

Reproductive biology and responses to threats and protection measures of the total population of a Critically Endangered Galápagos plant, *Linum cratericola* (Linaceae)

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We describe a reproductive and population dynamic study of the total population of a Critically Endangered plant over 10 years, during which part of the population was protected from the main threat, feral ungulates. *Linum cratericola* (Linaceae) was first discovered in 1966 at two sites on Floreana Island, Galápagos. It has since disappeared from one site and survives in three groups of plants at the other, where it has been threatened with extinction by introduced ungulates and invasive plants. Population size, and growth rate and mortality of individual plants, have been monitored since 1997. The population appears highly responsive to changes in threat levels: the three plant groups increased rapidly following protection by fencing and ungulate control, but temporarily declined when feral goat pressure increased and during dry periods. Natural factors that may contribute to population limitation include dry years, grazing by native snails and competition from native vascular plants and cryptogams. *Linum cratericola* has a single flowering period per year and produces abundant seed with 28% germination after scarification, but with no obvious adaptations for long-distance dispersal. Potential pollinators included the butterfly *Leptotes parrhasioides*, the hoverfly *Toxomerus crockeri* and the carpenter bee *Xylocopa darwinii*, all endemic to Galápagos. The continued survival of *L. cratericola* in the wild depends on effective protection from introduced herbivores and invasive plants. © 2009 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2009, 161, 89–102.

ADDITIONAL KEYWORDS: conservation – introduced ungulates – island endemic – phenology – pollination – population dynamics – seed production – threatened plant.

INTRODUCTION

The design of a successful conservation programme for a threatened species depends on an adequate understanding of its biology (Andersson, 1995; Tye, 2002a). It is necessary to know not just whether populations are stable, increasing or declining, but whether any such trends are likely to continue. In order to predict the latter and to decide what action needs to be taken to turn a decline into an increase, it

is essential to determine the limiting factors and at what stage or stages in the life cycle they act. Population viability analysis can be used to predict future trends in threatened plant populations (e.g. Crone & Gehring, 1998), but successful conservation intervention requires a deeper understanding. Standing size distributions can also be used to infer population dynamics (e.g. Crisp & Lange, 1976; Allen, Lee & Rance, 1994), but accuracy of conclusions is improved by observation over multiple reproductive cycles (Ogden, 1985). Similarly, analysis of threat impacts is often based largely on correlations between population changes and hypothesized threat factors, but more robust inferences can be drawn when correlational analysis is combined with direct observation of threat factors acting on individual plants (e.g. Kephart &

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Paladino, 1997; Fischer & Matthies, 1998). Many such studies are inevitably based on a population sample; multiple censuses of all individuals of a species or population are feasible only with extremely rare plants (e.g. Pfab & Witkowski, 1999; Coates, Lunt & Tremblay, 2006; Shapcott *et al.*, 2007). However, the results then provide direct insights into the importance of different threat factors and are by definition valid for the whole species or population, thus providing an excellent basis for conservation planning. We report here a 10-year reproductive and population study of the entire known population of a Critically Endangered Galápagos endemic plant, the Floreana flax, *Linum cratericola* Eliasson (Linaceae), aimed at obtaining the information necessary to achieve its long-term conservation.

Island endemics are particularly vulnerable to anthropogenic changes because of their small ranges and genetically homogeneous populations (e.g. Bernardello *et al.*, 1999; Sakai, Wagner & Mehrhoff, 2002; Tye, 2002b). About 180 of the 500 native Galápagos vascular plant species are endemic to the archipelago and many are restricted to a single island (Porter, 1983; Lawesson, Adersen & Bentley, 1987), where populations may be naturally small and vulnerable to new threats. Many Galápagos endemic plants are threatened by habitat destruction and species brought to the islands by humans, such as goats, insect pests and invasive plants (Tye, 2000, 2002b, 2009 in press).

So far, only three Galápagos endemic vascular plant species are regarded as having gone extinct in historical times: *Blutaparon rigidum* (B.L.Rob. & Greenm.) Mears (Amaranthaceae) was endemic to Santiago Island and collected only twice, while *Delilia inelegans* (Hook.f.) Kuntze (Asteraceae) and *Sicyos villosus* Hook.f. (Cucurbitaceae) were both endemic to Floreana Island and were collected only by Charles Darwin in 1835 (Hooker, 1847; Porter, 1980). However, several others are Critically Endangered (Tye, 2000, 2002b, 2009 in press), including *Linum cratericola*, currently one of the rarest Galápagos plants. Two species of *Linum* L. occur naturally in Galápagos, both endemic and each restricted to a single island (Wiggins & Porter, 1971). *Linum harlingii* Eliasson is found only on Darwin Volcano of Isabela Island, while *L. cratericola* occurs only on Floreana. In addition, *L. usitatissimum* L. has recently been introduced by humans.

Linum cratericola is a perennial subshrub growing up to 60 cm in height, with simple, alternate, narrowly oblong to lanceolate, subacute leaves, more or less appressed to the stem. It is able to reproduce sexually and by vegetative propagation. The cymous inflorescence bears several 5-petalled yellow flowers. The fruit is a globose capsule, brown when ripe,

which splits to release the shiny brown, oval seeds (Eliasson, 1968), which Porter (1983) presumed dispersed externally by birds, reporting that they had a 'viscid attachment . . . presumably mucilaginous when wetted'.

Floreana Island (Fig. 1) occupies 173 km², with a maximum altitude of 540 m at the summit of Cerro Pajas. The island was first settled about 1807 and many domestic animals and cultivated plant species have been introduced (Hamann, 1981), which have brought about dramatic changes in the structure and composition of its vegetation. As in the rest of the archipelago, there are two major seasons: the warm season from January to June, which is the rainier season in the drier lowlands, and the cool *garúa* season from July to December, characterized by grey skies and frequent misty drizzle (*garúa*), which especially affects the highlands. The west coast receives 200–250 mm of rain annually and the central plateau at c. 300 m altitude receives c. 800 mm (Hamann, 1981), except during major El Niño events, when these figures may be considerably exceeded.

Linum cratericola was discovered in December 1966. It has only been found in two localities: the rims of two neighbouring, extinct and weathered, small volcanic craters (Eliasson, 1968). The type locality is the south-west rim of one of the craters, at an altitude of 370 m (Eliasson, 1982); the second locality is the north-east wall of a larger crater, Cerro Alieri, at c. 380 m (U. Eliasson, pers. comm., Gothenburg), about 500 m from the type locality.

The species was still present at the type locality in 1981, when the second locality was not visited (Eliasson, 1982; U. Eliasson, pers. comm.), but it was feared extinct after it was not found during several searches of both sites from 1987 to 1997 (U. Eliasson, pers. comm.; Mauchamp *et al.* 1998). However, in April 1997, a group of plants was rediscovered in Cerro Alieri (Tye, 1997) and, in July of that year, C. Carvajal of the Galápagos National Park (GNP) showed one of the authors (A.T.) some additional *L. cratericola* plants on a cliff edge c. 50 m from this group, which he had known for some time but which had remained unidentified until then. It has still not been rediscovered at the type locality, which since 1981 has been severely damaged by gravel quarrying and almost covered by a dense invasion of the introduced shrub *Lantana camara* L.

The first group of plants found in 1997 was by the side of a pathway made by feral goats and donkeys, which were common in the area, and the largest individual was protected from herbivores by being enclosed by the stems of a shrub of *Macraea laricifolia* Hook.f. There were *Lantana camara* bushes present at the site, as well as several introduced herbaceous plant species. The second group of plants

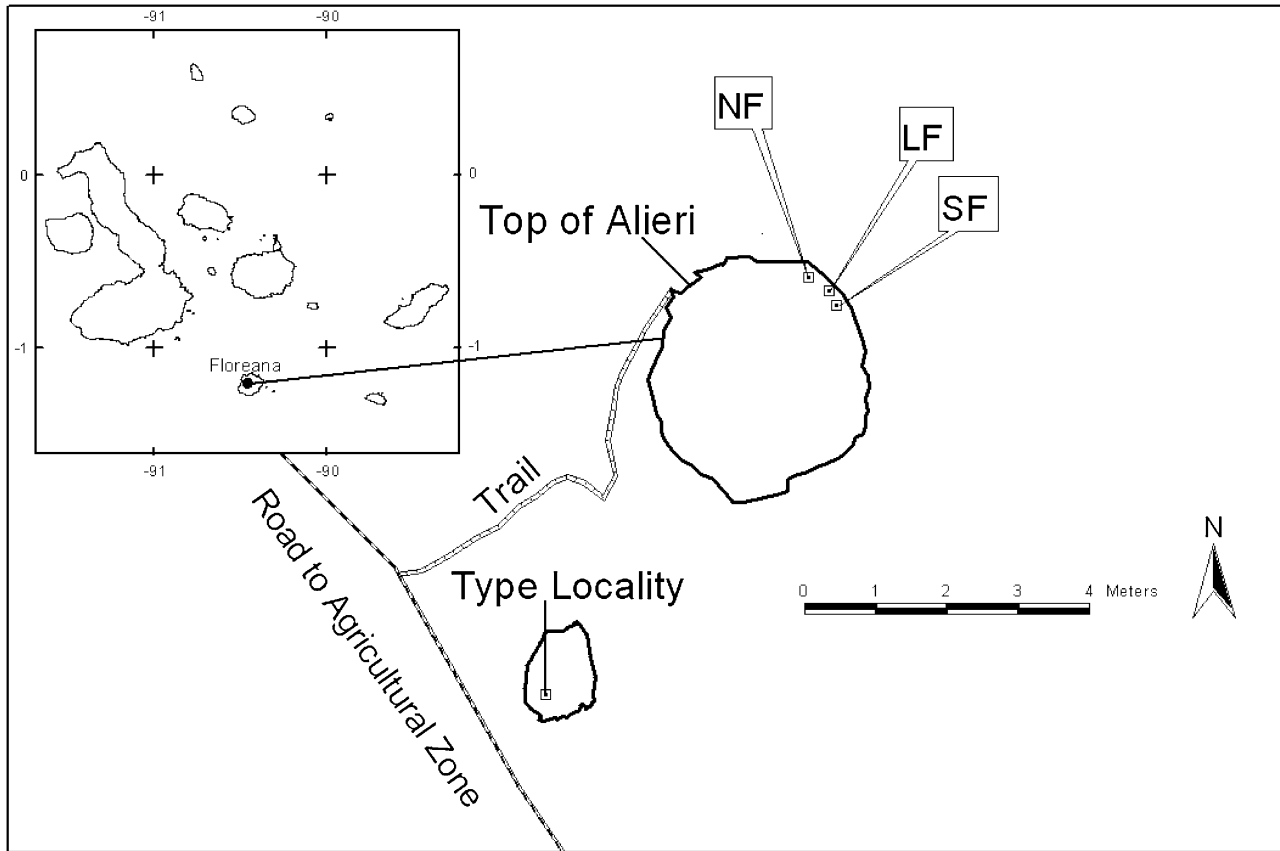


Figure 1. Galapagos, indicating the study area and location of three groups of *Linum cratericola* plants on Floreana Island. The three plant groups are: LF, large fence; NF, no fence; SF, small fence.

appeared to have survived because of the inaccessibility of their cliff-edge site to feral ungulates.

In November 1997, these two groups of plants (of 13 and five individuals), were each protected by an ungulate-proof chain-link fence and *L. camara* shrubs were removed from the area. In October 1998, the species was evaluated as Critically Endangered (IUCN, 1994), based on its small geographical range, tiny population and documented decline (Tye, 2000, 2002a, b). Apart from the habitat destruction at or near the type locality, the reasons for the decline were unclear, although it was speculated that grazing by feral ungulates and invasion by *L. camara* had contributed (Mauchamp *et al.*, 1998). In December 1999, one of the authors (W.S.) found a third group of 10 plants occupying c. 4 m², c. 60 m from the first group. This group remains unfenced.

Cerro Alieri (1°17'35"S, 90°27'25"W), lies in the north-west of Floreana, north of the road between the coastal village and the highland agricultural area (Fig. 1). It has a diameter of c. 300 m and internal depth of c. 80 m, with the highest walls on the north side. The crater contains evergreen forest with a

discontinuous canopy at 6–8 m height, dominated by *Scalesia pedunculata* Hook.f. and *Lippia salicifolia* Andersson. Other trees present include *Zanthoxylum fagara* (L.) Sarg., *Pisonia floribunda* Hook.f. and the invasive introduced species *Psidium guajava* L. and *Cedrela odorata* L. A well-developed shrub layer includes *Chiococca alba* (L.) Hitchc., *Macraea laricifolia*, *Cordia scouleri* Hook.f., *Croton scouleri* Hook.f., *Clerodendrum molle* Kunth, *Buddleja americana* L. and the introduced *Lantana camara*. The commonest herbaceous species are *Desmodium incanum* DC., *Paspalum galapageium* Chase, *P. conjugatum* Bergius, a variety of ferns and numerous epiphytes, especially lichens, bryophytes and the bromeliad *Racinaea insularis* (Mez) M.A.Spencer and L.B.Sm. In addition to *L. cratericola*, the site is an important refuge for other endemic and threatened plants, including *Lecocarpus pinnatifidus* Decne., *Lippia salicifolia*, *Opuntia megasperma* Howell, *Baccharis steetzii* Andersson, *Plantago galapagensis* Rahn and *Borreria dispersa* Hook.f.

Linum cratericola survives on the north-east upper edges and steep walls of the crater, among discon-

tinuous open evergreen scrub and woodland. We denote the three known groups of plants as 'large fence' (LF), 'small fence' (SF) and 'no fence' (NF). Site NF is on yellowish brown clayey soil at the base of a cliff, LF is on a coarse gravel slope mixed with lava blocks, with cliffs above and below, and SF is on a rocky cliff slope with gravelly soil in crevices.

Since 1997, feral ungulate control in and around Cerro Alieri was intensified by the GNP. However, goats became temporarily more common in Cerro Alieri during 2005, as assessed by observations of animals and fresh droppings. Goats managed to enter enclosure SF at some time between April and July 2005 and entered LF late in the same year. GNP staff and Floreana residents eliminated the goats in the enclosures and most of those in the surrounding area between January and April 2006 and blocked possible entry points to the enclosures. A programme to eradicate feral ungulates completely from Floreana then began, late in 2006.

Published information about *L. cratericola* is limited to taxonomy (Eliasson, 1968; Wiggins & Porter, 1971; Mildner & Rogers, 1978) and records of abundance and distribution (Eliasson, 1982; Lawesson, 1990; Tye, 1997, 2000; Mauchamp *et al.*, 1998). The present study was undertaken to extend our knowledge of its distribution and population dynamics, investigate its phenology and aspects of its reproductive biology and attempt to determine the reasons for its decline, in order to formulate a strategy for its long-term conservation (Tye, 2003). Here, we present results up to the beginning of the Floreana ungulate eradication programme.

MATERIAL AND METHODS

The study included all known individuals of the species. Plants with main stem basal diameter ≤ 1 mm were considered seedlings and larger plants adults. Each group of plants was mapped using Global Positioning System–Geographic Information System (GPS–GIS). In December 1999, all 43 plants known at the time (all of them adults) were individually tagged and young plants that appeared later were also tagged. We include here population data from all known counts at the sites up to 1999, monthly monitoring from December 1999 to April 2001 (except January 2001) and further censuses in April and October 2002, March and July 2003, January and December 2004, July and September 2005 and March 2006. The area occupied by each group was periodically measured, with the area defined by a line around the outermost plants of the group. In each locality the habitat was described and the vegetation surveyed, particularly within circular plots of radius 50 cm around each plant or cluster

of plants. During the study period, several more searches of the crater walls were carried out, and of similar sites on Floreana, but these did not reveal any additional populations.

At each visit from December 1999 onwards, for every plant within reach or where the feature could be seen with binoculars, the following data were recorded: plant height, basal diameter, state (signs of damage, etc.), mortality, evidence of threatening or damaging factors, distance of new seedlings from the nearest adult, number of flowers and number of fruits.

During the period December 2000 to January 2001, insects that visited flowers in groups NF and LF were observed during a 15-min period each hour of the day from 07:00 to 16:00 h (nine observation sessions per day) on 11 days. These observations were also used to determine the period of anthesis. Total observation time was 1485 min, but observation time when flowers were open was 825 min. All floral visitors and their behaviour were recorded. Insects were captured when necessary for identification.

To investigate seed viability, 50 mature capsules were collected from four plants, two in each of groups NF and LF, which contained a total of 454 seeds. Of these, 249 were extracted from the capsules using forceps. The rest (205) were extracted by placing the capsules on damp filter paper in Petri dishes for 30–60 min, when they opened, releasing the seeds. All seeds were then placed on filter paper in Petri dishes in natural light under a window and the papers dampened with distilled water twice a week. When the radicle attained 2 mm length, seeds were considered to have germinated. The experiments were run for 8–12 months.

RESULTS

POPULATION DYNAMICS

In 1966 up to 10 plants were present at the type locality and about six or seven plants were there in 1981 (U. Eliasson, pers. comm.); none has been seen there since.

In 1966, the Cerro Alieri site contained 'a fairly rich occurrence' (U. Eliasson, pers. comm.). In 1997, this population was only 13 plants, dropping to six in 1998, but since then it has greatly increased, with most growth in numbers from July 2000 to December 2004 (Fig. 2). From early 2005 there was a decline, which followed increased numbers of goats in the general area and their entry into both enclosures. Partial recovery seen in September 2005 coincided with a strong *garúa* season.

As the population grew in numbers, the area occupied by the plants expanded from the total of *c.* 4 m²

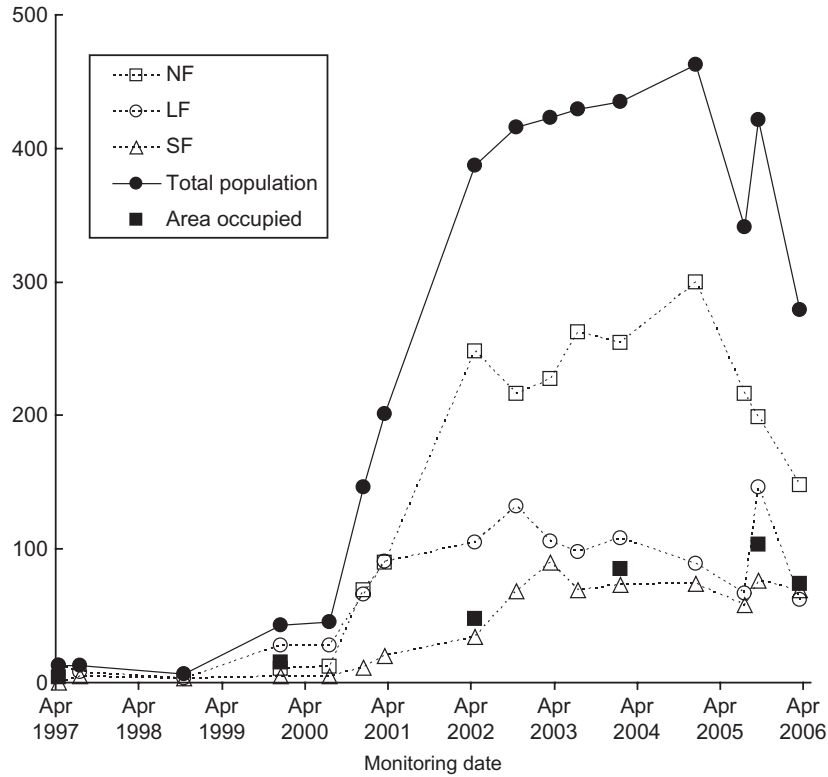


Figure 2. Population size (number of plants) and area (m²) occupied by *Linum cratericola*, 1997–2006, in three groups of plants: LF, large fence; NF, no fence; SF, small fence.

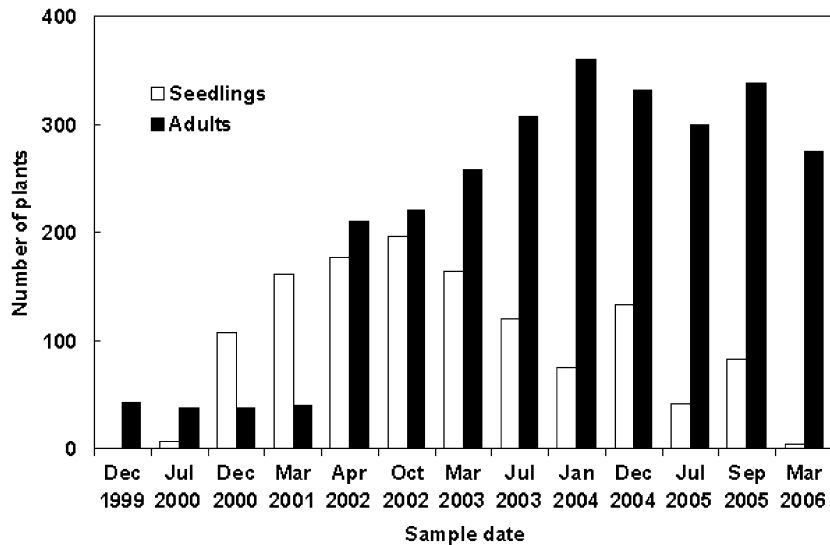


Figure 3. Size class distribution of the total known population of *Linum cratericola*, 1999–2006.

in 1997 (Fig. 2). During 2005–2006, the reduced population occupied a smaller area.

A size class analysis shows that the population was in a recruitment phase up to 2003, characterized initially by rising numbers of seedlings (up to October 2002, thereafter declining), followed by

rising numbers of adults (from April 2002) (Fig. 3). Regeneration was seen from July 2000, with new seedlings found in all three plant groups, but with group NF contributing more to the total population growth than the other two groups and with the greatest increase registered in April 2002

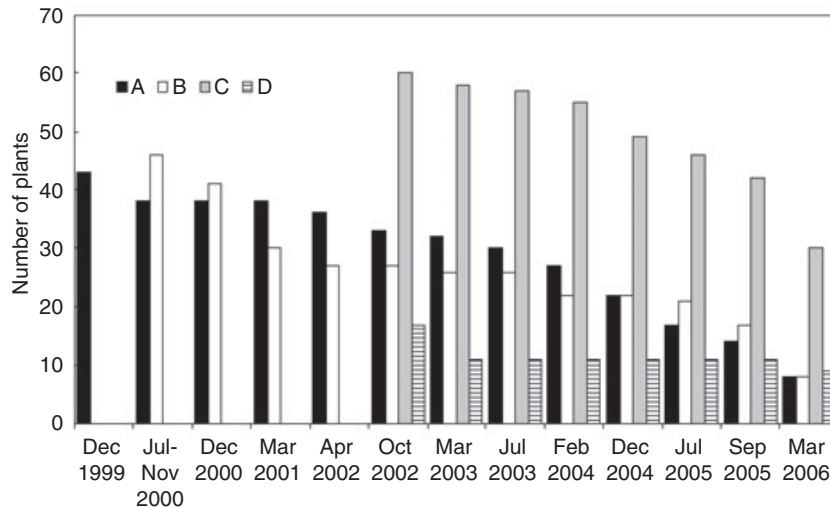


Figure 4. Mortality of four cohorts of *Linum cratericola* over > 6 years. Cohorts A and C tagged as adults, B and D as seedlings.

(Figs 2, 3). During 2004–2005, c. 80% of plants were adults.

Four cohorts were monitored for survival: cohort A (43 adults marked in December 1999), cohort B (46 new seedlings marked July–November 2000, all of which were adult by April 2002), cohort C (60 new plants first encountered as adults, marked in October 2002) and cohort D (new seedlings marked in October 2002, all of which were adult by July 2003). For the first 2 years after plants reached adult size, survival was high, with c. 5% mortality per year and a steady mortality of c. 15% per year thereafter (Fig. 4). Mortality was slightly greater among seedlings in their first year, at c. 20%. In the oldest cohort A, eight plants (17%) survived more than 6 years as adults. By March 2006, the ages of surviving plants in the four cohorts were: cohort A > 6.3 years (marked as adults, some of them possibly at least 9 years old, registered in 1997); cohort B 5.5 years; cohort C 4.5–5 years; and cohort D 4.5 years.

GROWTH

Growth in height of each cohort was approximately constant, although many plants of all cohorts suffered reversals in height in 2005–2006, apparently because of grazing by goats and snails (Figs 5, 6, left side). Growth in basal diameter was also approximately constant until reaching c. 11 mm (Figs 5, 6, right side, plus data on the plants surviving in 2006). Most seedlings reached adult size (basal diameter) in c. 1 year, with all having reached adult size within 2 years (Figs 5, 6, white bars).

There was no significant difference in mean diameter growth rate between the 14 adults of cohort A

and the 42 of cohort C that survived until September 2005, growth of which averaged 1.12 ± 0.07 mm per year ($N = 56$). There was also no significant difference between the mean growth rates of the seedling cohorts B and D, which grew at an overall rate of 1.30 ± 0.08 mm per year ($N = 28$). This was entirely as a result of faster growth in their first 3 years, when growth rate was 1.48 ± 0.11 mm per year, significantly faster than that of the adult cohorts A and C ($t_{82} = 3.01$, $P < 0.005$).

The cohort A and C adults that survived until September 2005 grew on average 6.3 ± 0.3 cm in height per year ($N = 56$) until December 2004, the last monitoring date before the entry of goats to the enclosures and the loss in height of many plants. Cohort B and D seedlings also grew significantly faster in height than adults (up to December 2004), at 9.1 ± 0.5 cm per year ($N = 28$) ($t_{82} = 5.28$, $P < 0.0001$).

HABITAT AND LIMITING FACTORS

The vegetation around the *L. cratericola* plants comprised 49 vascular plant species, of which seven are introduced and the rest native to Galápagos, or possibly so (Table 1). *Linum cratericola* plants commonly occurred among bushes of *Cordia scouleri*, *Croton scouleri*, *Darwiniothamnus tenuifolius* (Hook.f.) Harling, *Macraea loricifolia*, *Zanthoxylum fagara* and *Baccharis steetzii* and in sparse, mixed herbaceous vegetation of angiosperms (including the common epiphyte *Racinaea insularis*), ferns and liverworts of the genus *Frullania*, especially *F. brasiliensis* Raddi.

In group LF, two *Lantana camara* shrubs were found in May 2000 and one in March 2006, while in group SF one was found in April 2002 and two in July

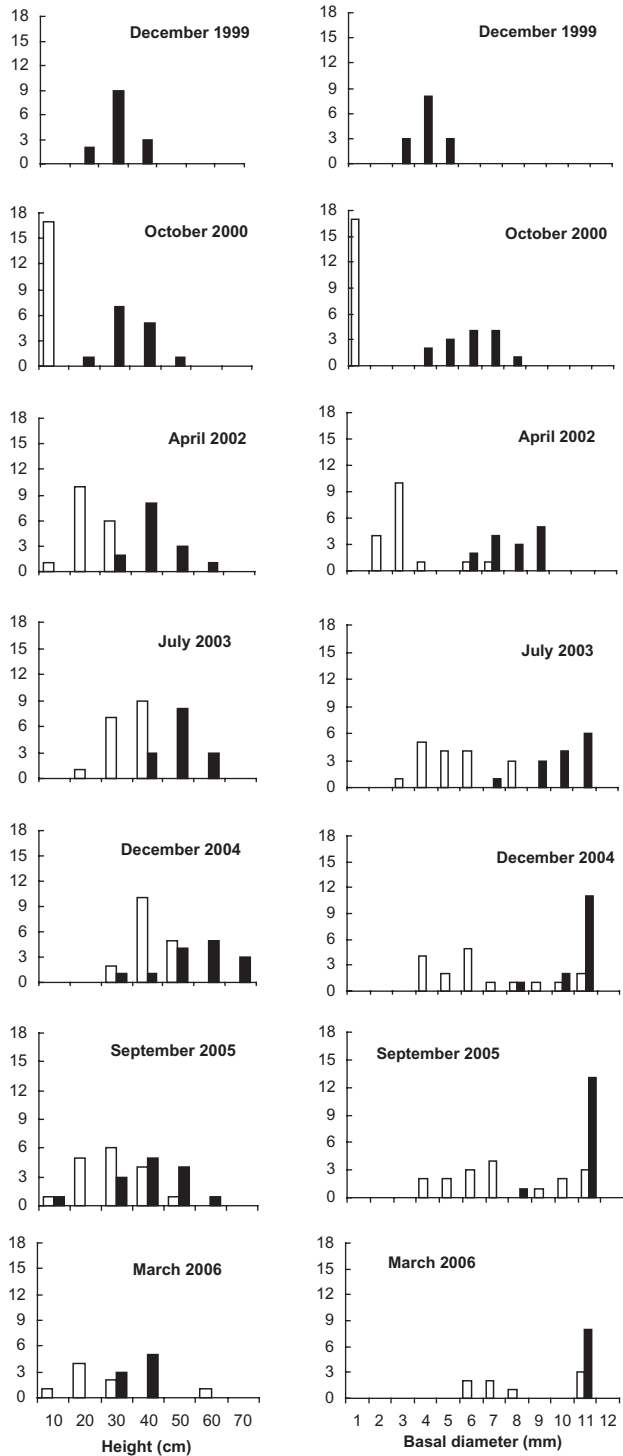


Figure 5. Growth in height and basal diameter of the 14 plants of cohort A (black bars) and 17 of cohort B (white bars) which survived until September 2005 and the eight plants of each cohort which survived in 2006. Frequencies are of plants measuring up to the figure cited on the x-axis.

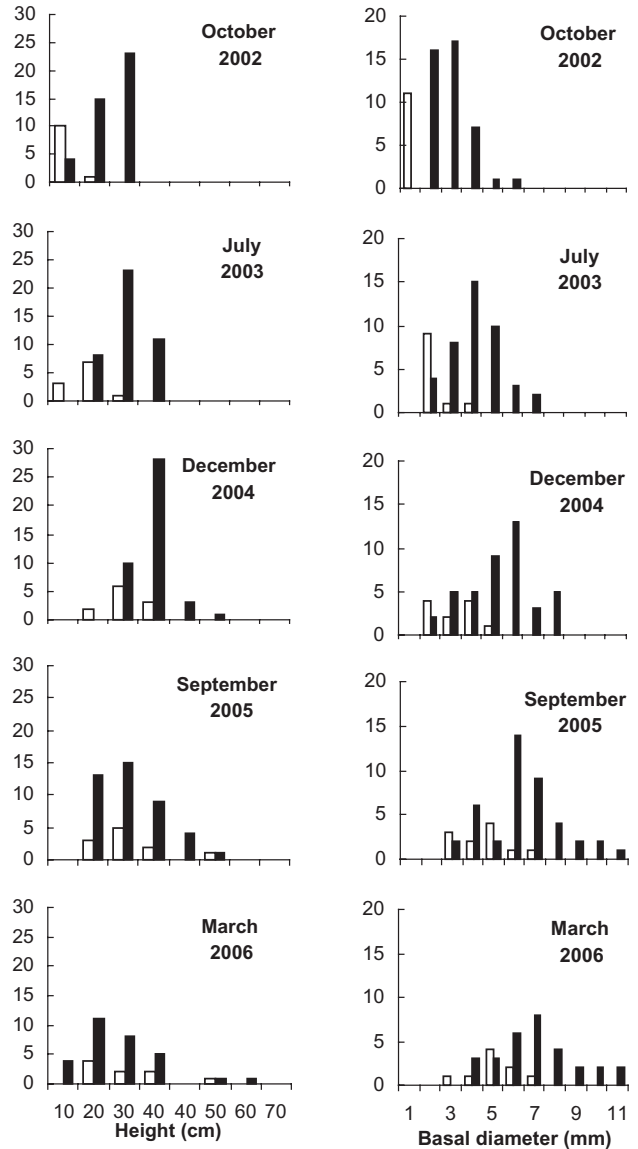


Figure 6. Growth in height and basal diameter of the 42 plants in cohort C (tagged in 2002 as adults, black bars) and 11 of cohort D (tagged in 2002 as seedlings, white bars), all of which survived until September 2005, and the 30 plants of cohort C and nine of D that survived in 2006. Frequencies are of plants measuring up to the figure cited on the x-axis.

and September 2005. They were growing within 50 cm of *L. cratericola* plants and all were manually removed immediately when found. However, in site NF, dense patches of *L. camara* still occurred in 2006, within 2 m of *L. cratericola* plants, and threatened to invade this area.

Physical damage to plants, correlated with goat presence, showed that goats ate *L. cratericola*. Snails of the genus *Succinea* (native to Galápagos) were first

Table 1. Vascular plants recorded within the populations of *Linum cratericola* at Cerro Alieri, Floreana. Species growing within 50 cm of one or more plants of *L. cratericola* are in bold type

Family	Species	Status*	Life form
Acanthaceae	<i>Blechnum pyramidatum</i> (Lam.) Urb.	N	Herb
Amaranthaceae	<i>Amaranthus hybridus</i> L.	I	Herb
Apiaceae	<i>Cyclosporum laciniatum</i> (DC.) Constance	N	Herb
Aspleniaceae	<i>Asplenium formosum</i> Willd.	E	Herb
Asteraceae	<i>Ageratum conyzoides</i> L.	N	Herb
Asteraceae	<i>Baccharis steetzii</i> Andersson	E	Shrub
Asteraceae	<i>Bidens pilosa</i> L.	N?	Herb
Asteraceae	<i>Darwiniothamnus tenuifolius</i> (Hook.f.) Harling	E	Shrub
Asteraceae	<i>Macraea laricifolia</i> Hook.f.	E	Shrub
Asteraceae	<i>Sonchus oleraceus</i> L.	I	Herb
Boraginaceae	<i>Cordia scouleri</i> Hook.f.	E	Shrub
Boraginaceae	<i>Heliotropium angiospermum</i> Murray	N	Herb
Boraginaceae	<i>Tournefortia psilostachya</i> Kunth	N	Shrub
Bromeliaceae	<i>Racinaea insularis</i> (Mez.) M.A.Spencer and L.B.Sm.	E	Herb
Cyperaceae	<i>Cyperus anderssonii</i> Boeck.	E	Herb
Cyperaceae	<i>Cyperus confertus</i> Sw.	N	Herb
Euphorbiaceae	<i>Acalypha parvula</i> Hook.f.	E	Herb
Euphorbiaceae	<i>Croton scouleri</i> Hook.f.	E	Shrub
Euphorbiaceae	<i>Phyllanthus caroliniensis</i> Walter	N	Herb
Fabaceae	<i>Desmodium incanum</i> DC.	N?	Herb
Lamiaceae	<i>Salvia occidentalis</i> Sw.	N	Herb
Malvaceae	<i>Sida spinosa</i> L.	N	Herb
Malvaceae	<i>Sidastrum paniculatum</i> (L.) Fryxell	I	Herb
Malvaceae	<i>Urena lobata</i> L.	I	Shrub
Nyctaginaceae	<i>Commicarpus tuberosus</i> (Lam.) Standl.	N	Herb
Oxalidaceae	<i>Oxalis corniculata</i> L.	I	Herb
Oxalidaceae	<i>Oxalis megalorrhiza</i> Jacq.	N	Herb
Passifloraceae	<i>Passiflora foetida</i> L. var. <i>galapagensis</i> Killip	E	Herb
Piperaceae	<i>Peperomia galapagensis</i> Hook.f. ex Mig.	E	Herb
Plumbaginaceae	<i>Plumbago scandens</i> L.	N	Herb
Poaceae	<i>Aristida repens</i> Trin.	E	Herb
Poaceae	<i>Paspalum conjugatum</i> Bergius	N?	Herb
Poaceae	<i>Paspalum galapageium</i> var. <i>galapageium</i> Chase	E	Herb
Polypodiaceae	<i>Pecluma dispersa</i> (A.M.Evans) M.G.Price	N	Herb
Polypodiaceae	<i>Polypodium tridens</i> Kunze	E	Herb
Pteridaceae	<i>Adiantum concinnum</i> Humb. & Bonpl. ex Willd.	N	Herb
Pteridaceae	<i>Cheilanthes microphylla</i> (Sw.) Sw.	N	Herb
Pteridaceae	<i>Trachypteris pinnata</i> (Hook.f.) C.Chr.	N	Herb
Portulacaceae	<i>Portulaca oleraceae</i> L.	N?	Herb
Rubiaceae	<i>Chiococca alba</i> L. (Hitc.)	N	Shrub
Rubiaceae	<i>Spermacoce remota</i> Lam.	N	Herb
Rutaceae	<i>Zanthoxylum fagara</i> (L.) Sarg.	N	Tree
Scrophulariaceae	<i>Capraria peruviana</i> Benth.	N	Herb
Scrophulariaceae	<i>Scoparia dulcis</i> L.	N	Herb
Solanaceae	<i>Solanum americanum</i> Mill.	N	Herb
Urticaceae	<i>Parietaria debilis</i> G.Forst.	N	Herb
Urticaceae	<i>Pilea baurii</i> B.L.Rob.	E	Herb
Verbenaceae	<i>Lantana camara</i> L.	I	Shrub
Verbenaceae	<i>Stachytarpheta cayennensis</i> (Rich.) M.Vahl	I	Shrub

*Status: E, Galapagos endemic; N, native; N?, doubtfully native; I, introduced.

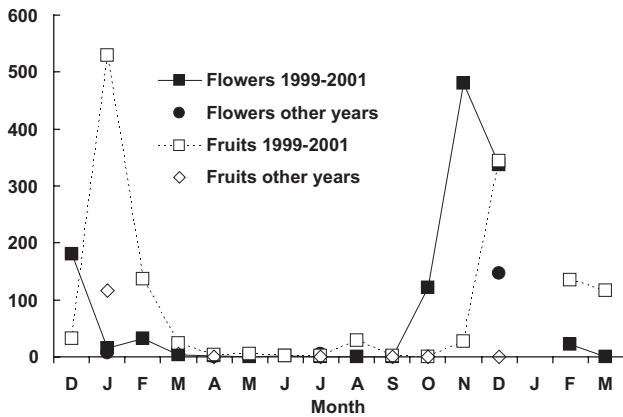


Figure 7. *Linum cratericola* total population flower and fruit counts. 1999–2001 data from adult cohort A. Data from other years were April and October 2002, March and July 2003, January and December 2004, July and September 2005 and March 2006.

noted on *L. cratericola* plants in April 1997. During the period March–December 2000, they were found on 28 of the 43 original adult plants, with up to five snails per plant (mean three). Snails were also observed on most subsequent visits. Snail grazing was followed by blackening, drying and death of damaged leaves and branchlets. When climatic conditions were favourable for growth of *L. cratericola* (much rain or *garúa*), lost branchlets were replaced by new growth from the main stems. However, in drier conditions, snail-grazed plants sometimes died. Five of the original 43 plants that died showed evidence of herbivory by snails.

On occasions, Galápagos doves (*Zenaida galapagoensis*) were observed foraging under adult *L. cratericola* plants. This predominantly granivorous bird may have eaten dropped *L. cratericola* seeds, but the doves were not seen to peck at capsules on the plants.

Competitors for space, such as the grasses *Paspalum galapageium* and *Aristida repens* Trin., ferns, liverworts and lichens, grew rapidly in height and cover in wet conditions and often almost covered plants of *L. cratericola*. However, we have no evidence that this caused mortality.

PHENOLOGY

Flowering occurred in plants of *L. cratericola* 19 cm or more in height and with a basal diameter 2.9 mm or more. Some of these plants were less than 2 years old, but most began flowering at 2–3 years of age.

Plants came into flower in October, with a peak in November and continuing to March (Fig. 7). The fruiting peak occurred 1–2 months after peak flowering, in December–January. The time from appearance of the

first flowers to their fruits attaining full size was less than 1 month. The largest number of flowers counted per individual was 130 (in November 2000) and the largest number of fruits on a single plant was 256 (December 2000).

The hermaphrodite flowers were borne on the terminal branchlets and opened from 07:00 to 12:00 h, being fully open (anthers and pistils fully exposed) by 08:00 h. They remained open at least until 09:00 h; flower wilting, which determined the end of anthesis, appeared to occur later on days with lower solar intensity, wind and flower visitor activity, although no data were collected to support this subjective impression.

The capsules, when mature, opened into five divisions, allowing the seeds to fall or be blown out by the wind. Ripe capsules measured 2.3–3.2 mm diameter (mean 2.6 mm; $N = 22$ capsules from eight individuals) and contained nine or 10 seeds (mean 9.5, $N = 40$ capsules from five individuals). The seeds measured 1.6×1 mm and, despite Porter's (1983) suggestion of a viscid attachment, seemed to have no obvious adaptations to promote dispersal.

FLORAL VISITORS

Three insect species were observed visiting *L. cratericola* flowers. The commonest visitor was the endemic Galápagos blue butterfly (*Leptotes parrhasioides*; Lycaenidae; Lepidoptera), with 34 visits of 2–420 s (mean visit length 58 ± 16 s); its overall visit rate (per 15-min observation period when flowers were open) was 0.62. The second most common was a Galápagos endemic hoverfly (*Toxomerus crockeri*; Syrphidae; Diptera), with 25 visits of 2–370 s (mean 69 ± 20 s; overall visit rate = 0.45). Both appeared to probe for nectar. The only other insect recorded visiting was the endemic Galápagos carpenter bee (*Xylocopa darwinii*; Apidae; Hymenoptera), with two visits of 1–2 s only (overall visit rate 0.04).

SEED VIABILITY

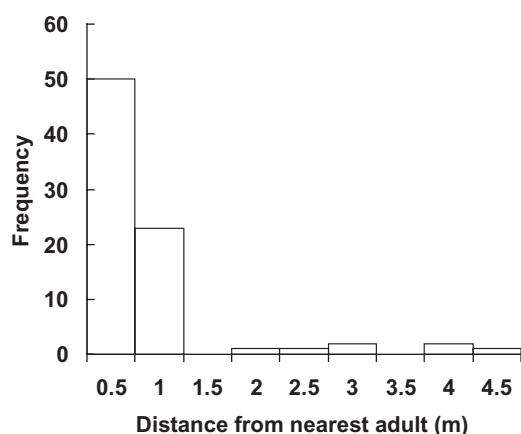
Mechanically extracted seed gave 28% germination, with the first seed germinating 14 days after sowing (Table 2). In contrast, none of the seed extracted by dampening the capsules germinated by the end of the experiments (8–12 months).

SEED DISPERSAL

The mean distance of seedlings to the nearest adult was 0.66 ± 0.09 m ($N = 80$, Fig. 8). The larger distances (≥ 3 m) refer to plants that germinated from seeds which appeared to have fallen from adults growing above them on the crater walls. This

Table 2. *Linum cratericola* seed germination trial results

Collection date	Sowing date	Seeds extracted by	No. of seeds	No. (%) germinated	Day first germinated	Day last germinated
31 January 2000	2 February 2000	Forceps	75	32 (41)	14	18
		Damp	1	0		
1 September 2000	1 September 2000	Forceps	80	18 (23)	58	222
		Damp	100	0		
28 December 2000	13 January 2001	Forceps	95	19 (20)	18	230
		Damp	95	0		
	Total	Forceps	249	69 (28)		
		Damp	196	0		

**Figure 8.** Distance of *Linum cratericola* seedlings from nearest adult. Frequencies are of plants at distances up to the figure cited on the x-axis.

occurred below all three groups, but in SF these lower seedlings germinated among denser vegetation outside the fence and did not survive.

DISCUSSION

Total population monitoring of *L. cratericola* for more than 10 years revealed marked positive and negative trends and demonstrated how the survival of this species depends on continued protection from introduced herbivores. With adequate protection the population can rapidly increase and with successful management of invasive animals and plants it can be expected to spread.

The critical effect of feral goats and donkeys was demonstrated by rapid population growth of *L. cratericola* during the period 2000–2003, following fence construction and local control of ungulates. The two fenced groups of plants regenerated and expanded rapidly and the unprotected group NF also increased following ungulate control. The effect of goats was further demonstrated by the death of many plants

and loss of height of many of the survivors, following a local increase in the feral goat population and the entry of goats into the exclosures in 2005. The decline may also have been exacerbated by 2005–2006 being drier than average, given that there was some recovery in September 2005 during the *garúa* season.

The short generation time (≤ 2 years), generous production and high viability of seeds (unlike many other Galápagos plants: Hamann, 1979, 2001, 2004) contribute to what appears to be a relatively high resilience of the species to temporary population reduction. Nothing is yet known of the *L. cratericola* soil seed bank, seed dormancy or longevity, although our seed germination experiments strongly suggest that mechanical scarification of the seed (as may have occurred during extraction of seeds from the capsules by forceps) is required to permit germination. The rapid initial recovery that occurred from the very small 1998 population might suggest a contribution from seeds produced in previous years. However, despite this local increase, the apparently limited dispersal ability of *L. cratericola* seeds will inhibit rapid spread beyond the established population in Cerro Alieri.

It is not known whether the recent reduction in the population of the species will have caused any significant loss of genetic diversity. There have been no investigations of its genetics but, given that most Galápagos plants which have been investigated show naturally low genetic variability [e.g. *Solanum* L. (Solanaceae), Rick & Fobes, 1975; *Galvezia* Ruiz & Pav. (Rutaceae), Elisens, 1989; *Gossypium* L. (Malvaceae), Wendel & Percival, 1990; Alvarez & Wendel, 2006; *Opuntia* (L.) Mill. (Cactaceae), Browne *et al.*, 2003; Helsen *et al.*, 2009], such a bottleneck might not have reduced variability at all. We do not know that the real population dropped as far as minimum plant counts indicated (six individuals), as it is not known to what extent a soil seed bank produced by a larger population of adults contributed to the recovery.

The fastest growth in both population size and plant size was in group NF, where the soil is deeper,

clayey, darker and with probably higher organic content than the other two sites, which are primarily on loose gravel and bare rock. NF is also more sheltered, perhaps with higher humidity, which may be important given the natural habit of this species of growing in sites that receive abundant misty precipitation, and its faster growth and regeneration during the *garúa* season.

Apart from feral ungulates and introduced shrubs, other potential limiting factors appear to be natural, including grazing by endemic snails, drought and competition from native plants. Although snail damage was followed by death of branchlets and sometimes of whole plants, *L. cratericola* has evolved with this factor and the species can presumably support it in the absence of anthropogenic threats. Reductions in plant and population size may also follow dry periods, but the climate of Galápagos is naturally cyclical, with annual, periodic (El Niño Southern Oscillation) and longer-term (glaciation-linked) cycles of dry periods, which have contributed to the evolutionary history of the species.

Linum cratericola may have low competitive ability, as its only known sites comprise predominantly exposed bare rock and gravel, even although it can reproduce more quickly in sheltered spots with good soil, when protected from competition and predation. Although growth of *L. cratericola* was faster in wet conditions, competitors for space, such as the grasses *Paspalum galapageium* and *Aristida repens*, ferns, liverworts and lichens, also grew rapidly in such conditions, more quickly than *Linum* plants and often almost covered them. Death of seedlings appeared to be higher in group NF and below SF, where greater competition was present. Competition with taller shrubs may also be limiting, even although some plants grew successfully under other species such as *Macraea laricifolia*, which sometimes provided protection from ungulate grazing.

The effect of the dense mats of epiphytic liverworts sometimes found on *L. cratericola* and other shrubs is unknown. On the one hand, such mats might hinder its regeneration, as many seeds of *L. cratericola* fall onto them, where their germination could be retarded, comparable with the lack of germination that we noted in experiments using only moisture (rather than mechanical means) to cause seeds to be released from the capsules. On the other hand, seeds in such mats might better survive the dry season and the mats could favour the survival of adult plants of *L. cratericola* in the dry season as they condense humidity which forms droplets, sometimes in quantities sufficient to fall to the ground (W. Simbaña, pers. observ.). This association perhaps merits further investigation: all three groups of *L. cratericola* occur in areas especially rich in liverwort cover compared

with the surrounding areas and it is not known whether this is simply a parallel response to environmental conditions or whether liverworts might favour the growth or survival of *L. cratericola*.

According to McMullen & Close (1993), many Galápagos highland plants flower during the cooler, *garúa* season. *Linum cratericola* begins to flower in the later part of this season, although the greater frequency of sunny weather from November onward favours greater abundance of pollinators. All three insect species seen to visit flowers of *L. cratericola* are among the most frequent insect visitors to the flowers of a variety of other Galápagos plants (Linsley, 1966; McMullen, 1985, 1987, 1993; McMullen & Close, 1993). The North American *Linum lewisii* Pursh, although self-compatible, depends on insects for seed production and bees and flies are both capable of pollination (Kearns & Inouye, 1994). It is not known whether *L. cratericola* is also self-compatible, as are many Galápagos angiosperms (McMullen, 1987), or to what extent it depends on insect pollination.

Linum cratericola appears to be restricted at present to the edge of the rim and steep interior walls of the north-east side of Cerro Alieri. However, its potential population is evidently much larger than its present small numbers and limited distribution suggest. We know that the species formerly occupied one other crater rim and similar sites are common, if widely separated, in the highlands of Floreana. Although many of the other potential crater sites for the species have been searched, a complete survey of them all has never been made, so it is possible that the species survives in one or more additional sites. However, feral ungulates have been present on Floreana in large numbers for at least 200 years and may have eliminated *L. cratericola* from all sites accessible to them. The survival of *L. cratericola* during the period 1981–1997, when goats and donkeys were common in its habitat, may have been because of its ability to grow on the upper edges and steep walls of the crater, out of reach of these animals, and perhaps also to a long-lived soil seed bank. Steep crater walls and other sites inaccessible to feral ungulates have saved several other Galápagos plant species from extinction during the past 100 years, including *Scalesia atractyloides* Arn. and *Galvezia leucantha* Wiggins on Santiago Island (Mauchamp, 1996; Tye & Jäger, 2000).

Mauchamp *et al.* (1998) suggested that invasion by *Lantana camara* may have brought about the extinction of *L. cratericola* in its type locality or the population may have naturally disappeared after a prolonged dry period, but goats were perhaps a contributory cause of its loss from the site. *Lantana camara* was introduced to Floreana in 1938, has spread widely in the western part of the island and is

regarded as a threat to several endemic plants (Cruz, Cruz & Lawesson, 1986), although no detailed study of its impacts has been carried out. In 1966, *L. camara* was uncommon in the area, with only scattered individuals present, and goats were scarce (U. Eliasson, pers. comm.). Since then, *L. camara* has multiplied and spread until it occupies the outer slopes of both craters where *L. cratericola* has been recorded, where it forms an almost continuous scrub layer, with extensive monospecific patches or with native bushes such as *Macraea laricifolia* (formerly the dominant shrub) and *Darwiniothamnus tenuifolius* intermixed.

With its restricted range on a single island, specialized habitat, small population and the requirement for continued management of ungulates and invasive plants in its habitat, *L. cratericola* is still highly vulnerable. Based on the results of this study, *L. cratericola* should clearly remain on the IUCN red list as CR, matching criteria B1a,b(ii,v),c(iv); B2a,b(ii,v),c(iv) of IUCN (2001), as it has a single known site of < 1 ha with a population subject to recent decline, with continuing habitat deterioration (invasive plants) and population fluctuations, and remaining at only a little over the threshold for criterion C of 250 mature individuals.

Thus, an important conservation goal for this and several other endangered Floreana endemic plants is the eradication of goats and other feral ungulates from the island, which began in late 2006. Although feral goats, donkeys and free-ranging domestic cattle have all been common there in the past, wild cattle have been rare for some decades now and goats and donkeys were subject to better control by the GNP from 1997, up to the commencement of the eradication attempt in 2006.

Ideally, invasive plants, especially *L. camara*, *P. guajava* and other habitat-transforming species, should be removed from and permanently controlled in the known sites of *L. cratericola* and surrounding areas. Preservation of seeds in a seed bank and a habitat restoration and reintroduction programme for the type locality could also contribute to population growth and security of survival, although we do not consider population enhancement at the sites where *L. cratericola* survives to be necessary. Searches of other potential sites should be completed to determine whether additional populations survive and a translocation programme planned in conjunction with introduced species control, in order to expand the number of sites where the species can be maintained. The present study suggests some criteria for artificial population establishment: for example, sites could be chosen to maximize seed spread downslope and to maximize survival by choosing suitable microclimate, substrate and vegetation. Propagation by seed or

cuttings could be used. Finally, should the ungulate eradication attempt fail, the NF group should be protected by a fence, the other exclosures enlarged and fence maintenance continued to prevent further breaches by goats.

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