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Status and declining trend of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) orchids in Pukaskwa National Park, Ontario, Canada

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Abstract

Pukaskwa National Park hosts part of a disjunct population of the perennial orchid species Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) on the north shore of Lake Superior, Ontario, Canada. Monitoring of *C. passerinum* within Pukaskwa National Park occurred between 1979 and 2019. During that period, the total number of stalks and the number of *C. passerinum* colonies within the park have declined, while the proportion of flowering stalks at colonies has increased. Although the number of stalks at extant colonies is stable, this population may be suffering from lack of recruitment and is at risk of extirpation. We hypothesize that the decline and lack of recruitment are a result of changing habitat conditions due to natural and anthropogenic influence.

Key words: Franklin's Lady's-slipper; Orchidaceae; Parks Canada; population decline; orchid conservation; dune succession; recruitment; climate change

Introduction

Sparrow's-egg Lady's-slipper (*Cypripedium passerinum* Richardson; Orchidaceae) is a perennial herbaceous orchid species distributed in boreal and subarctic regions of North America from Alaska to Hudson Bay and south to northern Montana (Sheviak 2002). Disjunct populations occur on the north shore of Lake Superior at the mouth of the Pic River and in the Mingan Islands near the north shore of the St. Lawrence River (Keddy *et al.* 1983; Rankou 2014).

The conservation status of *C. passerinum* is Secure globally (G5) and in Canada (N5) and is Apparently Secure (S4) in Ontario (NatureServe 2020). The Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has not yet assessed the species and therefore it cannot be considered for listing under the Canadian *Species at Risk Act*. In 2014, the species was added to the International Union for the Conservation of Nature (IUCN)'s Red List of Threatened Species as Vulnerable (Rankou 2014). The IUCN suggests that within the global range of this species (5 722 278 km²), there are 1200 to 10 000 mature individuals in 20 known locations, with an area of occupancy (the area within its extent of occurrence occupied by a taxon typically calculated by adding the number of occupied 2 km × 2 km grid squares) of 650 km² (Rankou 2014). This is likely a great underestimate dependent on the definition of location, as there were 105 sites of this plant mapped in the Northwest Territories (Porsild and Cody 1980), some likely overlapping with 28 sites in Ontario (Whiting and Catling 1986) and more than 50 sites in northwestern North America (Catling and Bennett 2007). Furthermore, there are likely additional unknown threats-based locations within the vast and botanically underexplored Hudson Bay Lowland (M.J. Oldham pers. comm. 11 September 2017). Human impacts, including deforestation, wildfire, tourism, urbanization, trampling, and plant collection for horticultural and medicinal use, may threaten the persistence of this species (Rankou 2014). However, much of the range occupies northern Canada, where there is relatively little human impact (M.J. Oldham pers. comm. 11 September 2017).

Pukaskwa National Park (PNP) encloses part of the disjunct population of *C. passerinum* on the north shore of Lake Superior, south of the mouth of the Pic River (48.6°N, 86.3°W), within an active cove dune system formed by glacio-fluvial deposits (Zoltai 1967; Bakowsky and Henson 2014). The other part of this population occurs on land managed by Biigtigong Nishnaabeg (formerly Ojibways of the Pic River First Nation), north of the mouth of the Pic River. This disjunct population was discovered in the 1800s (Macoun 1888) and rediscovered in 1964 (Soper 1965). Keddy (1979) characterized the distribution, morphology, phenology, growth, reproduction, and habitat of this population. In 1979, the population consisted of 57 "colonies" that contained 1–137 (average 17) stalks of *C. passerinum* each and a total of 919 stalks (Keddy 1979); 443 stalks were within PNP. Colonies were clusters of stalks (that may be clones of one or more individuals) ≥1 m from other clusters, except in the case of three clusters, which were <1 m apart, recognized as groups because of obvious habitat differences (Keddy *et al.* 1983).

Following Keddy's (1979) study, PNP recognized *C. passerinum* as a rare plant within the park and established a management plan for this species, which included a monitoring program to quantify changes in the number of stalks over time and thereby assess the effectiveness of management practices (Parks Canada Agency 1986). Many unpublished monitoring reports of the status and trends of the colonies within PNP have been written (Keddy 1984; Vien 1985a,b, 1987, 1988, 1989, 1990; Vien and Mosquin 1986; Reside 1992, 1993; Irvine and Drake 2017a,b; Irvine and Patterson 2021). Here we document the status of *C. passerinum* in PNP in 2019 and discuss trends in the population observed from monitoring conducted since 1979. Specifically, we determined the trends in the number of plants in all colonies and in extant colonies only, the trend in the percentage of flowering stalks, and whether habitat conditions (slope, aspect, canopy cover, and cover of downed woody debris) differed between extant and extirpated colonies.

Species biology

Cypripedium passerinum is a rhizomatous, perennial herb, capable of asexual (clonal) reproduction and sexual reproduction via seeds (Figure 1). Aboveground stalks of *C. passerinum* are erect, 12–50 cm tall, with 3–7 elliptic-lanceolate leaves (5–19 × 1.5–6 cm) arranged alternately along the length of the hairy stem (Sheviak 2002). Flowering plants have one (rarely two) flowers with two lateral and one dorsal sepals, two lateral white petals, and one central basal petal forming a pouch with purplish spotting at the lip and inside. Individuals of *C. passerinum* can take up to 15 years to flower, which occurs in June and July (Keddy *et al.* 1983). The population of *C. passerinum*

FIGURE 1. A flowering stalk of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) in Pukaskwa National Park in 2019. A cured seed pod, persistent from the year before, is visible in the left side of the photograph. Photo: Parks Canada Agency.

at the mouth of the Pic River is capable of self-pollination (Keddy 1979; Catling 1983; Catling and Bennett 2007); self-pollinated flowers produce seed pods (99% of healthy flowers produced seed pods; Keddy 1979), and seed pods (capsules) contain enormous numbers of lightweight seeds (Keddy 1979). *Cypripedium* spp. have specific requirements for seed germination, such as the presence of a symbiotic mycorrhizal fungus (Shefferson *et al*. 2005). If seed germination is successful, *Cypripedium* spp. must survive a subterranean protocorm life stage, relying on carbon production from their symbiont, to produce above-ground stalks (Curtis 1943; Shefferson 2006). Both vegetative and flowering stalks of *C. passerinum* can produce clonal offshoots along shallow-buried rhizomes, such that a large network of clonal stalks may eventually persist above-ground (Keddy *et al.* 1983) and may transition to and from periods of extended dormancy, as in other species of *Cypripedium* (Shefferson 2006). *Cypripedium passerinum* occupies a variety of habitats, including moist coniferous forests, thickets, forest openings, wooded ravines, littorals of streams, lakeshores, swamps, river terraces, edges of lakes and streams, and talus slopes in the montane and subalpine zones, on moist to dry substrates in bright light and on well-drained slopes (Sheviak 2002; Rankou 2014).

Methods

Monitoring

All colonies (clusters of stalks ≥1 m from other stalks; Keddy 1979) of *C. passerinum* in the population near the Pic River within and beyond PNP were identified in 1979 (n = 52) and given unique identifying numbers. All colonies within PNP (n = 22) were monitored annually from 1982 to 1990, and in 1992, 1993, 1999, 2001, 2016, 2017, and 2019. In 1983, PNP installed 13 permanent rebar stakes and recorded the directional distance between the nearest stake and *C. passerinum* colonies. This system was used to relocate the colonies in subsequent years until 2016, when the global positioning system coordinates of each colony was recorded. Surveys occurred between 16 July and 20 August of each year and consisted of counting the number of vegetative and flowering stalks at each colony. We used stalks (ramets) as a proxy for the number of individuals because the number of genets (true genetic individuals) within a colony could not be identified without soil excavation (Gregg 2004). Beginning in 1982, stalks at colonies 45–47 were combined into one colony (identified as colony 45-46-47 and considered one colony hereafter), as were stalks at colonies 50 and 51 (identified as colony 50-51 and considered one colony hereafter), for an unrecorded reason. In 1983, one additional colony (53) was found. Thus, we consider the historical number of colonies in PNP to be 20.

In 2019, we estimated the slope of the ground and directional aspect of the slope using a handheld compass, and we estimated the overstorey canopy cover and amount of downed woody debris in a ~1 m^2 area, or the area occupied by plants (mean = 1 m × 0.5 m), in four categories (0–24, 25–49, 50–74, 75–100%) at historical and extant colonies.

To determine the general trend of the *C. passerinum* population in PNP, we tested whether the number of *C. passerinum* stalks had increased, decreased, or remained stable between 1970 and 2019. We used a generalised additive model with a negative binomial error distribution to account for non-linearity, serial autocorrelation, and overdispersion in the count data (Wood 2011). Stalks within four colonies were excluded in the total count as these colonies were not surveyed every year, either to avoid trampling Northern Twayblade (*Neottia borealis* (Morong) Szlachetko; Keddy 1984) or because the nearest rebar stakes were not found (Irvine and Drake 2017).

To determine the trend of extant colonies of *C. passerinum* within PNP, we reported the number of colonies that have been extirpated compared to the number of historically known colonies. We tested whether the abundance of remaining colonies of *C. passerinum* increased, decreased, or remained stable between 1970 and 2019, using the number of stalks as a proxy for the number of individuals. We used a mixed effects linear model with "colony" as a random effect and a negative binomial error distribution to account for overdispersion in the count data (Bates *et al.* 2015).

To determine the trend in the percentage of flowering stalks, we calculated the proportion of flowering stalks out of the total number of stalks observed each year of monitoring and determined whether the proportion of flowering stalks was increasing, decreasing, or stable. We used a generalised linear model with a quasi-binomial error distribution to account for overdispersion in the proportion data (Bates *et al.* 2015). We excluded data from 1982 in this analysis because the number of flowering stalks was not recorded (Keddy 1984).

Lastly, we determined if microhabitat condition at colonies (slope, aspect, canopy cover, downed woody debris) contributed to the persistence of colonies. We tested whether slope, aspect, overstorey canopy cover, and downed woody debris were significantly different at colonies that were extant versus those that were extirpated using a two-sample *t*-test, Watson-Williams nonparametric test of homogeneity of means for circular data (Putman *et al.* 2014), or Fisher's exact test for frequencies, respectively. We considered all analyses significant at $\alpha = 0.05$. We completed all statistical analyses in R version 3.6.3 (R Core Team 2020).

Results

The total number of *C. passerinum* stalks found within PNP in 2019 was 162, representing only 36.6% of the 1979 population (443 stalks). The total number of stalks decreased significantly from 1979 to 2019 ($\chi^2_{2.3,\,2.8} = 66.05$, $P < 0.001$; Figure 2).

Nine of the 20 colonies identified in 1983 persisted in 2019. Note that we used the number of colonies in 1983 rather than the number of colonies in 1979 because some colonies were combined beginning in 1982 for the remainder of the monitoring years, and one additional colony was found in 1983. The number of *C. passerinum* stalks at extant colonies has remained stable ($\beta \pm SE = 0.004 \pm 0.005$, $z = 0.79$, $P = 0.427$; Figure 3, Table S1). The proportion of *C. passerinum* stalks flowering has increased by ~1.25% annually ($\beta \pm SE = 0.055 \pm 0.009$, $t = 5.942$, $P < 0.001$; Figure 4, Table S1).

Habitat conditions that were measured in 2019 did not differ among locations of extant and extirpated *C. passerinum* colonies. There were no significant differences in slope ($t_{16.6} = -0.433$, $P = 0.67$), directional aspect ($W_2 = 0.42$, $P = 0.81$), canopy cover (Fisher's exact test [two-sided]: $P = 0.67$), or downed woody debris (Fisher's exact test [two-sided]: $P = 0.21$) among locations of *C. passerinum* colonies that survived versus those that have become extirpated (Table 1).

Discussion

The decline in the total number of *C. passerinum* stalks, and the number of extirpated colonies in this population, is cause for concern, despite a small increase in the number of stalks since 2016 (Table S1: 162, 149, and 173 stalks in 2016, 2017, and 2019, respectively). Although the population trend in extant colonies is stable, a number of the extant colonies possess few stalks (6/9 extant colonies have fewer than 15 stalks each). Extirpation events of colonies decrease genetic diversity (Frankham *et al.* 2002), and the potential of small populations to adapt following chance events or novel conditions is reduced (Willi *et al.* 2006). The number of stalks in a colony is related to the survival of the colony in other species of *Cypripedium* (Shefferson 2006). The average number of stalks over the lifetime of *C. passerinum* colonies that were extirpated (12.9) was lower than in those that survived to 2019 (17.6) in PNP. Decreased population size increases risk of population extirpation in Clustered Lady's-slipper (*Cypripedium fasciculatum* Kellogg ex S. Watson; Kaye *et al.* 2019). As a disjunct population of *C. passerinum*, plants within PNP likely harbour some unique genetic material, thus extirpation could represent a loss of genetic diversity in this species.

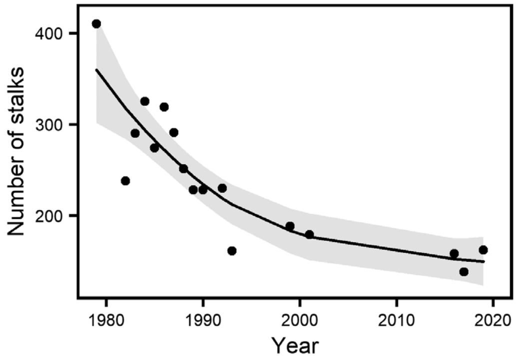

FIGURE 2. Total number of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) stalks counted within Pukaskwa National Park, Ontario, Canada between 1979 and 2019. The black line represents a generalised additive model with a negative binomial error distribution of the data and the grey ribbon represents the 95% CI of the predicted model.

The other finding of concern is the increase in the proportion of *C. passerinum* plants flowering within PNP since 1979. Individuals of this species take up to 15 years to flower (Keddy *et al.* 1983), and so the increasing proportion of flowering plants and declining number of stalks suggests that recruitment of new individuals may be limited in this population. A lack of recruitment can contribute to population declines in *Cypripedium* spp. (Nicolè *et al.* 2005). However, *C. passerinum* is not monocarpic nor is the transition between vegetative and flowering status necessarily linear. We did observe back-and-forth transitions between vegetative, flowering, and dormant (subterranean) life stages (e.g., Colony 43 in Table S1), as noted in other species of *Cypripedium* (Shefferson 2006). Thus, this result should be interpreted with caution, but could be clarified by identifying genets and true seedlings in the population.

A likely proximate explanation for the decline in numbers of stalks and ultimately in colonies of *C. passerinum* and the increase in the proportion of flowering plants is that recruitment of *C. passerinum* via sexual propagules (seedlings) is limited. Recruitment occurs via sexual and asexual reproduction in orchids. In 1979, true seedlings, identified by a tapering rhizome <1 cm long, occurred at only 5/20 colonies, and only in early successional habitat (Keddy 1979). We could not collect similar data because we did not dig up colonies. Seed production is an unlikely constraint in this population as self-pollination occurs and a large number of seeds are dispersed; seed germination and survival are more likely constraints (see

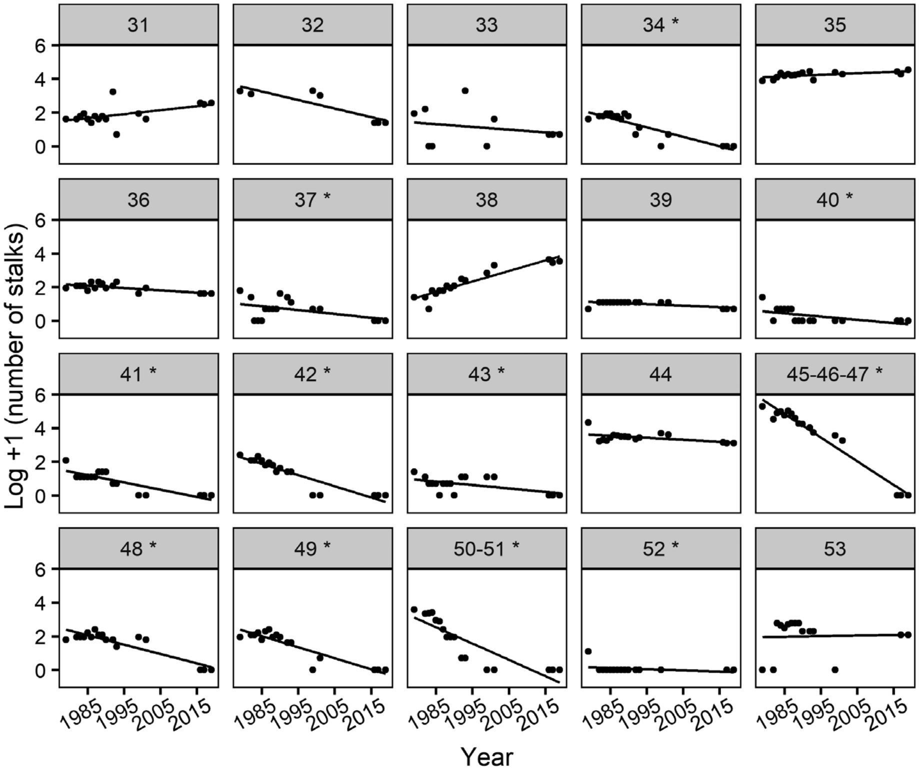

FIGURE 3. Number of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) stalks (log + 1) counted at each colony within Pukaskwa National Park, Ontario, Canada between 1979 and 2019. Trend lines represent linear models. Colony numbers followed by an asterisk are assumed to be extirpated.

Species biology section). The requirements for seed germination are not well understood in *C. passerinum*, but moisture regime, pH, light levels, and the presence of symbiotic fungi are likely all important factors (see Keddy 1979 for a thorough description). Germinated seeds of *Cypripedium* spp. are unlikely to survive the transition to above-ground stalks. For example, García *et al.* (2010) found that 1–10% of the 5000 seeds/fruit of Lady's Slipper Orchid (*Cypripedium calceolus* L.) were viable and landed in suitable microhabitats, 0.0001–1% of those seeds germinated and survived as protocorms over 3–7 years, and 1–10% of subterranean protocorms produced new stalks; the same pattern may be true for *C. passerinum*. An attempt to propagate *C. passerinum* via seed dispersal was unsuccessful in PNP (Keddy 1984).

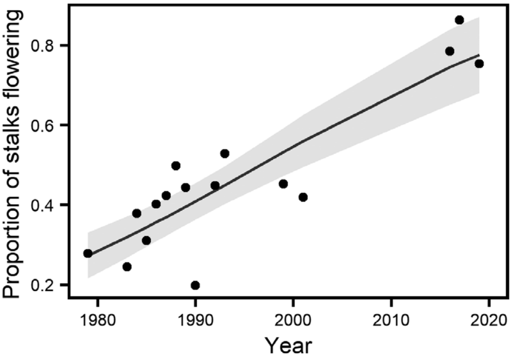

FIGURE 4. Proportion of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) stalks flowering between 1979 and 2019 in Pukaskwa National Park, Ontario, Canada. The black line represents a generalised linear model with a quasibinomial error distribution of the data and the grey error ribbon represents the 95% CI of the predicted model.

Asexual reproduction is an important mechanism of recruitment in orchids generally (Shefferson 2006) and of *C. passerinum* within PNP (Keddy 1979). Clonal offspring increase resource acquisition from a heterogeneous environment and can reduce mortality risk to the individual (Shefferson 2006). Asexual reproduction likely occurs more rapidly than sexual reproduction in *C. passerinum* and may improve survival of genetic individuals (Keddy 1979). Conditions

TABLE 1. Descriptive statistics for slope (°), directional aspect (°), canopy cover (%), and downed woody debris coverage (%) at locations of extant and extirpated colonies of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) in Pukaskwa National Park, Ontario, Canada in 2019.

	Summary statistic	Extant colonies (n = 9)	Extirpated colonies (n = 10)
Slope (°)	Mean ± SD	24 ± 12.86	21.5 ± 12.20
Aspect (°)	Circular median ± circular deviation	215 ± 1.34	48.5 ± 1.43
Canopy cover (%)*	Mode (*ns*†)	0–24 (5)	0–24 (6)
Downed woody debris (%)*	Mode (*ns*†)	0–24 (7)	0–4 (10)

*Canopy cover and downed woody debris were assessed using these categories: 0–24%, 25–49%, 50–74%, and 75–100%.
†The number of sites that scored in the category of the mode (*ns*) out of the total sample is represented in brackets.

for vegetative reproduction in *C. passerinum* are not well understood, but occur in both early and late stages of dune succession to forest (Keddy 1979).

Many orchids have specific habitat requirements, and lack of favourable habitat conditions may be limiting persistence and recruitment of *C. passerinum* in PNP. Keddy (1979) found maximum soil temperature, presence of sand, presence of canopy, and soil moisture were statistically different between sites with *C. passerinum* present and random locations where it was absent in 1979. This suggests that habitat conditions in space (i.e., site selection) and time (i.e., variation in precipitation, temperature) are important factors for survival and reproduction (Keddy 1979; Keddy *et al.* 1983).

Habitat requirements of *C. passerinum* may also vary during the life of an individual (Keddy *et al.* 1983). Seedlings in 1979 were found in early successional habitat at PNP, including White Spruce (*Picea glauca* (Moench) Voss) canopy with thick needle cover on the ground, Common Juniper (*Juniperus communis* L.) with needle cover, open dunes, and sand/litter including needles with no canopy (Keddy 1979; Keddy *et al.* 1983), while no seedlings were found at colonies where sphagnum moss (*Sphagnum* sp.) co-occurred despite abundant seed production (Keddy 1979; Keddy *et al.* 1983). This suggests that late-successional habitat (i.e., where canopy cover is sufficient for sphagnum moss to establish) is not suitable for seed germination but rather asexual reproduction alone and presents an increased risk of eventual extirpation (Keddy 1979; Keddy *et al.* 1983). Notably, the largest colony (45-46-47) of *C. passerinum* within PNP that became extirpated was located in a mossy area. Colonies 35 and 38, which have both increased in the number of total stalks since 1979 (Figure 3), are also located in sphagnum moss, suggesting that clonal reproduction is solely responsible for the stability in extant colonies of *C. passerinum* in PNP.

We did not find a difference in habitat conditions we measured (i.e., slope, aspect, canopy cover, and downed woody debris) in locations of colonies that survived versus those that were extirpated by 2019. However, sample size for this analysis was small (n = 19) and current conditions may not coincide with the conditions under which colonies disappeared. Moreover, we did not measure other microsite conditions that may influence survival and recruitment (e.g., Keddy 1979), such as soil pH, temperature, and moisture.

Habitat changes may be occurring in PNP's population of *C. passerinum* for several reasons. First, long-term climatic trends for the region include an increase in average air temperatures (Parks Canada Agency 2017), an increase in summer surface water temperature of Lake Superior (Austin and Colman 2008; Noël *et al.* 2019), and a corresponding decline in ice cover (Austin and Colman 2008; Wang *et al.* 2017; Parsons and Patterson 2020). Climate influences local habitat characteristics, such as soil temperature, moisture, and chemical composition, that affect vegetation growth. Climatic changes may also influence the persistence of species symbiotic with *C. passerinum*, such as the fungal mycorrhizal species necessary for seed germination (Keddy *et al.* 1983). The population of *C. passerinum* near the Pic River occurs as a southeastern disjunct of its distribution (Keddy 1979), meaning that warming temperatures may exceed what is suitable for this northerly species.

The second potential cause of habitat change is stabilization of the dune ecosystem where this population occurs. *Cypripedium passerinum* generally inhabits riverbanks and lakeshores—areas that are unstable but always present (Luer 1975; Keddy *et al.* 1983), which suggests this plant relies on some degree of disturbance. Dune stabilization results from a reduction in wind exposure, vegetation establishment, and, ultimately, succession to forest (Noël *et al.* 2019). In PNP, dune stabilization may have occurred due to driftwood accumulation (43–78% coverage) on beaches within the active cove dune system since 1978 (Noël *et al.* 2019) and the establishment of roads, campsites, and day-use trails in 1983. Succession from dunes to forest has occurred, as open sand

and low-lying vegetation has been replaced by mature forest, according to analysis of aerial images from 1937 to 2016 (Noël *et al.* 2019). The slow change of *C. passerinum* habitat due to forest succession was identified in monitoring reports (Keddy 1984; Vien and Mosquin 1986; Vien 1990; Reside 1993) and could be linked to lack of recruitment in the population.

Trampling is another potential factor that may impact the persistence of the *C. passerinum* population in PNP, and is identified as a threat to this species by the IUCN (Rankou 2014). The *C. passerinum* population in PNP is found in Zone I—Special Preservation, the highest protective level within Parks Canada Agency's zoning system (Parks Canada Agency 2015); the area is restricted to visitors unless accompanied by a PNP chaperone. The colonies are fenced and signed, and are rarely accessed by the public. However, there are 13 records of this population by 10 different people posted on iNaturalist (as of 6 January 2022; https://inaturalist.ca), suggesting that this population is visited by the public without knowledge of park management, even though the geolocation of the plants is obscured. Additionally, some colonies are within 5 m of a historical access trail used by PNP staff. Use of this trail ceased in 2017, but could have contributed to extirpation of some colonies. To reduce the impact of monitoring, staff wear soft-soled shoes to complete their monitoring work (Promaine and Nabigon 1997).

To better inform management and reverse this population trend, more research on the ecology of *C. passerinum* is necessary. Research should aim to define the habitat requirements of *C. passerinum*, including asexual reproduction and seed germination requirements, symbiotic fungi, and survivorship in different habitats (Keddy *et al.* 1983). Marking unique individuals could provide information on life history, recruitment, and dormancy. Active management strategies for restoration such as seed propagation experiments could be performed to further our understanding of germination, survival, and growth of sexual propagules and increase population size. *In vitro* reproduction could be a short-term solution to supplement population recruitment until habitat and reproductive requirements are better understood, as has been completed successfully for *C. passerinum* in the past (Curtis 1936).

Author Contributions

Writing – Original Draft: C.C.I.; Writing – Review & Editing: L.D.P.; Investigation: C.C.I and L.D.P.; Formal Analysis: C.C.I. and L.D.P.

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SUPPLEMENTARY MATERIAL:

Table S1. Number of flowering and total stalks of Sparrow's-egg Lady's-slipper (*Cypripedium passerinum*) within colonies in Pukaskwa National Park, Ontario, Canada monitored between 1979 and 2019.