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Only one subspecies of the scotch argus *Erebia aethiops aethiops* (Esper) exists in Britain

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ABSTRACT

The scotch argus (*Erebia aethiops*) is a locally abundant butterfly typically on the wing during August in large areas of Scotland and at two sites in northern England. It is currently accepted by many that in Scotland two subspecies – *Erebia aethiops caledonia* (Vérity) and *Erebia aethiops aethiops* (Esper) - exist in different areas and that these differ morphologically. *E. a. caledonia* is slightly smaller and has three ocelli (eyespots) on the upper fore and hind wing, whereas *E. a. aethiops* has four or more ocelli. We have surveyed four areas presumed to hold either one or the other subspecies but found that both forms exist in all areas and that *E. a. caledonia* was always the more common form. While there may be other areas that are the sole domain of one or the other form, our findings do not support the contention that two subspecies exist. These findings and the fact that there is continuous variation between the two variant extremes represented by *E. a. caledonia* and *E. a. aethiops* leads us to suggest that the subspecies *E. a. caledonia* is invalid and that this form ought to be considered only as a variant of the nominate species *Erebia aethiops aethiops* (Esper).

INTRODUCTION

The scotch argus is a butterfly of coarse damp grasslands with flushes, mires and wet woodland (Kirkland, 1995, 2004, 2012). It is the last non-migratory butterfly to peak in the late summer in Scotland and in areas with colonies is usually the most abundant species at that time. The species was first described in Scotland by Dr John Walker as "*Papillo amaryllis*" in a notebook now in the possession of the University of Edinburgh, having been discovered as early as 1760 in Bute (Stephens, 1827; Thomson, 1980). The butterfly was then renamed *Erebia blandina* (Stephens, 1856), this generic name perhaps being derived from the ancient Greek *Erebus*, meaning "darkness", in reference to the dark colour of this group. It was finally named *Erebia aethiops*, the specific name derived from the Greek for "red/brown". Subsequently it was claimed that a subspecies *caledonia* existed in Scotland (Vérity, 1911) but this was complicated by the fact that this author was comparing the *caledonia* subspecies found in Galashiels in the Scottish borders to continental "alpine" members of the species, not to other populations within the U.K. We know now that the British population differs substantially from continental European populations in habitat use in that the continental populations are dependent on forests (Slamova *et al.*, 2012; Wendt *et al.*, 2021), whereas many U.K. colonies do not seem to directly depend on forests (Kirkland, 1995). The status as a subspecies claimed by Vérity is also undermined by his own observation that there were transitions between *caledonia* and "the Alpine type", which is assumed to be equivalent to the nominate species *E. aethiops aethiops*. Also, the description given by Vérity of the subspecies *caledonia* was very brief indeed.

Other authors have given fuller descriptions of *E. a. caledonia* and differences between this and *E. a. aethiops* have been suggested. Riley (2007) and Easterbrook (2010) list four attributes. Subspecies *caledonia* is generally smaller, has more elongated and pointed forewings, the orange band is constricted centrally and only rarely contains more than three eyespots, and finally it has a less contrasting hindwing underside pattern. Newland *et al.* (2020) agree that *caledonia* is smaller and that the orange band has a constriction but point out that *E. a. aethiops* sometimes also has this. Thomson (1980) did not mention forewing shape but claimed that the orange band is narrower and nearly always constricted and rarely contains more than three eyespots. Eeles (2019) mentions the smaller size and "less prominent markings". It is notable that in the description of the nominate species Esper (1777) gave an illustration of the three-eye spotted form.

The existence of the two subspecies has become accepted by some, as has the distribution of the two subspecies within the U.K. (Thomson, 1980; Riley, 2007; Newland, 2012a; Newland *et al.*, 2020; *UK Butterflies* at https://www.ukbutterflies.co.uk). However, some other authors are less certain and for example Kirkland (2012, 2022) does not mention subspecies in otherwise full accounts, while Eeles (2019) points out that the "relative distributions of the two subspecies are not clear cut" and Easterbrook (2010) claims that it "is regarded as a subspecies by some lepidopterists". Those who do accept the validity of

these subspecies propose that *E. a. aethiops* exists in the east of Scotland and in surviving colonies in northern England, whereas *E. a. caledonia* is found in western Scotland and the Scottish borders (Fig. 1; Thomson, 1980). There is currently no indication of differences in behaviour between the two supposed subspecies except possible differences in foodplant choice (Newland, 2012a), but this is mostly due to the availability of grass species present (Kirkland, 1995, 2012, 2013). More generally, within Britain, there is no discernible differences in ecology or behaviour within the British populations (Kirkland, 2004).

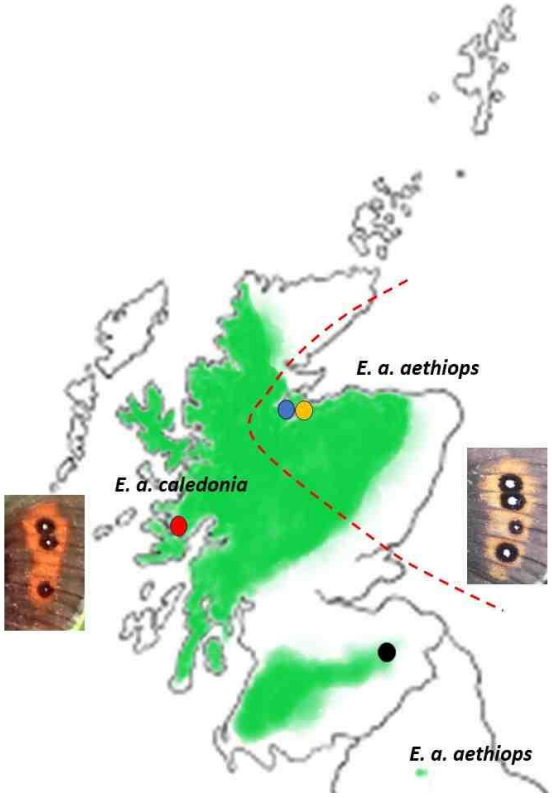

Fig. 1. The green areas show the known distribution of the scotch argus (*Erebia aethiops*) in Scotland and England (https://nbnatlas.org/; Thomson, 1980). The red dotted line shows the approximate separation of the two currently recognised subspecies: the three-spotted *E. a. caledonia* in western and southern Scotland, and *E. a. aethiops* in the eastern Scotland (Thomson, 1980). The northern English colonies are also proposed to be *E. a. aethiops.* The positions of the four study sites monitored during this work are shown by coloured circles (see Table 1). Red: Rhemore; blue: Belladrum; yellow: Milton of Leys; black: Melrose.

METHODS

Surveys were made of four areas in Scotland to determine the frequency of four-or-more (hereafter "≥four")-spotted versus three-spotted forms and other variable morphological features. These surveys were carried out mainly in August of the 2023 season, but data were also collected at the Rhemore near Lochaline, Lochaber site in August 2015 and in August 2022. Adults are generally to be found in the last week of July and throughout August (Kinnear, 2000), but some populations fly earlier (Hume, 2002). All four sites (Fig. 1) featured a similar mixture of damp, non-grazed or lightly grazed grasslands, proximal to mature trees. Wing measurements were made on limited numbers of live butterflies (Fig. 2) with as little handling as possible. We briefly detained "cold" specimens, found resting in tall grass, and measured the maximum wing length by extending the wings against the ruler. It was possible to find specimens resting deep in long grass during periods of dull weather and these could be handled gently for measuring. Adults also instinctively drop into deep grass when disturbed as a defence mechanism (Wilkie, 2019). However, the number of measured individuals (ten) was too low to justify the use of statistical tests, or to draw strong conclusions.

Fig. 2. (A) A "cold" male scotch argus (*Erebia aethiops*) with a wing span of 51 mm (Rhemore). (B) A pair of scotch argus hiding/resting in deep grass during a rain shower. (C) A female scotch argus with a fourth ocellus on one wing only (Rhemore). (D) A female scotch argus with five ocelli (Melrose).

RESULTS

No area was found to contain exclusively one variety of the species, all containing a mixture of both (Table 1). The *E. a. caledonia* phenotype (the three-spotted form) was dominant in all four areas investigated. Several individuals were found within areas supposedly of ssp. *caledonia* that were as large as or larger than the *E. aethiops aethiops* (Fig. 2A). Three-spotted forms also had three spots on the upper hindwing also and four spotted forms also had four spots on their upper hindwing.

DISCUSSION

In total we found that 23.5% of the sampled scotch argus butterflies had ≥four-spotted forewings and 76.5% were three-spotted forms. This agrees with the one-in-four estimate for the overall Scottish population (Thomson, 1980). However, the figure for southwest Scotland was only 2% (Thomson, 1980) while our Melrose site (within the southwest Scotland area) had 20%. It is possible that this is a very local difference, but it is also possible that our figure is higher as we recorded even a black dot at this position on the forewing as an eyespot and we do not know what criterion was used by

Site	Number of individuals with three ocelli	Number of individuals with four or more ocelli
Malthouse Burn beside golf course (Melrose, Scottish Borders) 55.583505ºN 2.728043ºW 199 m above sea level	62 (79.5%)	16 (20.5%%)
Rhemore (near Lochaline, Lochaber) 56.591512ºN 5.959346ºW 54 m above sea level	36 (75%)	12 (25%)
Belladrum (near Beauly, Inverness-shire) 57.444226ºN 4.465141ºW 44 m above sea level	14 (74%)	5 (26%)
Milton of Leys (south-east Inverness) 57.450128ºN 4.171381ºW 167 m above sea level	8 (66.6%)	4 (33%)

Table 1. Details of Scottish survey sites described in this paper. Sites are colour-coded as shown in Fig. 1.

Fig. 3. (A) A male scotch argus with three ocelli on the forewing, corresponding to the *E. a. caledonia* phenotype. (B) A female scotch argus with four ocelli on the forewing, corresponding to the *E. a. aethiops* phenotype.

Thomson. This fourth spot (between veins 3 and 4) (Thomson, 1980) is very variable, from a single black punctum to a full ocellus with a white centre. We have found that some individual images have a fourth small ocellus on one wing but not on the other (Fig. 2C). Furthermore, some specimens have an additional fifth spot (Fig. 2D) (Mercer *et al.*, 2009), and some even have a sixth (Newland *et al.*, 2020).

Like many satyrid butterflies, variations in the patterns and colour of the wings of scotch argus have been reported. An unusual form in which the orange band on the forewing was greatly expanded and in which there were no bands on the underside of the hindwings was recorded in northern England (Russwurm, 1971). A form known as *croesus* in which the eyespots are enlarged is reported (Thomas & Lewington, 2016). Newland (2012b) described variants of spot patterns in the upper hind wings in a population near Lochaline. This was only 13.5 miles from the Rhemore site and yet we found no such variants in this area in searches conducted in 2015, 2022 and 2023. Within the populations studied here, it is the number and pattern of eyespots on the upper forewing surface that are the most obvious variant feature. Three-spotted forms are known as *E. aethiops* subsp. *caledonia* (Fig. 3A) and four-spotted forms have become known as *E. aethiops* subsp. *aethiops* (Fig. 3B). Although Newland (2012b) did not mention numbers from his study at Lochaline, he did publish four photographs of *E. a. caledonia* phenotypes and none of *E. a. aethiops* in his paper, in agreement with our findings.

The definition of what constitutes a subspecies has been controversial (Mallet, 2007), but a generally accepted version has been offered. According to Patten & Unitt (2002) a subspecies "is a collection of populations occupying a distinct breeding range and diagnosably distinct from other such populations". We argue here that the current available information concerning *E. a. caledonia* is not compatible with this definition by multiple criteria. None of the reported differences are unique to the alleged populations, which is incompatible with the "diagnosably distinct" requirement for the status of a subspecies. Also, as the areas occupied by *E. a. aethiops* and *E. a. caledonia* share a border, this is

incompatible with the requirement for a "distinct breeding range".

However, there are two distinct subspecies of the related meadow brown (*Maniola jurtina*) found in east and west Europe, separated by intermediate forms (Thomson, 1969, 2011). Genetic studies have been conducted on populations of scotch argus from northern England and the Highlands and islands of Scotland (Gunson, 2019; Gunson *et al.*, 2023) and, although this study did not directly address the question of the validity of the subspecies *caledonia*, the results showed a general cline between the Highlands/islands and northern English populations. There was no evidence for overall differences between, for example, populations in Skye and Mull on the west coast (previously presumed to be *caledonia* territory) (Fig. 1), and the Insh marshes, Highland, Tomnavoulin, Moray, and Craigower, near Pitlochry, Perth & Kinross, towards the centre and east (presumed to be *aethiops* territory). This genetic study utilised a polymerase chain reaction (PCR) based amplified fragment length polymorphism (AFLP) technique that amplifies subsections of the genome, thereby creating a genome-wide fingerprint (Paun & Schönswetter, 2012). If *E. a. caledonia* were to be a genuine subspecies this method would be predicted to demonstrate differences between *E. a. caledonia* and *E. a. aethiops.* For example, AFLP was used to demonstrate that the butterfly species considered to be the Demeter longwing (*Heliconius demeter*) was actually two subspecies despite the fact that no difference could be detected in the adults' morphology (Rosser *et al.*, 2019).

It is still possible that areas exist in which exclusively three-spotted or ≥four-spotted forms exist. These may be individual colonies or groups of colonies, but even if they were found to exist, we suggest that they would not justify a subspecies status. Certainly, more accurate wingspan measurements should be made to test the hypothesis that the *caledonia* variety are significantly smaller than the *aethiops* variety, as previously stated, or whether there are significant differences in overall wingspan between the 3-spotted and ≥4-spotted forms. It would be helpful to measure male and female of both types also. Our initial crude measurements indicate that no such differences exist, but we would need many more, and more accurate, measurements from populations across Scotland and England to be conclusive on this point.

We conclude that the subspecies *Erebia aethiops* ssp. *caledonia* does not exist, the U.K. population instead containing a variety of forms, some of which may show local differences in the frequency of various morphological features. Genetic studies (Gunson *et al.*, 2023) indicate that whereas a general cline of variation is evident from north to south, there is no evidence to support the existence of a *bona fide* subspecies *caledonia* within the Scottish population. We suggest that the three-spotted form is only a variation and should be described as *Erebia aethiops* var. *caledonia* rather than *Erebia aethiops* ssp. *caledonia.*

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