but did not occupy the caves on Mt. Gingera in order to take advantage of caves at higher elevations. Moths were in abundance from October until December but declined rapidly from the beginning of January (Caley and Welvaert 2018), i.e. at least 1-2 months prior to the main return migration, possibly reflecting a move to higher elevations.

Table 5. Average maximum temperatures (°C) in January and February during different years from caves in the NSW and ACT Alps

Location	Year	January	February
Mt. Gingera NSW/ACT ^a 1840 m	1952	14.5	12.3
Mt. Gingera NSW/ACT ^a 1840 m	1953	10.5	9.5
Mt. Gingera NSW/ACT ^a 1840 m	2020	16.2	13.1
Charlotte Pass NSW 1755 m	2010	13.8	12.2
Unnamed peak “Ken Green Bogong” NSW 1940 m	2006	13.7	12.3
•	2007	12.1	12.0
•	2008	12.8	8.5
•	2009	12.3	11.3
•	2010	12.4	11.1
•	2014	12.5	12.7
•	2015	10.5	11.8
•	2016	10.8	12.1
•	2017	13.4	11.4
•	2018	12.8	11.2
•	2019 ^b	15.7	11.4
Unnamed peak “Ken Green Bogong” NSW 1940 m	2020	13.3	10.9

Notes

- a. Common 1954. The cave monitored by Common on Mt. Gingera was at about 1840 m, just below the summit at 1857 m. This was also the cave where temperatures were measured in 2020.
- b. During the latter half of December 2019, the average maximum temperature reached 15.6°C

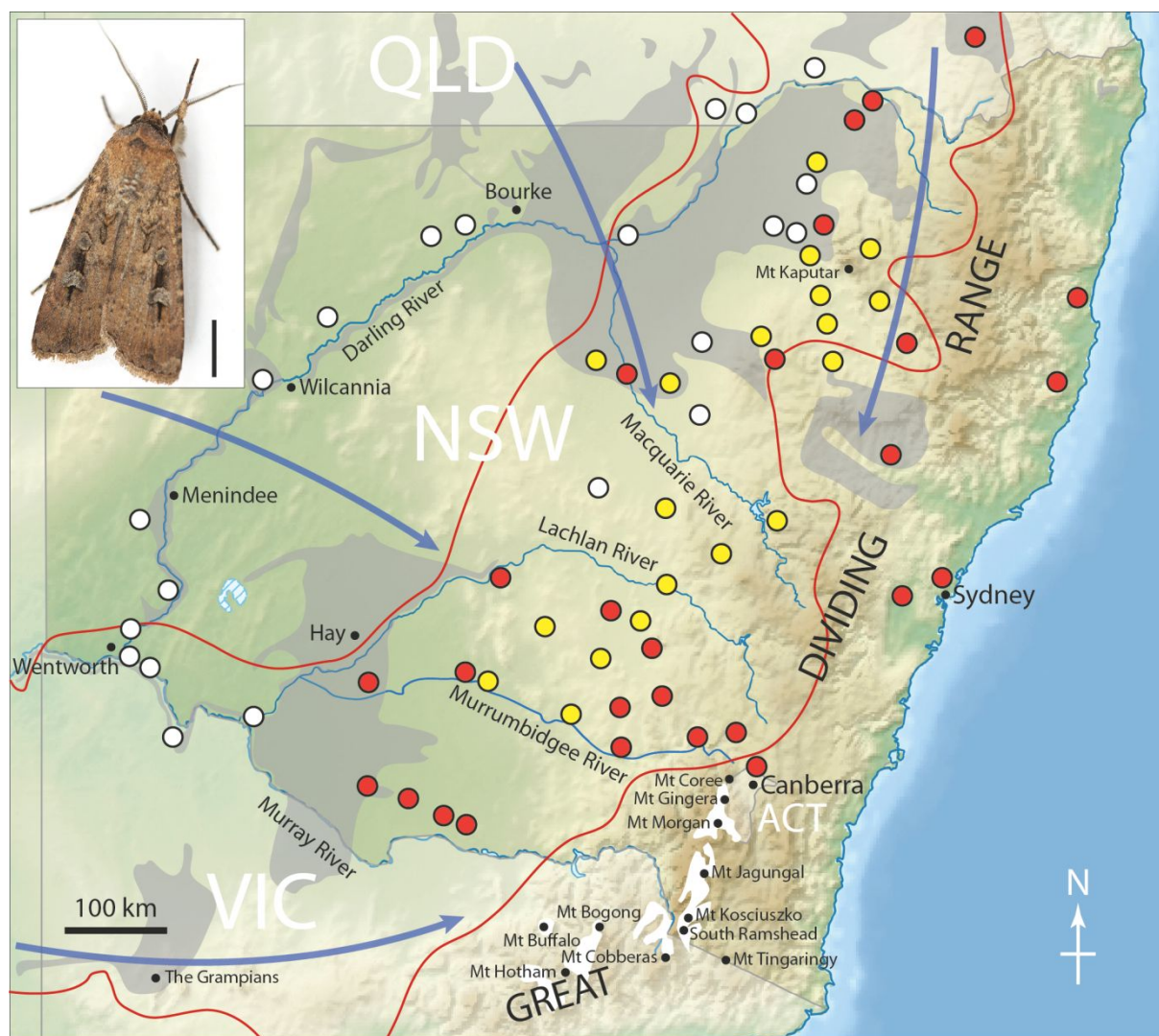


Figure 1. Map of south-eastern Australia showing the locations where larvae have been collected by Froggatt (1900, *yellow circles*), Common (1954, *red circles*) and Green (2008, *white circles*). Also shown are the names of the major rivers in NSW, and the locations of various towns and mountain peaks mentioned in the text. The area of broadacre cropping farms across south eastern Australia during 2014-2015 is delineated by the *red line* (from ‘The Conversation’ 2017), while areas of grey cracking clays are shown in *grey*. Bogong moths fly towards the Australian Alps (*white areas*, elevations > 1500 m) from various regions of southeast Australia, from as far distant as eastern South Australia, western Victoria, western and northwest New South Wales and southern and southeast Queensland (*blue arrows*). Adapted from Warrant *et al.* (2016), after Green (2008). **Inset:** The Australian Bogong moth *Agrotis infusa* (Boisduval, 1832). Scale bar = 5 mm. Reproduced with the kind permission of the photographer; Ajay Narendra, Macquarie University, Australia.

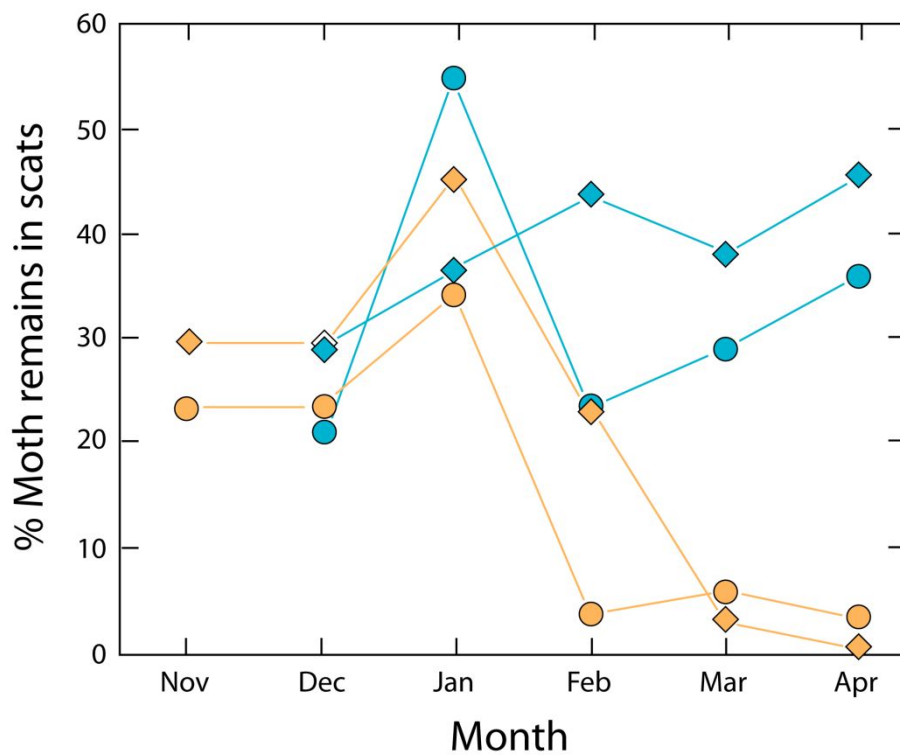


Figure 2. Mean proportion of individual fox scats consisting of Bogong moth remains at subalpine (orange lines and symbols) and alpine altitudes (blue lines and symbols) over two summer seasons: 1996-1997 (diamonds) and 1997-1998 (circles). Redrawn from Green (2010b).

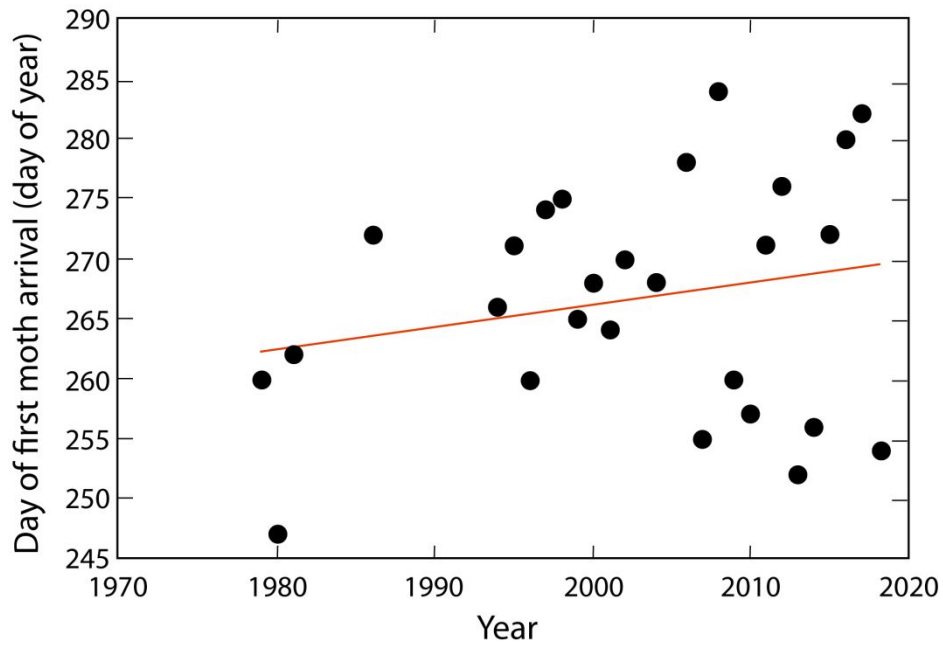


Figure 3. Date of first arrival of the Bogong moths above the snowline in the Snowy Mountains from 1979 until the present. *Regression line* has the following equation: $D = 0.19Y - 114$ ($R^2 = 0.050$) where D is the day of the year for the first moth arrival, and Y is the year.

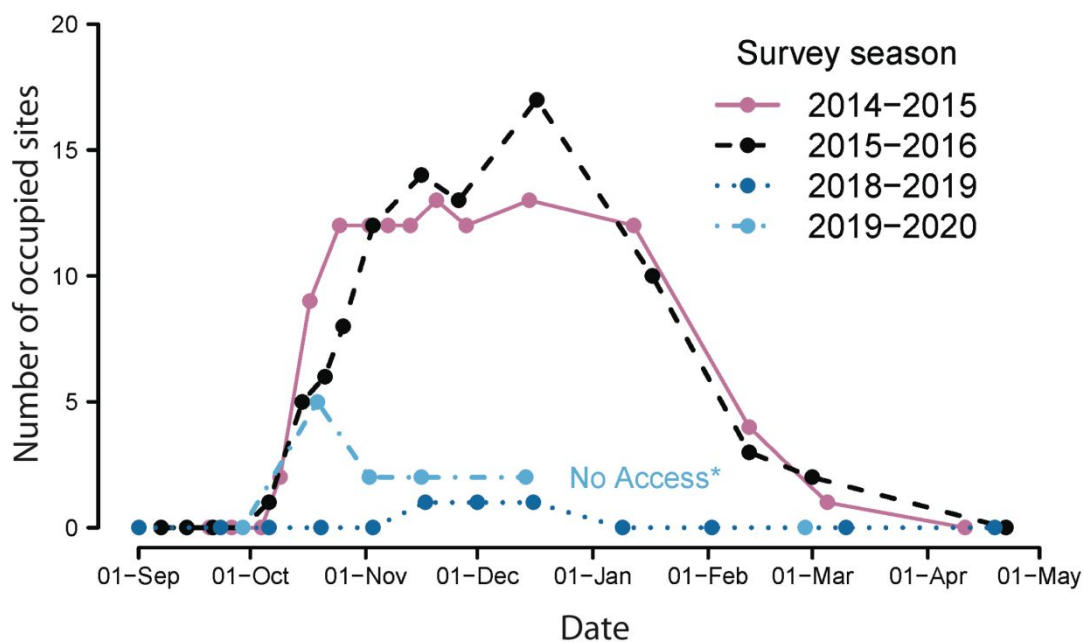


Figure 4. Seasonal changes in site occupancy of aestivating Bogong moths close to the summit of Mount Gingera in the Brindabella Ranges (on the NSW and ACT border), based on 37 sites surveyed by Caley & Welvaert (2018) during 2014–2016 (reproduced with permission), and during the recent extreme drought.

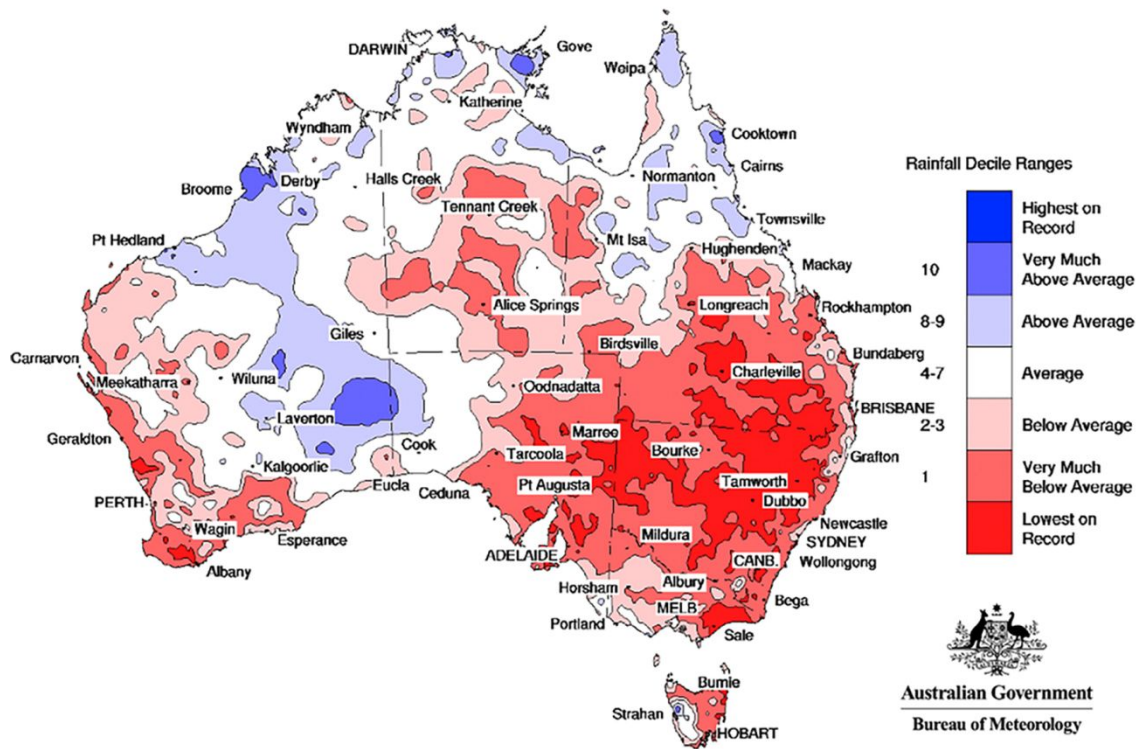


Figure 5. Australian rainfall deciles (1 January 2017 – 31 December 2019). Source: Bureau of Meteorology, Australian Government. Distribution based on gridded data.

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The Australian Bogong moth *Agrotis infusa* (Lepidoptera: Noctuidae), 1951-2020: Decline and crash

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Running title: ~~P~~**Dramatic** population decline in Bogong moths

Abstract

The Bogong moth *Agrotis infusa* is well known for its remarkable long-distance migration – a return journey from the plains of southeast Australia to the Australian Alps – as well as for its cultural significance for Indigenous Australians. Each Spring, as many as 4 billion moths are estimated to arrive in the Australian Alps to aestivate in cool mountain caves and in boulder fields, bringing with them a massive annual influx of energy and nutrients critical for the health of the alpine ecosystem. However, a massive decline in moths present at their aestivation sites has occurred over the past three years, with only a few individuals present where hundreds of thousands could earlier be found. In order to understand the possible sources of decline, we analysed historical records of Bogong moth numbers at aestivation sites in the Australian Alps, including observations on Mt. Gingera (NSW) in the early 1950s, observations from 1980 onwards in the Snowy Mountains (NSW), and an almost-unbroken series of observations each summer over the past 53 years in three caves at different elevations on Mt. Buffalo (Victoria). This analysis shows that moth numbers were probably steady from 1951 until about 1980, fluctuated and slowly fell from then until 2016 and dramatically crashed in 2017. In the Murray–Darling Basin, the main winter breeding ground of Bogong moths, changes in farming practices, such as increasing land clearing for crops (which has removed around a quarter of a billion moths annually from the mountains compared to pre-European levels) has probably driven some of the decline in Bogong moth numbers observed from 1980 to 2016. The impact of insecticide remains unclear and is in urgent need of further study. Even though we found little evidence that increasing global temperatures *per se* are responsible for the Bogong moth decline, the Australian climate has nonetheless become drier and warmer over past decades, possibly hampering the survival of immature stages in the breeding areas and confining adult aestivation to gradually higher elevations. The crash in moth numbers from 2017 is most likely due to the recent severe drought in the moth’s breeding grounds.

~~The Bogong moth *Agrotis infusa* is well known for its remarkable long-distance migration – a return journey from the plains of southeast Australia to the Australian Alps – as well as for its cultural significance for Indigenous Australians. Each Spring, over 4 billion moths are estimated to arrive in the Australian Alps to aestivate in cool mountain caves and crevices, bringing with them a massive annual influx of energy and nutrients that is critical for the health of the alpine ecosystem. However, a massive decline in moths present in their aestivation caves has occurred over the past three years, with only a few individuals present where hundreds of thousands could be found just two years earlier. In order to understand the possible sources of decline, we analysed historical records of Bogong moth numbers at aestivation sites in the Australian Alps, including observations~~

on Mt. Gingera in the ACT/NSW in the early 1950s, observations from 1980 onwards in the Snowy Mountains of NSW, and an almost unbroken series of observations each summer over the past 53 years in three caves at different elevations on Mt. Buffalo in Victoria. This analysis shows that moth numbers were probably steady from 1951 until about 1980, but began to fall from then until 2016 before the current dramatic crash in numbers beginning in 2017. In the Murray–Darling Basin, the main winter breeding ground of Bogong moths, changes in farming practices, such as increasing land clearing for crops (which currently removes around a quarter of a billion moths annually from the mountains compared to pre-European levels) and an elevated use of insecticides, may have facilitated the decline in Bogong moths observed from 1980 to 2016. Even though we found little evidence that increasing global temperatures *per se* are responsible for the decline in Bogong moths, the Australian climate has nonetheless become continuously drier and warmer over past decades, possibly hampering the survival of immature stages in the breeding areas and confining adult aestivation to gradually higher elevations. The crash in moth numbers from 2017 is likely due to the recent severe drought in the moth's breeding grounds.

Key words: ~~Bogong moth, *Agrotis infusa*, alpine ecosystem, migration, drought, climate change, drought, pesticide, historical record, migration, pesticide, population decline, mountains, alpine ecosystem~~

IntroductionINTRODUCTION

The Bogong moth (*Agrotis infusa*) is well known for its remarkable long-distance migration (Common 1952, 1954; Warrant *et al.* 2016; Dreyer *et al.* 2018) and its cultural significance for Indigenous Australians (Flood 1980, 1996). Newly emerged ~~Bogong moths~~Bogong moths escape the increasing heat of ~~the breeding grounds in western and north-western New South Wales (NSW), southern Queensland, western Victoria and South Australia, their breeding grounds, in western and north-western New South Wales (NSW), southern Queensland, western Victoria and South Australia,~~ by migrating during spring to the ~~mountains~~mountain regions of south-eastern Australia, a journey of up to 1000 km. Once ~~at high elevation~~ in the mountains, moths ~~eventually~~

seek out the shelter of cool caves, and the deep hollows and crevices of boulder fields at high elevation, where they aestivate in vast numbers until autumn (aestivation is a state of dormancy similar to hibernation but instead occurring in summer). Bogong moths – which tile the cave walls at a density of around 17,000 individuals per square metre – are capable of aestivating for up to four months (Common 1954), ~~but the numbers of moths present at aestivation sites can vary markedly~~. Following this period, the same individuals that arrived months earlier return to the breeding grounds where they mate, lay their eggs and die (Common 1952, 1954; Warrant *et al.* 2016). The larvae then develop during the coming winter, being found in soils across a variety of land types, where they feed on the stems of broad-leaved plants at ground level. Pupation occurs in late winter, about 2-3 cm underground, with eclosion occurring during the following spring (Common, 1981; Warrant *et al.* 2016).

Bogong moth aggregations in the mountains were first reported in NSW by Bennet (1834) and later by Scott *et al.* (1872) but no satisfactory explanation for the moth assemblages was offered until that by Common (1952). In this and his later paper (Common ~~Common~~ 1954), Common argues that the reason for migration, and subsequent aestivation, is the increasingly unfavourable conditions of the breeding grounds. the basis was set for the scientific study of Bogong moths and their extraordinary migratory abilities.

Before Bogong moths begin to congregate at high elevations in the mountains to aestivate over the summer, a number of lower sites are usually occupied temporarily (Common 1954), most often at lower sub-alpine elevations in the mountains. However, in some years, and these lower sites may can also occur at a great distance from the mountain aestivation sites. ~~In particular years Bogong moths can occupy sites for instance~~ in houses, Parliament House in Canberra or other similar locations (such as sports grounds) where large bright lights attract them. These are 'accidental' sites, however, and away from lights Bogong moths may use a variety of ground-based sites such as dead trees. Moths have even been observed to congregate in small animal traps that have been used in dietary studies of mammals. The dates of the first Bogong moth arrivals at these lower sites can vary depending on the year and the location. ~~For example, at Mt. William (1167 m) in the Grampians in western Victoria – which is en route to the Victorian Alps – Bogong moth arrivals were recorded during October in 1976, during December in 1977 and during November in 1978 (Coekburn 1981). At a location near Nelligen on the NSW south coast, Bogong moths were flushed from their hiding places in a roadside embankment in mid-October, and near Braidwood in~~

~~southeast NSW, Bogong moths were seen feeding on *Eucalyptus* trees in bright sunshine (Common 1954).~~

Bogong moths eventually cease feeding and ascend to the caves to aestivate. The moth's aestivation sites include a variety of granitic locations in the Brindabella Ranges of the [Australian Capital Territory \(ACT\)](#) and NSW, and in the Bogong Peaks and Snowy Mountains of NSW, and at a number of granitic sites in Victoria, including Mt. Buffalo and the Jaithmathangs. These mountains are characterised by granitic outcrops and boulder fields (Common 1954), and include the highest sites where Bogong moths can aestivate and be observed throughout the summer. The basalt boulder fields of Victoria (e.g. on the Bogong and Hotham High Plains) also provide aestivation sites (Mansergh 1988; Mansergh and Heinze 2019). ~~Other sites in the Victorian Alps (such as Silurian schist and gneiss) do not provide sites where Bogong moths can easily be observed and numbers measured. In the summer of 1951-52, Bogong moths arrived at their aestivation caves on Mt. Gingera (at 1857 m in the Brindabella Ranges on the border of the Australian Capital Territory (ACT) and NSW) in late October, but in the exceptional peak summer of 1952-53 they arrived in much higher numbers, but not until after November 20th (Common 1954; Common 1980 & pers. com; Blakers 1980). Before this time the moths clustered gregariously during the day at lower elevations in the Brindabella Ranges between 1220 m and 1580 m.~~

The first 30 years of Bogong moth research ([1950-1980](#)) established the numbers of Bogong moths at a time when climate change was becoming an issue of concern, with the global mean surface temperature having now been established relative to the 1951–1980 mean (ASA Goddard Institute for Space Studies). In 60 years of recorded measurements from the central Snowy Mountains, there has been a steady decrease in the maximum depth of the snowpack, and a shortening of the mean duration of the snowpack, by 18.5 days. ~~This-These changes has-have~~ resulted from a mean temperature increase of 0.36°C per decade (Sánchez-Bayo and Green 2013), ~~and this which must also be accounted for when discussing may have also impacted~~ Bogong moth numbers.

~~There-Although there~~ has been some suspicion that moth numbers at aestivation sites have declined over the years (Flood 1980; but see a discussion in Blakers 1980), ~~but~~ records of Bogong moth abundance collated and/or collected by the authors over nearly 70 years ([detailed below](#)) indicate that we have now experienced a sudden and major decline (see also Mansergh and Heinze 2019). This occurred in the summer of 2017-18, the worst summer ever recorded for Bogong moth numbers, with very few moths seen in a continuously monitored cave on an unnamed peak above

Dead Horse Gap near Thredbo (2020 m), a boulder outcrop near South Ramshead in the Kosciuszko Main Range of NSW (which we, the first author's co-authors, in recognition of his long history of visits to the site, have dubbed "Ken Green Bogong"). In January 2019, no moths at all were found in this cave. This situation was mirrored in caves at a number of other mountain locations that had been studied over many years: Mt. Gingera (ACT/NSW/ACT—see Fig. 4), Mt. Morgan (NSW), Mt. Buffalo (Vic.) and the Bogong and Hotham High Plains (Vic.) (Mansergh and Heinze 2019). ~~Improvements-Increases~~ in moth numbers were observed in the NSW and ACT caves during the summer of 2019-20, but the population was still ~~significantly~~ depleted. This rapid decline ~~has~~ probably ~~created-had~~ a tremendous impact on the health of the alpine ecosystems of south-eastern Australia ~~which depend on~~as the massive influx of energy and nutrients that Bogong moths provide via their summer migration to the mountains (Green 2011) ~~had evaporated~~. The aim of this review is to examine the timing and causes of the dramatic decline in Bogong moth numbers in the Australian Alps.

To examine this decline, ~~we re-examined data collected in the early 1950s by Ian Common from Mt. Gingera, on the border between NSW and the ACT (Common 1952, 1954), and analysed our own data collected from a number of locations over the past 53 years—were analysed. This—These~~ data includes notes on Bogong moth arrivals ~~on the snow~~ and moth activity over four decades in ~~13 regularly surveyed aestivation sites across~~ the Snowy Mountains of NSW (KG: personal field notebooks and PhD data), data from ~~over four decades of~~ studies of the diet of foxes in the Snowy Mountains (KG: ~~biannual 6 km transects~~), Bogong moth activity on Mt. Gingera ~~in the ACT/NSW~~ (PC: ~~37 separate aestivation sites, observed approximately bi-weekly from September to May since 2014, excluding the summers of 2016-17 and 2017-18~~), records of Bogong moth numbers from aestivation sites at three elevations on Mt. Buffalo ~~in Victoria~~ over the past 53 years (MB), and moth collections from the Snowy Mountains, the Brindabella Ranges and the Mt. Kaputar National Park (northern NSW) for studies of Bogong moth migration (EW, DD and JW: ~~each year during spring and autumn since 2010~~).

OBSERVATIONS OF BOGONG MOTH NUMBERS IN SOUTHEAST AUSTRALIA

Observations of Bogong moths in southeast Australia

Larvae ~~in~~ the breeding grounds ~~and during migration to the mountains~~

Even though Bogong moths can be recorded elsewhere, regions of inland south-eastern Australia that possess grey cracking clays are the most common breeding grounds (Common 1954). We measured these areas in NSW and Queensland to obtain an approximate area of 101,180 km². Bogong moth larvae were ~~collected~~ surveyed from 29 sites in 2001, primarily in locations with grey cracking clays (Green 2008 – see Fig. 1). This resulted in a calculated density of 0.78 Bogong moth larvae per 10 m², (or 78,000 larvae km⁻²) giving a total of around ~~7.8992 b~~ million larvae within the region of grey cracking clays of NSW and Queensland. Adult Bogong moth numbers were also calculated for the Snowy Mountains, based on calculations of predation and other sources of mortality (Green 2010b) together with a percentage survival from Blakers (1980), to give a total number of ~~2,200 million-billion~~ adult Bogong moths. According to the Interim Biogeographic Regionalisation for Australia (IBRA), developed by the Australian Government, the Australian Alps consists of two subregions: the Snowy Mountains (IBRA code AUA01: area 713,114 Ha) and the Victorian Alps (IBRA code AUA02: area 519,866 Ha). The areas of these two subregions indicate that the Victorian Alps cover around 73% of the area of the Snowy Mountains (see the white alpine regions shown in Fig. 1). If we assume that moths are evenly spread over both alpine regions, this would imply that around 1.6 billion adults moths. Assuming the same number of adult moths are present in Victoria, this gives a total of 443.800 b million Bogong moths overall in the Australian Alps. If the figures above (~~7.8992~~ and ~~43.8400 b~~ million) are reliable, this would suggest an attrition of ~50% from Bogong moth larvae to post-migration adults. There are occasional records of Bogong moth adults occurring far from the Australian Alps during the summer (and at other times of the year), but these moths are in low numbers and none of them have been recorded aestivating in any other cave system outside the Australian Alps, either in NSW or Victoria. These moths may represent individuals from small non-migratory populations (Common 1954; Warrant *et al.* 2016).

Adults during migration

During migration, Bogong moths are apparently not attracted to caves along the route, and in areas where moth migration is commonly recorded, for example on Mt. Kaputar (EW), no evidence of Bogong moth aestivation was found in the bat-free caves around the summit (at 1510 m); although However, some of these caves housed other species of moths, such as the Granny's Cloak moth *Speiredonia spectans* (investigations in caves near the summit by KG in October 2015: Warrant *et al.* 2016).

As part of ~~ongoing~~ studies of the Bogong moth migration, adult moths were collected at light traps during spring on Mt. Kaputar in northern NSW. These moths were flying south-southwest (Dreyer *et al.* 2018) so had most likely originated in south-eastern Queensland (see Fig. 1). Moths were captured every third night with hundreds being caught during most trapping sessions from 2011 to 2015. In 2017, trapping re-commenced at Mt. Kaputar and in the first 10 days of November only 70 moths were caught. In 2018 ~~only~~ around 100 moths were caught over a two-week period in October. Trapping of adult moths – when moths were presumably at the beginning of their migration – was also undertaken at various locations along the Darling River in western NSW in mid-October 2016, with 41 moths taken over 2 nights with a light trap near Wentworth ~~good numbers of moths being caught on favourable nights using a light trap near Wentworth (41 moths over 2 nights)~~ and at Wilcannia (42 moths on a single night at Wilcannia). Some nights had adverse weather conditions (very low temperatures and/or rain) and on these nights no moths were trapped. The winter and spring of 2016 were very wet across NSW with major flooding occurring in several regions of the central west – the grasslands of western NSW were dense and lush during that particular spring.

In the following year – 2017, the first year of ~~our~~ the recent current extreme drought – light trapping of adults was again undertaken on the Western Plains during the last two weeks of October – at Hay, Wentworth, Wilcannia and Bourke. Of the 44 Bogong moths caught over that two-week period, 42 of them were caught over several nights at Hay. Trapping was again undertaken for the entire month of October in 2018 near Hay, Wentworth, and west of the Grampians in Victoria, with even lower numbers than the previous year – around 30 moths in almost as many nights.

Thus, although light-trapping observations of adult migrants, many hundreds of kilometres from the Australian Alps, have only been made since 2010, Bogong moths were highly abundant from 2010 until 2016 but suffered a dramatic drop in their numbers from 2017 to 2020. This implies that the crash in Bogong moth numbers observed in the Australian Alps over the same period was primarily due to losses in their breeding grounds, and not to conditions prevailing at their high elevation aestivation sites (albeit some further losses may also have occurred in the mountains). During migration, Bogong moths are apparently not attracted to caves along the route, and in areas where moth migration is commonly recorded, for example on Mt. Kaputar (EW), no evidence of Bogong moth aestivation was found in the bat free caves around the summit (at 1510

m), although some of these caves housed other species of moths, such as Granny's Cloak moths *Speiredonia spectans* (investigations in caves near the summit by KG in October 2015; Warrant *et al.* 2016).

Arrival in the mountains

As Bogong moths arrive in the vicinity of the caves in the Australian Alps, they first arrive at lower elevations where they shelter and feed until conditions improve sufficiently at higher elevations to ascend to their aestivation caves (Common 1954; Warrant *et al.* 2016). In the Brindabella Ranges, 'temporary camps' are occupied at lower elevations between 1220 and 1580 m (Common 1954). They have also been observed and Bogong moths were observed on the summit of Mt. Coree (1275 m) in December 2013 (Ben Keaney, pers. com.). On 2 November 2015, many Bogong moths were found sheltering under some of the myriad loose rocks on the summit of Mt. Coree (KG and Mary Green pers. obs.) but none were found in December 2018 (Ben Keaney, pers. com.). In spring at lower elevations in the northern parts of the Snowy Mountains, notably Mountain pygmy-possums *Burramys parvus* were observed feeding on Bogong moths in spring at low elevations, including Happy Jacks (1240 m) and Snow Ridge (1495 m) (Gibson *et al.* 2018).

During weekly surveys of several aestivation sites on Mt. Gingera, during two summers (2014-2015 and 2015-2016), Caley and Welvaert (2018) found that moths arrived approximately one month earlier (in the first week of October) and left one month earlier (during early March) than they did during the surveys conducted by Ian Common during the early 1950s (arrival in mid-November, and departure during early April: Common 1954). This is consistent with the recent decades of warmer climate, but further surveys are needed to ascertain whether confirm this trend truly holds.

When the Bogong moths arrive at these lower elevations, it is likely that snow still blocks the entrances to their aestivation caves at higher elevations, and Bogong moths may avoid them during this period. However, Bogong moths can shelter at higher sites without snow blockage, even where sub-zero temperatures have been recorded using temperature loggers (e.g. in a subalpine tree stump at 1860 m on 14 October 2001 and in an alpine cave at 1940 m on 10 November 2001). Most moths, however, are likely to be elsewhere, feeding or waiting at lower elevations to move up

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hill to the aestivation sites. The lack of suitable sites at these elevations makes it difficult to obtain data on these locations. However, predators such as as mountain pygmy possums and foxes provide a suitable source of data. The diet of ~~these animals~~foxes was studied along a transect from 1500-1800 m elevation at Schlink Pass in the Kosciuszko National Park (Green and Osborne 1981), with fox scats collected monthly from December 1978 to February 1980 (although these were not studied according to elevation). Of the 1159 scats collected and ~~studied~~analysed, 151 contained only Bogong moth remains (Green and Osborne 1981). The number of Bogong moths present in scats increased from October to peak in December-January, both in 1978 and 1979, and declined to zero in May 1979 (Green and Osborne 1981). This indicates that moth numbers rose early post snow-thaw, ~~correlated with high numbers of scats~~ below ~~the elevation~~the elevation of Schlink Pass (1800 m). As moth numbers fell in scats from the 1500-1800 m elevation band after their December peak, foxes were probably still feeding on moths at elevations above 1800 m – at aestivating sites such as that at Dicky Cooper Bogong (1985 m, above Schlink Pass) – possibly defecating up there rather than at lower elevations where scats were being studied.

Fox diet was ~~further~~also studied at well separated alpine and subalpine study sites (Green 2010b). This showed that Bogong moth numbers in scats at subalpine sites again peaked in December-January, declining rapidly from January with low numbers thereafter (Green 2010b). By contrast, at alpine sites, numbers remained high and in fact increased (Green 2010b) (Fig. 2). The year 1996-97 showed a later arrival than in 1997-~~1998~~ but received more Bogong moth arrivals later in the season (Fig. 2). This indicates that Bogong moths were moving to higher elevations as summer progressed, and the same pattern can be observed from studies of the scats of the Mountain pygmy-possum *B. parvus* (Gibson *et al.* 2018, Table 1).

The first arrivals of Bogong moths above the snowline have been recorded by one of us (KG) by ski surveys occurring on an almost daily basis from August until October since 1979 (Fig. 3). The earliest arrival ever recorded was in 1980 ~~— day 247 (on 3 September)~~. There is a considerable spread in arrival days across years, certainly due to yearly differences in weather conditions (e.g. harshness of winter). The latest arrival was recorded in 2008 – on ~~day 284 (10 October)~~ – although for the years before and after, Bogong moths arrived almost a month earlier.

Ascent and occupation of aestivation caves

~~When conditions become less favourable at lower elevations, for instance due to rising temperatures, Bogong moths ascend to their aestivation ceaves in the alpine zone above the tree-line. Temperature is probably a major factor setting the lowest elevation where aestivation is possible, and this is likely to be related to summer temperatures within the caves, although significant variation in this temperature occurs depending on the location (Table 2).~~

Feeding limits may trigger ascent

~~Once moths ascend to the alpine zone (i.e. above the treeline), food availability is significantly lessened, and this may be a trigger that initiates aestivation. Of 62 alpine plant species recorded in a study from December 1983, only one species—Epaeris paludosa—was recorded with ‘many’ Bogong moths (observed on 31 December: Inouye and Pyke 1988). Thus, although Bogong moths are recorded feeding from alpine plants in the Snowy Mountains, the major last-chance food source prior to the commencement of aestivation is flowering snow gums Eucalyptus pauciflora niphophila. The earliest record for snow gums flowering at alpine treeline elevations in the Snowy Mountains is, on average, around the end of December (Table 2). This is also the case at Mt. Buffalo in Victoria (MB, pers. obs). Flowers then remain available for 4-6 weeks. This may also vary with location. For instance, snow gums E. p. niphophila on Mt. Morgan in NSW were flowering profusely on 7 January 2019, but just 2 days later, at nearby Mt. Gingera, there were no snow gums flowering at all. If food availability becomes limited, aestivation would become the only option for Bogong moths.~~

Minimum elevation of aestivation sites

~~When conditions become less favourable at lower elevations, Bogong moths ascend to their aestivation ceaves. But what is the lowest elevation where aestivation is possible? The answer is almost certainly related to summer temperatures within the caves, although surprising variation occurs depending on the location (Table 3).~~

Numbers of aestivating moths Aestivation from 1951-2017: the decline

Qualitative observations of Bogong moth numbers at four main locations in the Australian Alps

Commented [EW1]: I realise that I am not sure what we are trying to say here, and the reviewers questioned it too. The tree-line snow gums start flowering only after 99% of Bogongs are already aestivating. Are we trying to say here that because of this, there is really no food at aestivation elevations as moths are arriving during November and December (since the snow gums don't flower until new year), and because of this dearth of food the moths might as well enter aestivation after arrival.

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10 have been made continuously or sporadically by a number of individuals (including the authors)
11 over the past 70 years (Table 4). A number of aestivation sites at each location were typically
12 sampled. The locations were Mt. Gingera in the Brindabella Ranges, on the border of the ACT and
13 NSW, Ken Green Bogong on the Main Range in the Snowy Mountains in NSW and Mt. Buffalo
14 and Mt. Higginbotham in the Victorian alps.

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18 The Mt. Gingera site, is the site used by where Ian Common first described the aestivation and
19 natural history of Bogong moths in the early 1950s (Common 1954). Common's counts revealed
20 as many as 17,000 aestivating moths tiled onto every square metre of cave wall (subsequent
21 estimates from the three-dimensional spaces provided by a boulder field suggest >50,000
22 moths/m³; Mansergh and Heinze 2019). does appear to have been affected by climate change.
23 Common made at least one visit to Mt. Gingera every summer at the peak of the aestivation from
24 1951 until 1980, but made no mention of declining numbers over this period in his final paper on
25 Bogong moths in the early 1980s (Common 1981), suggesting that moth numbers probably
26 changed little. Records were not kept or available at from Mt. Gingera from about 1980 until 2014.
27 However, since 2014, one of us (PC) has made weekly or fortnightly surveys of 37 aestivation sites
28 around the summit of Mt. Gingera. As mentioned above, during the summers of 2014-2015 and
29 2015-2016, Caley and Welvaert (2018) found that although Bogong moth numbers were high (Fig.
30 4), most had arrived, and also departed, one month earlier than observed by Common in the early
31 1950s (Common 1954). had departed from Mt. Gingera before the end of January (Caley and
32 Welvaert 2018). Their early arrival, as well as their early departure, long before the expected end
33 of the complete aestivation period, suggests that moths were departing because conditions
34 (possibly temperature and humidity) were no longer suitable for aestivation, a shift consistent with
35 recent decades of climate warming.

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42 Through until about 1980 it did not demonstrate major changes (or at least none were recorded by
43 Common in 1980). In the summer of 1972-73 the only site in NSW where Bogong moths were
44 recorded was in the Bogong Peaks (Flood 1980) suggesting that there may have been low numbers
45 at Mt. Gingera. Long-term records of Bogong moth numbers, have also been kept from caves on
46 Mt. Buffalo (1600-1723 m) in Victoria (started in the mid-1960s) and caves at different elevations
47 at on the unnamed peak "Ken Green Bogong" (1860-2020 m), a boulder outcrop above Dead
48 Horse Gap, near South Ramshead in the Kosciuszko Main Range of NSW (started in the mid-
49 1970s), also reveal interesting trends (Table 5 Table 4). At both locations, moth numbers were high
50 and stable until the early 1980s. For all summers between 1966-1967 and 1981-1982 (with the
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exception of 1968-1969), Bogong moths were found regularly at the lowest site on 'The Horn' on Mt. Buffalo, at an elevation of around 1600 m, even during the drought period of 1979 to 1983 which revealed little impact on Bogong moth numbers either here or at Ken Green Bogong (Table 4). During the final summer of this drought (1982-1983), moths declined at Ken Green Bogong and possibly also at Mt. Buffalo (Table 4). This summer experienced the arrival of heavy deposits of red soil from drought-impacted lands in the west of NSW (KG pers. obs., 20 November 1982).

From the early 1980s, moth numbers at Ken Green Bogong began to fluctuate significantly from year to year, and on average began to decline (Table 4). Similar fluctuations were also noted within the basalt boulder fields of the Bogong and Hotham High Plains in Victoria's alpine region (Mansergh and Heinze 2019). At Mt. Buffalo, moths continued to occupy one or both of the two lower sites (at similar elevations) until at least the summer of 1992-1993; however, observations over the following 20 years do not reveal whether moths continued this trend or whether during some years they could only occupy the highest (coolest) caves.

Records over the drought periods of 1979 to 1983 showed little impact on Bogong moths at Ken Green Bogong or Mt. Buffalo until the final summer (1982-83) when moths declined on both Mt. Buffalo and Ken Green Bogong (Table 5). This summer experienced the arrival of heavy deposits of red soil from drought-impacted lands in the west of NSW (KG pers. obs., 20 November 1982). Records were not kept or available at Mt. Gingera from about 1980 until 2014. In the summers of 2014-15 and 2015-16, although Bogong moth numbers were high (Fig. 4), most had departed from Mt. Gingera before the end of January (Caley and Welvaert 2018). This early departure, long before the expected end of the complete aestivation period, suggests that moths were departing because conditions were no longer suitable for aestivation. At Ken Green Bogong populations were recorded differently but showed a variety of good and bad years (Table 5). For all summers between 1966-67 and 1981-82 (with the exception of 1968-69), Bogong moths were found regularly at the lowest site on 'The Horn' on Mt. Buffalo, at an elevation of around 1600 m, and continued at a mid-level site (at about the same elevation) until the summer of 1992-93 (Table 5). By summer 1994-95 a poor moth year commenced a regular decline in moth numbers in the Snowy Mountains, and possibly also on Mt. Buffalo (Table 5).

Numbers of aestivating moths Aestivation from 2017-2020: the crash

From the summer of 2017-2018, the numbers of aestivating Bogong moths we encountered in the Australian Alps fell dramatically (Table 4). In addition to the aestivation sites listed in Table 4, two

~~others have also been A number of aestivation caves were visited~~ regularly visited since 2013 (in conjunction with studies of the sensory basis of the Bogong moth migration, ~~(based at Lund University: Warrant *et al.* 2016; Dreyer *et al.* 2018), with moth samples taken from the same sites as used in a study of arsenic (Green 2008): Mt. Gingera (Fig. 4), Mt. Morgan (1852 m) and South Ramshead in the northern and southern Snowy Mountains and at Mt. Tingaringy (NSW/Vic 1434 m) in the northern and eastern Snowy Mountains respectively).~~

In the summer of 2017–2018 moths were absent from Mt. Morgan and Mt. Gingera (observations were made on 7 and 8 January, respectively, and again on 4 and 2 February, respectively). At the summit of the “Ken Green Bogong”, which was visited on 10 January and 5 February 2018, the walls of the main cave ~~was were~~ empty, with moths only found in deep crevices. This was ~~reported as~~ the lowest number of Bogong moths ever recorded for this location (KG), with a similar report from Mount Buffalo for 18 and 19 January 2018 (MB).

~~Expecting During~~ the following summer season of 2018–2019 ~~to be equally bad~~, Mt. Buffalo was investigated on 16 December 2018 and no moths were found (KG). The following day, ~~on 17 December, Bogong~~ moths were observed in three deep locations of the major upper cave on “Ken Green Bogong (2020 m)”. Three other caves at lower elevations near “Ken Green Bogong” were empty, apart from three moths inside one cave (KG). At the same time ~~at on~~ Mt. Gingera very few moths were observed (Fig. 4). On 7 January 2019 only one live Bogong moth was found on Mt. Morgan and three were found on Mt. Gingera. On 9 January, seven moths were observed at “Ken Green Bogong”. At higher elevations on the Kosciuszko Main Range, ~~larger numbers of —and somewhat later in the season —~~ moths were however found at two locations (KG): Club Lake (1950 m) on 10 February and Mt. Kosciuszko (2100 m) on 21 February 2019 ~~(2100 m) where in 2014 the January–February mean temperature was measured as 11.7°C (KG)~~. Further south in Victoria, in early January 2018, the only Bogong moths observed on Mt. Buffalo were a handful of moths in the upper cave under ‘The Horn’ (1723 m), while in January the following year (2019) moths were entirely absent (MB). This ~~almost sudden total complete~~ absence of Bogong moths in previously richly populated caves, both in NSW and Victoria, ~~has had~~ never previously been observed in over half a century of observations.

During the spring of 2019, unexpectedly high numbers of Bogong moths flew into the Snowy Mountains and the Victorian Alps, despite little relief in the ~~current~~ drought. Why or how this was possible is not ~~entirely~~ clear. There were localised heavy falls of rainfall in areas of southwest

Queensland from February to April 2019, leading to flooding in some areas of southern Queensland that extended into northern NSW. These weather patterns also led to reasonable falls in localised areas of western NSW that may have promoted Bogong moth reproduction and survival. However, no matter what the cause, the improved-increased numbers of moths entering the mountains during the spring of 2019 translated into considerably healthier-larger aestivating cave populations than seen in the previous two summers (but nowhere near as healthy-high as before the drought), although apparently only at higher elevations. On Mt. Gingera (1760 m, Fig. 4), a lower elevation site, the number of aestivation sites occupied were many fewer than during previous recent summers (with the exception of the 2018-2019 summer when the numbers of occupied sites were even fewer). Following the devastating sub-alpine fires of early January 2020, few Bogong moths remained at these high elevation aestivation sites after mid-February, either having succumbed to smoke, or having been washed out of the caves by heavy rains that came in the first half of February or having departed for the breeding grounds earlier than normal.

Maximum temperature for aestivation

~~To determine the impact of climate change on the population size of aestivating Bogong moths, we require knowledge of the maximum temperature at which aestivation can occur. There is little evidence that this has ever been studied scientifically, or even noted. Bogong moths aestivate in a sexually immature condition and do not feed (Common 1954). Temperatures at aestivation sites in the Snowy Mountains were recorded using Plus 2 Tiny Tags over the summer of 2009-10, every hour throughout January and February. Temperature measurements from the main study site on Mt. Gingera (1760 m) were made over two years (1952-53) by Common (1954). A lower elevation site at Mt. Little Ginini (1525 m) would have been 2.1°C warmer due to the lapse rate (Green 2014). Common used this (temperature un-measured) site only in the cooler of these two years (1953) when its extrapolated average January-February temperature would have been 12.1°C (Table 4) – during 1952 this mean temperature would likely have been 14.8°C. This then is a suggested maximum temperature for aestivation. [The average January-February temperature was 10.0°C at Mt. Gingera in the cooler year (1953) and 12.7°C in the warmer year (1952, Table 4). Sites in the Snowy Mountains where Bogong moths are common in spring but depart during January and February include Charlotte Pass (1755 m, Jan-Feb mean of 13.8°C) and “Ken Green Bogong” (1940 m, Jan-Feb mean of 11.9°C). At Mt. Buffalo, Bogong moth aestivation was recorded during the summer of 1966-67 in the lower cave at 1600 m which, being 1.16° of latitude south of Mt. Gingera, would have an adjusted elevation of 1700 m and a January-February temperature (based~~

Commented [EW2]: For the reasons/worries listed below, I wonder if we should leave this section out? I think we might be in a position to say which maximum daily cave temperatures moths have been shown to aestivate in (i.e. all of the data given below), but I am not sure we can say with any certainty what the exact upper permissible temperature is. This is still something that needs to be carefully investigated. I think it is unlikely they would aestivate happily at 20°C, but it is clear they happily do so at 14.8°C (at Little Ginini in 1951-52 – see below). I suspect that the maximum temperature will lie somewhere between 15 and 20°C, although my guess is closer to 15°C than 20°C. But exactly which temperature remains unknown.

Commented [EW3]: I realise now I don't understand the arguments in this section nor the "evidence" to support them. We claim here that 14.8°C is likely to be the highest temperature that permits aestivation. But how did we arrive at that conclusion? The data from Common 1954 argues the opposite. At the top of page 229 he writes that moths occupied Mt Little Ginini all summer in 1951-52 (the warm year with the 14.8°C mean Jan-Feb max temperature), but in the cooler year they were only present during the spring and early summer (and had presumably moved upwards)

Commented [EW4]: Shouldn't this be *before* January and February? I think by January they will all have ascended to higher elevations, plus that would support the argument better because the implication is that it gets too warm at these lower locations to aestivate, although all the temperatures here are well below the suggested max temperature of 14.8°C, so his shouldn't have been the motivation to seek higher ground.

on Mt. Gingera ~~—corrected~~) of 13.2°C.

~~Discussion~~ DISCUSSION

Our results, taken together with ~~earlier~~ observations by Ian Common in the early 1950s, suggest that the Bogong moth population ~~was stable until the early 1980s but since then~~ has fluctuated, been and on average slowly declining-declined, over the past half century, and has until crashed crashing over the last 2-3 years. This rapid decline has probably ~~created-had~~ a tremendous deleterious impact on the health of the alpine ecosystems of south-eastern Australia which depend on the massive influx of energy and nutrients that Bogong moths provide via their summer migration to the mountains (4929 GJ of energy, 7.2 tons of nitrogen and 0.97 tons of phosphorus: Green 2011).

The years 1951-1980 can probably be considered a basis-baseline for 'normal' post-European population numbers of Bogong moths (Common 1954, 1981~~0~~). In winter 1980, there was an extensive outbreak of caterpillars in south-western NSW, with Bogong moths being particularly numerous (Drake and Farrow 1985). This winter outbreak also coincided with the earliest records of Bogong moth arrivals above the snowline of the Snowy Mountains (Fig. 3), and that summer moth numbers were not only high in the Snowy Mountains but also in the Victorian Alps, at Mt. Buffalo (Mansergh pers. com. 2019), ~~at Mt. Buffalo and Mt. Gingera~~. Moth numbers subsequently began to decline in Victoria (~~Table 5~~ Table 4) although there ~~appear to be~~ no data for Mt. Gingera (Ian Common last wrote of Bogong moths on Mt. Gingera in 1981~~0~~), nor for the Snowy Mountains (between 1983-1994 only one record is available: from 1988 – KG pers. obs.). From the mid-1990s moth numbers started to fall in the Snowy Mountains and likely also on Mt. Buffalo (~~Table 5~~ Table 4).

Admittedly the data we present here are necessarily sketchy. Until very recently, data on moth numbers were collected either for scientific reasons (to answer completely different questions from those presented here), or as a result of curiosity and interest (e.g., the long-term records of MB from Mt. Buffalo). In the past, few could have predicted that Bogong moths, usually common and plentiful in the Australian Alps, could now become so threatened, thus motivating the type of extensive population monitoring that would have strengthened the conclusions of this review (and which are likely warranted in the future). Thus our data only represent a handful of aestivation sites

– fewer than 70 – although these are spread across their full latitudinal range and at a number of elevations. But this admittedly fragmented data – complemented by analyses of the faeces of Bogong moth predators – show that Bogong moth numbers are worryingly in decline.

There are several possible causes of ~~the Bogong moth~~ this decline, including agricultural practices (~~including e.g.,~~ habitat loss and insecticides), climate change (particularly drought), and other factors (e.g., foxes, pigs, traditional hunting, urban light pollution). These factors have been implicated in the recent dramatic declines of insects across the globe, both in terms of population loss and species extinctions (with Lepidoptera prominent: Hallmann *et al.* 2017; Sánchez-Bayo and Wyckhuy 2019; Goulson 2019; Wagner 2020). We discuss each of these factors in turn. We discuss each of these three key factors in turn.

~~Are agricultural practices influencing decline?~~

Agricultural practices in the landscape are very likely to have had an impact on Bogong moths. Unfortunately, there is no consistent data on whether Bogong moth numbers have declined in the breeding areas of western NSW (and hence in the mountains). If, after 1980, farming practices gradually reduced the number of Bogong moths in the breeding areas over the following 35 years, it is still difficult to disentangle agricultural impacts (e.g., habitat loss and pesticide use) from impacts arising from the increasing temperatures that have resulted from climate change.

To address the possible impacts of pesticides, Bogong moths were collected in 2001 from a cave at “Ken Green Bogong” (1940 m) and were analysed by the New South Wales Department of Agriculture for sub-lethal levels of 59 chemicals currently used in agriculture. These analyses revealed no traces of these agricultural chemicals. Bogong moths killed by spraying in Parliament House in Canberra were collected in spring 2003 and were analysed for 139 different chemicals by the Australian Environmental Protection Authority. The pesticide used – Deltamethrin (USEPA/OPP Pesticide Code: 097805) – was recorded at a rate of 0.95 mg kg⁻¹. Deltamethrin is a pyrethroid ester insecticide and the main constituent of Cislin 10, one of the most popular insecticides in the world, ~~and this chemical was used to kill Bogong moths at Parliament House (Hansard 2003).~~ Apart from Deltamethrin, the moths collected at Parliament House ~~in spring 2003~~ contained only trace concentrations of other pesticides. ~~(Hansard 2003).~~

When deltamethrin enters the soil, it binds tightly to soil particles (National Pesticide Information Centre 2010). Deltamethrin is commonly used ~~on moths against Lepidoptera~~ and kills on contact, or by larval consumption in the soil (EXTOXNET 1996). It does not persist ~~for a long time~~ in soil, with degradation occurring within 1-2 weeks (EXTOXNET 1995). This suggests that Deltamethrin would generally kill Bogong moths, ~~and that even sub-lethal levels would not persist long enough to allow it to be found in moths collected in the mountains~~. The recent use of neonicotinoids (which has a persistence in plants of 1-2 years) has also very likely impacted the survival rate of Bogong moth larvae in the breeding areas where applied. New chemical analyses of Bogong moths are urgently needed to check whether neonicotinoids are present in their tissues. ~~Insects have recently declined dramatically across the globe, both in terms of biomass and diversity (with Lepidoptera prominent), and this has been blamed on habitat loss, synthetic pesticides, biological factors and climate change (Hallmann *et al.* 2017; Sánchez-Bayo and Wyckhuy 2019; Goulson 2019).~~

Chemical spraying of pesticides at Bogong moth breeding sites occurs mainly on broadacre farm land in areas of grain production that lie ~~(in 2014-15)~~ in the central-east and southern regions of NSW and extend into southern Queensland (Fig. 1). The biggest farming change in this area has been the southward shift of cotton growing, taking in large areas ~~of the country~~ along the Murrumbidgee River (Michael Nash, pers. com.). The pesticides now used ~~(and their quantities: Zalucki *et al.* 2009)~~ may well have changed since Bogong moths were collected and analysed in 2001 and 2003 (Green 2008). Indeed, the introduction of neonicotinoids in the late 1990s to broadacre farming regions of southeast Australia (Nash *et al.* 2019) may now be having an impact on Bogong moth populations. These insecticides are currently under heavy scrutiny for their adverse effects on economically beneficial insects such as bees and were partially banned in Europe in 2013. Even though the specific effects of neonicotinoids on ~~Lepidopterans~~ lepidopterans is currently unknown, various species of moths (and particularly noctuids) are considered agricultural pests and are no doubt a target of these insecticides.

~~The total cost of pesticides targeting invertebrate pests in Australian agriculture during 2016-17, including those used in broadacre farming, was \$613 million (Nash *et al.* 2019). However, little insecticide was used on arable dryland country in the Murray-Darling Basin (Fig. 1) over the 'last couple of years' due to drought conditions (Michael Nash, pers. com.). Further west, in rough grazing and native vegetation country (Fig. 1), traditional pastoral lease holders would have used even lower amounts of pesticides. Thus, the extent to which neonicotinoids and other types of~~

insecticides may have contributed to the Bogong moth decline is presently unknown.

Two agriculture activities made possible by the availability of irrigation water – the production of rice and cotton – may also adversely affect Bogong moth numbers. In Australia, rice is grown in ~~immense~~ irrigated ~~paddocks~~ ~~fields~~ which ~~means that exclude~~ Bogong moths ~~cannot use these areas~~ (since the larval and pupal stages are subterranean). On average, the annual production area of rice is between 65,000–90,000 hectares (most of which is in the Murrumbidgee and Murray valleys – Plant Health Australia 2020). Since Bogong moth density in these areas is estimated at 0.78 moths per 10 m² (Green 2008, see above), the loss of moths due to habitat loss would be 50.7–70.2 million moths annually, compared to pre-European conditions.

~~C~~Cotton ~~plantations~~ ~~plantings~~ may have also impacted Bogong moth numbers. ~~D~~(disregarding any impacts by spraying, ~~which has decreased since the 1996 introduction of genetically modified cotton (which expresses a bt toxin gene: Zalucki et al. 2009, Zalucki 2015), cotton fields are~~ monocultures without any grass between the cotton plants – hence resulting in no suitable food ~~plants~~ for Bogong moth larvae. Although some cotton has been grown in Australia since ~~about~~ the 1820s, by 1951 an established cotton industry was still essentially non-existent. Using water from newly constructed dams, cotton production ~~reached~~ ~~increased to~~ 435,000 bales per annum by 1980, and by 1985 it had more than doubled to 1.1 million bales per annum. A further doubling occurred by 1992, and by 2011–2012 production was 5.3 million bales per annum (de Garis 2013). ~~Even though the combined area of cotton fields that have successfully produced cotton has fluctuated significantly over the last two decades due to drought (Zalucki 2015), the area of cotton fields themselves (productive or otherwise) has grown.~~ For Bogong moth areas in NSW and southern Queensland cotton fields cover an area of 483,890 hectares. ~~Whether productive or not, these cotton fields remain fallow and empty over winter and are thus highly unsuitable as Bogong moth breeding grounds.~~ Again, assuming 0.78 Bogong moths per 10 m², and assuming cotton growing areas do not support Bogong moths, this means the loss of a further 377.4 million moths annually, compared to pre-European conditions.

Thus, cotton and rice cultivation in the grey cracking clays natal areas has resulted in a current-day ~~deletion of close to~~ ~~reduction of almost~~ half a billion moths from the Bogong moth population annually. Of these, around half would likely have arrived in the mountains (where ~~around close to~~ 4 billion are thought to arrive annually in regular years: Green 2010b, ~~and see above~~). This loss – currently around 1/16 of total moth arrivals – gradually grew from 1980.

Thus, habitat loss via rice and cotton farming ~~and the use of synthetic pesticides~~, have almost certainly ~~had a significant role in~~ contributed to the slow long-term decline of the Bogong moth. The role of synthetic pesticides is much less clear, and longer-term monitoring studies, particularly to determine the impact of neonicotinoids and other commonly used insecticides on Bogong moth decline, are urgently required to quantify these roles more precisely.

Climate change

Effects of temperature

Climate change and Bogong moth arrivals in the mountains.

Increasing temperatures through climate change appears to have had no impact on the arrival time-date of Bogong moths in the Snowy Mountains as arrivals have been highly variable (Fig. 3). However, the arrival time-date of Bogong moths does have an impact on alpine fauna because for many species they provide the only available food immediately after the snowmelt. Animals dependent upon winter snow cover are becoming active earlier because of a decreasing snow mass and an increasingly earlier snowmelt (on average, about 2.75 days earlier per decade since the early 1950s: Green 2010a). With little else as a food source, an earlier arrival time-date of for Bogong moths thus becomes critical. However, ~~the moths are there~~ is no evidence for this as arrival dates are highly variable arriving significantly later relative to the date of snowmelt – in fact, 25 days later (Fig. 3, Green 2010a). For instance in 1952, a good moth year, the Brindabella Range, in early September 1952 (a good moth year), Bogong moths were recorded arriving nearly a month in the Brindabella Ranges in early September, nearly a month earlier than in 1951 (Common 1954). A similar difference in first arrival dates (37 days, from 4 September to 11 October) occurred in the Snowy Mountains during 40 years of observations (Fig. 3). As with Common's 1952 record, the earliest arrival date recorded in these later observations (Fig. 3) was in 1980, which was also a “good” moth year. However, an early arrival date is not necessarily associated with a “good” moth year – the early arrival years of 2007 and 2009 were years with low numbers of moths, as appears to be the case for the third earliest arrival in 2019, while the late arrival years of 2012 and 2016 were years with high numbers of moths. These observations suggest that some other factor, rather than the snow duration in the mountains, determines either the arrival date in the mountains or the date of departure from the breeding areas. Indeed, factors along the migratory route – such as

weather conditions or the availability of food from flowering plants such as eucalypts – may affect the length and/or duration of the migratory journey and thus the arrival time in the mountains.

Climate change and aestivation

Aestivation. Despite differences in arrival date, the movement of Bogong moths into the aestivation caves is more likely to be affected by the climate in the mountains themselves. In both 1951 and 1952 on Mt. Gingera, Common (1954) first recorded Bogong moths in the ‘chief observational cave’ (an aestivation cave) on 20 November in 1951 and 26 November in 1952. However, the arrival of moths in their aestivation sites in 2014 and 2015 was approximately six weeks earlier (Fig. 4, Caley and Welvaert 2018). Moreover, Caley and Welvaert (2018) noted that the greatest numbers of moths occurred on 1 November 2014 and 5 November 2015 and that moth numbers had already declined before the date that Common recorded the maximum moth number in the same cave in 1951 and 1952 (1 January). This suggests that Mt. Gingera is no longer a preferred aestivation site, but rather has become a temporary camp before ascent to caves at higher elevations. Indeed, even as early as 1954, Common had hypothesised that Bogong moths might use Mt. Gingera as merely a stopover during their migration route between it and higher elevations in the Snowy Mountains, both in the autumnal migration (~~definitely~~) and possibly in the summer, as in the hot summer of January-February 1952 (~~Table 6~~Table 5).

The fact that moth declines are becoming noticeable at lower elevations, such as those ~~on close to the summit~~ Mt. Gingera (ca. ~~1760-1840~~ m), can be explained by either of two possible (non-mutually exclusive) scenarios: (1) lower elevation aestivation sites are becoming less suitable due to climate change, or (2) higher elevation aestivation sites have always been preferred by the moths, but when high numbers of moths filled the higher sites, additional moths were forced to aestivate at the lower (and less-preferred) sites, so that when moth numbers began to decline, these lower sites emptied first.

~~The first~~Both of these scenarios ~~is~~are supported by the long-term moth declines observed at lower elevations on Mt. Gingera in the Australian Alps. Similar lower elevation declines occurred in the lower caves on Mt Buffalo during the summers of 1982-83 and 1993-94 and these too could have been a result of unsuitable conditions.The lower cave on South RamsheadKen Green Bogong has almost always had a high number of moths in early spring-summer, but numbers decline to zero

in mid-summer as moths move higher. This situation could well have ~~been the case~~ been mirrored on Mt. Gingera during the summers of 2014-~~2015~~ and, 2015-16 and 2019-2020 when Bogong moth numbers ~~first rose and then~~ declined (up to two months earlier than they did during the summer of 1953-~~1954~~; (Common 1954; Caley and Welvaert 2018; Fig. 4). ~~Unfortunately, during the summers of 2011-12 and 2013-14, which we recorded as “good years” higher in the mountains, we visited Mt. Gingera only in January, and by then most moths may have moved to higher elevations. During the summer of 2019-20 on Mt. Gingera (Fig. 4) there was again an early peak in Bogong moth numbers, followed by an early decline (in December).~~ Based on the January 2019 mean maximum temperature of 15.7°C in the lower ~~(1860 m) South Ramshead cave at~~ (Ken Green Bogong; ~~(Table 6) Table 5~~), the mean maximum temperature of the upper cave ~~(2020 m)~~ would have been 15.0°C (Green 2014). This temperature, higher than that measured by Common (1954) in the cave near the summit of Mt. Gingera ~~(ca. 1840 m)~~ during the hot summer of 1951-~~1952~~, suggests that Ken Green Bogong ~~was probably~~ may have been unsuitable for Bogong moths and that they ~~likely might have~~ migrated further up hill. Indeed, during the summer of 2018-~~2019~~, Bogong moths appeared to be in good numbers only in locations just below the summit of Mt. Kosciuszko where cave temperatures would have been around 13.0°C (Green 2014). ~~Thus, during this summer the upper cave at Ken Green Bogong was either too warm (at 15.0°C) for aestivation (scenario 1), and/or the lower numbers of moths in the mountains were entirely accommodated within the highest (and preferred) aestivation sites, leaving the lower sites (like those at Ken Green Bogong) empty (scenario 2).~~

Hence, during this summer — even at the highest elevations in Australia — Bogong moths experienced temperatures approaching the maximum permissible for aestivation. In other words, quite irrespective of other causes of decline, Bogong moths face a significant future threat from climate change.

The first scenario – that lower aestivation sites are becoming less suitable due to climate change – would require that these sites have acquired average maximum temperatures that exceed the maximum for which aestivation is permitted. However, this maximum temperature has never been determined scientifically.

The second of these scenarios is supported by the following events. The summer of 1952-53 was cold at Mt. Gingera, even colder than many subsequent years at the higher “Ken Green Bogong” (Table 4). If space was a limiting factor, Bogong moths would have likely moved from Mt. Gingera to higher elevations in the Snowy Mountains, but instead they chose to stay at lower less favourable

sites at Little Ginini (1525-1585 m). In 1953, Bogong moths were most numerous in January when there was an average temperature of 10.5°C (Table 6), but with the coldest January temperatures between 2006-2017 occurring in 2015 (10.5°C) and 2016 (10.8°C), this suggests that unsuitable temperature was not the reason for low Bogong moth numbers in the caves but that they were presumably migrating onwards.

The maximum known aestivation temperature from 1951 to about 1993 appears to be about 14.5°C (with an estimate of 14.8°C in a non-aestivating year at Mt. Little Ginini). From the turn of this century, Bogong moths at aestivation sites on Mt. Gingera have declined during a 0.9°C temperature increase (i.e. 0.36°C per decade: Sánchez-Bayo and Green 2013). These aestivation sites, together with those on Mt. Buffalo, are among the lowest aestivation sites known, with records of aestivation at 1760 m on Mt. Gingera and 1600 m at Mt. Buffalo (which is equivalent to 1700 m when accounting for Mt. Buffalo's 1.15° more southerly latitude). If temperatures increase further with climate change, the elevations of aestivation sites are only likely to increase.

For Bogong moths to aestivate, there is presumably What might this a maximum temperature (and lowest elevation) at which they can spend the summer be? The lowest definitely known and regularly frequented whole-summer aestivation elevation is 1600 m at Mt. Buffalo – equivalent to 1700 m at Mt. Gingera when one accounts for Mt. Buffalo's 1.15° more southerly latitude. This is only slightly lower than the lowest known aestivation sites below the summit of Mt. Gingera (which are located at 1760 m: Table 2). the peak at 1760 m. Nonetheless, In the northern Snowy Mountains, Mountain alpine pygmy possums have been recorded eating Bogong moths in January at Boltons Hill in January (1581 m, above Happy Jacks Valley; Linda Broome, pers. comm.), suggesting whole-summer aestivation at that location, and also in late summer at. In contrast, almost 100 m lower at nearby Snow Ridge (1495 m), pygmy possums are found to consume Bogong moths almost exclusively in Spring (as revealed by scat analyses in 2011: Gibson *et al.* 2018) – presumably the moths do not remain here but instead migrate to higher elevations in the early summer, Gibson *et al.* 2018), with both locations within the northern Snowy Mountains. In the eastern Snowy Mountains, m Moths have also been observed in good numbers until at least 2015 at Mt. Tingaringy (1440 m), although it is not certain that they are there for the entire summer (Table 2, note e), or if they move to higher elevations in January (the more likely scenario).

Thus, the lowest elevation for regularly frequented whole-summer Bogong moth aestivation sites is likely to be around 1600 m, both in New South Wales (Boltons Hill) and Victoria of even lower

~~elevations than those on (Mt. Buffalo). What do these elevations suggest about the maximum permissible aestivation temperature? Data given in Table 5 reveal that between 2006 and 2020, the average maximum temperature measured from a cave at Ken Green Bogong (1940 m) during January was 12.7°C. Using a lapse rate for the Snowy Mountains of 9.1°C per kilometre of elevation (Green 2014), one can calculate that during the same period the average maximum temperature from the lowest suspected aestivation site on Boltons Hill (1581 m) would have been 16.0°C. We suggest that this is likely to be close to the highest temperature that permits aestivation. Supporting this notion is an unusual observation made by ~~may potentially still be possible, which assumes summer temperatures at these sites are still acceptably low for aestivation. Ian Common during the summer of 1951-52 on Mt. Little Ginini in the ACT (1525 m, and close to Mt. Gingera). Common noted that Bogong moths aestivated on Mt. Little Ginini for the entire summer when the average January-February maximum temperature was projected to be 14.8°C (Table 3; Common 1954). This suggests that aestivation is permitted at temperatures at least as high as 14.8°C, only 1.2°C lower than our predicted maximum. Thus 16°C seems to be a reasonable estimate for the maximum temperature that permits aestivation.~~~~

~~From the turn of this century, Bogong moths at aestivation sites on Mt. Gingera have declined during a 0.7°C temperature increase (i.e. 0.36°C per decade; Sánchez-Bayo and Green 2013). The mean maximum January temperature in the currently preferred aestivation site (at around 1840 m) was 16.2°C during 2020 (Table 4) – at or above our estimated maximum permissible temperature for aestivation. These aestivation sites, together with those on Mt. Buffalo, are among the lowest aestivation sites known. This suggests that our estimates for the maximum allowable temperature for aestivation may be too low, but~~ there is no question that if climate change advances and global temperatures continue to rise, aestivation will become more and more restricted to sites at higher elevations. To determine the actual maximum temperature where aestivation is permitted, the temperatures of caves at different elevations where moths aestivate need to be monitored using temperature loggers. Such measurements will allow us to forecast the impact of climate change on the Bogong moth population in the mountains; and ~~will~~ allow us to predict the impacts that changes in this population will have on the alpine ecosystem.

Effects of dDrought

From 2017 to 2019 much of the agricultural lands of the Murray–Darling Basin in western New South Wales and southern Queensland ~~have been~~were ~~extremely~~ affected by extreme drought, the most severe in the recorded history of the Murray–Darling Basin. This drought has had a major impact on the Bogong moth population, whose main breeding areas occur in ~~these same agricultural lands~~this region. The Bogong moth crash seen in the Australian Alps over the summer of 2017–2018 was sudden, widespread across all mountain areas, and continued into the summers of 2018–2019 and to a lesser extent 2019–2020.

There is no doubt that the major cause of the recent Bogong moth crash is the ongoing latest drought, which may have affected moths in a number of ways. Firstly, a lack of food for the larvae in the breeding areas would have been a major problem, coupled ~~with~~to unfavourable soil temperatures and moisture levels. We do not know the direct effect of temperature on the larvae, but temperatures were higher than normal, and coupled with a considerably drier soil and a lack of food, there were probably very few larvae that survived the dry winter of 2017, and thus very few adults that emerged and flew to the mountains in spring. Of course, even fewer of those that migrated to the caves would have survived to return in autumn for the winter breeding season of 2018. Those few that did return would have encountered the same drought-stricken landscape that they had experienced the previous year, leading to even fewer of their offspring surviving to adulthood. Because the winters of 2018 and 2019 were equally dry (Fig. 5), it is not difficult to understand how Bogong moth numbers ~~have~~ plummeted.

The effect of drought on Bogong moths numbers prior to 2017 is less clear, although significant fluctuations are apparent (as has also been noted in Victorian alpine areas: Mansergh and Heinze 2019). Almost all of eastern Australia was affected by major droughts in 1958–1968 and 1979–1983, with the 1982–1983 El Niño that developed from June to August creating severe conditions in terms of lack of rainfall and extreme heat. There was no noticeable impact of these droughts on Bogong moth numbers at Mt. Buffalo apart from the significant temporary reduction experienced in summer 1968–1969. However, by the summer of 1969–1970 Bogong moth numbers were back to ‘normal’ (Table 5Table 4). In the summer of 1972–1973 the Bogong Peaks were reported as the only site in NSW with Bogong moths in any quantity (Flood 1980). However, it is not clear whether any other major aestivation sites in NSW were checked by Flood (1980 – see Blakers 1980). Initially, the drought from 1979 to 1982 made no difference to Bogong moth numbers on Mt. Buffalo, in the Snowy Mountains or during the one summer recorded at Mt. Gingera. Moth numbers in the Snowy Mountains and on Mt. Buffalo declined in the summer of 1982–1983, and remained lower

at Mt. Buffalo but there are no records available elsewhere.

The Millennium Drought in southeast Australia (2001–2009) was particularly severe and badly affected the Murray-Darling Basin and virtually all of the southern cropping zones (Australian Bureau of Meteorology 2015). Bogong moths continued to be found at lower levels on Mt. Buffalo but the drought had major impacts on moth numbers in the Snowy Mountains during the summers of 2006–2007 and 2008–2009 (Table 5 Table 4). However, the successive La Niña events during the summers of 2010–11 and 2011–12 were associated with record rainfall over much of Australia (Australian Bureau of Meteorology) and resulted in good years for Bogong moth numbers in the Australian Alps. At this point it was obvious that there had been a long-term decline in overall numbers of Bogong moths, with declines that followed the drought of 1981–1983 and further declines that commenced in 1993–1995 that pre-empted the ~~coming~~ Millennium drought (Table 5 Table 4). The decline in numbers from 2014–2015 on Mt. Higginbotham, coupled to the progressive movement of Bogong moths to higher elevations, suggest that when numbers are low, Bogong moths on Mt. Buffalo move to higher, cooler locations. This also appears to be occurring further north in NSW on Mt. Gingera (35.58°S), where the lowest aestivation sites lie ~~between-at~~ 1760 m and continue upwards to just below the summit at 1857 m. This is essentially the same elevation band for aestivation sites a little further south at Charlotte Pass (36.43°S): 1755 to 1837 m. Bogong moths found here are generally spring arrivals that migrate to higher elevations as summer develops (see above). ~~The current latest~~ drought began in NSW in mid-2017, with Bogong moth numbers crashing within the breeding areas ~~(as they did not arrive in the mountains in high numbers as a result of migration)~~. Since then, there ~~has been was~~ no reprieve in the drought until well in to 2020 – NSW was declared to be 100% in drought by August 2018 and Queensland 65.2% by May 2019 (NSW Department of Primary Industries 2019). By July 2019 the drought was officially recorded as the worst on record in the Murray–Darling Basin (Farm Online National 2019), exceeding the Millennium drought, Federation Drought (1895–1903) and the World War II drought (1937–45). By the end of March 2019 rainfall deficiencies in the Murray–Darling Basin were the third lowest on record. Temperatures were extremely high, with the nearest equivalent temperatures, according to paleo-climatic data, being a hot period that occurred 2–3 million years BP (Dr. David Jones: Australian Bureau of Meteorology). Together, these conditions suggest that the ~~current-recent~~ drought, mediated by climate change, is sufficient in itself to have caused the Bogong moth collapse.

Other factors ~~causing decline~~

In addition to agricultural practices and climate change, annual declines of Bogong moth numbers may have occurred for the following reasons: (1) attrition as larvae in soil that is too dry and/or too warm (as likely occurred during winter 2017 and 2018), or attrition during adult migration as a result of (2) introduced predators, (3) environmental factors (such as increasing light pollution) or (4) because of attrition once the moths reach the mountains (e.g. due to climatic factors, and introduced predators and parasites). Obtaining a measure of the numbers of moths existing as larvae (see Green 2008), or as adults during migration, is difficult, particularly if relying on light traps. Local and synoptic weather systems can both affect the moth catch in light traps due to thunderstorms and the passage of cold fronts or depressions. The wind speed, air temperature and levels of moonlight may also have an affect (Gregg *et al.* 1994). The aestivating population of Bogong moths, from their arrival at their caves in December until the beginning of their departure in early March, is the part of the lifecycle where numbers of moths can be most accurately measured.

Ten years ago, a total number of ~~220.20~~ billion aestivating Bogong moths was estimated to exist in the Snowy Mountains over the summer (Green 2011). This number suggested that observed losses of moths in cities such as Canberra – where in occasional years migrating moths have been lured by city lights after presumably being blown off course by unusually strong winds – may not have had an overwhelming impact on overall numbers in the mountains as most moths eventually leave their city refuges and continue their journeys. These losses from light pollution were probably comparatively small (although the loss of moths by any cause is now becoming important). Apart from light pollution, another major change since European settlement is the arrival of feral predators such as foxes (arriving in the Snowy Mountains around 1900, after the first capture of a fox in NSW in 1893: Rolls 1969). Fox predation now accounts for a loss of 55 imperial tons of Bogong moths annually in the Snowy Mountains (Green 2011). However, fox baiting from 1999 onwards (which still continues annually above the treeline) had an immediate impact on fox numbers, with a decline of about 80% based on three criteria: fox scat counts, fox tracks found on snow transects, and numbers of foxes counted at Charlotte Pass (K. Green, unpublished data). A recent report indicates that wild pigs have also become significant predators of Bogong moths, following the introduction of these feral animals to the Snowy Mountains in 1959 (Caley and Welvaert 2018). Before European settlement a major impact on Bogong moths was hunting by Aboriginal people, and there are estimates that this would have taken several tons of moths (Jardine 1901). However, without the actual figures, the impact of these hunting activities on moth numbers

cannot be calculated.

CONCLUSIONS

Records of Bogong moths collected over the past 70 years from around 50 to 60 aestivation sites, and more recently along the migratory route, coupled with the analysis of Bogong moth remains in mammalian predator faeces, reveal noticeable patterns in the numbers of moths present over summer in the Australian Alps. Even though the data (our own and that of others) are admittedly fragmentary, this analysis has revealed that Bogong moth numbers were fairly stable from 1950 until around 1980, apart from temporary falls in numbers due to occasional drought. From 1980 until 2016 Bogong moth numbers in the mountains began to fluctuate, with some years having very high numbers of moths, while others had many fewer. Even though overall numbers remained high, these years showed evidence of a slow decline. From 2017-2020 a sudden and worrying crash in Bogong moth numbers occurred.

Although the causes for the decline and recent crash in Bogong moth numbers remain uncertain, one or more factors may be responsible. ~~Even though we~~We currently have little evidence to suggest that increasing global temperatures *per se* are responsible for the decline in Bogong moths seen across the mountains, however the Australian climate has nonetheless become continuously drier and warmer over past decades. This change in climate has possibly had a serious impact on the ability of Bogong moth eggs, larvae and pupae to survive the winter in their breeding grounds, which in turn may have slowly been reducing the number of moths entering the mountains. Moreover, our analysis also suggests that the maximum temperature for aestivation may be around 16°C, and that a warming climate is thus likely restricting aestivation to higher and higher elevations. These possible effects of climate change, added to known changes in farming practices, such as increasing land clearing for crops and an elevated use of insecticides, may account for the gradual decline in moth numbers observed from about 1980 until 2016. These declines were followed by the catastrophic Bogong moth ~~years- summers~~ of 2017-~~2018~~ and 2018-~~2019~~ (and to a lesser extent 2019-2020) for which only drought can be seen as the cause. This drought is very likely to have severely impacted the survival of Bogong moth immature stages in their breeding grounds, a speculation supported by the sudden disappearance of Bogong moths that we observed along their migratory routes during Spring. The latest drought – the worst in recorded history in the Murray–Darling Basin – is almost certainly the result of climate change (CSIRO 2018). Whether

the current drought — the worst in recorded history in the Murray–Darling Basin — is the result of climate change, remains to be seen.

Finally, as with the alarming worldwide decline of insects in general (Wagner 2020), the decline of Bogong moths in the Australian Alps should be seen as a worrying development. The delicate alpine environment is already severely threatened by climate change and the massive annual influx of energy and nutrients provided by Bogong moths is of major importance for the health of this ecosystem (Green 2011; Mansergh and Heinze 2019). Just a few years ago it would have been difficult to believe that such an abundant and iconic insect – with 17,000 aestivating individuals crowding onto each square metre of alpine cave wall, in untold numbers of caves and boulder fields across the great expanse of the Australian Alps – could ever be threatened. But our analysis has revealed that Bogong moths have been slowly declining for the last 40 years, and the latest drought has made it glaringly obvious that in highly unfavourable conditions the Bogong moth population can actually crash. Hopefully their numbers will rise again as conditions improve, but our analysis, as well as that of Mansergh and Heinze (2019), suggest that further research is urgently needed. Regular quantitative monitoring of Bogong moths during their migration (e.g. using light-trapping, vertical radar and lidar methods), during aestivation in alpine caves and during development in their breeding areas, coupled with long-term and frequent temperature and air/soil humidity readings in these locations, is greatly warranted. Moreover, the currently unknown effects of neonicotinoid insecticides on the health of Bogong moth breeding populations should be urgently investigated.

The Bogong moth is an iconic and culturally significant Australian insect whose remarkable highly-directed migration (Warrant *et al.* 2016), and its use of stellar and magnetic compass cues for nocturnal navigation (Dreyer *et al.* 2018; Adden *et al.*, in preparation), places it on-par with its better-known diurnal counterpart in North America, the Monarch butterfly *Danaus plexippus* (Reppert and de Roode 2018). This, in addition to its importance for the health of the alpine ecosystem (Green 2011; Mansergh and Heinze 2019), and its significance as a food source for critically endangered alpine marsupials such as the Mountain pygmy possum (Gibson *et al.* 2018; Mansergh and Heinze 2019), makes the Bogong moth both unique and exceptional among Australian insects, and worthy of every effort to ensure its long-term survival and protection.

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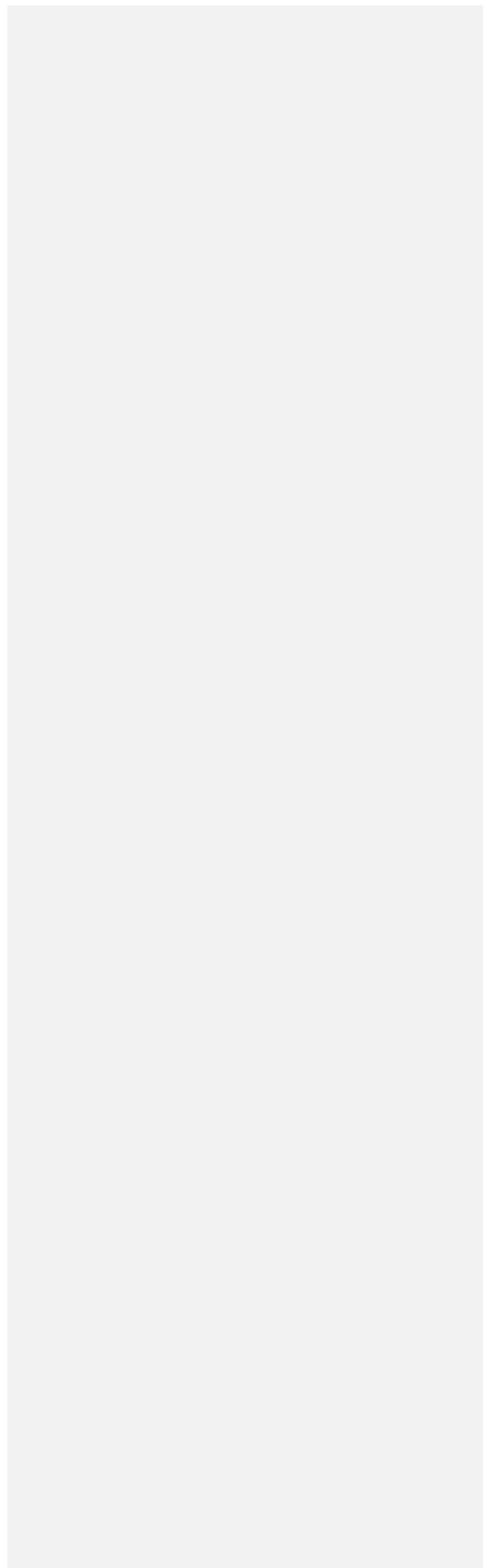


Figure Captions FIGURE CAPTIONS

Figure 1. Map of south-eastern Australia showing the locations where larvae have been collected by Froggatt (1900, *yellow circles*), Common (1954, *red circles*) and Green (2008, *white circles*). Also shown are the names of the major rivers in NSW, and the locations of various towns and mountain peaks mentioned in the text. The area of broadacre cropping farms across south eastern Australia during 2014–2015 is delineated by the *red line* (from ‘The Conversation’ 2017), while areas of grey cracking clays are shown in *grey*. Bogong moths fly towards the Australian Alps (*white areas, elevations > 1500 m*) from various regions of southeast Australia, from as far distant as eastern South Australia, western Victoria, western and northwest New South Wales and southern and southeast Queensland (*blue arrows*). Adapted from Warrant *et al.* (2016), after Green (2008). **Inset:** The Australian Bogong moth *Agrotis infusa* (Boisduval, 1832). Scale bar = 5 mm. Reproduced with the kind permission of the photographer; Ajay Narendra, Macquarie University, Australia.

Figure 2. Mean proportion of individual fox scats consisting of Bogong moth remains at subalpine (*orange lines and symbols*) and alpine altitudes (*blue lines and symbols*) over two summer seasons: 1996–1997 (*diamonds*) and 1997–1998 (*circles*). Redrawn from Green (2010b).

Figure 3. Date of first arrival of the Bogong moths above the snowline in the Snowy Mountains from 1979 until the present. *Regression line* has the following equation: $D = 0.19Y - 114$ ($R^2 = 0.050$) where D is the day of the year for the first moth arrival, and Y is the year.

Figure 4. Seasonal changes in site occupancy of aestivating Bogong moths atop around the summit of Mount Gingera in the Brindabella Ranges (on the NSW and ACT borderACT), based on 37 sites surveyed by Caley & Welvaert (2018) during 2014–2016 (reproduced with permission), and during the recent extreme drought.

Figure 5. Australian rainfall deciles (1 January 2017 – 31 December 2019). Source: Bureau of Meteorology, Australian Government. Distribution based on gridded data.

Tables

Table 1. Maximal shade temperatures T in boulder fields on the Main Range of the Snowy Mountains at four elevations during the snow-free season^a, together with proportion of Bogong moths in Mountain pygmy possum (*Burramys parvus*) scats recorded over 17 years in different seasons^b and frequency of occurrence of Bogong moths in scats of Dusky antechinus (*Antechinus swainsonii*) in 1981-1987^{c,d}.

Location	Mean T (°C)	Late Spring	Late Summer
Charlotte Pass, 1755m	12.3±2.9	30% ^b	≈1% ^b
South Ramshead, 2000 m	10.7±3.5	62% ^{c,d}	2% ^{c,d}
Mt. Townsend, 2209 m	9.5±3.1	40% ^b	40% ^b
Mt. Kosciuszko, 2228 m	8.6±2.5	32% ^b	49% ^b

Notes

- The average maximum temperature over the period November 2009-March 2010, measured using a temperature logger placed in a shaded place within the boulder field at each location (Green 2010a). Temperatures measured at Charlotte Pass from a Bureau of Meteorology Stevenson Screen over the same time period ($12.3^{\circ}\text{C} \pm 3.5^{\circ}\text{C}$) was not significantly different to that measured by the logger placed in the nearby boulder field.
- Data from Mountain pygmy possum (Gibson *et al.* 2018)
- Data from Dusky antechinus
- See [Table 2](#), Note d.

Table 2. First observed date of flowering of snow gums *Eucalyptus pauciflora niphophila* above the winter snowline in the Snowy Mountains. (Data KG)

Year	First summer flowering
1982	January 11
1986	January 3
1987	February 8
1995	January 6 ^a
1995	December 5 ^b
2001	January 8
2006	November 30
2007	December 5
2010	December 14
2012	January 3 ^c
2012	December 28 ^d
2015	November 30
2016	December 23
2018	December 16
2020	December 30

Notes

- a.— Late flowering onset for the summer of 1994-95
 b.— Flowering onset for the summer of 1994-95
 c.— Late flowering onset for the summer of 2011-12
 d.— Flowering onset for the summer of 2012-13

Table 2. The lowest elevations (m) at which aestivation of Bogong moths takes place at different locations in the Australian Alps (with notes)

Location	Latitude	Lowest elevation (m)
Mt. Gingera, NSW/ACT	-35.583° S	1760 ^a
Bogong Mountains Big Plain/Mt. Jounama, NSW	-35.576° S	1680/1710 ^b
Charlotte Pass, NSW	-36.427° S	1755 ^c
Unnamed peak "Ken Green Bogong", NSW	-36.517° S	1860 ^d
Mt. Tingaringy, NSW	-36.998° S	<1440 ^e
Mt. Higginbotham, Victoria	-36.987° S	1720 ^f
Mt. Buffalo (The Horn), Victoria	-36.736° S	1600 ^g

Notes

- The lowest 'camp' used as an aestivation cave was on nearby Little Ginini was at 1525-1585 m but in 1952-1953 it was only used as a 'temporary camp' in spring and early summer (Common 1954, p229). Apart from that record, in current years the lowest major aestivation site ~~commonly was has been on at Mt. Gingera~~ (1760 m, below the peak of Mt. Gingera (which is at 1857 m)).
- On 23 February 1999 Bogong moth remains were found in fox scats on the Bogong Peaks and Bogong moths were seen flying around camp from about 7 pm (KG, pers. obs.). Moths flying at this time usually do so for approximately an hour before returning to the caves. Even though the reason for this flight is unknown, it may possibly be to drink, to gauge atmospheric conditions in preparation for their return migration, or for some other purpose. The location of the lowest cave used as an aestivation site is not known. At one site on Big Plain, Bogong moths were found on 26th January 2015 but not in large agglomerations (Ben Keaney, pers.com). The higher site on Mt. Jounama has not been examined.
- At Charlotte Pass, the Mountain pygmy possum *Burramys parvus* was recorded with a diet consisting of 30% Bogong moths in spring, falling to ~1% in summer (Table 1, Gibson *et al.* 2018). This contrasted with higher elevation sites, where in summer the proportion of Bogong moths in the pygmy possum diet at Mount Townsend (2209 m) remained about the same as it was in Spring, while at Mount Kosciuszko the proportion increased throughout summer (Gibson *et al.* 2018). This suggests that Charlotte Pass was not a summer aestivation site and that the local lower limit for aestivation was thus at or above 1755 m.
- Bogong moths occurred in high numbers in pitfall traps and sheltered areas in the study sites of the Dusky antechinus *Antechinus swainsonii* at 1860 m and 1940 m (PhD data, KG). This mainly occurred in spring over the 1981-1987 seasons. Lepidoptera, mainly Bogong moths, were the most common food through the spring in the diet of *A. swainsonii*, but this declined through summer (Green 1989). Frequency of occurrence of Bogong moths in scats of *A. swainsonii* was 75% in a high sub-alpine site in spring and 62.5% in a low alpine site (Green 1989). Numbers then appeared to decline over summer (see Table 3 in Green 1989). However, this is a result of using "season" rather than month in the published study, and when the data were re-examined by month, the decline was found to occur in February with scats generally gone by March (PhD data, KG). In January at high subalpine sites, Bogong moth frequency of occurrence was 58.3% in *A. swainsonii* while in low alpine sites it was 66.7% (PhD data, KG). In contrast, this had fallen to 11% and 2% respectively in February and 1% and 0% respectively in March, indicating that as summer became warmer (or moth numbers declined) the moths moved higher (PhD data, KG).
- On 13th October 2001, Bogong moths were captured in their thousands whilst flying around the summit of Mt. Tingaringy. These moths smelled strongly of nectar and were being preyed upon by White-throated needletails (a type of swift) as well as unidentified bats. On 15th October, moths were lined up inside a cave on the north-west face of Mt. Tingaringy, with Quoll scats outside (which had been feeding on them). On 16th October "The Amphitheatre" was found, a crack in the mountain estimated to be an 80 m length of accessible cave, with dead moths 8-10 cm deep on the floor (KG and Tony Stubbs). A big catch of moths was also collected on 5th and 6th January 2013, with a smaller catch on 7th Jan 2016 (KG, EW). Although many moths use the site, there is no record of occupation later than 7th January, so despite its size, there is currently no data to prove that Mt. Tingaringy is an aestivation site.
- Aestivation sites up to a maximum of 1720m (Ian Mansergh, pers. com.)
- For all summers from 1966-1967 and 1981-1982 (with the exception of 1968-69), a cave (at 1600m) on 'The Horn' on Mt. Buffalo (at 1600m) was the lowest site used by Bogong moths to aestivate (MB).

Table 3. Mean daily maximum temperature T from January to February at aestival sites ~~in the Snowy Mountains (2010)~~, on Mt. Gingera^a and Mt. Little Ginini (1952-1953)^a, ~~in the Snowy Mountains (2010)~~, and on Mt. Buffalo (1967)

Location	Elevation (m)	Mean T (°C)
Mt. Gingera 1952	4760 1840	12.7 ^b
Mt. Gingera 1953	4760 1840	10.0 ^c
<u>Mt. Gingera 2020</u>	<u>1840</u>	<u>14.7</u>
Mt. Little Ginini 1952	1525	14.8 ^c
Mt. Little Ginini 1953	1525	12.7 ^c
Charlotte Pass	1755	13.8
Unnamed peak "Ken Green Bogong"	1860	11.8
Unnamed peak "Ken Green Bogong"	1940	11.9
Unnamed peak "Ken Green Bogong"	2020	11.5
Mt. Ramshead North	2140	11.7
Mt. Twynam	2150	8.9
Mt. Townsend	2150	10.4
Mt. Kosciuszko	2200	10.2
Mt. Buffalo (Vic)	1600	13.2

Notes

- a. Common 1954. The cave monitored by Common on Mt. Gingera was at about 1840 m, just below the summit at 1857 m. This was also the cave where temperatures were measured in 2020.
- b. In 1952, it appears that temperatures were measured in a location that may not have been fully shaded (Common 1954, p 254). If we assume that January temperatures did not exceed those at Kiandra, and set Mt. Gingera's January temperature at 13.0°C, the corrected 1952 January-February mean temperature would then be 12.7°C.
- b-c. Extrapolated from temperatures measured at the summit of Mt. Gingera.

Table 4. Records of Bogong moth occurrence and relative abundance at aestivation sites on four mountains in the Australian Alps^a. ~~The~~ numbers 1-4 refer to relative abundance of moths at their aestivation sites, as follows: (1) good, (2) normal to poor, (3) bad, or (4) absent. ~~whether the year was good for moth numbers (1), normal to poor (2), bad (3) or moths were absent at their aestivation sites (4).~~ For Mt. Buffalo, three cave sites were checked on one peak known as The Horn^b: two separated lower elevation sites (A and B at 1600 m), and several higher caves in close vicinity (C) ranging from 1680 m to the summit of The Horn at 1723 m – all sites may have been visited, but in certain years if site A had Bogong moths the other sites (B and C) were not visited. A single letter indicates the lowest cave that moths were found in (e.g. C); A or B indicates that moths were found in one or both of these cave sites (and were thus also found at cave site C), but no exact record was kept. P indicates that moths were present in one or more of these cave sites, but no exact record was kept.

Summer	Mt. Gingera	Ken Green Bogong	Mt. Buffalo	Mt. Higginbotham
1951-52	1			
1952-53	1			
1953-54	1			
1954-55	1			
1955-56	1			
1956-57	1			
1957-58	1			
1958-59	1			
1959-60	1			
1960-61	1			
1961-62	1			
1962-63	1			
1963-64	1			
1964-65	1			
1965-66	1			
1966-67	1		A	
1967-68	1		A	
1968-69	1		C	
1969-70	1			
1970-71	1			
1971-72	1			
1972-73	1 ³			
1973-74	1			
1974-75	1		A	
1975-76	1		A	
1976-77	1	1	A	
1977-78	1	1	A	
1978-79	1	1	A ^{be}	1
1979-80	1	1	A ^{be}	1
1980-81		1	A	
1981-82		1	A	
1982-83		2	A or B ^{be}	1
1983-84			A or B	

1984-85			A or B	
1985-86			A or B	1
1986-87		2	A or B	1
1987-88		1	A or B	
1988-89			A or B	
1989-90	1		A or B	
1990-91				
1991-92			A or B	
1992-93			A or B	
1993-94		3	P	
1994-95		3	P	
1995-96		1	P	
1996-97		2	P	
1997-98		2	P	
1998-99		2	P	
1999-00			P	
2000-01		1	P	
2001-02		1	P	
2002-03		2	P	
2003-04			P	
2004-05		1	P	
2005-06		1	P	
2006-07		3		
2007-08		2	P	
2008-09		3	P	
2009-10		2	P	
2010-11		1	A	
2011-12	1	1	P	
2012-13	1	2	P ^{cd}	
2013-14	1	2	A ^{be,cd}	1
2014-15	3 ^{fg}	1	A	3
2015-16	3 ^{fg}	1	C ^{cd,de}	3
2016-17		1	C ^{cd,de}	3
2017-18	4	4	C ^{cd,de,ef}	4
2018-19	4	4	4 ^{cd}	4

Notes

- a. Data was collected on (1) Mt. Gingera, NSW/ACT: 1952-1979 data from Common (1954, 1980) and pers. com.), 1979 & ~~and~~ 1989 KG, 2011-2014 EW, 2015-2019 PC, (2) The unnamed peak "Ken Green Bogong", close to South Ramshead in the Kosciuszko Main Range, NSW: 1977-2019 KG, (3) granite boulder fields around Mt. Higginbotham, Victoria: data from Mansergh and Heinze (2019), (4) Mt. Buffalo, Victoria: 1966-2019 (as A, B and C) MB, with other Victorian Records 1988-1989 Ian Mansergh - during 2013-2014 Dean Heinze reported that Bogong moth numbers were high, but did not appear to occupy either the low or medium cave sites.
- b. ~~For Mt. Buffalo, a single letter indicates the lowest cave that moths were found in (e.g. C); A or B indicates that moths were found in one or both of these cave sites (and were thus also found at cave site C), but no exact record was kept.~~
- ~~e.b.~~ This was considered a good moth year on Mt. Buffalo
- ~~d.c.~~ Visit made in January
- ~~e.d.~~ Bogong moths were only present in the summit cave on The Horn (1723 m)
- ~~f.c.~~ Only a handful of Bogong moths were present
- ~~g.f.~~ There is a possibility that Bogong moths were in good numbers during these years but did not occupy the caves on Mt. Gingera in order to take advantage of caves at higher elevations. Moths

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were in abundance from October until December but declined rapidly from the beginning of January (Caley and Welvaert 2018), i.e. at least 1-2 months prior to the main return migration, possibly reflecting a move to higher elevations.

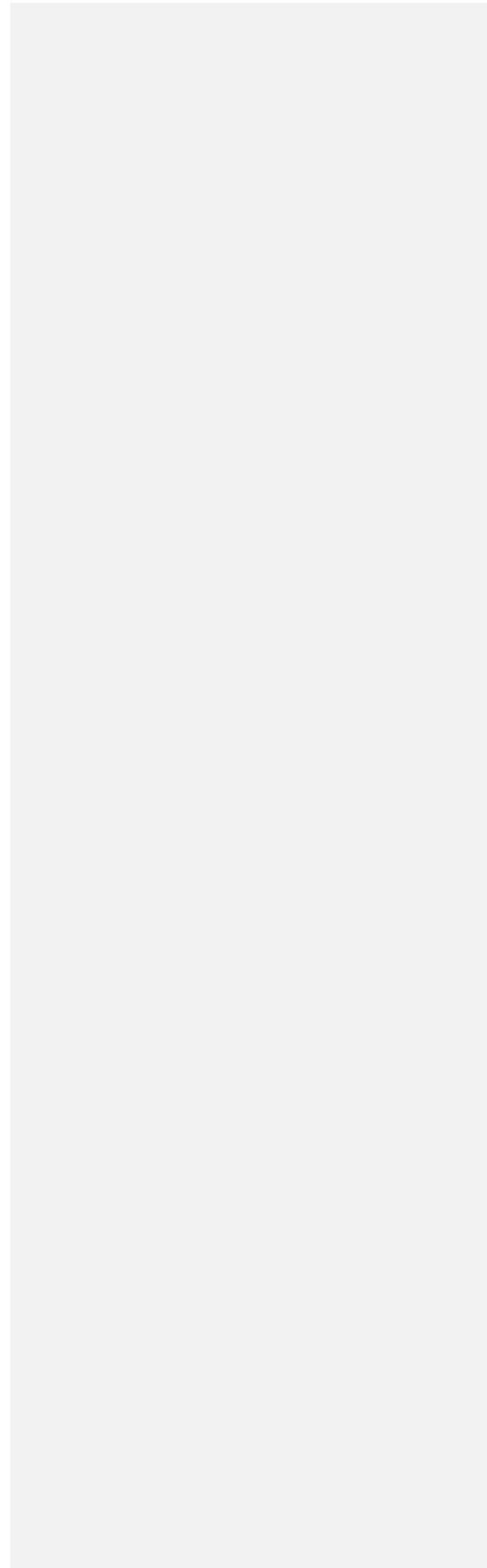


Table 5. Average maximum temperatures (°C) in January and February during different years from caves in the NSW and ACT Alps

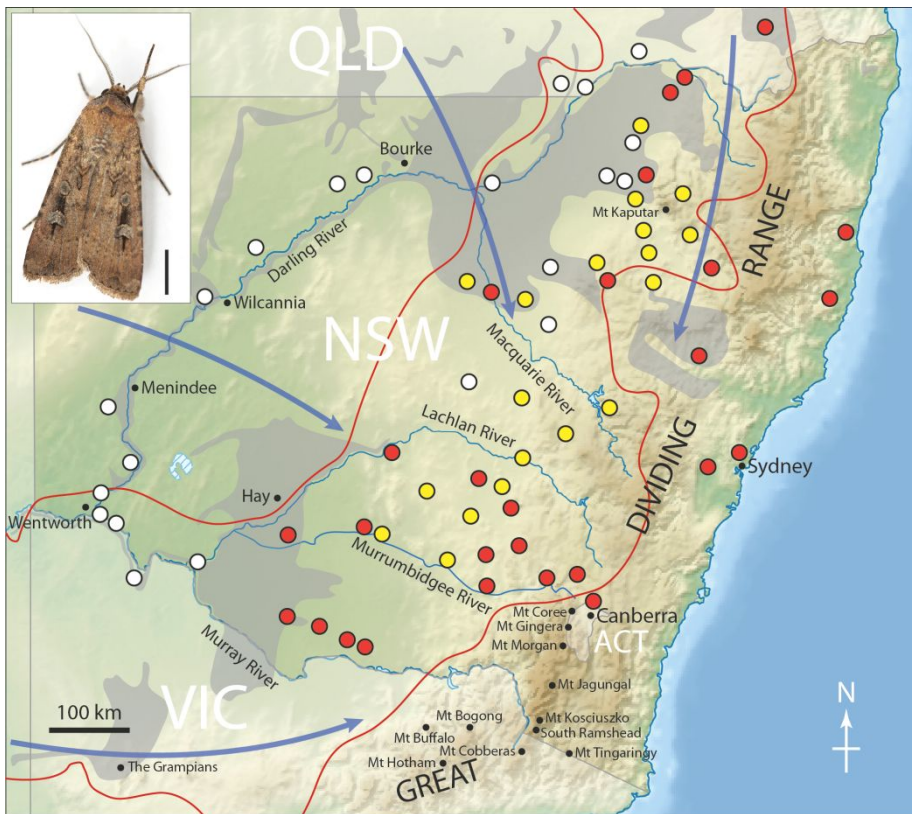
Location	Year	January	February
Mt. Gingera NSW/ACT ^a 1760-1840 m	1952	14.5	12.3
Mt. Gingera NSW/ACT ^a 1760-1840 m	1953	10.5	9.5
Mt. Gingera NSW/ACT ^a 1840 m	2020	16.2	13.1
Charlotte Pass NSW 1755 m	2010	13.8	12.2
Unnamed peak “Ken Green Bogong” NSW 1940 m	2006	13.7	12.3
•	2007	12.1	12.0
•	2008	12.8	8.5
•	2009	12.3	11.3
•	2010	12.4	11.1
•	2014	12.5	12.7
•	2015	10.5	11.8
•	2016	10.8	12.1
•	2017	13.4	11.4
•	2018	12.8	11.2
•	2019 ^b	15.7	11.4
Unnamed peak “Ken Green Bogong” NSW 1940 m	2020	13.3	10.9

Notes

- a. Common 1954. The cave monitored by Common on Mt. Gingera was at about 1840 m, just below the summit at 1857 m. This was also the cave where temperatures were measured in 2020.
- b. During the latter half of December 2019, the average maximum temperature reached 15.6°C

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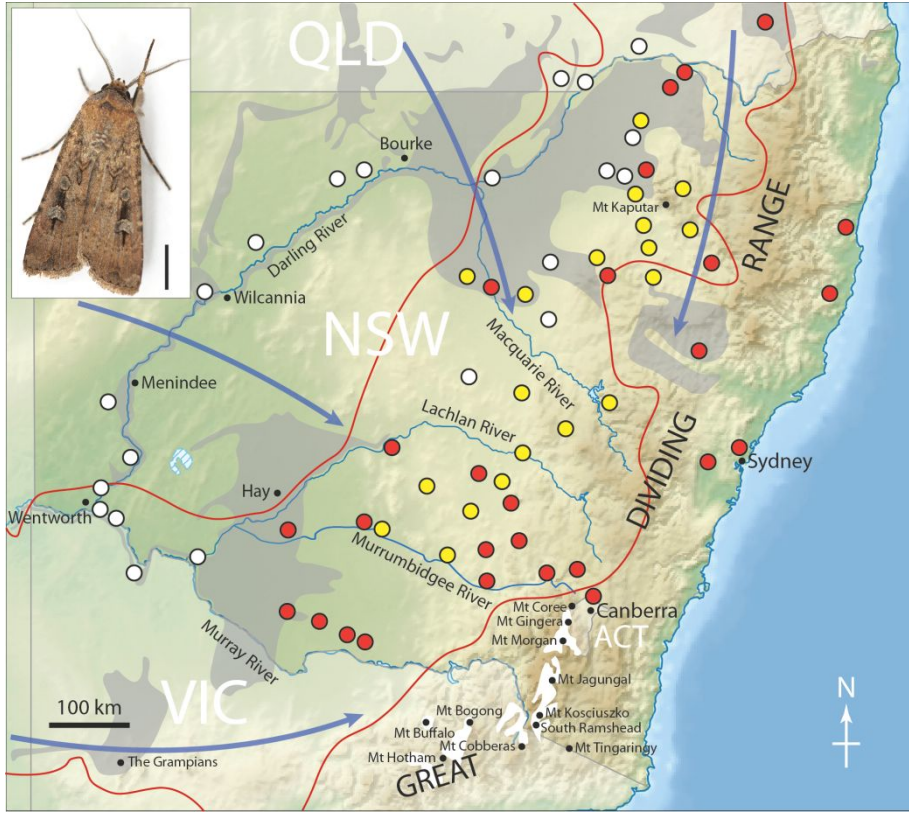


Figure 1. Map of south-eastern Australia showing the locations where larvae have been collected by Froggatt (1900, *yellow circles*), Common (1954, *red circles*) and Green (2008, *white circles*). Also shown are the names of the major rivers in NSW, and the locations of various towns and mountain peaks mentioned in the text. The area of broadacre cropping farms across south eastern Australia during 2014-2015 is delineated by the *red line* (from ‘The Conversation’ 2017), while areas of grey cracking clays are shown in *grey*. Bogong moths fly towards the Australian Alps (*white areas, elevations > 1500 m*) from various regions of southeast Australia, from as far distant as eastern South Australia, western Victoria, western and northwest New South Wales and southern and southeast Queensland (*blue arrows*). Adapted from Warrant *et al.* (2016), after Green (2008). **Inset:** The Australian Bogong moth *Agrotis infusa* (Boisduval, 1832). Scale bar = 5 mm. Reproduced with the kind permission of the photographer; Ajay Narendra, Macquarie University, Australia.

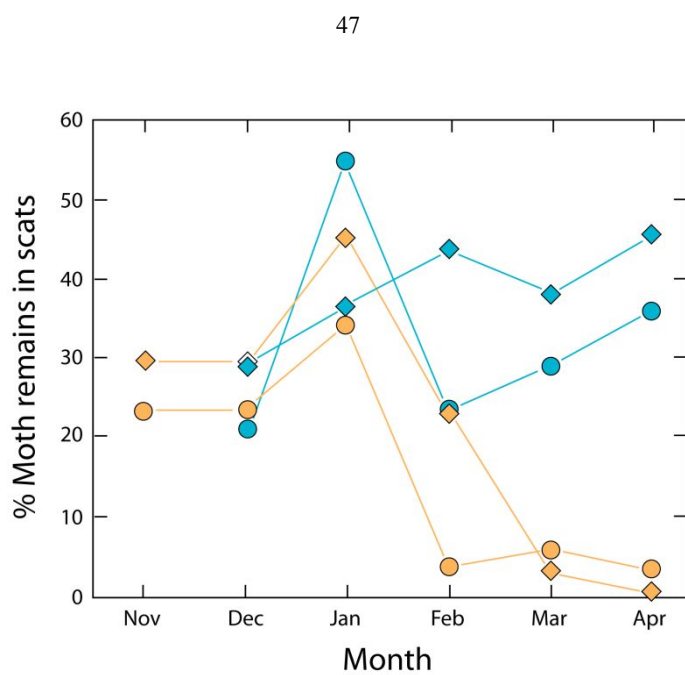


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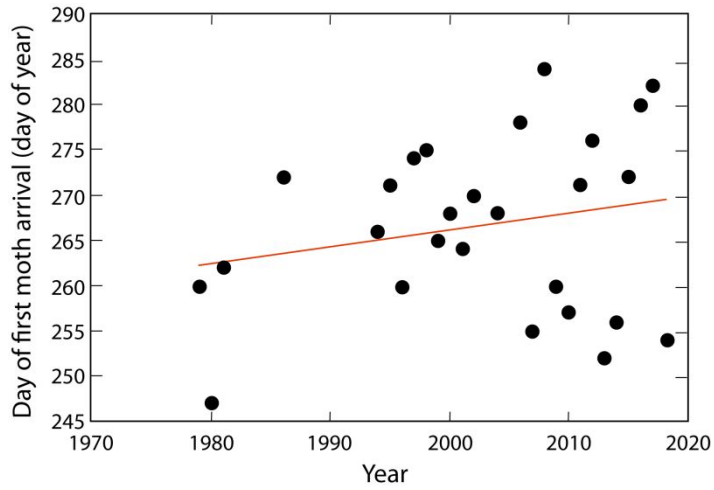


Figure 3. Date of first arrival of the Bogong moths above the snowline in the Snowy Mountains from 1979 until the present. *Regression line* has the following equation: $D = 0.19Y - 114$ ($R^2 = 0.050$) where D is the day of the year for the first moth arrival, and Y is the year.

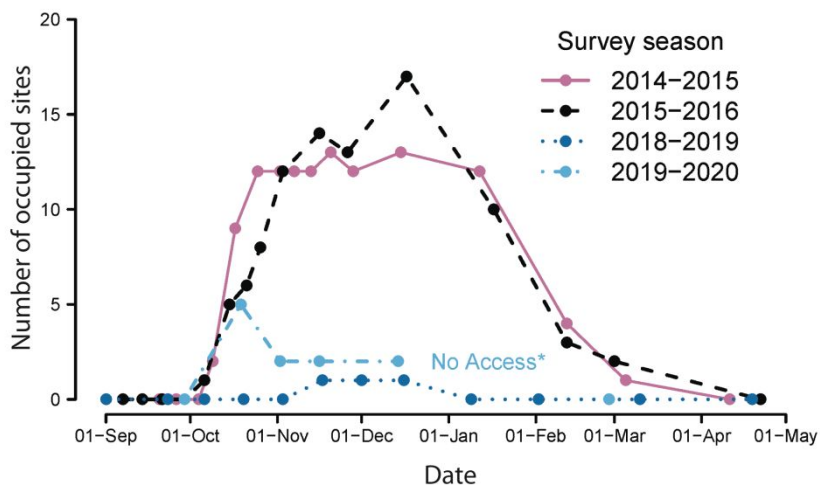


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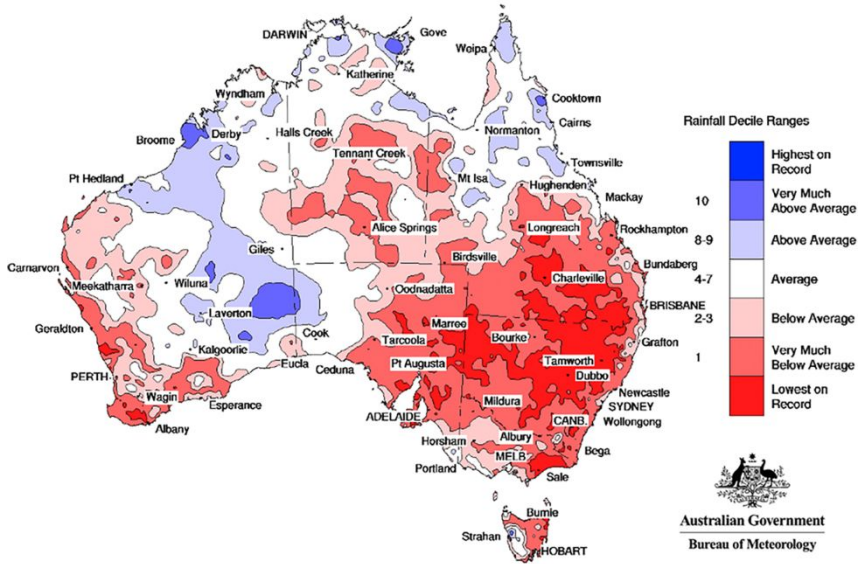


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