

The Rise and Demise of the Glanville fritillary on the Isle of Wight

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Received: 2 June 2014 / Accepted: 20 November 2014 / Published online: 29 November 2014
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Abstract The Glanville fritillary is one of Britain's rarest breeding butterflies, and is predominantly restricted to the south coast of the Isle of Wight. Populations have been monitored annually at a high proportion of known sites by counting the number of larval 'webs' during spring since 1996. In this paper, we present population time series for eight core sites. Populations have been observed to fluctuate considerably over the last 18 years, with a high degree of synchrony between sites. Recently, numbers of larval webs have shown a severe decline, with simultaneous extinctions occurring across many former strongholds. We combine our web count data with counts of adult butterflies from five sites of the UK Butterfly Monitoring Scheme. Together, these data suggest that the Glanville fritillary is threatened by extinction on the Isle of Wight, and that the total area used for breeding is likely no more

than a few km². The results flag up the need for a national census of remaining populations and further research to understand causes of decline, so that a conservation recovery plan can be developed.

Keywords *Melitaea cinxia* · Metapopulation · Extinction · Abundance · Habitat quality · Temperature · Butterflies

Introduction

The abundance and distribution of a species is a reflection and response to environmental conditions (Brown 1984). All species populations fluctuate in response to environmental changes over time (Andrewartha and Birch 1954), and the direction and scale of the response can be influenced by many factors, for example, climate, resources, predators and diseases and often the complex interactions between them (Begon et al. 1986). Clarifying the importance of the various factors that determine species distributions and abundance is a key question in ecology (Whittaker 1975; MacArthur 1984), as although there are general patterns, the mechanistic explanations do not yet appear to be definitive (Storch and Gaston 2004; McGill 2006; Mattila et al. 2011). However, there are key drivers of these processes, and temperature and resource availability influence both the distribution and abundance of nearly all species (May 1975; Krebs 1978).

Like most ectothermic insects, butterflies are extremely sensitive to changes in temperature and restricted by both climatic restraints (Thomas 1995; Bryant et al. 2002; Davies et al. 2006) and limitations in resources (Dennis 2010). The high degree of specialisation required to successfully utilise both differing temperature gradients and

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resources within the smallest habitats means that many butterflies are short lived thermophilous species, often showing rapid and clear responses to changes in the environment making them ideal indicators to gauge the health of habitats and ecosystems (Erhardt and Thomas 1991; Oostermeijer and van Swaay 1998; Thomas et al. 2004). Indeed, they have long attracted population biologists as convenient model organisms (Ford 1945; Ehrlich 1983), and are one of the few insect groups for which annual abundance monitoring is possible (Roy et al. 2007).

The Glanville fritillary *Melitaea cinxia* is one of the most intensively studied butterfly species in the world. In Finland, long-term dynamics have been monitored within a large network of 4,000 habitat patches in the Åland Islands since 1991 (Ojanen et al. 2013). This research has focussed on the role of patch size, shape and isolation on the persistence of individual populations (Hanski 1994, 1999). The insights from the Åland Islands have been influential in the development of metapopulation theory (Hanski 1998) and its extensions to biodiversity conservation in fragmented landscapes (Ross et al. 2008; Johst et al. 2011; Jones 2011; Leidner and Haddad 2011).

In the UK, Glanville fritillary females are highly selective in their egg-laying preferences, choosing to oviposit only on small hostplants in warm microclimates (Thomas et al. 2001). The availability of *Plantago lanceolata*, the host-plant, in this suitable condition is a convenient measure of habitat quality that explains much of the variation in occupancy and abundance between sites (Thomas et al. 2001). Within sites, both habitat quality and spring temperature are strongly correlated with population dynamics, with dramatic population increases in warm years corresponding with a good supply of plantains in suitable condition (Curtis and Isaac 2014).

In Britain, Glanville fritillaries are largely restricted to early-successional habitat on south-facing slopes on the Isle of Wight, although in the nineteenth century it was more widespread and occupied several sites on the mainland (Asher et al. 2001). It is univoltine and monophagous, with a typical flight period lasting from May to July. Eggs are laid in clusters on the underside of Ribwort plantain (*P. lanceolata*) leaves, with most oviposition occurring in June. During summer the larvae live and feed gregariously and spin a silken web around the plantain leaves. They enter diapause within the web during early autumn, and emerge the following spring, when they again feed communally and spin a conspicuous web around plantains before pupating in April.

The Glanville fritillary is highly conducive for research and monitoring, principally because the larvae form conspicuous ‘webs’, making it possible to conduct accurate population counts within just a couple of weeks each year (Thomas and Simcox 1982). As a monophagous species

with limited distribution and narrow niche breadth the Glanville fritillary is predicted to be extremely sensitive to climate change (Diamond et al. 2011).

In this paper, we describe the population dynamics of the UK Glanville fritillary population across eight sites from 18 years of monitoring data. We combine our data with adults counts from five transects of the UK Butterfly Monitoring Scheme, to produce a synthetic overview of the status of this species on the Isle of Wight. These sites harbour the bulk of the British population of this species, so our results define the national conservation status of this species, which is one of the rarest in the UK.

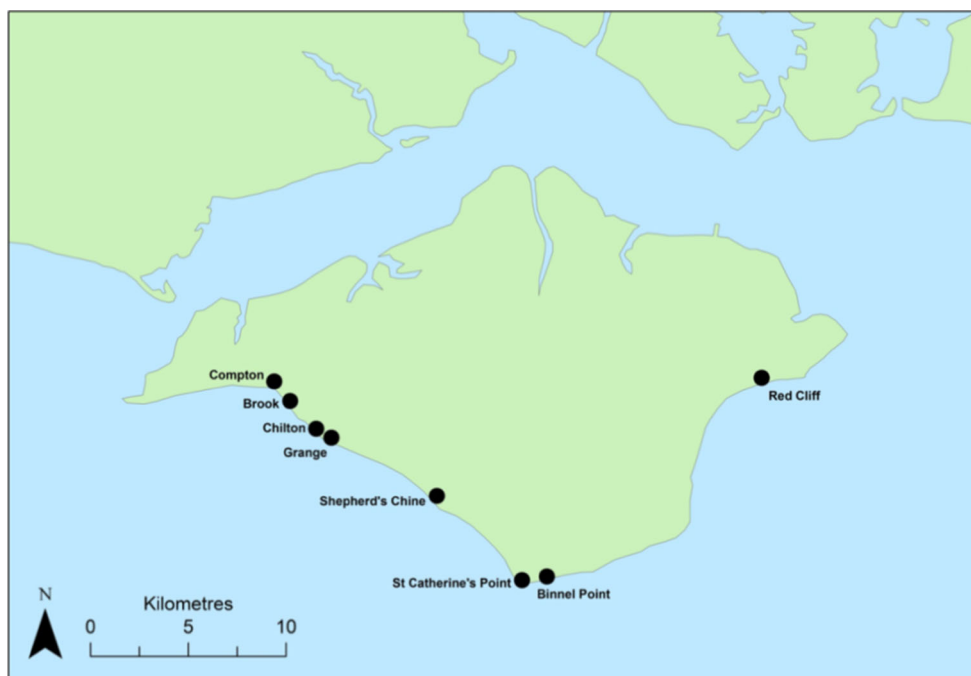
Methods

A survey of Glanville fritillary larval webs in 1979 (Simcox and Thomas 1979) repeated in 1996 (Thomas et al. 2001) established that over 95 % of the British population occurred on eight sites along the south coast of the Isle of Wight (see Fig. 1; Table 1), between Compton Bay in the west, and Red Cliff at the south-eastern end of the Island.

Four of these sites (Brook, Chilton, Grange and Shepherds) are centred on chines or riverine valleys, where small land slippages and erosion produce patches of bare ground that are ideal breeding habitat for Glanville fritillaries. Compton and Red Cliff comprise large areas of rapidly-eroding cliffs characterised by frequent landslips, creating a dynamic patchwork of suitable and unsuitable habitat patches. Finally, two sites (St. Catherine’s Point and Binnel Point) are semi-permanent grassland.

The abundance of Glanville fritillary has been monitored at these sites annually since 1996. All sites were surveyed every year, except Brook (1997 and 2001) and Chilton (2001). Surveys were conducted during March, which is when the larval webs are largest and most conspicuous (Simcox and Thomas 1979). Abundance was calculated as the total number of larval ‘webs’, which were counted by walking briskly along a series of survey lines spaced 5 metres apart until the entire area had been surveyed. Webs were recorded within an area of approximately 2.5 m², as per the transect methods used for adult butterflies (Pollard and Yates 1993; Botham et al. 2009).

We also extracted counts of adult Glanville fritillaries from the UKBMS dataset for the five transect routes on the Isle of Wight. Whilst adult Glanville fritillaries are occasionally recorded on transects on the English mainland, it is widely suspected that most are introduced populations that are supplemented by collectors, so the index for these sites is unlikely to reflect natural population dynamics. We also excluded counts from the Channel Islands, as these are not in the UK. We constructed separate collated population indices (Pollard and Yates 1993) from the eight web count

Fig. 1 A map of study sites on the Isle of Wight**Table 1** Summary statistics on population time series for each site

| Site name | Ordnance survey grid reference | Mean count | Coefficient of variation |
|----------------------|--------------------------------|------------|--------------------------|
| Compton | SZ371848 | 102.3 | 1.05 |
| Brook | SZ387831 | 75.2 | 1.05 |
| Chilton | SZ410821 | 127.9 | 1.01 |
| Grange | SZ421817 | 123.7 | 1.27 |
| Shepherd's Chine | SZ447798 | 156.6 | 0.83 |
| St Catherine's Point | SZ499753 | 32.1 | 1.64 |
| Binnel Point | SZ525758 | 54.6 | 1.45 |
| Red Cliff | SZ620854 | 17.8 | 1.69 |

Sites are listed from west to east

sites in this study and the five transects with adult counts, as well as a combined index for the whole island, with all 13 sites together.

Results

Populations fluctuated considerably over the 18 years of the survey (note the log scale on Fig. 2). However, some sites are clearly much more variable than others (Table 1). A variance components analysis reveals strong synchrony across sites, with over 2.5 times as much variance among years as among sites. In 2013 the population appeared to go extinct at five sites, and fell to historically low levels at the

other three (Fig. 2). Prior to 2013 there were just three extinction events: at two of these the population returned the following year but Red Cliff (the most isolated site) remained unoccupied between 2000 and 2005.

A collated index based on adult counts (UKBMS transects) was not possible every year (Fig. 3), since the number of sites is small and not all were surveyed in all years. At four of the five sites, Glanville fritillaries were observed in a minority of survey years: three of these are in the northern part of the Isle of Wight and the butterflies seen here probably represent transient individuals rather than breeding populations. Not surprisingly, the collated index for our eight sites shows 2013 as the lowest overall abundance since the survey began in 1996 (Fig. 3). The whole island index is almost indistinguishable from the index based on our eight sites, reflecting the larger number of contributory sites and the fact that adult Glanville Fritillaries are generally recorded at low numbers on UKBMS transects. The overall trajectory of larval and adult-based indices is broadly similar, with a steep increase during 2008–2009 followed by a sharp decline in 2012–2013 (Fig. 3).

Discussion

Our results reveal wide fluctuations in Glanville fritillary abundance, both on web count sites (Fig. 2) and the sites where adults are counted (Fig. 3). Thus, there are ‘boom’ years, where the population increases dramatically, but these

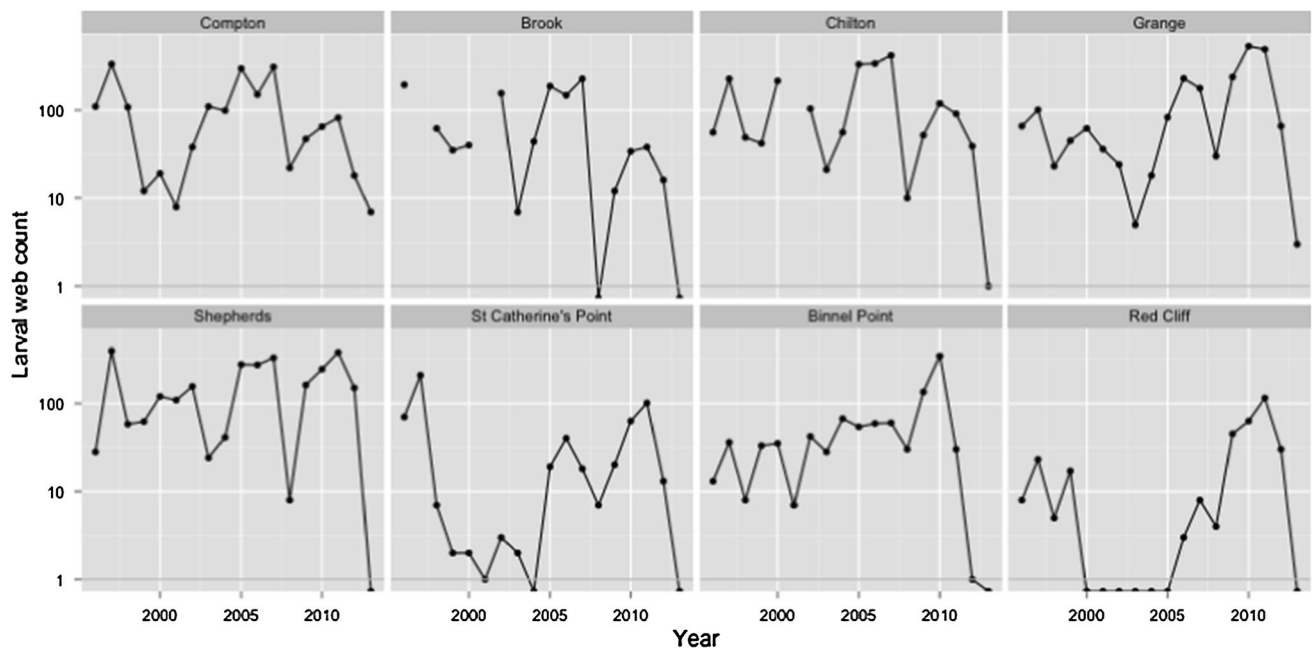


Fig. 2 Larval web counts for Glanville fritillary at eight sites, 1996–2013

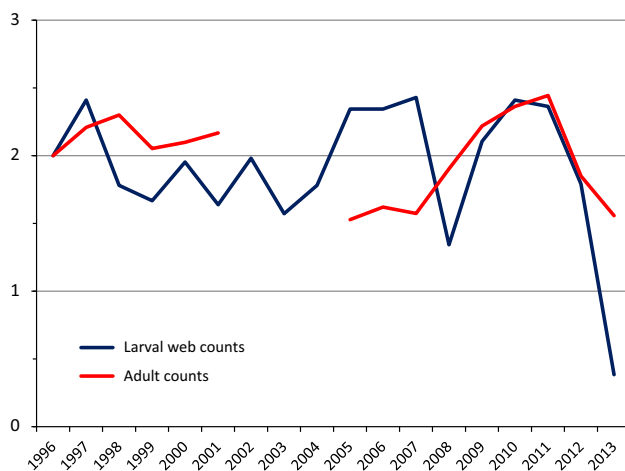


Fig. 3 Collated population indices for the Glanville fritillary on the Isle of Wight

are followed by ‘bust’. Boom years are clearly identifiable as 1997, 2006/2007 and 2010, with bust years in 2003, 2008 and 2013.

Thermophily and boom-bust dynamics

The British population of Glanville fritillary is at the very edge of its thermal tolerance. Its hostplant is widespread, but its distribution is restricted to the warmest microclimate (early-successional habitat) on south-facing slopes in one of the warmest parts of the country (Thomas 1993).

The preference for warmer hostplants and earlier successional stages can be understood by examining the larval ecology, and particularly the reliance on effective thermoregulation (Thomas 1991). Glanville fritillary larvae are gregarious until the final instars: this behaviour is more effective at raising body temperature than basking individually (Porter 1982; Bryant et al. 2000). Glanville fritillary larvae are able to raise their body temperature by up to 20° Celsius above ambient, at which point larvae leave the web to feed on the surrounding plantains (Thomas and Lewington 2010). The body temperature of a caterpillar then falls sharply, so larvae feed in short bouts between basking. This post-feeding basking is believed to be important in maximising the efficiency of a gut enzyme (J. Thomas pers. comm.). Thus, microclimatic temperature is crucial for the metabolism and development of Glanville fritillary larvae.

Adult females select hostplants that provide the warmest microhabitats (Thomas et al. 2001; Curtis and Isaac 2014), in order to maximise thermoregulation and metabolic efficiency, thus expediting development time (Bryant et al. 2002). Furthermore, fast larval development may also be important to minimise the risk of attack from host specific parasitoids, as synchronicity between parasitoid and host is much greater during cooler years (van Nouhuys and Lei 2004). However, parasitism had minimal impacts on population dynamics on the Aland Islands (Hanski and Meyre 2005), and our data support a similar interpretation: populations at Red Cliff and Binnel Point are highly

synchronous (Fig. 2), despite the parasitoid occurring on the latter site only since 2005 (Curtis, unpublished data).

Microclimate is partly determined by ambient temperature (i.e. weather), which means that not all hostplants are suitable for oviposition in all years. In years when June is relatively cold, only a small subset of plantains are used for oviposition, but in warmer years the females will lay eggs on plants on cooler aspects (Davies et al. 2006) and slopes (Weiss et al. 1988). This leads to a strong correlation between June temperature and the number of webs the following March (Curtis and Isaac 2014). The larvae are voracious feeders in the final instars, at which stage they are large enough to individually thermoregulate and thus feed without the need for gregarious basking. In years of high larval density, it is common for sites to be stripped bare of plantains in April. These same larvae then emerge in May on a site with few plantains on which to lay eggs. We speculate that this scenario creates strong density dependence and leads to population crashes the following year. It's not clear whether the primary mechanism is female dispersal in search of alternate (but nonexistent) egg-laying habitat, or larval mortality through competition for scarce food resources. Regardless of the mechanism involved, it seems clear that the boom-bust dynamics we observe are a consequence of extreme thermophily and the patchy nature of the breeding habitat.

The boom-bust dynamics we observe in the Glanville fritillary are consistent with other butterflies at northern limits of their range (Thomas et al. 1994). The amplitude of fluctuation for many British species has dampened in recent decades, as the climate has warmed (Oliver et al. 2012): if anything, the fluctuations in Glanville fritillary appear to be getting more extreme (Fig. 2), in spite of a strong warming trend on the Isle of Wight (Fig. 4).

Demise or conservation?

The 2013 survey within the eight core sites showed widespread synchronous dramatic declines. This pattern was mirrored on the UKBMS transect routes (Fig. 3), suggesting that the Isle of Wight population is at its lowest recorded level, with the total area used for breeding no more than a few km². Our results highlight the urgent need for a more wide-ranging survey of the butterfly on the Isle of Wight to determine current status and assess any extent to which the butterfly has shifted local distribution due to changing habitat conditions.

While the boom—bust nature of population dynamics exhibited by this species would suggest that recovery is possible, it could take many years to recolonize all of the former range. Indeed, the 2,000 extinction at Red Cliff, which is the most isolated of the eight monitored sites, took 5 years to be recolonized (Fig. 2). What, then, are the

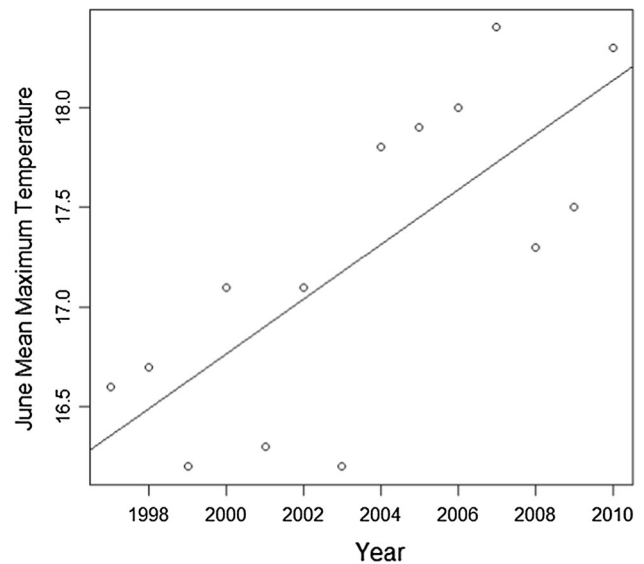


Fig. 4 June mean maximum temperatures from 1997 to 2010 at St. Catherine's Point lighthouse, Isle of Wight, with least squares regression line

prospects for the long-term survival of the species in Britain?

Most of the known sites occur on soft cliff habitats where few management options are available. Two sites, St. Catherine's and Binnel Point, are characterised by semi-permanent grassland, on which management is possible through grazing. The majority of St. Catherine's Point is overgrazed, and most of the suitable habitat lies within a small livestock enclosure where the sward height is at risk of becoming too long for oviposition. Binnel Point is a very small site, where tamarisk is encroaching onto the suitable breeding habitat: recent control efforts have been linked to increasing erosion.

We are aware of at least one other population which is not included in this survey, at Wheeler's Bay near Ventnor. Much of the breeding area is on an escarpment, which is impossible to survey without climbing equipment. However, counts from the base of the escarpment suggest that Wheeler's Bay is an important population (A. Butler pers. comm.). In the west of the Island there are extensive areas of chalk downland around Afton and Compton, which contain large areas of potentially suitable habitat. This area includes the UKBMS transect at Mottistone Down, where just three adult Glanville fritillaries were observed in 2013 (UKBMS 2013). Larval webs have been observed intermittently in this area (RJC, pers. obs.) and it's possible that small colonies persist here.

Our review of sites known to recently support Glanville fritillary on the island, suggest there is no single change in habitat or land management that is causing decline, whilst the strong degree of synchrony in annual change implicates climate as a factor. Once a census has been carried out to

determine the location and size of all remaining populations, further research is required to fully understand the causes of decline, so that a recovery plan can be formulated.

The prospects for the butterfly away from the Island look bleak. On the mainland, Glanville populations have occurred at Hurst Castle in Hampshire (close to the Isle of Wight) and at Sand Point in Somerset, in addition to scattered sightings elsewhere in southern England. The Glanville is known to have been subject to numerous unauthorized introductions (Asher et al. 2001) and it's likely these populations are not self-sustaining but a result of frequent supplementation.

The Glanville fritillary has always been one of Britain's rarest breeding butterflies, but our results indicate that it is vulnerable to extinction in its stronghold sites on the Isle of Wight. Even if the numbers can be stabilised in the short term and unoccupied sites recolonized, the Glanville will always carry a high intrinsic risk of extinction in Britain. Indeed, it could be seen as an archetype of the small population paradigm in conservation biology (Caughley 1994), as it suffers from the triple whammy of few occupied sites, large fluctuations in abundance and synchronous population dynamics across sites. In addition, the possible erosion of genetic diversity and changing climate present extrinsic threats to future persistence. Whilst the future is highly uncertain, it's not too late to act.

Acknowledgments This work was supported by NERC Grants NE/D009448/1 and NE/F007930/1. We are also grateful to the Isle of Wight Natural History and Archaeological Society (IWNHAS), Andy Butler, David Simcox, Jeremy Thomas, Wightlink and two anonymous reviewers.

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