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Long-term study of the Sword-leaved Helleborine *Cephalanthera longifolia* (Orchidaceae) in Knapdale, Argyll

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Abstract
The results of detailed monitoring of four populations of Sword-leaved Helleborine, *Cephalanthera longifolia* (L.) Fritsch over a 22-year period at Knapdale, Argyll are presented. Flowering and vegetative plants were recorded each year, with individuals relocated using triangulation. There were marked differences in the population changes at the four sites with the likely causes being grazing and changes in light intensity. In addition, a few large plants were recorded over a 31-year period. A few, large, plants flowered for the majority of the study and were probably of disproportionate importance to the long-term survival of the plant at Knapdale. The flowering, survival and occurrence of the other plants varied considerably. In addition, observations from other sites in Knapdale were noted.

Key Words: orchid; flowering; recruitment; survival; vegetative

Introduction

Cephalanthera longifolia (L.) Fritsch (Sword-leaved Helleborine) is a long-lived rhizomatous perennial, which flowers from May to June. It persists until the autumn when it dies off, but some stems with seed capsules can remain until the following spring. The plant normally produces one stem but occasionally there may be more. Each stem has a flowering spike of usually 5-20 white flowers with a yellow-edged labellum. Flowering usually occurs only if conditions are favourable and there is sufficient light but the plant can survive in dense shade for many years. The number of plants and rate of flowering varies markedly each year. The flowers are pollinated by solitary bees but only a few seed capsules are produced from one spike. Little is known about seed germination and establishment (Harrap & Harrap, 2005).

Cephalanthera longifolia grows in a variety of woodland situations, mainly on calcareous soils, where there are open areas allowing light. It is usually found in places where woodland has persisted for a long time, however it doesn't appear to be capable of colonising new areas (Summerhayes, 1951). The species has declined during the last century, especially pre-1970, mainly due to changes in woodland management, including coniferisation. It is found in fewer than 100 sites with the majority having only a few plants (Rumsey, 2010). Argyll is the current stronghold for the species in Scotland and the UK as a whole. *C. longifolia* is classed as Vulnerable in the GB Vascular Plant Red Data List (Cheffings & Farrell, 2005).

In Kintyre (v.c.101), *C. longifolia* was known from five sites in three hectads (BSBI Distribution Database). Since 2000, it has been recorded from only one hectad in Knapdale, Mid Argyll, where there are three areas containing a number of colonies. Here it likes semi shaded conditions at the edge of tracks or in glades, most often on steep rocky south east facing slopes in oak woodland.

One of the areas is located at the Fairy Isles, a long narrow peninsula with ridges and valleys enclosing small islands. It is owned by Forestry and Land Scotland. Much of the area was afforested with conifers but pockets of natural woodland remain on steep slopes and along the coast. As the site is now a Site of Special Scientific Interest and a Special Area of Conservation it is managed with the aim of restoring the native woodland. Blocks of mature conifers were felled in 1992, 1996 and 2001/2002 and were not replanted. These areas are being colonised by natural regeneration, mainly of willow and birch. A stock fence was erected across the peninsula in 2008, and cattle were introduced into the southern area as part of a woodland grazing scheme. They were present from May 2009 to September 2011 and ranged widely throughout the woodland.

There are historical records for *C. longifolia* at the Fairy Isles from 1899 but the species was first located by the author in 1990, and by 1999 it had been found in eight separate locations when walking through the area during the flowering season. Four of these are discrete colonies and the other sites are point locations with a small number of plants. The sites were mainly on SE facing slopes under oak canopy where outcrops of richer schist occurred. Four sites were at the edges of forestry tracks where glades had been created. All were in semi-shaded conditions with moderate light levels.

Methodology

Plants have been recorded annually since 1990, including non-flowering plants, which were more difficult to locate. However, in 1999 more detailed recording was started to provide data on the ecology of the plant in four colonies: Main, Jetty, Quarry and Ridge. The other point location sites and any other plants found were recorded in less detail.

Fixed points were established for each of the four colonies to enable coverage of the whole site. Using two measurement points each plant could be given co-ordinates to enable it to be relocated each year. As the plants die back completely over winter a plant found at approximately the same co-ordinates in future years was considered to be the same plant.

The whole area at each site was searched and all plants found were recorded with details of the number of leaves and flowers if present. The height of each plant was measured from the base to the top of the flowering stem. For vegetative plants measurements were taken to the tip of the longest leaf. Plants were recorded as damaged if the flowering stem was grazed off or trampled, or the leaves substantially eaten so that it was not possible to tell if the plant would produce a flower. With damaged plants any remaining leaves were counted. If there were any dead flowering stems with seed capsules from the previous year this was noted. From 1999 to 2020 data were collected once a year with a visit in mid to late May, when conditions and time allowed. Detailed recording began in 2000 at the Ridge site.

Only small numbers of plants were present in other areas and these were recorded using GPS. At three locations plants had disappeared by the start of the detailed study in 1999 however small numbers of plants appeared at four additional point locations during the study period. All plants seen were counted.

Site Descriptions

Main site

The Main site (NR763879; Fig. 1) is located in a narrow strip of oak woodland on a rocky rib, running NE/SW, close to the sea. It is open to the south east. The site is approximately 35 x 15 m, with a flat central area and sheltered to the east by the rocky rib and to the west by a steep bank. The area is partly shaded by *Quercus* (oak) and *Ilex aquilifolium* (Holly). A large *Rhododendron ponticum* (Rhododendron) bush in the northern part was cut down in 1990 and subsequent regrowth removed. Growing in semi-shade the grasses in the ground layer are sparse and interspersed with mosses and herbs, however during the study grasses in the more open areas have become rank.

Figure 1. The Main site with *Cephalanthera longifolia* growing under oak and Holly.

Jetty site

The Jetty site (NR765882; Fig. 2) is to the north of the Main site and is near an old jetty. One plant was first found here in 1993 in dense *Luzula sylvatica* (Greater Wood-rush)*,* growing between two large concrete mooring blocks under a *Pinus sylvestris* (Scots Pine) tree. The site is open to the south. Plants were mainly seen amongst *L. sylvatica* or in the adjacent sparse grasses over an area of 4 x 3 m.

Extensive windblow has occurred just north of the site and along the access track, mainly of a *Salix* species (willow) but also a large oak that continues to grow. This restricts deer movement along the coast. Saplings and *Rubus fructicosus* agg*.* (Brambles) have started to colonise the area in the past two years. The site is just outside the stock fence erected in 2008. The jetty was used pre-1990 and there was an access path adjacent to the orchid site which has become disused.

Figure 2. The Jetty Site where *Cephalanthera longifolia* grows under a Scots Pine amongst Greater Wood-rush

Quarry site

The Quarry site (NR764882; Fig. 3), 5 x 3 m, lies east of a disused quarry by the side of a forestry track and is close to the Jetty site. One plant was first seen here in 1997. The quarry was used to store felled timber in 2001/2. The quarry was originally fenced and the site being adjacent to it was kept relatively open. When the quarry was used to store timber in 2001/2 the fence fell into disrepair. A new stock fence erected in 2008 by the edge of the site partly using the original fence and preventing cattle access. This altered the drainage and the site became muddy and waterlogged in winter maintaining some bare ground. Since 2009 *L. sylvatica* has gradually spread into the site and along the edge of the fence affecting the

drainage. Additionally, a willow (*Salix* sp.) and *Betula pubescens* (Birch) regeneration has been filling the open areas. The willow was over 10 m in height by 2020 shading the site.

Figure 3. The Quarry site where *Cephalanthera longifolia* grows under a willow in bare ground and amongst *Luzula sylvatica*.

Ridge site

To the NW of the Main site is a steep wooded rocky ridge and the Ridge site (NR763880; Fig. 4) is at the top under *Fagus sylvatica* (Beech) and *Pinus sylvestris*. It is less open than the other sites but not densely shaded because of the steepness of the SE facing slope.

A conifer plantation just above and to the NW was felled in 2001 which is likely to have increased light levels. At 20 m a.s.l., the site is higher than the other sites which are all virtually at sea level. The ground vegetation is sparse grasses. Plants were first recorded here in 1996 in an area of 7 x 7 m.

Figure 4. The Ridge site under *Fagus sylvatica* with *Cephalanthera longifolia* growing in open shaded ground.

Results

All sites in the Fairy Isles area

The population change for all known plants from the four colonies and other sites from 1990 to 2020 is shown in Fig. 5.

As vegetative plants can easily be overlooked in general counting pre-1999 the number of flowering plants seen can be compared with the earlier years. The total population fluctuated between 11 and 24 flowering plants per year from 1990 to 1998 before plants were marked. After this it reached a peak of 69 flowering plants (total 103 plants) in 2008 and 66 flowering (total 109 plants) in 2007. Numbers crashed in 2012 and continued to decline to reach a low of 10 flowering (total 22 plants) in 2014. From 2015 the population gradually recovered with 23 flowering (total 42 plants) in 2020.

From 1999 the four marked sites were recorded in more detail and these are considered separately below.

Main site

The Main site had a total population of 38 plants over 1990-2020, with 10-25 plants being seen each year (Fig. 6). There was a maximum of 25 plants in 2007 and the population remained high at 24 in 2008 and 2009. The maximum number of

flowering plants since 1999 was 17 (however 20 were found in 1992). The population crashed to just 3 plants with 2 flowering in 2012 and is recovering slowly with a maximum of 13 plants (9 flowering) in 2017. There was a similar decrease in numbers in 1998 which prompted the detailed study and the population recovered from this. However, there are now fewer plants in the more open areas.

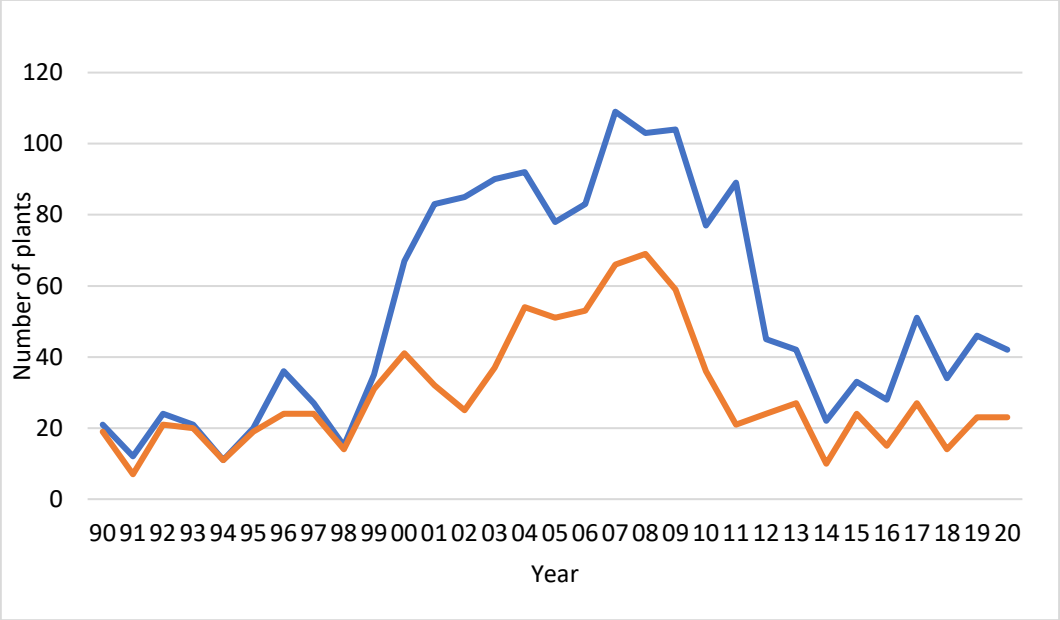

Figure 5. Number of *Cephalanthera longifolia* plants at all sites at the Fairy Isles 1990 -2020. Blue = total number of plants; brown = number of flowering plants.

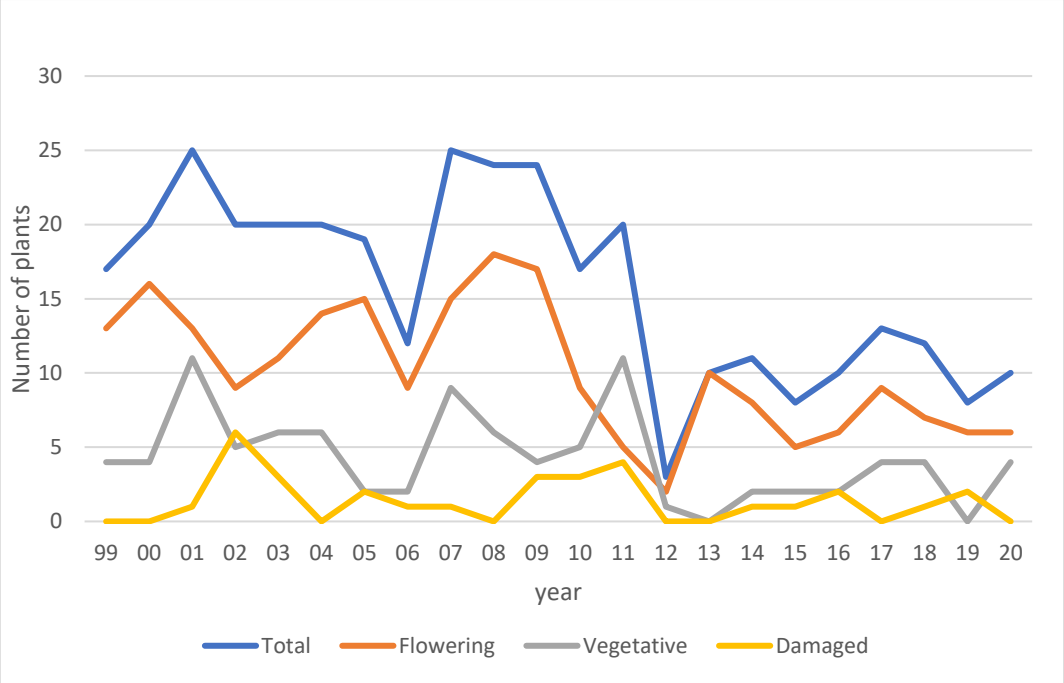

Figure 6. Number of *Cephalanthera longifolia* plants seen at the Main site 1999-2020.

There were small numbers of vegetative plants at the Main site. Of the 38 plants recorded during the study, 32 (83%) flowered at least once during their lifetime, 5 (13%) were vegetative and one was damaged so could not be classed as vegetative or flowering.

Jetty site

This site had the most stable population. One (damaged) plant was first recorded here in 1993 and from 1996-1998 there were 5 flowering each year. Since 1999, 10-12 plants were regularly seen over the majority of years until 2014 (Fig. 7). There were only four plants seen in 2016 but it was a late flowering year and all the plants were in bud. There has been a reduction in the population to 7-8 since then. Of note is plant J5 that produced 2 flowering spikes from 2000 until 2007 and then 3 spikes every year 2008-2016 apart from 2014 when 4 spikes were seen. No other site produced plants with multiple flowering spikes. There were few vegetative plants. Growing in dense *Luzula sylvatica* it will be more difficult for vegetative plants to develop or to be spotted, and those seen were in sparse grass at the edge of the colony.

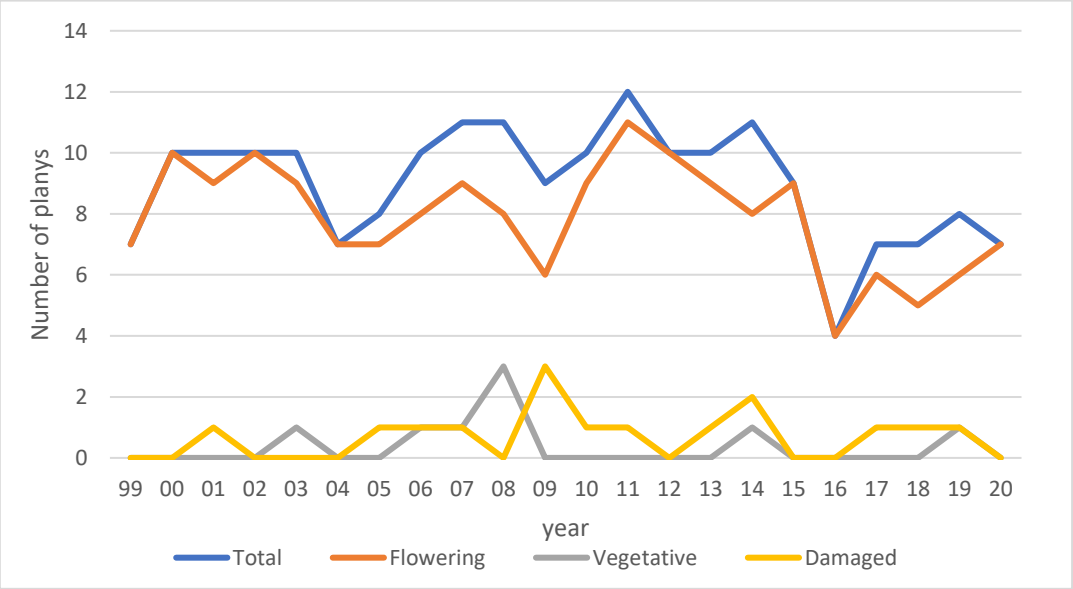

Figure 7. Number of *Cephalanthera longifolia* plants seen at the Jetty site 1999-2020.

The total population recorded during the study was 16 plants, of which 14 produced flowers (88%) and 2 were vegetative only.

Quarry site

The Quarry site is a colony that seems to have established itself during the study period. It started as one large flowering plant first seen in 1997 which continued to flower annually until 2000 when the flower buds were damaged. It was then vegetative for two years before flowering again in 2003. The plant was still flowering in 2020 with the occasional periods of absence and damage. This plant occasionally produced seed capsules prior to 1999 and since then vegetative plants have appeared and developed into flowers. From one plant the population has expanded

to 43 plants in total over the study period. A maximum of 21 plants was seen in 2012 and 2017 and the maximum number of flowering plants, 11, was recorded in 2008 and 2017. New plants developed along both the new and old fences, the majority just outside the fence on the grazed side and most appeared after the cattle were removed. This was the only site with substantial bare ground during the study period. There was a reduction in plant numbers in 2009 with only 9 plants (4 vegetative, 4 damaged and 1 flowering) when the site was particularly wet.

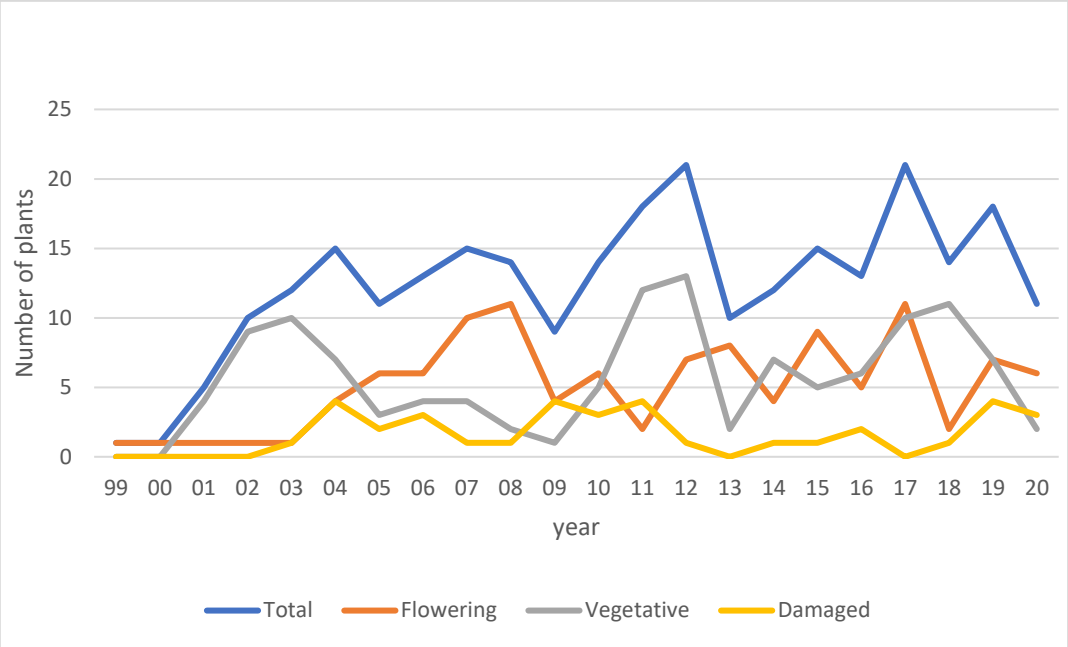

Figure 8. Number of *Cephalanthera longifolia* plants seen at the Quarry site 1999-2020.

Of the 43 plants recorded during the study at the Quarry site 30 (70%) flowered during their lifetime, 12 (28%) were vegetative and one was seen as damaged.

Ridge site

Twelve plants, eight flowering, were first seen here in 1996. Between then and 2000 when detailed recording began 5-8 plants were seen each year, with a maximum of 8 flowering (Fig. 9). The Ridge site had the most plants overall with 94 during 1999-2020. The 52 (55%) plants that flowered were mainly seen before 2012. The peak of flowering was between 2006 and 2009 when 19-23 were seen, but the maximum number of 46 plants was seen in 2009. The population crashed in 2012 to 8 plants in total then four in 2014 and none at all in 2015 and 2016.

Of the 94 plants recorded during the study at the Ridge site 52 (55%) flowered during their lifetime, 40 (43%) were vegetative and 2 (2%) were only seen as damaged.

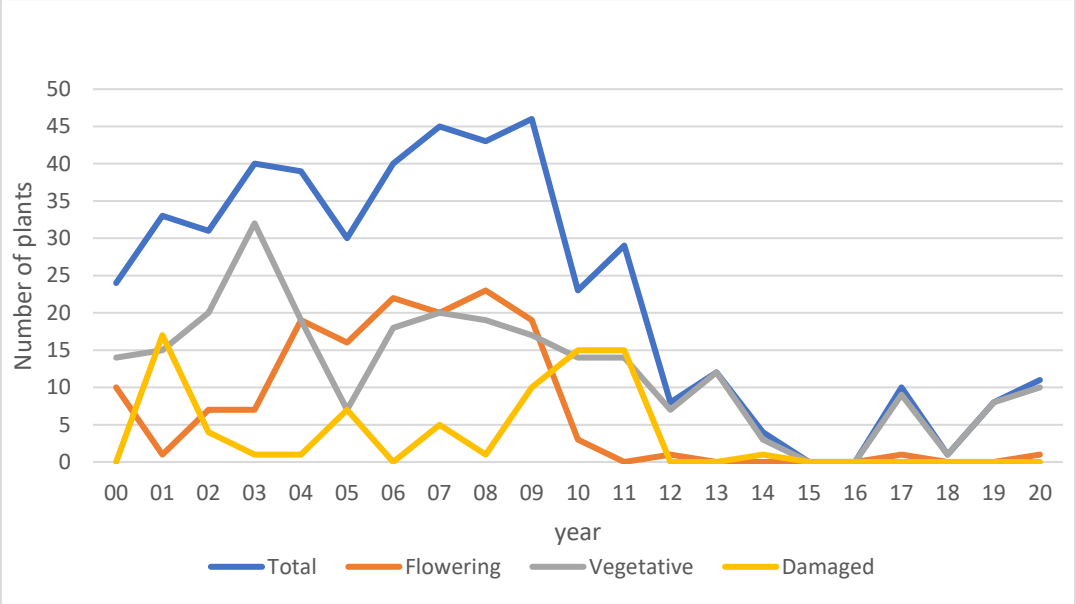

Figure 9. Number of *C. longifolia* plants seen at the Ridge site 2000-2020.

Life span of plants

In total 191 plants were recorded during 1999-2020, and of these 18 (9%) were seen for 21 -22 years, the majority of which were at the Jetty and Main sites (Fig. 10). The marked plants have been recorded for 22 years but general recording started in 1990. From their position at the Main site nine plants can be traced back for 30 or 31 years and a further 7 plants for 24-29 years. At the Jetty site five plants are likely to be at least 25 years old with a further two 21-22 years. One plant at the Quarry site was seen for 24 years. These plants were substantial flowering plants and were regularly seen.

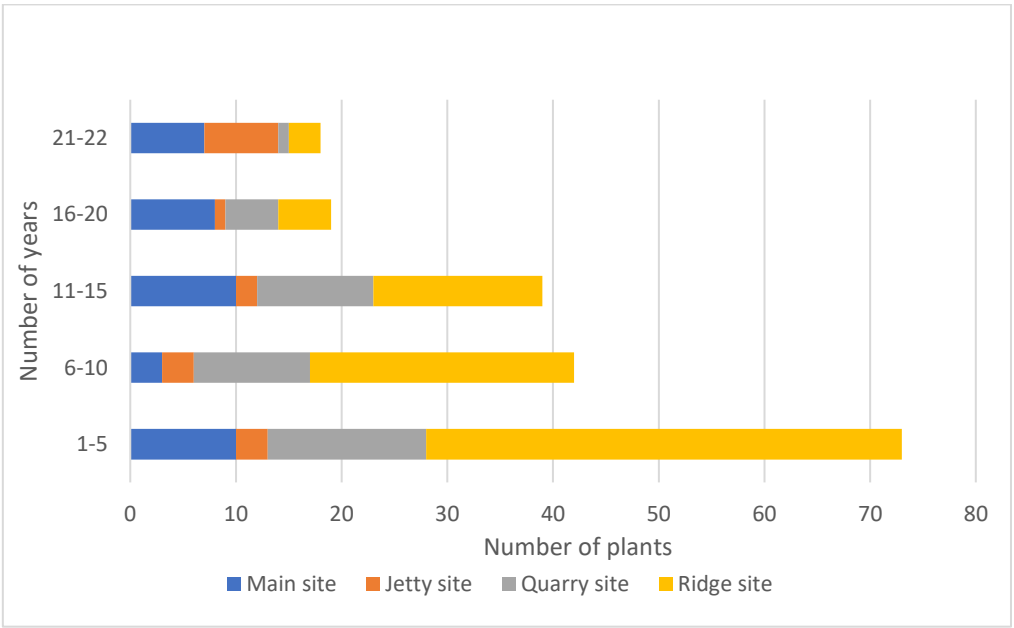

Figure 10. Stacked bar chart showing the number of years between when plants were first and last seen at each site, 1999-2020.

During 1999-2020, 58 plants (30%) were recorded for 11-20 years but the majority 115 (60%) were present for 10 years or less. The Ridge and Quarry sites had the youngest plants (Fig. 10). At all four sites combined 15% of all plants were present for one year only and 33% of plants were present for up to 5 years.

It is impossible to say if this is the actual age of a plant because plants could have been present before recording began and plants can be absent for a number of years and then reappear. Some extreme examples are four plants, originally two vegetative and two flowering, which were absent for 9 -13 years and then a vegetative plant appeared at the same locations. It is not possible to say if this was the same or a new plant after such a long absence. It is more likely to be the same if a plant can be tracked over a number of years, but two vegetative plants found for one year only at the same co-ordinates 11 years apart are likely to be different individuals.

Heights of flowering plants

The heights of flowering plants were recorded but plants in bud were not included as they had not reached their full height. The largest plants were over 50 cm tall with the maximum 59 cm, but only 1% of measured plants were in this category (Fig. 11). The majority, 67%, were between 20-39 cm tall, and no plant was less than 10 cm. The average height varied between 20-35 cm during 1999-2020.

Figure 11. Range in heights of flowering plants at sites 1999-2020 (n=538).

The Jetty site consistently had the tallest plants. Plants at the Main site varied considerably with the majority being between 20 and 40 cm, but those growing at the base of trees were smaller and those growing amongst *Luzula sylvatica* were taller.

The tallest plants at the Quarry site were (53 cm and 57 cm) but 40 (51%) were less than 30 cm. The Ridge site being more shaded had consistently smaller plants with the majority 90 (68 %) less than 30 cm. At both these sites some of the smaller plants could originally have developed from seed during the study.

Number of flowers

The number of flowers per plant varied considerably from 1-35 flowers. 60% of plants had 1-10 flowers and only 5% more than 20 flowers (Table 1). The smallest plants had one to five flowers. These were mainly at the Ridge where 59% plants had 1-5 flowers and 90% less than 10 flowers per plant. In contrast at the Jetty 70% of plants had more than 10 flowers per plant.

Table 1. Numbers of flowers per plant 1999-2020

Number of Flowers	Main site	Jetty site	Quarry site	Ridge site	Total	%
1-5	53	7	25	78	163	30
6-10	61	32	26	42	161	30
11-15	48	46	20	10	124	23
16-20	24	34	4	2	64	12
21-25	10	9	2	1	22	4
26-30	1	2	0	0	3	1
31-35	0	0	1	0	1	<1
Total plants	197	130	78	133	538	

The Quarry site had one plant with 35 flowers, but the majority of plants (91%) had between 1 -15 flowers, whilst the smaller, presumably younger, plants had 1-5 flowers. At the Main site the number of flowers per plant varied with the size of the plant as would be expected. Most were in the 6-10 category (31%), and 82% had 1-15 flowers, with only 6% having more than 20 flowers. The average number of flowers per plant for the four sites during 1999-2020 varied between 6 and 12 depending on the year.

Flowering during the plant's life span

For well-established plants, defined as present for 10 years or more, the percentage of years a plant flowered during its life span was investigated (Table 2). 83 (63%) plants out of the total of 128 flowering plants met this criterion.

A quarter of plants flowered for over 60% of their life span and these were mainly at the Jetty and the Main sites. The Jetty site was the most consistent site with four plants flowering for over 90% of their life span and only two plants flowered for less 50% of the time. At the Main site the flowering period varied considerably ranging from 10- 80%. Eight long lived plants flowered for more than 70% of the life span, others flowered well for 5-6 years then had periods when they were either vegetative or absent. The original large plant at the Quarry site flowered for at least 64% of the time, as it was present since 1995. However, it did not flower as regularly after it was damaged.

66% of plants in total flowered for less than 50% of their life span and these were mainly at the Ridge and Quarry sites where there were smaller flowering plants.

Table 2 Flowering Frequency for plants 10 years old or over 1999-2020.

Flowering frequency %	Main site	Jetty site	Quarry site	Ridge site	Total	% Plants
1-10	4	0	4	5	13	16
11-20	5	0	5	4	14	17
21-30	0	1	2	3	6	7
31-40	4	1	1	6	12	14
41-50	3	0	3	4	10	12
51-60	3	1	1	2	7	8
61-70	0	3	2	0	5	6
71-80	5	1	0	0	6	7
81-90	3	2	1	0	6	7
91-100	0	4	0	0	4	5
Number plants	27	13	19	24	83	

Development of flowering plants

The majority of flowering plants were first seen with flowers, mainly at the start of the study in 1999. Some appeared later as flowers at the edge of the colonies. 57 (45%) of the 128 flowering plants appeared to develop from vegetative plants during the study. The majority of these were at the Ridge and Quarry sites (27 plants and 20 plants, respectively). Nine were at the Main site and one at the Jetty site.

The number of years before a flowering stem appeared was examined (Fig. 12). Plants could be vegetative for several years and then flower, but also absent and damaged for some years in that period.

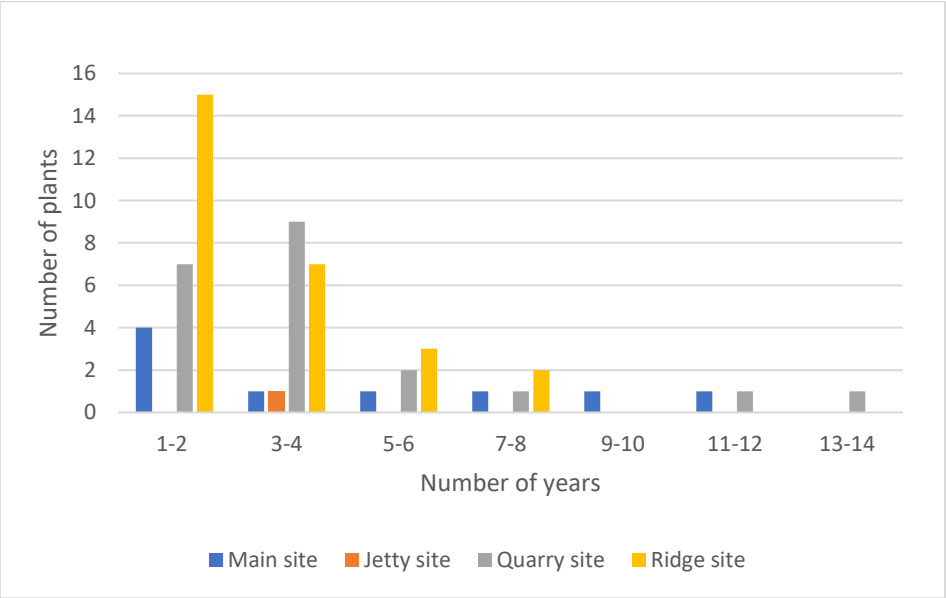

Figure 12. Number of years as a vegetative plant before flowering (n=58)

26 plants (46%) took 1-2 years to flower, particularly at the Ridge site where 15 (56%) flowered within this time. 18 (31%) of plants took 3-4 years thus 77% produced flowers within 4 years (Fig. 12). The three plants which took longer than ten years were vegetative for 5-7 years during this time with periods of absence and damage in between at the Quarry site. A plant at the Main site was only vegetative for one year with long periods of absence and damage before flowering once only. When flowering for the first time, small plants were produced with 1-5 flowers. They often spent several years as smaller plants and then presumably built up the necessary reserves to produce taller plants with more flowers, though there were sometimes periods as vegetative plants, absence and damage in the process.

The Main site being more established had fewer developing plants during the study period but 5 plants appearing before 1999 were first seen as vegetative plants. Two plants could be traced from 2-3 leaves in 1995 to flowering in 1999 and continued to flower most years to 2020. The number of flowers produced by these two plants gradually increased, in one case from one flower in 1999 to 14 flowers in 2003, and in the other case from two flowers in 1999 to 8 flowers in 2005 and then 10 in 2007. Interestingly these plants produced smaller numbers of flowers in poor flowering years after this.

At the Jetty site only one flowering plant developed from a vegetative plant; it was vegetative for 3 years, absent for a year and then flowered most years to 2020. It had stored sufficient reserves to produce 12 flowers when first flowering. The only other two vegetative plants seen were present for a year only.

Vegetative only plants

Of the 116 vegetative plants seen between 1999 and 2020, 59 (51%) never developed flowers. The majority of these (40) were at the Ridge site, with 12 at the Quarry site, 5 at the Main site and only 2 at the Jetty site. Of these 59 plants, 28 (47%) survived for 1-2 years. However, 12 (20%) survived as vegetative plants for over 6 years (Table 3).

Table 3. Number of years vegetative only plants were present

Number of Years	Main site	Jetty site	Quarry site	Ridge site	Total	% plants
1-2	3	2	6	17	28	47
3-4	0	0	3	11	14	24
5-6	1	0	0	4	5	8
7-8	0	0	2	3	5	8
9-10	1	0	0	1	2	3
11-12	0	0	1	0	1	2
13-14	0	0	0	3	3	5
15-16	0	0	0	1	1	2
Total plants	5	2	12	40	59	

Of the plants seen for longer than 10 years there were occasional periods of absence. One plant was present for a total of 16 years; in the first 10 years it was vegetative with the occasional absence but then it was damaged and it was 5 years

before another vegetative plant was seen at the same co-ordinates. The latter may have been a different plant. At the Ridge site 60% of the vegetative plants never flowered compared with 36% at both the Main and Quarry sites. 31% (59) of the total number of plants (191) recorded during the study were vegetative only.

Recruitment and Losses

The pattern of recruitment and losses over the study period is shown in Fig. 13. After the first two years (detailed recording began in 2000 at the Ridge site) most recruitment took place between 2002 and 2007 when 11-14 new plants were seen each year. Further large additions of 7-9 new plants occurred between 2010 and 2012. There were only 1-5 new plants or none in other years and less recruitment after 2012. These additional plants were mainly developing vegetative plants, however there were a small number that first appeared as flowering plants at the edge of the sites.

There was a sharp increase in the numbers of plants last seen between 2009 and 2011. This varied between 14 to 25 plants per year, making 55 plants in total over these 3 years. Fewer than 10 plants per year were apparently lost in the other years, discounting 2018 onwards as it is too early to know the fate of these plants. As plants can be absent for a number of years it is possible that they may reappear in the future especially ones absent in more recent years. No losses were recorded in 2020 as losses are only known the following year.

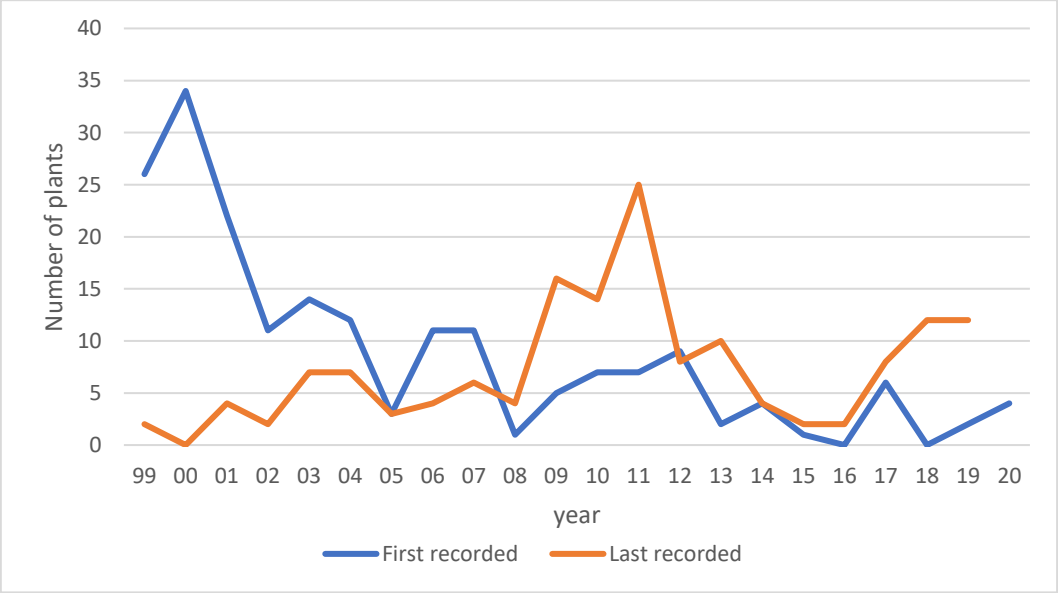

Figure 13. The number of plants first recorded and last recorded each year at sites 1999-2020.

Damaged plants

Damage to plants was mainly through grazing by deer, voles, cattle or trampling. Slugs can also eat the main stem. Only those plants that had been severely affected were included, plants where there was minor leaf damage were excluded. Of the 191 plants, 92 (48%) were damaged at least once during the study period. All sites were affected and damage varied between 45% and 56% at the four sites. Most plants (52 or 57%) were only damaged once, 21 (23%) twice and the other 19

plants (20%) plants between 3-5 times. Eight plants were damaged twice in consecutive years and one three consecutive times. This latter plant was not seen again. One plant at the Ridge site was first seen as a small flowering plant and then damaged 4 times in 5 years appearing as a vegetative plant in between. It was then vegetative for 4 years, flowered, then was damaged again. After this it was vegetative or absent, the longest absence being for 5 years. The plant was last seen in 2019 and appeared to have survived for 20 years but this was exceptional.
What happened to individual plants the year following damage was investigated. For all sites 31 (34%) plants were lost, not seen at all in subsequent years, 18 (20%) were absent for 1-6 years. The outcome of the rest of the plants was evenly split between flowering directly afterwards or producing a vegetative plant which could flower in future years (Fig.14).

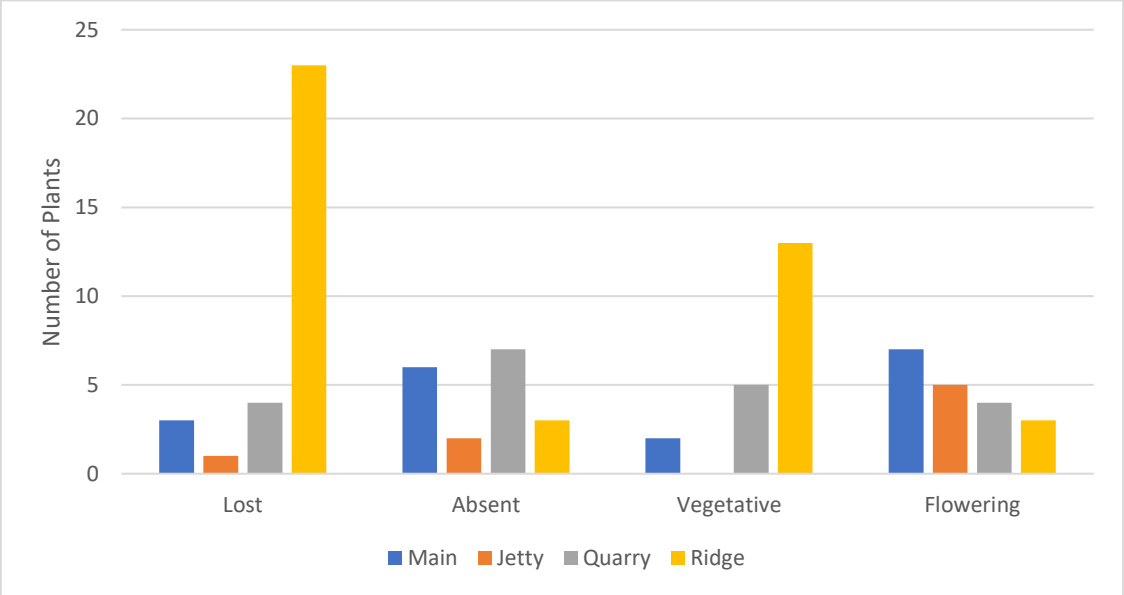

Figure 14. The fate of plants in the year after damage 1999-2020.

Well established plants could be damaged one year and flower again the next. The smaller and probably younger plants, that were establishing themselves, were more affected.

The Ridge site suffered most effects from the damage, 23 plants (53%) were not seen again and a further 18 plants (42%) were absent for 1-5 years after damage. From the signs left it appeared that deer grazing contributed to most of the damage at this site. Here there appears to be a correlation between the number of plants damaged in 2009-2011, 31 in total, and plants last seen in these years, 37 plants. However, in 2001 when 17 plants were damaged, though weakened these plants survived and the population continued to increase. The Quarry site had the greatest percentage of plants damaged 24 (56%), of these 5 (21%) disappeared, and 7 (29%) were absent for 1-6 years. Four plants were absent in each of 2019 and 2020, 3 in both years and one in 2019, the fate of these is not yet known. At the Jetty site though 50% of plants suffered damage they were large, robust, mature plants and most of them flowered the next year and subsequent years.
The Main site suffered a huge decrease in numbers in 2012 from 20 plants to three. However, only three plants were lost after damage in 2011 suggesting that damage

had much less of an effect here than at the Ridge site in that year. At the Main site, of the 18 plants damaged overall, 3 (17%) were lost, and 6 (34%) were absent for 1-7 years directly afterwards. Most of the rest, 7 (39%) continued to flower the year following damage though sometimes sporadically after that.

Seed Capsules

The sites were only visited in May and hence only a few plants developing seed capsules were seen. However, these are persistent and can sometimes be present the following year. When present they were counted though, of course, others will have been missed. At the Jetty site seed capsules were found in six years during the study period, including five years between 2000 and 2007. A maximum of four seed capsules were produced (range 1-4) and the maximum number of plants producing them was four in 2002. Additionally, two plants produced three and four capsules in 2020 following an exceptionally good spring. The Main site had one plant with one seed capsule in 2000 and the Quarry site two plants with seed capsules present in 2007.

Discussion

Observing a population of *C. longifolia* for over 30 years, with individual plants marked for 22 years, at four sites has provided detailed information about the species and its ecology. Although in close proximity the four sites performed differently over the period with two declining considerably, one stable and the other expanding.

Numbers of plants rose and then fell. This appears to be a real situation and is not due to closer searching from 1999 as the number of flowering plants also rose and fell. There was consistency in recording flowering plants from 1990 onwards. The population change is mostly be linked to two factors, changes in light levels and recruitment and loss.

Mature conifers were felled in 1996 near the Main and Quarry sites and during 2000/01 above the Ridge site. *C. longifolia* appeared to quickly respond to these changes, including four point-locations by forestry roads the year after felling. However, they were only present for 2-5 years until the ground vegetation grew dense.

For new plants to become established a combination of factors is needed; open ground, sufficient light, seed source and adult plants close by. The underground rhizomes have an association with particular fungi which are needed for development. Though few plants with seed capsules were recorded in the study (no late summer visits were made) many flowers were present and so it is likely more capsules were produced. Orchid seeds are like dust and a capsule can produce many seeds which will disperse widely.

The Quarry site had ample bare ground and what appeared to be new seedlings developed into flowering plants during the study period. At the Ridge site some new small vegetative plants occurred over a five-year period. It is not known if these grew directly from seed or how long seed takes to develop. Some may have grown from existing underground rhizomes, particularly at the Ridge site which is a more shaded site and may not have provided enough light for all plants to develop flowers until the conifer felling.

Just less than half vegetative plants produced flowers, and of those 44% within 2 years and 77% within four years. Small, few-flowered, plants were produced first and it took several more years of favourable conditions to produce large flowering plants. Just over half the plants, 51% remained vegetative and of these 47% survived for only 2 years. At the ridge site there was a greater proportion of vegetative plants where conditions seemed less favourable.

The decrease in numbers, which was a major population crash, could have been caused by grazing and/or decreased light levels. Cattle were present from 2009-2011 at the Main and Ridge sites. The other two sites outside the grazed area did not suffer the same population reduction. The Main site was particularly affected with evidence of cattle trampling as well as grazing. A temporary fence was erected here in 2010 to reduce this but unfortunately some plants at the edge of the colony were not included and there was further damage in 2011. The Main site is now recovering slowly.

Cattle had access to the Ridge site but there was more evidence of deer grazing here. From Met Office data the winters of 2010 and 2011 were amongst the coldest in recent years with more days of frost (Met Office, 2022). 2001 also had more days of frost in spring. As the plants die right down over winter and they are in sheltered woodland this may not have been a direct affect. However, during years when the spring is late the succulent orchid spikes appear before the surrounding growth and are very attractive to deer. At the Ridge site over 50% of plants disappeared after they were damaged and there seemed to be a correlation between the damaged plants and disappearance over this period. However, after similar grazing damage in 2001 plants were weakened but continued and the population expanded, so the orchid can withstand grazing in some circumstances.

The more established plants are not as affected by damage as developing ones and can flower again the following year. However, they may instead produce vegetative plants or be absent for a period of time before they gain enough reserves to flower again. When conditions at a site are less favourable the impact of grazing is more pronounced. The Ridge site had not recovered from the crash by 2020 when only 11 plants remained and no plants were seen at all in 2015 and 2016.

There has been considerable scrub regeneration in the clear fell areas and throughout the site. The tree canopy at all the sites is increasing gradually and thus light levels have decreased. The ground vegetation has also increased in cover and density, so there is more competition for orchid growth. At a different site on a road verge mowing clearly illustrated the effect of this. In the two years the verge was cut in the autumn, plants appeared in the following spring and disappeared when mowing ceased and the vegetation became coarse again. Plants growing amongst grasses were more affected and this may be contributing to the decline at the Main site.

There were concerns at the start of the study that *Luzula sylvatica* would outcompete the orchid at the Jetty site but these plants have the best survival rate. The Jetty site has shown that plants can have a capacity to flower for 90% of their lifetime under the right conditions. Plants can live for over 30 years and still be vigorous. These large long-lived plants which consistently flower with large numbers of flowers (and hence probably seed) will have a significant effect on the survival of the orchid at the main colonies and its survival in the area. These larger plants also seem to have the ability to survive some grazing damage and continue flowering.

Some of these plants are over 30 years old with an unknown life span. By contrast the study has shown that some plants can develop from the vegetative form to produce flowers and gradually over the years increase in size and flower production. Some plants, however have the ability to appear for the first time as a large flowering plant.

Conclusions

The study has shown how sensitive the colonies of *C. longifolia* are to habitat change, competition with coarse vegetation and grazing damage. The efforts of Forestry and Land Scotland to control deer to allow natural woodland regeneration may have had an unintentional effect on the shading of the main colonies. Some localised removal of regenerating scrub might be necessary in the near future at some of the sites to allow the orchid to survive.

The importance of a small number of long-lived plants that flower almost every year to the population survival has been demonstrated.

The Fairy Isles has a very small population of *C. longifolia* with scattered isolated sites in restricted areas. It is possible there was once a much larger population in Knapdale. The species is still just surviving here. The study has shown that under the right conditions, particularly the appropriate light intensity, the species can persist and expand.

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