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AUTECOLOGICAL STUDIES OF *DROSERA LINEARIS*, A THREATENED SUNDEW SPECIES

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ABSTRACT

The linear-leaf sundew has been extirpated from several stations at the southern edge of its range. Cedarburg Bog is believed to harbor the largest of the remaining southern colonies of this species. Drosera linearis has a lower reproductive output at Cedarburg Bog than at other sites, and produces fewer seeds per plant than the three sundew species which share its range. The population studied at Cedarburg Bog declined in population size and reproductive output from 1980 to 1982, and revealed characteristics associated with high rates of local extinction. Populations experienced rapid turnover of individuals, and population size was closely coupled to the size of the previous year's seed crop. Sustained flooding in the flarks of the patterned fen further decreased population stability. The species may have persisted at Cedarburg Bog because the patterned fen is sufficiently large to allow the recolonization rate to keep pace with the rate of local extinction.

INTRODUCTION

Recent publications on threatened and endangered plants have stressed the need for long-term autecological studies of species' population dynamics, reproductive biology, and life history (Bradshaw and Doody 1978; Mustard 1982). Such comprehensive studies allow greater understanding of the reasons for a species' decline and enable the formulation of recovery plans. The number of species warranting such study is large, and continues to increase. Wisconsin, for instance, accords threatened or endangered status to nearly 100 plant species. A large proportion of endangered plants in this region inhabit wetland or aquatic habitats (Beaman 1977). In 1980, I began an autecological study of Drosera linearis Goldie, a threatened wetland plant of national significance (Crow et al. 1981). My study was focused on the population of linear-leaf sundew in the Cedarburg Bog State Scientific Area, Ozaukee County, Wisconsin. Characteristics of the species were compared to more abundant North American sundews. This report summarizes results from the first three years of this continuing study.

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All correlations are Spearman Rank, and multiple comparisons among means use Duncan's method (Brown and Hollander 1977). The significance level is $P < 0.05$.

RESULTS

Description

Drosera linearis is a carnivorous, perennial herb. Expansion of the winter bud begins in April (at Cedarburg Bog), producing a rosette of up to eight linear-shaped leaves. Leaf blades on mature rosettes may attain 50 mm in length and 2 mm in width, according to Gleason and Cronquist (1963), although the longest blade observed at Cedarburg Bog during the study period was 35 mm. Blades are adorned on the adaxial surface with reddish, glistening, mucilage-capped secretory glands, which trap mosquitoes, damsel flies, and other insects (Wynne 1944; Gleason and Cronquist 1963). Petioles are glabrous and up to 7 cm long. Juvenile rosette leaves are held erect, while senescing leaves become prostrate, providing anchorage in unconsolidated substrates. The root system consists typically of one to five 10 mm by 0.5 mm diameter unbranched roots.

A scorpioidal cyme unfurls in mid-summer, revealing one to seven (or to four at Cedarburg Bog) actinomorphic flowers, 6 to 8 mm in diameter (Wood 1955). Color in the flowers is provided by pink stigmas, orange anthers, and green nectar lines and pink tips on the white petals. Pollen is trinucleate, and unique among boreal angiosperms in having proximal apertures (Kuprianova 1973). Seeds ripen in one month, in capsules, and are ca. 1 mm long, rhomboidal, and black. The two cotyledons on seedlings are linear in shape and up to 2 mm in length, while the immature seedling leaves are reminiscent of mature leaves of Drosera rotundifolia in their rotund shape and possession of 'spoon' glands (see Krischan 1981).

Geographic distribution

Historically, Drosera linearis has occurred with low frequency throughout a relatively large range (Fig. 1). Within Canada, Drosera linearis has been reported from no more than five stations in any one province (Argus and White 1978; Cody et al. 1979; Cruise and Catling 1974; Maher et al. 1979; White and Johnson 1980). Drosera linearis was only recently discovered in the Northwest Territories, and thus may be expanding in range northward. In contrast, along the southern border of its range, it clearly is declining in frequency and numbers. It has been extirpated from six Wisconsin counties (Bayfield, Columbia, Iron, Jefferson, Polk, St. Croix) and remains now in only two (Wisconsin Department of Natural Resources 1979). The Ashland Co. population is extremely small (Brynildson 1982), while the population in Ozaukee Co. numbers into the thousands and is scattered throughout the 70 ha of patterned fen (string bog portion) in the Cedarburg Bog.

Habitat description

Areas of the Cedarburg Bog and Red Lake Peatland (Minnesota) complexes in which D. linearis grows are best described as rich mineratrophic patterned fens (sensu Glaser et al. 1981); rich mineratrophic refers to the input of mineral-rich

Fig. 1. Extant (E) and extirpated (X) *D. linearis* stations known to author.

groundwater, and patterned to the string bog type of topography. The habitat of D. linearis may be characterized as mineratrophic, calcareous wetlands with a sand, peat, or marl substrate. The substrates supporting D. linearis throughout its range, including those at Cedarburg Bog, are chemically similar; they have high concentrations of calcium (ca. 25 ppm) and magnesium (ca. 10 ppm), high electrical conductivity (140 to 420 uMhos), and a circumneutral pH (6.2 to 8.0) (Grittinger 1969; Schnell 1980; Vitt et al. 1975; Stromberg 1981; S. C. Rooney, pers. comm.). In contrast, the most abundant sundew in Wisconsin, D. rotundifolia, typically occurs in acidic, oligotrophic peatlands such as Sphagnum bogs.

Habitat differences between the two sundews are readily observed at Cedarburg Bog. Patterned peatlands are so named because of their parallel, often anastamosing, ridges and furrows (flarks), that are oriented perpendicular to the slope. Drosera linearis occurs within the flarks, while D. rotundifolia is restricted to the Sphagnum-covered ridges and hummocks. As mentioned, peat in the flarks is circumneutral and calcareous, and is derived primarily from sedges. Compared to the peat from the ridges, which is more acidic (pH ca. 5) and derived from Sphagnum, the flark peat has a lower 'unrubbed' fiber content (70% vs. 77%), higher 'rubbed' fiber content (47% vs. 33%), less organic matter by weight (74.6% vs. 84.9%), and a lower (darker) pyrophosphate index (3 vs. 6). These latter tests indicate the flark peat to be more decomposed, and suggest classification of the flark peat within the Medihemist Great Group of the Histosol Order, and of the ridge peat within the Medifibrist Great Group.

Flarks possess temporary pools after rain and snow melt. Depth ranges from a few millimeters to several centimeters, with both depth and duration varying spatially and temporally (Fig. 2).

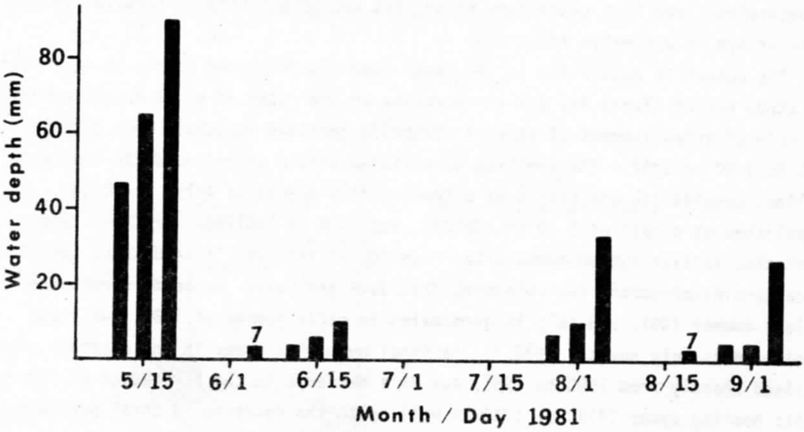

Figure 2. Water depth (mm) in three permanent quadrats in 1981. Left bar indicates Quadrat #2; middle bar, Q#4; right bar Q#7. No water was present on July 1 or July 15.

Flarks support less vegetation than the ridges and hummocks. Drosera rotundifolia commonly occurs on sites that have 100% ground cover of Sphagnum and herbaceous plants, and that are shaded by Thuja occidentalis and Larix laricina. In contrast, D. linearis is sometimes found on sunny moss (Campyllium stellatum) and (Scorpidium scorpioides) covered hummocks, but is more common in the open flark, where ground cover is generally less than 60%. Sedges dominate the D. linearis community, and carnivorous and rare species are well represented (Table 1).

Population dynamics

Drosera linearis individuals have a rapid turnover rate; the half-life for the composite population is estimated to be 9.9 months. Two-hundred and twenty-two plants "passed through" the quadrats during the study period, in addition to the initial population of 248 plants. Establishment occurs as a result of sexual and asexual processes; seeds from a given year's crop germinate in late summer immediately after ripening, and throughout the next summer after overwintering, while asexual offspring arise in spring from the buds on hibernaculum leaves and throughout the growing season on damaged or detached leaves (gemiparous reproduction). Plants (ramets) also arise from axillary buds any time during the growing season; these asexual offspring are equal in size to the mother plant, and remain attached for a period of time. Survivorship of seedlings and gemiparous offspring is low in comparison to mature plants and axillary ramets (probability of survival to six months is 38% for seedlings, 40% for gemiparous offspring, and 65% for mature plants), although those seedlings that do survive may reproduce sexually and/or asexually when one year old. The maximum lifespan of D. linearis cannot be determined from this short-term study, but the probability of survival to two years of age is estimated to be 60%.

The composite population in the seven quadrats decreased nearly by half over the study period (Table 2), due to decreases in the rates of plant establishment. The rate of establishment of asexual offspring declined somewhat, from 0.18 in 1981 to 0.07 in 1982. The seedling establishment rate experienced the sharpest decline; considering one season as extending from August to July, seedlings established at a rate of 0.30 in 1980/81, and 0.06 in 1981/82. (Fifteen seeds germinated in late summer 1980, after ripening of that year's seed crop, and 75 seeds germinated during the following May, June and July. No seeds germinated in late summer 1981, and only 15 germinated in early summer of 1982. No seeds germinated in late summer, 1982.) The total number of cymes in the quadrats also declined sharply from 1980 to 1981, due to a decrease in the percentage of mature plants bearing cymes (41% vs. 17%) as well as to the decrease in total population size. Cyme number declined again in 1982, although the percentage of cyme-bearing plants remained near 1981 levels (15%). Thus, the seedling establishment rate appears to be closely coupled to the size of the previous year's seed crop.

Table 1. Domin-Krajina cover - abundance scale for flark vegetation at Cedarburg Bog.

Tracheophytes	Scale Value
Rhynchospora alba	5
Sarracenia purpurea	5
Carex chordorrhiza	4
Carex lasiocarpa	4
Carex limosa	4
Eleocharis sp.	4
Equisetum fluviatile	4
Lobelia Kalmii	4
Menyanthes trifoliata	4
Triglochin maritima	4
Utricularia intermedia	4
Calopogon pulchellus	3
Carex tetanica	3
Drosera linearis	3
Phragmites communis	3
Pogonia ophioglossoides	3
Utricularia cornuta	3
Campanula aparinoides	2
Solidago uliginosa	2
Utricularia vulgaris	2
Chamaedaphne calyculata	1
Eupatorium perfoliatum	1
Galium labradoricum	1
Gerardia purpurea var. parviflora	1
Habenaria dilatata	1
Habenaria leucophaea	1
Kalmia polifolia	1
Potentilla palustris	1
Vaccinium Oxycoccus	1
Bryophytes	
Campyllium stellatum	3
Scorpidium scorpioides	3

Table 2. Population's size, plant size, inflorescence production, and demographic data for quadrat populations.

	Hummock	Flark						
		Dry-					-Wet	
Quadrat	Q1	Q2	Q3	Q4	Q5	Q6	Q7	TOTAL
Population size								
Sept. 1980	28	78	69	42	3	1	27	248
Sept. 1981	30	78	55	52	6	11	4	236
Sept. 1982	26	28	47	26	10	8	3	148
Number of:								
New plants*	34	74	50	20	9	24	11	222
Deaths*	36	124	72	36	2	17	35	322
Population growth rate	-0.07	-0.64	-0.32	-0.38	2.33	7.00	-0.89	
Cyme number								
1980	12	30	31	8	0	1	1	83
1981	12	0	6	9	2	1	1	31
1982	10	0	4	0	0	0	1	15
Blade length (mm)								
1980	24(9)	23(10)	26(14)	26(11)	16(7)	32(0)	22(5)	
1981	20(7)	12(4)	16(6)	28(14)	22(13)	26(5)	20(12)	
1982	26(7)	21(7)	23(13)	13(7)	35(5)	26(14)	21(6)	

* = From July 1980 to August 1982.

Mortality remained constant during the study period. Mortality causes were not quantified, but causes were identified as frost heaving of the peat and trampling by deer. Sustained high water levels and high population densities also appear to decrease population stability.

Overall, there was a significant negative correlation between initial population density and population growth rate, with only those quadrats with a density of 6 plants per m^2 or less experiencing a gain in population. The four high density quadrats declined substantially in population; each experienced high mortality rates as well as significantly lower mean leaf lengths during either the year of, or the year preceding the crash. Plant size is negatively correlated with reproductive output (see Reproductive Output), and decreases in cyme densities and percentages of cyme-bearing plants also accompanied the population crashes.

Sustained high water levels also appear to decrease population stability. Of the four quadrats that declined in population, the wettest, Q7, experienced the greatest reduction in size. Only three of the initial 27 plants remained alive in 1982. The other 'wet' quadrats had initially low densities, perhaps indicative of the plants' inability to attain high densities on such sites. The wetter areas of the flark have higher densities of invertebrate 'casting' mounds, which cause mortality of liner-leaf sundews via burial of the plants. Flooding also increases turbidity, decreases light penetration, and reduces insect-trapping activity. Seedlings float on the surface of the flood waters, and may in this fashion, disperse to drier areas of the flark or to edges of moss hummocks, resulting in lower population sizes in the wet flark areas and probably higher overall rates of seedling mortality.

The moss hummock quadrat, where plant densities were moderate and flooding is infrequent, was the only one in which cyme numbers, and establishment and death rates remained stable. However, linear-leaf sundew colonies are infrequently found on these hummocks; long-term colonization may be hindered by drought, runoff of the seeds to the flarks, or overgrowth by sedges and other species. Additionally, recolonization of these raised areas may occur infrequently.

Mortality, establishment and population growth rates in the quadrats do not appear to be correlated with rainfall totals by year or by month. It may be that intensity and duration of the rainfall is equal in importance to the total amount fallen, due to effects on turbidity levels and duration of the flark pools.

Reproductive output

Reproductive output of D. linearis appears to be lower at Cedarburg Bog than at other areas in its range. Compared to values collected at two Michigan intertidal flats, the linear-leaf sundew at Cedarburg Bog produces significantly fewer capsules per cyme and fewer seeds per cyme (Table 3); values reported in taxonomic descriptions also are high by comparison. Seed weight is constant between areas and over time, while seed number per capsule is significantly higher at one

Table 3. Reproductive output of Drosera linearis. Values for seeds per capsule, capsules per cyme, and blade length are mean (standard deviation); sample size = 50. Seed weight is a pooled value for 50 seeds. Other variables were obtained by multiplication.

Site and year	Seed weight (mg)	Seeds per capsule	Capsules per cyme	Seeds per cyme	Seed wt. per cyme (mg)	Blade length (mm)*
Emmet Co. Mich. 1982	0.033	60(16)	3.2(1.3)	192	6.3	35.1(9.2)
Cheboygan Co. Mich. 1982	0.033	39(10)	5.1(1.8)	199	6.6	30.3(8.4)
Cedarburg Bog Flark 1980	0.033	50(13)	2.1(0.9)	105	3.5	21.4(6.7)
1981	0.033	42(11)	1.4(0.7)	59	1.9	16.9(6.2)
1982	0.033	65(15)	2.1(1.0)	136	4.5	21.9(8.2)
Cedarburg Bog Moss hummock 1982	0.033	62(14)	2.4(1.1)	149	4.9	25.5(8.3)

* = Measured ca. August 1. Sample excludes juvenile plants.

Michigan site. Seed production per cyme (more specifically, capsule number per cyme) is positively correlated with the mean leaf length of mature rosettes, as indicated by comparison among sites, and among years at Cedarburg Bog.

Three sundew species have ranges which overlap with that of D. linearis. The linear-leaf sundew produces substantially fewer seeds per cyme than these species, reflecting both a smaller number of capsules per cyme and of seeds per capsule (Table 4). Drosera linearis also produces fewer grams of seeds per cyme, its greater seed weight notwithstanding.

Breeding system

Drosera linearis is predominantly self-fertilizing (autogamous). Each flower on the cyme is open for a single day, for approximately three hours. Self-pollination occurs when the flower closes, in early afternoon. Under overcast conditions, flowers do not open and D. linearis is environmentally cleistogamous. I found no significant differences in mean number of viable seed per capsule among nylon-mesh encased flowers (45 seeds), chasmogamous (open) flowers to which pollinators had free access (42 seeds), and cleistogamous (closed) flowers (40 seeds). I observed no insects visiting the flowers of D. linearis, but did see Dipteran insects pollinating the structurally similar flowers of the sympatric D. rotundifolia. The round-leaf sundew has a more effective floral display at Cedarburg Bog than does the linear-leaf sundew, producing denser, taller cymes (mean height of 124 mm; sd=24; n=20). In contrast, the cymes of the linear-leaf sundews are infrequent and barely surpass its leaves. Mean height of cymes with only one capsule (the modal number of capsules in all years) was 38 mm (sd=8, n=30), while mean height of all cymes was 68 mm (sd=14, n=40).

Table 4. Reproductive output of four Drosera species.

	Seed weight (mg)	Seeds per capsule	Capsules per cyme	Seeds per cyme	Seed wt. per cyme (mg)
D. anglica*	0.022	108	6.6	716	18.6
D. intermedia*	0.026	85	6.3	535	13.9
D. rotundifolia*	0.022	74	6.3	462	10.2
D. linearis#	0.033	52	5.1	199	6.6

* = From Salisbury (1942).

= Average of 1980, 1981, and 1982 values at Cedarburg Bog.

In each of the three years, there was little overlap in flowering dates between the June and July flowering D. linearis and the July and August flowering D. rotundifolia. Britton and Brown (1913) also reported asynchronous anthesis for sympatric populations of the two sundew species, although they report that the round-leaf sundew flowers before the linear-leaf.

Transplant experiments

Transplant experiments revealed the intolerance of D. rotundifolia for the flark habitat; all of the transplants died within two weeks of being transferred from hummocks to the flarks. The D. linearis transplants grew nearly as well on the Sphagnum hummocks as they did in portions of their natural flark habitat. Establishment from asexual offspring offset the transplant population decline to 20%; leaf blade means declined significantly, from 25 mm to 9 mm; and cyme number declined to zero in 1982. However, similar reductions occurred in several of the natural flark quadrats. Several transplants were completely overtopped by the Sphagnum moss at the end of the third year.

DISCUSSION

D. linearis is protected as an endangered species in Maine and a threatened species in Wisconsin, and many D. linearis populations occur on state-owned nature preserves. However, the pattern of decline observed in D. linearis supports contention of White and Bratton (1981) that, because of the omnipresent impacts of humans and the dynamic nature of the landscape, habitat preservation alone may be insufficient to insure the long-term survival of the species. For instance, Drosera linearis has disappeared from apparently pristine peatlands in northern Wisconsin counties (Tans 1981). It is one of only two of the six regionally rare species which were collected by John Goldie in 1819 near Lake Simcoe, Ontario and which could not be relocated in 1976, despite assiduous searching in areas harboring Triglochin maritima, Carex chordorhiza, Carex livida, Lobelia Kalmii, Utricularia minor, and other usual associates (Reznicek 1980). In Cedarburg Bog, as well, D. linearis may be declining in numbers and in reproductive output (P. Matthiae, pers. comm.). Some of the extirpated D. linearis populations owe their demise to habitat conversion for agricultural and commercial uses (Brynildson 1982; Smith 1981), but the causes of decline within Cedarburg Bog and other preserves are more elusive.

To explain the rarity of D. linearis and other uncommon Saskatchewan species, Argus and White (1978) speculate that, "habitat tolerances are either so narrow, or the required habitat so infrequent as to represent a major factor in restricting their distribution". Smith (1981) also suggests that a cause of the decline of D. linearis is its narrow niche, rendering it more vulnerable than other wetland species to changes in hydrology or water chemistry. Evidence supports at least the hypothesis of a narrow potential niche along the moisture dimension. My studies indicate that D. linearis germinates within a narrower range of water potentials than other sundews, and demonstrate that flooding suppresses germination and decreases population size (Stromberg 1981). The absence of D. linearis from those portions of the Red Lake Peatland (Minnesota) which have been ditched provides indirect evidence of intolerance to drought and its consequences (Smith 1981), while Wood (1955) attributes the extirpation of a Michigan population of the sundew to an artificial increase in the water level of the lake along which it grew. Schnell (1976) states, "The species is on a marked decline, particularly in recently well-documented locations in southeastern Michigan. The decline seems to be correlated with the deterioration of marl bogs to acid conditions and with a persistent string of rainy seasons with flooding to the extent that plants of D. linearis were totally submerged. While the species does grow in shallow water to a depth of a centimeter or so, it will not tolerate prolonged flooding."

Less evidence exists on the impacts of natural or artificial changes in peatland chemistry on D. linearis abundance. Gorham et al. (1978) documented elevated levels of iron, aluminum, and other wind-deposited minerals in Cedarburg Bog and other wetlands surrounded by agricultural fields, but the impact on D. linearis is unknown. In this study, and in those of Schnell (1976) and Korolas (1982), D. linearis has demonstrated a broad potential niche in terms of substrate chemistry; seedlings and mature plants have been grown as successfully on acidic, oligotrophic substrates as on calcareous, alkaline peats, and transplant experiments have demonstrated the potential of D. linearis to survive, at least in the short term, in habitats dominated by Sphagnum spp. The absence of D. linearis from Sphagnum bogs, which are more abundant than fens in Wisconsin and other parts of the sundew's range, may be a consequence of its reproductive allocation strategy. Drosera linearis produces fewer seeds than D. rotundifolia and other sundews of Sphagnum bogs, perhaps because adaptation to alkaline conditions is energetically costly. Thus, it may be limited to areas where mortality is low, such as the expansive competition-free peat flats that occur in Cedarburg Bog. Open peat is rarer in Sphagnum bogs, and is limited mainly to deer trails, where mortality from trampling presumably is high. Additionally, the morphology of the round-leaf sundew's rosette allows it to pre-empt space and successfully compete with Sphagnum plants, while the erect D. linearis plants become engulfed by the rapidly growing, dense moss colonies. As a final note, the positive correlation between reproductive output within a genus and frequency of the attendant species observed by Salisbury (1942) and others (Primack 1979; Moran et al. 1981) holds true for D. linearis and the other three sundews discussed herein.

Characteristics of D. linearis population dynamics suggest that populations are subject to frequent local extinction. Populations possess short half-lives, experience rapid turnover of individuals, and have unstable growth rates. Factors which decrease seed production, such as high population density or sustained high water levels, may jeopardize populations because of dependence on the previous year's seed crop. However, it is possible that D. linearis may respond similarly to D. intermedia and many other wetland species, persisting at the site in seed form during adverse conditions (Keddy and Reznicek 1982). Drosera linearis shares with the intermediate sundew key adaptations to in situ dormancy; both produce seeds that have limited dispersal ability (neither possesses adaptations for aerial dispersal, as do the round-leaf and English sundews) and that exhibit temporal variation in dormancy requirements (Skogen 1979). The spate of recent discoveries and rediscoveries of linear-leaf sundew populations supports the idea that D. linearis is a colonizing species that has adapted to the cyclic vegetation processes of wetland habitats by a strategy of dispersal in time rather than space. Alternatively, the species may have been overlooked because of its inconspicuous nature, or because of the inaccessibility of many of its habitats.

The continued survival of D. linearis depends on preservation and management of existing habitat as well as of pristine historical sites that may possess viable linear-leaf sundew seed banks. Water levels within the preserves should be closely monitored, because of the critical influence on population dynamics. Management of the linear-leaf sundew within threatened preserves such as the Red Lake Peatland (which may be mined for peat in coming years; Luoma and Shaw 1981) should include establishment of extensive buffer zones around sundew populations to prevent hydrological changes from causing adverse impacts. Recovery management suggestions for smaller D. linearis preserves include clearing of vegetation from selected areas, and seeding of the areas with the linear-leaf sundew. This would compensate for any decline in seed dispersal via flowing water or water birds that has resulted from the fragmentation and reduction in size of the species' habitat (Gadgil 1971). Population dynamics of the linear-leaf sundew at Cedarburg Bog will continue to be monitored, to determine whether the observed downward trends in population size are permanent, and whether they typify the response of the species throughout the entire patterned fen. The fen may be sufficiently large to allow for rates of local extinction and recolonization that are compatible with maintenance of a viable population.

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