

# Size is not a reliable measure of sexual fecundity in two species of lichenized fungi

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**ABSTRACT.** Since a number of studies have shown a strong positive correlation between apothecia production and lichen thallus size, it has been suggested that size can serve as an easy measure of lichen sexual fecundity. The reliability of the relationship between size and apothecia production among different environments has not been studied. We measured apothecia development and thallus area in populations of the lichenized fungi *Xanthoparmelia cumberlandia* and *Xanthoparmelia coloradoënsis*. Our data suggest that while size is a significant predictor of apothecia production, the relationship between size and apothecia production is not consistent among various environments, nor does size adequately explain variation in apothecia production.

**KEYWORDS.** *Xanthoparmelia cumberlandia*, *Xanthoparmelia coloradoënsis*, population structure, apothecia, thallus size, sexual reproduction, lichen, fecundity, elevation.



Many ecological studies require an estimate of fitness. The fitness of an organism in response to environmental variables (parasite abundance, light intensity, competitor abundance, wind exposure, etc.) can lead to interesting conclusions concerning the evolutionary impact of those variables. Since a direct measurement of reproductive output is often difficult, other more easily measured correlates have been sought.

In lichenology, the possibility that size can be used as an estimate of fitness has been explored. Because height can be ignored in effectively two-dimensional organisms like crustose and most foliose lichenized fungi, size is a fairly simple measurement. In contrast, measuring fitness (i.e., contribution to the next generation) directly is extremely difficult in lichenized fungi due to their long life-span and the

cryptic nature of much of their life history (e.g., microscopic fertilization, dispersal, photobiont capture, and colonization).

For a few lichen species, studies suggest that larger thalli may be better equipped to survive (Gauslaa & Solhaug 1998; Hestmark 1997). The enhanced ability of larger lichen individuals to retain more water for a longer time gives them a competitive edge. Due to increased water retention, larger individuals of the lichen species *Degelia plumbea* (Lightf.) P. M. Jørg. & P. James and *Lasallia pustulata* (L.) Mérat tend to remain photosynthetically active longer than smaller thalli (Gauslaa & Solhaug 1998; Hestmark 1997). Hestmark (1997) found that increased water retention allows larger thalli to expand over other individuals, thereby gaining more access to sunlight.

Another competitive advantage exhibited by lichen individuals of a larger body size relates to the onset of sexual reproductive ability (Hestmark 1992; Pringle et al. 2003; Ramstad & Hestmark 2001). *Lasallia pustulata*, *Xanthoparmelia cumberlandia* (Gyeln.) Hale and *Umbilicaria spodochoa* (Hoffm.) DC. all appear to have a size threshold above which most individuals have apothecia (sexual spore-bearing structures) and below which most do not (Hestmark 1992; Pringle et al. 2003; Ramstad & Hestmark 2001), thus indicating that a critical mass must be reached before energy is made available for sexual reproduction.

Beyond its association with the onset of sexual maturity, thallus size often exhibits a positive correlation with the number of apothecia produced. A study of the species *Xanthoparmelia cumberlandia* found that the number of apothecia produced by an individual is positively correlated with size (Pringle et al. 2003). Apothecia and size show a similar relationship in *Umbilicaria spodochoa* (Ramstad & Hestmark 2001). In *Lasallia pustulata*, a positive correlation was found between size-class and the presence of apothecia (Hestmark 1992).

However, studies demonstrating a strong relationship between size and apothecia production have been carried out in homogenous environments, raising the question of how consistently this relationship between size and fecundity holds across varying conditions experienced by natural populations of lichens. The afore mentioned study on *X. cumberlandia* study was conducted in Berkeley's

Botanical Garden (Pringle et al. 2003), while the findings for *U. spodochoa* came from observations within a narrow range of habitats (Ramstad & Hestmark 2001). Though the average positive relationship between size and apothecia development in *Lasallia pustulata* was persistent when sampled over a variety of microhabitats (Hestmark 1992), statistical variation in this trend was not reported. Thus, while an average trend has been noted in these organisms, the degree of error which can be expected when this trend is viewed across habitats is unknown. The reliability of size as an estimate of fecundity must be known if size is to be used to compare the fitness of individuals from different habitats, as has been suggested (Pringle et al. 2003).

We must also emphasize that this relationship between size and sexual fecundity is different among various genera. *Xanthoparmelia cumberlandia* shows a non-linear relationship between size and apothecia number, in that larger thalli produce disproportionately more apothecia (Pringle et al. 2003). *Umbilicaria spodochoa*, on the other hand, exhibits a simple linear relationship between size and sexual fecundity (Ramstad & Hestmark 2001). Rather than increasing in size and fecundity with time, *Cladonia furcata* (Huds.) Schrad., *Cetraria islandica* (L.) Ach. and *Peltigera canina* (L.) Willd. terminate growth altogether after onset of sexual maturity (Jahns & Frey 1982; Jahns et al. 1978; Jahns & Schuster 1981). Whether this variability in the relationship between size and apothecia production is due to environmental variation or variability in species traits is not clear.

Before thallus size is used as a replacement for more direct measures of fitness, its ability to predict variation in sexual fecundity must be ascertained. We assess the validity of the hypothesis that size is an adequate predictor of sexual fecundity in *X. cumberlandia* and *X. coloradoënsis* (Gyeln.) Hale by studying the reliability of this relationship when faced with variation in elevation.

#### MATERIALS AND METHODS

**Study organisms.** A lichen consists of two or more species: a fungus and its photosynthetic partner(s) (an alga and/or a cyanobacterium).

When measuring sexual reproductive fitness of a lichen, one usually focuses on the fitness of the

fungus. The photosynthetic partner is generally understood to be asexual, though recent studies have indicated that cryptic recombination is occurring within putatively clonal algal populations (Taylor et al. 1999). Apothecia on lichenized fungi are essentially permanent once formed, and so provide a record of the sexual effort of an individual.

*Xanthoparmelia cumberlandia* is distinguished from its closely related sister taxon, *X. plittii* (Gyeln.) Hale, by the presence of apothecia and absence of isidia, specialized asexual structures which disperse viable cells of both symbionts. *Xanthoparmelia cumberlandia* is facultatively sexual, meaning that it can engage in both sexual and asexual reproduction; thus the lichen can produce offspring through spore production or unspecialized asexual thallus fragments. More information concerning *X. cumberlandia* and *X. plittii* can be found in Hale (1990) and Brodo et al. (2001).

*Xanthoparmelia cumberlandia* is morphologically indistinguishable from *X. coloradoënsis*, though slight overlapping differences in rhizine length, and size of thallus, lobes, conidia, apothecia and spores have been proposed (Hale 1990). Thalli, medullae, lower surfaces and rhizines are reportedly the same color, except for the hazy distinction that the lower surface of *X. cumberlandia* is “pale brown to darkening,” while that of *X. coloradoënsis* is just “pale brown.” The only solid difference that has been described involves the secondary chemicals produced by these two lichens. *Xanthoparmelia cumberlandia* purportedly produces stictic, constictic, norstictic and usnic acids, while *X. coloradoënsis* produces salazinic, usnic and possibly consalazinic acids.

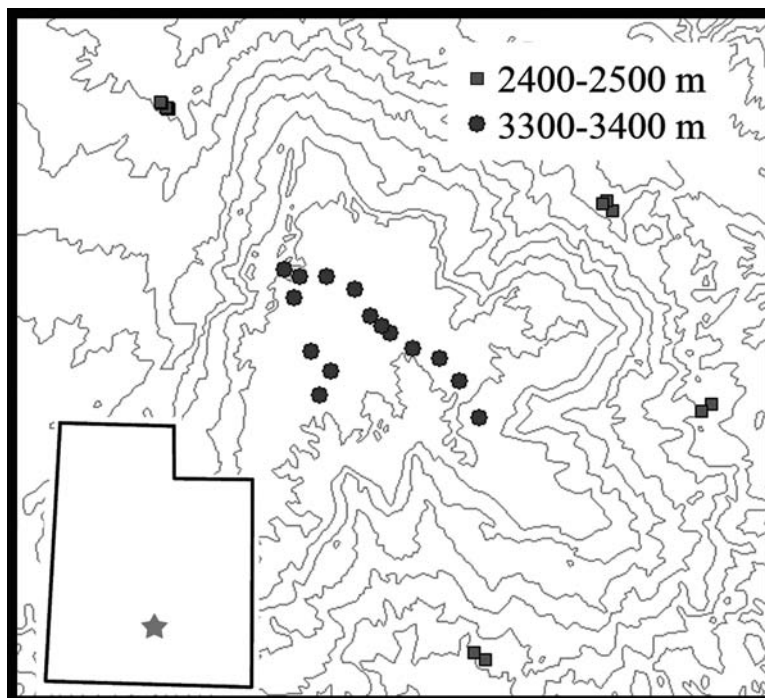
To ensure correct species identification, thin layer chromatography (TLC) was performed in order to distinguish *X. cumberlandia* from *X. coloradoënsis* (sensu Hale 1990). Both *X. cumberlandia* and *X. coloradoënsis* were present in our sample (see Jackson 2004 for more details) and we assume the relationship between size and sexual fecundity is comparable in these closely related species. This assumption was tested by considering species identity during the model building process, as described below.

**Sampling strategy.** Due to the abundance of *Xanthoparmelia cumberlandia* and *X. coloradoënsis*, Boulder Mountain, Aquarius Plateau, Utah, was the

site selected for this investigation. With approximately ten individuals measured in each population, 15 populations were observed at an elevation of 2400–2500 m, and 18 populations at 3300–3400 m (Fig. 1). The resulting 325 samples provided us with ample statistical power. Eight of the lower elevation populations occurred on the western slope of Boulder Mountain, while the other seven occupy the eastern slope. Poor access to the northern and southern slopes prevented observations in those areas. The higher elevation observations were made along Rt. 178 which effectively transects the upper plateau from northwest to southeast. Populations were chosen at random distances from the road.

**Abiotic conditions.** In general, the lower elevations of Boulder Mountain can be characterized as warm and dry, while the upper elevations are cooler and more moist (U.S. Department of Agriculture et al. 1999). Weather sensors near the study sites indicate that the average yearly temperature near the upper elevation (Donkey Reservoir, 3064 m) is more than 4°C cooler than at the lower-west elevation site (Boulder City, 2150 m) and 7°C cooler than at the lower-east elevation (Loa City, 2035 m) (Western Regional Climate Center: [www.wrcc.dri.edu](http://www.wrcc.dri.edu)). Average yearly precipitation at the higher elevation sensor is 75 cm, while Boulder City (lower-east) receives only 27 cm per year, and Loa (lower-west) receives only 6.3 cm per year (National Water and Climate Center: [www.wcc.nrcs.usda.gov](http://www.wcc.nrcs.usda.gov)).

**Measurement.** Thallus area was measured by photographing each lichen thallus with a ruler placed beside it, and then estimating area using NIH image 1.62 (freeware downloaded from NIH at [rsb.info.nih.gov/nih-image/download.html](http://rsb.info.nih.gov/nih-image/download.html)). When more than one picture was required due to large size or extension of the thallus around the edge of a rock, a straight object was used to mark the cutoff between the two pictures. The pictures were later opened in Adobe Photoshop CS (Adobe Systems Inc. 2003) where the photographed ruler was used to calibrate the size of the picture using the “image size” menu. The paintbrush tool was used to outline the thallus, and the paintbucket tool was used to fill it in. Saved as a TIF file, these pictures were opened in NIH Image 1.62, and thallus area was calculated. More instructions for using NIH image are found in Ruzin (2002; <http://microscopy.berkeley.edu>).



**Figure 1.** Collection sites on Boulder Mountain, Aquarius Plateau, UT. Collection sites. Inset shows the location of Boulder Mountain in Utah. Approximately ten individuals were collected at each site, and sites were located at random distances from the road. In order to have enough apotheciate lichens to include in a regression model, extra apotheciate individuals were collected non-randomly from the upper population. Topographic lines indicate a 500 ft change in elevation (downloaded from Utah Coalition for Geographic Information Systems Education: [www.edtechsupport.net/gis](http://www.edtechsupport.net/gis)).

Three sexual fitness correlates were considered: presence of apothecia, number of apothecia and total area of apothecia. Apothecia were counted according to the procedure followed by Pringle et al. (2003). The cumulative area of apothecia on each thallus was measured in the same way as thallus area; using Adobe Photoshop CS (Adobe Systems Inc. 2003), each apothecium was painted and the sum of all apothecial areas for each individual was calculated using NIH Image 1.62.

Additionally, average ascospore production per ascus was measured to assess the consistency of spore production. In *X. cumberlandia* and *X. coloradoënsis*, eight ascospores are generally found in each ascus. A sample from each thallus was collected in the field, and ascospores were counted using an Olympus microscope. Three apothecia from each thallus were selected and sectioned. Ascospores from three asci from each apothecium were then counted. So that apothecia of similar size and development would be

compared, apothecia  $>5$  mm in diameter were selected for ascospore counts, when available.

**Statistical analyses.** Models were selected after using forward-selection regression in SAS (SAS Institute Inc. 2001) and S-PLUS (MathSoft Inc. 1999). The adequacy of parameters included in the final models was evaluated using drop-in-deviance chi-square tests and extra sum of squares F-tests for logistic and linear regressions, respectively.

In the last decade much attention has been paid to information-theoretic methods as a replacement for the more traditional null-hypothesis testing methods used here (Anderson et al. 2000; Stephens et al. 2005). Particular concern has been expressed for the use of null-hypothesis tests in observational studies. However, since our main interest in this study is whether or not biologically significant variance in apothecia production exists between populations located at different elevations (as opposed to what the causes of those differences are), the null-hypothesis method is appropriate for this study (Stephens et al. 2005).

**Table 1.** Summary of models predicting sexual fecundity. On Boulder Mountain, apothecial production in *Xanthoparmelia cumberlandia* and *X. coloradoënsis* is generally correlated with thallus size and elevation.  $R^2$  values indicate that this correlation is not strong. All models were developed using forward-selection regression.

Linear Regression Models						
Response	Model	F	d.f.	d.f.	p-value	$r^2$
number of apothecia	$N = A + E$	9.03	2	96	<0.0001	15.83%
area of apothecia (cm <sup>2</sup> )	$S = A + E$	28.20	2	96	<0.0001	37.00%
Maximum Likelihood Models						
Response	Model	$\chi^2$	d.f.		p-value	
presence of apothecia	logit ( $\pi$ ) = $A + E$	96.39	2		<0.0001	
ascospores per ascus	no model significant					
Parameters						
A = ln (thallus area) (cm <sup>2</sup> )						
E = elevation (2400–2500 m, 3300–3400 m)						
N = ln (number of apothecia)						
S = ln (area of apothecia) (cm <sup>2</sup> )						
$\pi$ = probability of apothecia						

Because most lichens had no apothecia, the response variables number of apothecia, area of apothecia and ascospores per ascus were evaluated after removing non-apotheciate individuals from the model. On a follow-up visit, additional apotheciate individuals were non-randomly collected from the upper elevation in order to increase sample size for these analyses. Thus, these models attempt to answer the question: if apothecia are present, how well does size predict the number and area of apothecia? Data collected in the random sample were used to develop a binary logistic regression model predicting the presence of apothecia.

The distribution of both number of apothecia and area of apothecia were heavily skewed to the right, even when zeros were removed. These responses were log-transformed before evaluation using linear regression. Using Bonferonni's correction for multiple

analyses, we accepted as significant those explanatory variables with p-values less than or equal to 0.010.

## RESULTS

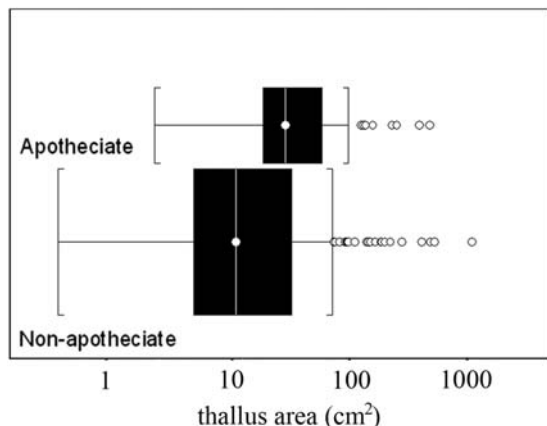
Thallus size was a significant positive predictor of apothecial presence, number and size for *Xanthoparmelia cumberlandia* and *X. coloradoënsis* on Boulder Mountain. For every 10% increase in thallus area, there is on average a corresponding 31% increase in the probability that an individual has apothecia ( $Z = 5.9$ ;  $p < 0.0001$ ; **Tables 1–2; Fig. 2**), a 5% increase in the average number of apothecia ( $Z = 3.53$ ;  $p = 0.0002$ ; **Tables 1 & 3; Fig. 3**), and a 10% increase in the average area of apothecia ( $Z = 7.50$ ;  $p < 0.0001$ ; **Tables 1 & 4; Fig. 4**).

However, much of the variation in the number of apothecia per thallus remains largely unexplained (**Tables 3–4**); only 15.83% of the variation is

**Table 2.** Presence of apothecia. Individuals in lower elevations and with larger thalli are more likely to have apothecia. This analysis includes all randomly selected individuals.

Parameter	DF	Estimate	SE	Type III		Odds Ratio	99% min	C. I. max	Z	p-value
				Drop	in Deviance					
(Intercept)		–2.95	0.47						–6.24	<0.0001
elevation	1	–2.86	0.42	68.94		0.06	0.02	0.17	–6.84	<0.0001
ln(thallus area) cm <sup>2</sup>	1	0.88	0.15	44.55		2.41	1.64	3.54	5.90	<0.0001

Presence of Apothecia and Thallus Area

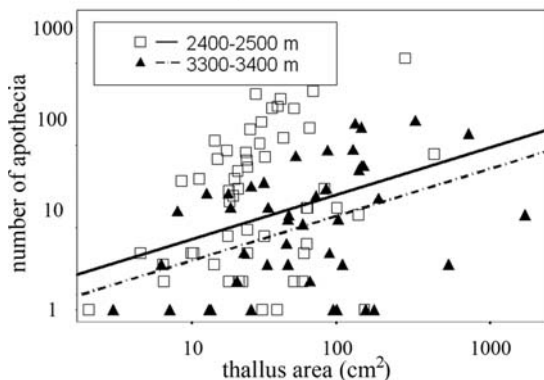


**Figure 2.** Predicting the presence of apothecia using thallus size. A 10% increase in the size of a thallus is associated with a 31% increase in the probability of having apothecia.

explained by thallus size and elevation (Table 3; Fig. 3). Thallus size and elevation explain more of the variation in total area of apothecia ( $r^2 = 37.00\%$ ; Table 4; Fig. 4). None of the variables measured significantly predicted variation in ascospore production.

The effect of elevation was less clear than the effect of thallus size on apothecial production. As measured by a drop in deviance test, elevation was negatively correlated with the presence of apothecia (Fig. 5) and number of apothecia, but was only marginally significant in predicting total area of apothecia on an individual (presence:  $p < 0.0001$ ,  $F_{2,313} = 43.21$ ; number:  $p = 0.0014$ ;  $F_{1,96} = 10.84$ ; size:  $p = 0.0171$ ;  $F_{1,96} = 5.89$ ; Tables 1–4). Compared to the lower elevation individuals of the same size, upper elevation individuals were 6% as likely to have apothecia ( $p < 0.0001$ ;  $Z = -6.84$ ; Tables 1–2; Fig. 5), had only 59% as many apothecia ( $p = 0.0002$ ;  $Z =$

Number of Apothecia and Thallus size



**Figure 3.** Number of apothecia and thallus size. Though thallus size is positively correlated with the number of apothecia, substantial variation still exists in the data ( $r^2 = 15.83\%$ ; Table 3). The relationship between thallus size and apothecia number is negatively affected by increasing elevation.

3.53; Tables 1 & 3; Fig. 3), and 69% as much apothecia in terms of area ( $p = 0.0005$ ;  $Z = -3.29$ ; Tables 1 & 4; Fig. 4).

Species distribution is strongly correlated with elevation ( $r = 0.91$ ). *Xanthoparmelia coloradoënsis* was generally located at 2400–2500 m ( $95.86\% \pm 4.3\%$  were in the lower elevation; 99% confidence) while *X. cumberlandia* was commonly found at 3300–3400 m ( $95.56\% \pm 4.0\%$  were in the upper elevation; 99% confidence). Because species and elevation were so highly correlated, these two effects are impossible to separate.

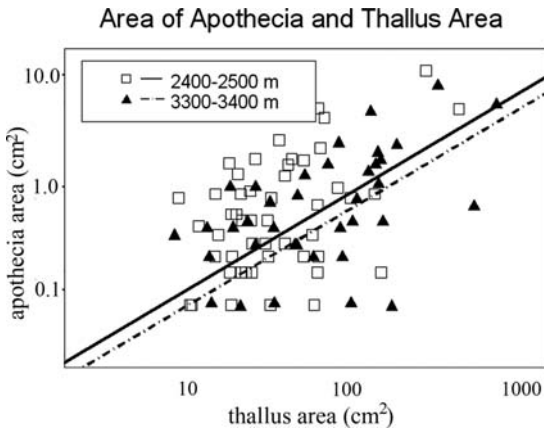
The average number of ascospores per ascus was consistent regardless the variable considered.

DISCUSSION

While thallus size was significantly associated with all measures of sexual fecundity, the relationship

**Table 3.** Number of apothecia. Both increased thallus size and decreased elevation are correlated with greater numbers of apothecia on an individual. The  $r^2$  value indicates that much variation is left unexplained. Non-apotheciate individuals were not considered in this model.

Parameter	DF	Estimate	SE	99%		Z	p-value	F	p-value
				min	max				
Intercept		0.49	0.56			0.88	0.1885		
$\ln(\text{thallus area}) \text{ cm}^2$	1	0.50	0.14	0.14	0.87	3.53	0.0002	7.22	0.0085
elevation	1	-0.52	0.16	-0.92	-0.11	-3.29	0.0005	10.84	0.0014
$r^2 = .16$									



**Figure 4.** Area of apothecia and thallus size. Only 37% of the variation in area of apothecia can be explained by thallus size and elevation.

between the two variables was not consistent across habitats. Sexual fecundity was negatively correlated with elevation, and variation within populations at the same elevation was high. That ascospore production per ascus among populations and individuals of different sizes was not significantly different indicates that area of apothecia is a comparable measure of reproductive output.

Though statistically significant, the correlation between thallus area and apothecia production explains little of the variance in sexual fecundity. Large amounts of variation in apothecial production remain unexplained in our models (number of apothecia:  $r^2 = 15.83\%$ ; area of apothecia:  $r^2 = 37.00\%$ ; **Table 1**; **Figs. 3–4**).

The onset of sexual reproduction was not reliably predicted by thallus size. Pringle et al. (2003) found a distinct size cutoff at  $10 \text{ cm}^2$  after which most *X. cumberlandia* individuals produced apothecia; however, we found that *most* individuals had *no* apothecia, regardless of size (**Fig. 6**). We did, however, find a

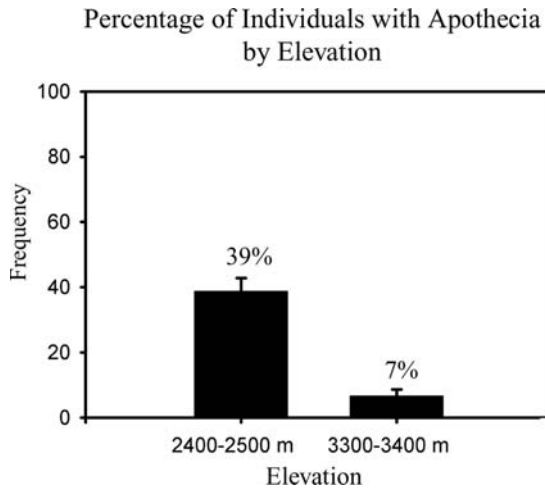
threshold at  $15 \text{ cm}^2$  after which roughly 37% of all individuals had apothecia, while before only 6% had apothecia (**Fig. 6**), an indication that a size threshold may exist, but that other variables besides size play an important role in sexual development.

Lichens are known for their variability and flexibility (Jahns & Ott 1997). Plainly, in populations of *X. coloradoensis* and *X. cumberlandia* variation in the relationship between apothecia production and thallus size is more marked than the correlation. While this study indicates that mesohabitat conditions associated with elevation have a significant relationship with apothecia production, microhabitat variables are also likely to affect sexual fecundity. Microhabitat characteristics affecting light and water availability have shown strong correlations with individual growth (Dahlman & Palmqvist 2003) and lichen community structure (Lücking 1999; Ott et al. 1996, 1997; Peck et al. 2004). In our study, there is enough variation within populations to suggest that size will not provide a reliable comparison of fecundity, even within the same population.

Other lichens have shown a propensity for sterility in extreme climates. Gaßmann and Ott (2000) observed a greater proportion of sterile thalli in populations of *Ochrolechia frigida* (Sw.) Lyngby with increased latitude. A similar pattern in which asexual or clonal reproduction is more common at higher latitudes and elevations is widespread among vascular plants and animals (termed “geographic parthenogenesis;” Bell 1982; Bierzychudek 1987a). Many advantages of asexuality have been called upon to explain this pattern including the ability to reproduce without a mate in areas of low-density (Bierzychudek 1987b; Gerritsen 1980), asexual’s avoidance of outbreeding depression in areas of high migration (i.e. frequent disturbance; Peck et al. 1998), and the idea

**Table 4.** Cumulative area of apothecia. Greater thallus size and decreased elevation are associated with larger area of the apothecia produced by an individual lichen. Non-apotheciate individuals were not considered in this model.

Parameter	DF	Estimate	SE	99% C.I.		Z	p-value	F	p-value
				min	max				
Intercept		-4.90	0.54			-9.06	0.0000		
$\ln(\text{thallus area}) \text{ cm}^2$	1	1.04	0.14	0.68	1.39	7.50	0.0000	50.50	0.0000
elevation	1	-0.37	0.15	-0.76	0.02	-2.43	0.0076	5.89	0.0171
$r^2 = .37$									

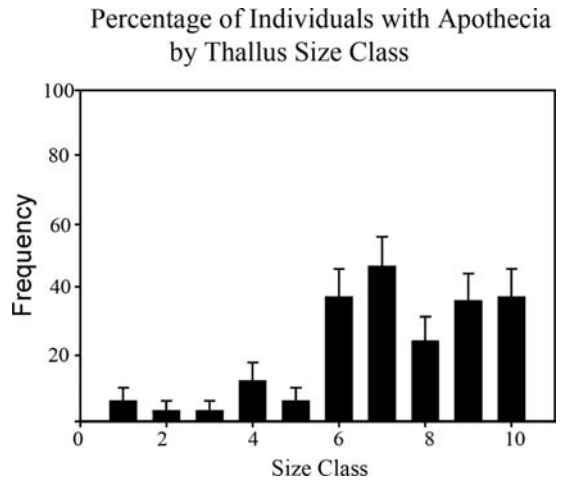


**Figure 5.** Predicting the presence of apothecia with elevation. Individuals from the upper elevation (3300–3400 m) are less likely to have apothecia than those from lower elevation locations (2400–2500 m). Standard error bars are shown.

that in marginal habitats, the costs of sex (Maynard Smith 1971) may outweigh the advantages (Bell 1982; Glesener & Tilman 1978). Kappen (1993) provided an explanation specifically for lichens, stating that thallus fragments are ideal for short-distance dispersal in areas with limited plant cover.

Whatever the reason for increased sterility within *Xanthoparmelia cumberlandia* and *X. coloradoënsis* populations on top of Boulder Mountain, it is clear that climatic effects associated with increased elevation have an impact on lichen life history strategies thus making comparisons of fitness defined by sexual fecundity or size difficult. Not only is size an unreliable predictor of sexual fecundity both within and among populations at different elevations, but perhaps sexual fecundity itself is not always indicative of fitness. As the widespread pattern of geographic parthenogenesis suggests, fitness at higher elevations and latitudes may depend on an organism's ability to reproduce asexually.

Mesoclimatic change (and probably microclimatic change as well) is associated with variation in the relationship between size and sexual fecundity. Though this relationship is consistent in the homogeneous environment of a botanical garden, the use of size in natural environments as an easy measure of sexual fecundity is unwarranted. Apothecial production is simply too variable across the landscape to allow for size and fecundity to be used interchangeably.



**Figure 6.** Presence of apothecia by thallus size class. Though most individuals in all size classes have no apothecia, a distinct difference in the proportion of individuals with apothecia is seen between size classes above and below 15 cm<sup>2</sup>. Size classes were chosen by percentiles, with size class 1 containing individuals in the 10<sup>th</sup> percentile and lower and so on. Sizes in each size class are as follows: 1: 0.39–3.35 cm<sup>2</sup>, 2: 3.42–5.10 cm<sup>2</sup>, 3: 5.10–7.42 cm<sup>2</sup>, 4: 7.61–11.74 cm<sup>2</sup>, 5: 11.87–15.81 cm<sup>2</sup>, 6: 15.94–22.77 cm<sup>2</sup>, 7: 22.90–33.03 cm<sup>2</sup>, 8: 33.35–51.42 cm<sup>2</sup>, 9: 52.90–91.16 cm<sup>2</sup>, 10: 93.94–1174.26 cm<sup>2</sup>. Standard error bars are shown.

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