

CONSERVATION OF A FLORIDA ENDEMIC CARNIVOROUS PLANT:
GODFREY'S BUTTERWORT (*PINGUICULA IONANTHA*)

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CONSERVATION OF A FLORIDA ENDEMIC CARNIVOROUS PLANT:
GODFREY'S BUTTERWORT, *PINGUICULA IONANTHA*

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A Thesis

Submitted to

the Graduate Faculty of

Auburn University

in Partial Fulfillment of the

Requirements for the

Degree of

Master of Science

Auburn, Alabama
December 15, 2006

CONSERVATION OF A FLORIDA ENDEMIC CARNIVOROUS PLANT:
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THESIS ABSTRACT

CONSERVATION OF A FLORIDA ENDEMIC CARNIVOROUS PLANT:

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Master of Science, December 15, 2006
(B.S., Florida State University, 2000)

85 Typed Pages

Directed by Craig Guyer

For conservation and recovery efforts to be effective under the Endangered Species Act, knowledge of the factors which make a species rare must be gained. In order to meet conservation goals, this study focuses on the habitat availability and demography of a federally threatened carnivorous plant species, *Pinguicula ionantha*.

The majority of existing *P. ionantha* populations occur in the Apalachicola National Forest (ANF), the largest National Forest east of the Mississippi. Presence data from 28 confirmed populations and a randomly generated pseudo-absence dataset were overlaid onto spectral data from Landsat 5 TM images and a Digital Elevation Model (DEMs).

Generalized additive models were used to develop spatially explicit predictive models to identify potential *P. ionantha* populations within the ANF. Validation tests of this map ranged in accuracy between 75 - 83%. The resulting predictive map found 36.4 km² (3.0%) of potential *P. ionantha* habitat in the Apalachicola district of the ANF and aided the in the discovery of seven previously unrecorded populations of this rare plant.

The bog/savannah habitat, where *P. ionantha* occurs, is defined as a fire-dependent community. Prescribed fire is a common management tool in this ecosystem yet, until the current study, no information on the influence of fire on *P. ionantha* was available. Multi-state mark recapture models with dead recoveries were used to estimate survival and transition probabilities for over 2313 individuals in 12 populations. These estimates were then used to parameterize matrix models used in a regression-based Life Table Response Experiment (LTRE). Nearly 60% of the variation in population growth rate was explained by days since last fire. Population growth rate (λ) was greater than 1.0 and increased with days since fire until 430 days. After this time, λ decreased, becoming less than one after 1200 days. Positive growth rates were found for both dormant- and growing-season burns, but the timing of these effects were different. Frequent fires (1-3 year interval) were predicted to maximize population growth of *P. ionantha* populations. Fecundity and growth contributed the most to post-fire population growth. Current prescribed fire intervals used at the study sites are effective at maintaining populations of this rare species.

ACKNOWLEDGEMENTS

I acknowledge the support of my committee members Sharon Hermann, Craig Guyer, and Barry Grand. Their guidance and advice have greatly improved this work. I also thank my wife, Jennifer Trusty. Without her unconditional love for plants and me this document would not have been possible. She has assisted in every phase of this project and I thank her for making every day an unforgettable one. I appreciate the support of my mother and father, Herbert and Sandra Kesler. They have consistently supported all endeavors school related or otherwise. I would like to acknowledge Louise Kirn, Brian Martin, and Florida Natural Areas Inventory for assistance locating populations and logistics in Apalachicola national Forest and Tate's Hell State Forest. A special thanks to Frank Thompson for going out of his way to make every stay in the Apalachicola National Forest a great one.

The following individuals have provided support essential to the completion of this document, including critiques of early versions, advice regarding data analysis and assistance in the field: Luke Marzen, Mark McKenzie, Nedret Billor, Kyle Barrett, Roger Birkhead, Sydney Grubb, Shannon Hoss, Christina Romagosa, Geoff Sorrell, John Steffen, and Matt Williams. This project was supported by a U. S. Environmental Protection Agency Greater Research Opportunity (GRO) fellowship. Additional funding was generously provided by the Florida Native Plant Society.

Style manual or journal used:

Ecography (Chapter 2)

Ecological Applications (Chapter 3)

Computer software used:

SAS v9.1, S-Plus v7.0, Program MARK v4.2, MATLAB, ERDAS, ArcView v3.2,

ARCGIS® v9.1, Hawth's Analysis Tools for ArcGIS, Generalized Regression Analysis

and spatial Prediction (GRASP), Microsoft Word, Microsoft Excel, Microsoft Access

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INTRODUCTION

The goal of the Endangered Species Act (ESA) is the recovery of listed species to levels where protection under the Act is no longer necessary. In many cases, the recovery of the endangered and threatened species is dependent on conservation of their ecosystems. Recovery efforts may take many forms, such as protective measures, consultation to avoid adverse impacts, habitat acquisition or restoration and activities in managing and monitoring endangered and threatened species (U.S. Fish and Wildlife Service 1994).

For conservation and recovery efforts to be effective under the ESA, knowledge of the factors which make a species rare must be gained. Understanding whether a species is rare due to habitat loss and/or as the result of stochastic or deterministic processes is essential to making informed recovery efforts. The interaction between habitat availability and demography is tightly linked for non-mobile species such as plants. Understanding the relationship of growth, fecundity and survival of a rare plant species to the biotic and abiotic factors of its native habitat and knowledge of the amount and quality of available habitat are critical to conservation planning. Finally, a recovery plan must include data on how management options influence population growth.

The current study focuses on the demography and habitat availability of a federally threatened carnivorous plant species, *Pinguicula ionantha* R. K. Godfrey

(Lentibulariaceae). Godfrey's butterwort is one of five species of *Pinguicula* found in the Southeastern United States. The range of *P. ionantha* is limited to the lower Apalachicola River region in the Florida panhandle (Figure 1). The species is a perennial carnivorous rosette-form herb that is up to 15 cm in diameter and has pale purple flowers. *P. ionantha* is endemic to a 25-mile radius in the panhandle of Florida and primarily occurs in the herb bog or savannah zone located between long-leaf pine flatwood and cypress stringer habitats (Godfrey and Stripling 1961). In these bog/savannah habitats overstory trees and shrubs are absent or nearly so and soil surface can remain saturated for weeks (Clewell 1985).

P. ionantha was listed as federally threatened in 1993 (U.S. Fish and Wildlife Service 1993). The primary threat to this plant has been the adverse modification of its habitat. Large-scale modifications are primarily related to pulp wood industry and fire suppression (U.S. Fish and Wildlife Service 1994). Site preparation and subsequent growth of planted pine trees and perhaps increase numbers of hardwood stems due to lack of fire may severely disrupt the hydrological and light regimes required by this species (Kral 1983).

Fire suppression is detrimental to many species of the pineland savannah flora (Platt et al. 1999). Until recently, fire as a management tool was viewed as a legal liability on private property (U.S. Fish and Wildlife Service 1994). In addition, on public land, past alteration of fire regimes may have promoted encroachment of hardwood species such as titi (*Cyrilla racemiflora*) into herb bogs (Drewa et al. 2002). Kral (1983) suggested that *P. ionantha* needs a reduction in vegetative cover to grow, flower, and fruit. This periodic reduction probably occurred naturally through wildfires but is now

accomplished by means of prescribed fire. Prescribed burns have now become a common management tool in this ecosystem yet until the current study no information on the influence of fire on the federally threatened *P. ionantha* was available.

Based on information provided by the Florida Natural Areas Inventory (FNAI), there are 62 historically documented populations. Locations of forty-one of these populations were revisited in the current study (Table 1). Plants were present at twenty-two (54%) of these populations. Of the populations in which plants were present, 20 (90%) were within the boundaries of the Apalachicola National Forest (ANF). One population was within the Tate's Hell State Forest (THSF) and one Gulf county population contained *P. ionantha*. Searches did not locate plants at nineteen (46%) previously-recorded sites. Within the ANF nine populations were not found of which, seven of these populations were not observed in the 1992 survey conducted by Gholson and Baker (FNAI, pers. comm.). Three additional THSF populations were not relocated, and four populations on private land were not found. Additionally three previously recorded populations in Gulf County were not located because high water prevented access to these populations.

At some sites, *Pinguicula ioanantha* populations may become extirpated in a short amount of time. In the current study one population in Franklin County contained approximately 100 individuals in 2004 and was reduced to two individuals by 2005 (see Chapter 3). It appears as if the severe reduction of this population was associated with saltwater inundation from a nearby tidally influenced river during Hurricane Francis (September 2004).

It is not known how commonly populations succumb to natural stochastic events. The majority of local extinctions are likely to be deterministic and due to habitat loss and degradation.

Information from herbarium specimen label and recorded observations by workers who conducted earlier field surveys were summarized and suggest possible reasons for population declines. Three main situations were implicated (Table 1). First, habitat descriptions indicated that of nine extirpated populations were located on roadside, railroad, or drainage ditches. These conditions may cause sites to become unstable over the long term. Second, sites of three populations were logged one year prior to the last observation period. Mechanical disturbance associated with timber harvesting practices may negatively impact the hydrological requirements of this species (Kral 1983). Three sites were noted to have dense ground cover, indicating a lack of fire necessary to reduce competition (Kral 1983).

The objective of the recovery plan for *P. ionantha* is its eventual delisting. This can occur when 15 populations throughout its historic range are adequately protected and managed (U.S. Fish and Wildlife Service 1994). In order to meet this goal accurate knowledge on the location and status of existing populations must be obtained and the management practices that have the greatest positive impact on population growth must be determined. Based on the results of the current study, although the existing *P. ionantha* populations within ANF and THSF are growing, the continued loss of populations outside of protected areas and the inexorable extirpation of protected populations due to stochastic events precludes the delisting of this species in the near future.

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County	Location	Last observed	Found	Explanation for loss	Notes
Franklin	ANF	1982	n	1	Drainage ditch
Franklin	ANF	1992	n	2	Dense overgrown vegetation
Franklin	THSF	1961	n	?	Shallow depression
Franklin	THSF	1961	n	?	Shallow depression
Franklin	THSF	1961	n	?	Wet Flatwoods
Franklin	P	1981	n	1	Ditch
Franklin	P	1988	n	3	Logged several years prior
Franklin	THSF	1988	y		Area clearcut, one plant observed
Gulf	P	1960	n	?	Flatwoods depression
Gulf	P	1991	n	3	Clearcut, ground cover left intact
Gulf	P	1999	n	?	Possible presence, high water
Gulf	P	1996	n	?	Possible presence, high water
Gulf	P	1996	n	?	Possible presence, high water
Gulf	P	1998	y		Two plants observed, high water
Liberty	ANF	1982	n	?	Savannah
Liberty	ANF	1992	n	1	Roadside ditch
Liberty	ANF	1992	n	1	Roadside ditch
Liberty	ANF	1992	n	2	Dense overgrown vegetation
Liberty	ANF	1992	n	1	Roadside ditch
Liberty	ANF	1992	n	2	Dense overgrown vegetation
Liberty	P	1990	n	3	Bedded slash pine
Liberty	ANF	1994	y		Located in savannah along a ditch and on border of <i>Taxodium ascendens</i> interface, population used in demographic study
Liberty	ANF	1992	y		10-20 plants observed, shrub edge seems to be increasing
Liberty	ANF	1992	y		Locally abundant in along savannah and cypress edge, population included in demographic study

County	Location	Last observed	Found	Explanation	Notes
Liberty	ANF	1992	y		Locally abundant in along savannah and cypress edge, population included in demographic study
Liberty	ANF	1992	y		On island located in center of drainage ditch passing under SR 379
Liberty	ANF	1992	y		30 m from road side, plants found on border of cypress pond, population used in demographic portion of study and population growth appears to have been negatively impacted by SR 65 road widening project.
Liberty	ANF	1992	y		Edge of <i>Taxodium ascendens</i> / <i>Magnolia</i> pond
Liberty	ANF	1992	y		aprox 100 plants observed in 2004
Liberty	ANF	1992	y		Savannah/ pond cypress edge
Liberty	ANF	1992	y		Located on the edge of <i>Taxodium ascendens</i> area, population included in demographic study
Liberty	ANF	1992	y		Three plants observed along roadside ditch
Liberty	ANF	1992	y		At the end of small cypress pond, population included in demographic study
Liberty	ANF	1992	y		<i>Ilex myrtifolia</i> / <i>Nyssa biflora</i> pond. 100 plants observed
Liberty	ANF	1992	y		Located in narrow ecotone between <i>Pinus palustris</i> / <i>Aristida</i> upland and lower <i>Taxodium ascendens</i> drainage pond, population included in demographic study.
Liberty	ANF	1992	y		<i>Taxodium ascenden</i> , graminoid/pond interface, population used in demographic portion of study
Liberty	ANF	1992	y		<i>Taxodium ascendens</i> , graminoid/pond interface, population used in demographic portion of study
Liberty	ANF	1992	y		<i>Taxodium ascendens</i> , graminoid interface, population used in demographic portion of study

County	Location	Last observed	Found	Explanation	Notes
Liberty	ANF	1992	y		Plants located under <i>Taxodium ascendens</i> overstory, 10 plants observed
Liberty	ANF	1992	y		Edge of <i>Taxodium ascendens</i> pond approx 100 plants observed
Liberty	ANF	1992	y		Plants located under <i>Taxodium ascendens</i> overstory, 100-300 plants SW edge along ecotone with pond cypress stand, population included
Liberty	ANF	1992	y		in demography study

Table 1. *Pinguicula ionantha* populations monitored by FNAI that were revisited during current study. P= private land, ANF = Apalachicola National Forest, THSF = Tate's Hell State Forest, n = not found. Explanation describes possible reason for disappearance of population: 1=ditch, 2=shading, 3=clearcut.

PREDICTING RARE CARNIVOROUS PLANT (*PINGUICULA IONANTHA*) HABITAT USING REMOTE SENSING

Abstract

Pinguicula ionantha (Lentibulariaceae) is a federally-listed carnivorous plant found only within the Apalachicola River Basin of Florida. Most existing *P. ionantha* populations occur in the Apalachicola National Forest (ANF), the largest national forest east of the Mississippi. The small size and growth habit of *P. ionantha* make locating new populations in this extensive area labor intensive and difficult. Currently, over 90% of the known *P. ionantha* populations are located within 100m of a well-maintained road despite the presence of a much larger potential habitat. The existence of 28 previously-recorded populations within the ANF was confirmed. These presence data combined with randomly generated pseudo-absences were overlaid onto two Landsat TM5 scenes and digital elevation model (DEM) data. Generalized additive models were used to predict the probability of *P. ionantha* occurrence throughout the ANF. The resulting predictive map aided the discovery of eight previously unrecorded populations of this rare plant. This predictive map has the potential ofr aiding in the discovery of additional populations of this and other co-occurring rare plant species.

Introduction

The emergence of geographical information systems (GIS) combined with ecological modeling provides a valuable approach to locating unknown populations of rare plant species (Vogiatzakis 2003). This methodology is able to incorporate both biotic and abiotic factors such as soil type, elevation, and the reflective signatures of differing vegetation types to identify potential habitat based on analysis of data from known populations (Sperduto and Congalton 1996, Wiser et al. 1998). Predictive maps created using this approach have identified suitable habitats and have aided in the location of new populations of rare plant species (Wiser et al. 1998, MacDougall and Loo 2002, Engler et. al 2004).

The current study focused on the Apalachicola river basin, recognized by The Nature Conservancy as one of six biodiversity hotspots in the United States (Stein et al. 2000). This ecologically complex region covers 6,215 km² of northern Florida and is made up of a mosaic of 16 recognized habitats defined mainly by the interactions of hydrology and small changes in elevation (Myers and Ewel 1990). These habitats are home to over 1300 plant species (Clewell 1985), including numerous carnivorous plants.

Two unique habitats found within the Apalachicola river basin are herb bogs and seepage savannahs. Both habitat types are seasonally moist to wet and dominated by grasses and forbs. Herb bogs exist in small areas where gradually sloping land intersects the water table (Wolfe et al. 1988). Areas where seepage occurs over a wide area are referred to as savannahs (Myers and Ewel 1990). Human impacts have drastically reduced the abundance of these unique communities and their representative species. At one time herb bogs and savannahs covered a large portion of the land from the Florida

Panhandle through the Gulf Coastal Plain of Alabama and Mississippi. Today it is estimated that between 85 and 98% have been lost due to a variety of factors including creation of drains, conversion into farm ponds, urbanization, and road construction (Folkerts 1982, United States Fish and Wildlife Service 1994).

Many rare plant species are restricted to the herb bog/savannah habitat of the Apalachicola River basin. Within this habitat twenty-five plant species of special concern are monitored by the Florida Natural Areas Inventory (FNAI). Most of these species are endemic to the area and many are protected by federal and/or state regulations (Kindell 1997). *Pinguicula ionantha* (Lentibulariaceae), Godfrey's Butterwort, is a carnivorous plant that is limited to herb bog/savannah habitats and is listed by the federal government as Threatened and by the state of Florida as Endangered.

Pinguicula ionantha is a carnivorous plant species endemic to the Gulf Coastal Plain of Bay, Franklin, Gulf, Wakulla, and Liberty counties, Florida. There are 61 historically known populations (Florida Natural Areas Inventory 2002). The majority of extant *P. ionantha* populations occur in the protected area of the Apalachicola National Forest (ANF) (Fig. 1). The ANF is the largest national forest east of the Mississippi river and covers 2656 km². The small size and growth habit of *P. ionantha* (see below) make locating new populations in this extensive area labor intensive and difficult. Currently, the majority of the known *P. ionantha* populations occur within 100 m of a well-maintained road despite a much larger potential habitat (Florida Natural Areas Inventory 2002). Due to the cost and difficulty of surveying large areas, the true number of populations is not known. In order to comply with federal Threatened and Endangered Species guidelines, an accurate assessment of populations is needed. In addition, the

United States Fish and Wildlife Service (USFWS; 1994) recovery plan for *P. ionantha* recommends further field surveys to locate previously unrecorded populations.

In order to find new populations, the USFWS recovery plan for *P. ionantha* recommends that an attempt be made to identify more conspicuous associates that co-occur with *P. ionantha* in hopes that exploring for associated species would result in identification of new locations for the species. However, this type of survey requires extensive fieldwork by trained botanists. Since the majority of *P. ionantha* populations occur in high-quality herb-bog/savannah habitat, enhancing the ability to identify these habitats within the ANF and throughout the historic range should help focus time and effort spent in locating new *P. ionantha* populations and their rare associate species.

The current study developed spatially-explicit models for the prediction of herb-bog/ savannah habitat within the ANF. I used presence/absence and location information and spectral data from Landsat 5 TM images to predict locations of herb-bog/savannah habitat in order to identify potential *P. ionantha* populations. In addition, GIS predictive maps created by this approach estimated the total remaining area of herb-bog/ savannah habitat within the ANF. This approach was able to locate new *P. ionantha* populations. Based on the amount of high probability habitat and the accuracy of the predictive models, an estimate of the true conservation status of this rare habitat can be made. This knowledge will not only help *P. ionantha* but aid in making management recommendations and assist in restoration planning for the unique flora and fauna within this unique habitat.

Materials and Methods

Description of Habitat

The herb-bog and savannah habitats occupied by *Pinguicula ionantha* are frequently burned and this maintains a grassy ground cover with an open canopy. These areas are dominated by wiregrass (*Aristida beyrichiana*), spurned panic grass (*Panicum spretum*), flattened pipewort (*Eriocaulon compressum*) and Chapman's beakrush (*Rhynchospora chapmanii*) (Kindell 1997). Often, *P. ionantha* habitats are found between a lower elevation habitat dominated by a cypress (*Taxodium ascendens*) overstory and a slightly higher elevation pine flatwoods dominated by an overstory of longleaf pine (*Pinus palustris*).

Mapping and Predicting Populations

Existing location information for *P. ionantha* was gathered from the FNAI data base. Field searches were conducted in February-April 2004 to confirm the existence of previously recorded populations. Within the ANF a total of 28 populations were re-sighted and sub-meter GPS point locations were recorded. A pseudo-absence point data set was created using Hawth's Analysis Tools for ArcGIS (Beyer 2004). The pseudo-absence data set consisted of 30 randomly generated points within a polygon representing the ANF. The random point generation procedure was not weighted because the relative rarity of bog and savannah habitats within the ANF decreased the probability of generating pseudo-absences in favorable *P. ionantha* habitat (Engler et al. 2004). All data were projected into UTM WGS 1984 zone 16.

Two cloud-free Landsat 5 TM images (path 20 row 39) dated 8th January 2003 (JTM) and 27th April 2005 (ATM) were obtained. These dates represented the dormant (January) and growing (April) season in this area and can be useful in distinguishing deciduous and evergreen vegetation types. These images contain 6 bands of different reflective wavelengths. A Digital Elevation Model (DEM) data of the area was used as a surrogate for hydrology; lower elevations in the Florida coastal plain often represent mesic vegetation while xeric communities occupy higher elevations (Myers and Ewel 1990). Presence and pseudo-absence points were overlaid onto the raw bands and (DEM) data. Digital numbers (DNs) were extracted from each layer using the intersect tool in Hawth's Analysis Tools for ArcGIS (Beyer 2004).

Pairwise correlations between bands were assessed. Bands with high correlations (> 0.4) were dropped from the analysis and separate starting models were constructed that did not contain the highly correlated variables. Strong correlations can cause problems when estimating additive surfaces and influence stepwise selection procedures (Brauner and Shacham 1998). Bands 1, 2, 5 and the mid-infrared band 7 were highly correlated with bands 3 and 4 and were therefore removed from the analysis. Landsat bands used in this study included two 30m resolution bands TM3 0.63-0.69 and TM4 0.75-0.90 from each landsat image and a DEM for a total of five predictor variables: JTM3, JTM4, ATM3, ATM4 and DEM. Bands TM3 and TM4 are particularly useful for distinguishing differences in plant biomass and species composition (Jensen 2000).

A Generalized Additive Model (GAM; Hastie and Tibishirani 1990) was used to predict herb-bog/ savannah occurrence. These semi-parametric regression techniques allow predictors to be modeled with a smoothing function. GAMs with a logit link

function were implemented with Generalized Regression Analysis and Spatial Prediction (GRASP) developed by Lehmann et al. (2002). GRASP consists of a set of functions implementing spatial predictions with GAMs in the S-plus statistical package. Each predictor variable was restricted to a maximum of three degrees of freedom. This constrained the complexity of the fitted GAM function to that comparable of a cubic function. However GAMs exhibit more flexibility because of their ability to model asymmetrical response curve shapes (Bio et al. 2002).

A forward/backward stepwise selection procedure was used to select predictor variables with the highest statistics of cross validation (Lehmann et al. 2005, Maggini et al. 2006). In this method predictors are added or removed according to the Bayesian Information Criteria (BIC). At each step a cross-validation procedure using Receiver Operating Characteristic (CVROC; Fielding and Bell 1997) is calculated. In the end, the model with the highest CVROC is selected. This method has been shown to be the best compromise between model stability and performance (Maggini et al 2006).

GAMs are often referred to as data-driven models (as opposed to model driven) because it is the data not the model that determines the shape of the response curve (Yee and Mitchell 1991). Unlike Generalized Linear Models (GLMs), GAMs do not impose the assumption of linearity. The relaxation of the linearity assumption can allow for the development of more realistic ecological models (Austin 2002). GAMs have been used successfully to model species occurrences in both terrestrial (Bio et al. 2002, Ferrier et al. 2002, Clarkson et al. 2004) and aquatic (Garza-Pérez et al. 2004) ecosystems. Despite the added flexibility of GAM models, it is suggested that the GLM equivalent be used if the fit is comparable (Hastie and Tibshirani 1990).

GLM models may be preferable over GAMs for several reasons. First, GLMs produce interpretable parameter estimates under conditions for which GAM estimates are not directly calculable. Second, GAMs often have difficulty predicting at the tails of the distributions (Hastie and Tibshirani 1990, Frescino et al. 2001) while GLMs can constrain the behavior of functions at these extreme ranges of the data (Hastie and Tibshirani 1990). Finally, GLMs have been shown to perform better when predictors show medium to high correlation. This correlation is known as concurvity (non-parametric analogue to multicollinearity). For GAMs concurvity has been shown to bias parameter estimates upward and underestimate their variances (Ramsey et al 2003, He et al. 2006).

A parametric GLM was fit for the best GAM model selected by the CVROC procedure under a generalized linear model framework in S-Plus. Second- and third-order polynomial fits were compared to the GAM model by examining the number of parameters and residual deviance and performance of the GLM and GAM models (Cressie 1991, Frescino et al. 2001). An Analysis of Deviance was used to test differences between models.

Look-up tables (LUTs) were produced from the best GAM and corresponding GLM models for prediction within the ANF. Look-up tables were imported into ArcView 3.2 using the GRASP ArcAvenue LUT script. The predictive map for the corresponding best parametric model was created by specifying the model in the Spatial Analyst raster calculator of ArcGIS 9.1. Maps were then reclassified into areas having $\geq 90\%$ and $< 90\%$ probability of occurrence. Sixty random points were generated in areas

with > 90% probability of herb-bog/ savannah habitat on maps produced by the GAM and GLM models. Random points were then overlaid on 1m resolution digital orthographic quarter quads (DOQQs). A visual check was made to determine if the random points were in herb-bog/ savannah habitat. A field test of the GAM predictive map occurred in February 2006. Ground truthing by field surveys of random points generated on the final maps was also used to evaluate model performance.

Results

The top GAM model included JTMB3 ATMB4 and DEM (Table 1.). Graphs of the fitted function to the response indicated nonlinear relationships (Fig. 2). This model had a CVROC of 0.8859, a residual deviance of 19.12 with approximately ten parameters. The corresponding cubic GLM had a residual deviance of 31.6 and ten parameters. The quadratic model had seven parameters and a residual deviance of 34.2. There was a significant difference between the GAM and GLM models but not between the two GLMs as tested by analysis of deviance. There was no significant difference between the polynomial and linear GLMs ($\chi^2 = 0.47$). Significant differences were found between the best GAM and both GLMs ($\chi^2 = 0.01$).

The contribution of each predictor in the best GAM model was determined in two ways. First I calculated the explained deviance for a model that included only the predictor. Then I calculated the drop in deviance that occurred in a model that excluded the predictor (Fig. 3). JTM3 explained the most deviance when it was the only parameter included in the model (33.0) and resulted in the largest drop in explained deviance when it was excluded from the model (14.6). The contribution of ATM4 and DEM alone in the

model was nearly equal (23.6 vs 22.3) as was the drop in explained deviance when each parameter was excluded from the model (7.9 vs 8.3).

Because the map produced by the GAM model (Fig. 4) is more accurate than either GLM map (according to the DOQQ test) it was used as the final predictive map for *P. ionantha* search locations. The GAM map predicted the presence of potential *P. ionantha* habitat correctly 83% of the time. In contrast the quadratic GLM map predicted presence 68% of the time and the cubic GLM map predicted 62% of the randomly generated presences correctly.

In the final GAM map 36.4 km² (3.0%) of the western portion of the ANF had a probability $\geq 90\%$ of being herb-bog/savannah habitat type and, therefore, of potentially supporting *P. ionantha*. The predicted herb-bog/savannah habitat sizes ranged from small herb bogs (616m²) to large savannah habitats (1.4 km²). A total of ten savannahs were identified as having areas greater than 0.5 km² in the ANF. These habitats are irregular in shape and are interspersed among other habitat types.

Field surveys

Nineteen of the 20 random points in areas predicted to have $>90\%$ *P. ionantha* habitat were visited in the equivalent of 40 work hours. High water prevented visitation to one site. The GAM model was able to correctly discriminate herb-bog/savannah habitats in 79% of the field survey points visited. Seven of 20 points (37%) contained previously-undocumented *P. ionantha* populations and eight points (42%) were in herb-bog/savannah habitat where no *P. ionantha* currently occur. Four points (21%) were not

located in herb-bog/savannah habitat; although the sites were open and grassy, they appeared to be too dry to contain *P. ionantha*.

Discussion

Prediction of Herb Bog/Savannah Habitats

Remotely-sensed data were able to aid in distinguishing the open, grass-dominated herb-bog/savannah habitats from the general landscape. The GAM model was found to best predict potential *P. ionantha* habitat. Smoothed functions of the three predictor variables, JTM3, ATM4 and DEM were better at predicting potential habitat than the polynomial linear models. This is consistent with other studies (Austin 1987, Austin 2002, Lawesson and Oksanen 2002) in which the relationship between the predictor variable and plant presence was not always best described by symmetric response curves.

Status and Conservation of *P. ionantha*

Human activity has drastically reduced the abundance of herb-bog savannah communities and their unique representative species. At one time these communities were nearly continuous from the Florida Panhandle through the Gulf Coastal Plain of Alabama and Mississippi (Folkers 1982). It has been estimated that between 85 and 98% of these communities have disappeared due to a variety of factors including draining, conversion into farm ponds, urbanization, and highway construction (Folkerts 1982). This study is the first attempt to quantify both the location and area of these remaining habitats within ANF. The majority of predicted herb-bog/savanna habitats are found in the southwest portion of the national forest (Fig. 3). In the top model only 3.0% of the portion of the

ANF studied had a probability $\geq 90\%$ of being high quality herb-bog/savannah habitat type that could potentially support *P. ionantha*. This low percentage of habitat found within the protected confines of the ANF suggests that these habitats, and their associated plants and animals, may now be rarer than previously thought.

The predictive map will also aid in the conservation of *P. ionantha* by increasing the ability to target useful management techniques. The interaction of fire and hydrology play an important role in maintaining *P. ionantha* habitat. Currently, the ANF manages *P. ionantha* habitat with prescribed burns applied at four year intervals in alternating winter and summer seasons. Herb-bog/savannah habitats are often flooded during the winter and so burning during wet periods may reduce the coverage and effectiveness of prescribed fires. Knowing the locations and area of herb-bog/savannah habitat within each ANF burn compartment can help managers plan prescribed burning at the most effective times. Finally, this map can serve as a basis for identifying future changes to the area and locations of herb-bog/savannah habitat under different management regimes.

Future research should focus on predicting and locating *P. ionantha* habitat outside of the ANF. The model developed in the current study serves as a starting point for building predictive maps to identify potential populations outside the boundaries of the National Forest. Additional mapping efforts would provide information on the extent of the total remaining habitat and the locations of high-quality habitat that could be added to a conservation management program. Many of the locality points of historic populations outside of the ANF are based on herbarium label information and an effort must be made to verify these historical populations. Additional herb bog habitat needs to be identified and further populations of *P. ionantha* located and protected to meet the

federal conservation mandate of this species. The long-term goal of delisting *P. ionantha* is dependent on the success of these efforts. The discovery of new populations, the correct designation of historical populations and the proper management of known populations will improve our ability to ensure the long-term success of *P. ionantha* and other rare species on wet savannahs of the Apalachicola River basin.

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Band	absence	presence
jb3	21.533 ± 1.1201	27.615 ± 0.8613
ab4	68.767 ± 2.2199	56.308 ± 1.6914
dem	4.5 ± 0.394	2.6 ± 0.237

Table 1. Band means with standard errors for predictors selected by cross validation.
Absence n=30 presence n=28.

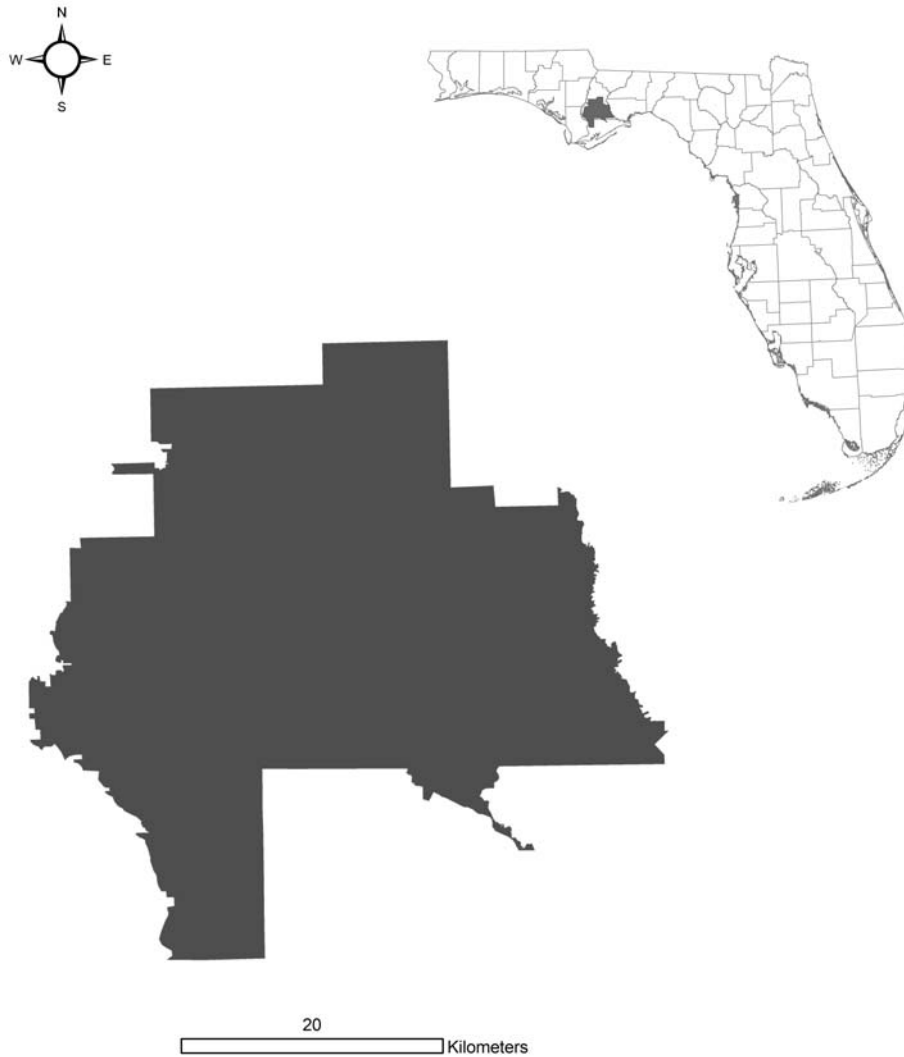
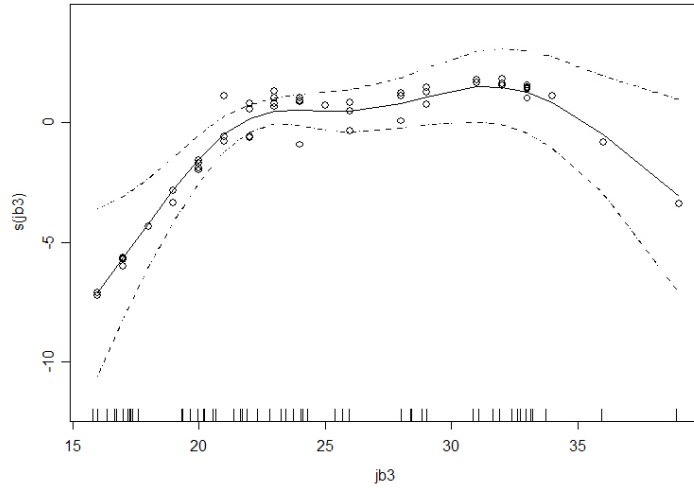


Figure 1. Western portion (Apalachicola District) of the Apalachicola National Forest used in mapping project.

a.



b.

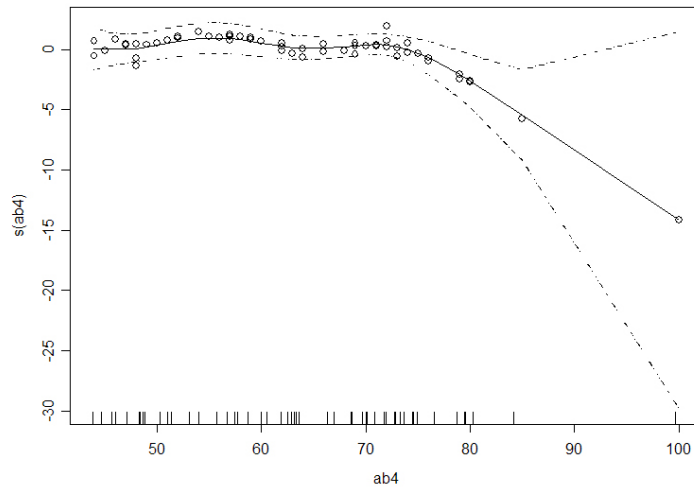


FIG. 2. Explanatory variables selected from the stepwise CVROC procedure as contributing to the binomial response variable *P. ionantha* presence. Each plot shows the relationship of the fitted function to the response and scaled to zero. The plots include 95% pointwise confidence intervals. At the base of each plot is the univariate histogram (rug plot) showing the distribution of each observation. (a) JTM3, (b) ATM4, (c) DEM.

c.

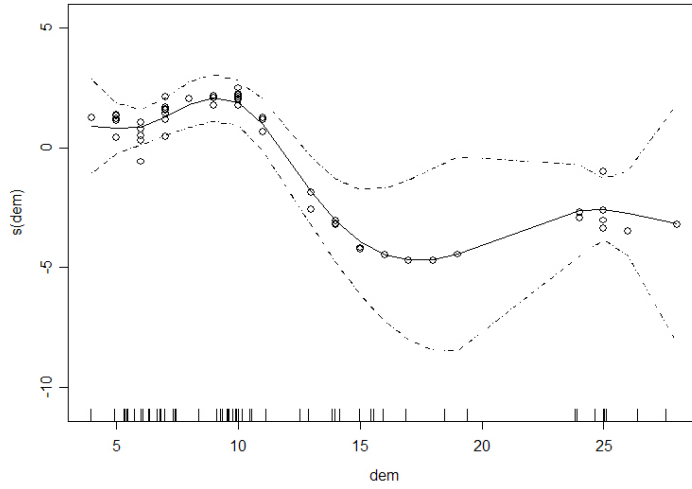
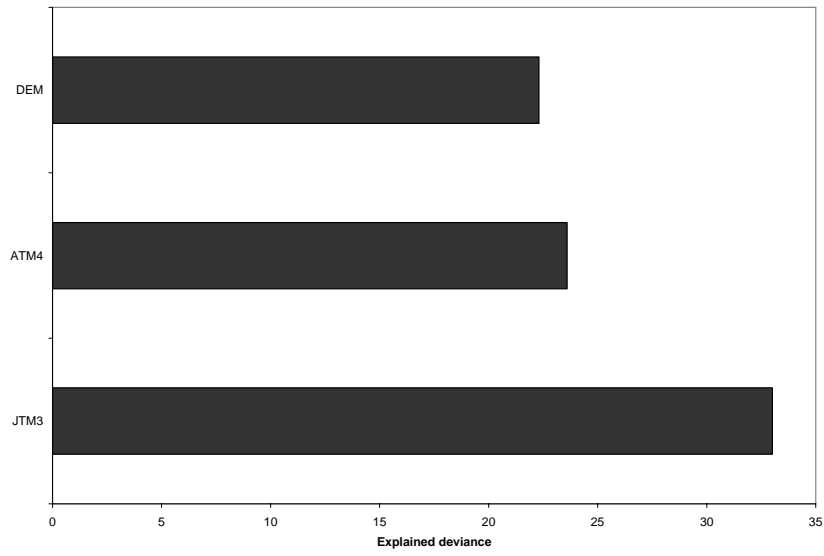


FIG. 2 cont. Explanatory variables selected from the stepwise CVROC procedure as contributing to the binomial response variable *P. ionantha* presence. Each plot shows the relationship of the fitted function to the response and scaled to zero. The plots include 95% pointwise confidence intervals. At the base of each plot is the univariate histogram (rug plot) showing the distribution of each observation. (a) JTM3, (b) ATM4, (c) DEM.

a.



b.

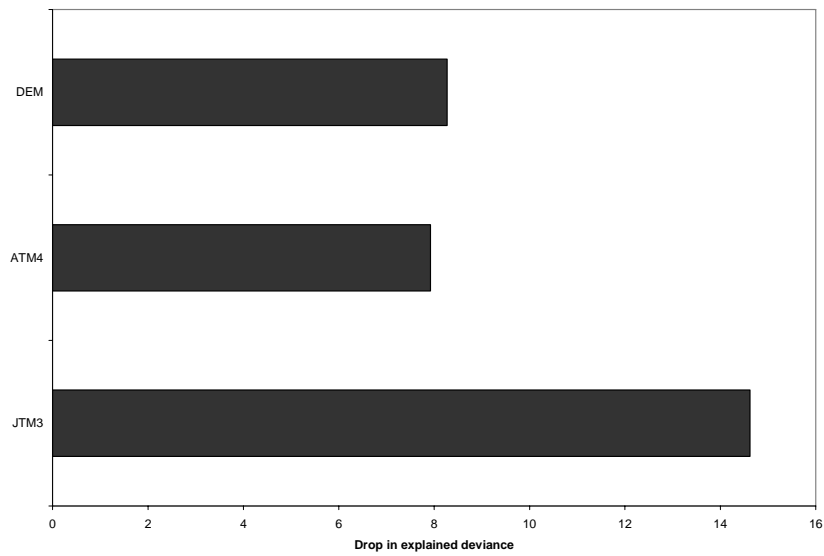


FIG. 3. Contributions of bands in the model selected from the stepwise CVROC procedure. (a) deviance explained when band is the only predictor in the model (b) drop in deviance explained when the band is excluded from the model.

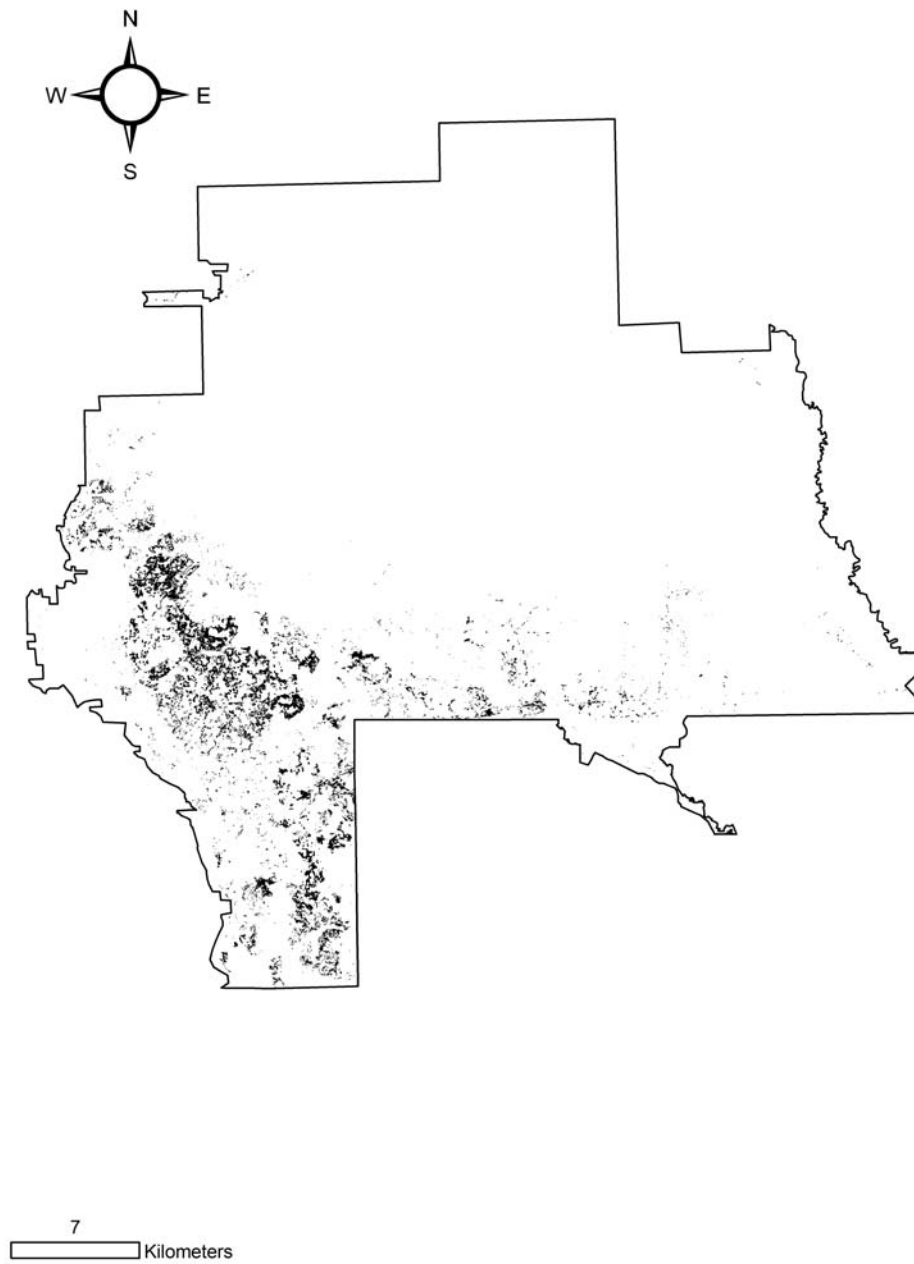


FIG. 4. The predicted distribution of *P. ionantha* within the Apalachicola District of the ANF.

DEMOGRAPHIC RESPONSES OF *PINGUICULA IONANTHA* TO PRESCRIBED FIRE

ABSTRACT

This study investigates the effects of prescribed fire on demographic responses of *Pinguicula ionantha*, a federally listed species endemic to the herb bog/savannah community in north Florida. Previous to this study there was little information on how burn frequency and timing affect species of this unique community. Multi-state recapture models with dead recoveries were used to estimate survival and transition probabilities for over 2313 individuals in 12 populations of *P. ionantha*. These estimates were applied to parameterize matrix models used in a regression based Life Table Response Experiment (LTRE). Nearly 60% of the variation in population growth rate was explained by the number of days since last fire. Population growth rate (λ) was greater than one and increased with days since fire from 100 to 430 days. After this time, λ decreased, becoming less than one after 1200 days after a burn. Positive growth rates were associated with both dormant and growing season burns, but the timing of these effects varied. Frequent fires (1-3 year interval) were predicted to maximize population growth of *P. ionantha* populations. Fecundity and individual growth contributed the most to post-burn population growth. Current prescribed fire intervals used at the study sites are effective at maintaining populations of this rare species.

Understanding the role of fire in creating and maintaining appropriate habitat for this species may aid in the conservation of *P. ionantha* and other rare herb bog/savannah species.

INTRODUCTION

Fire is one of the most universal disturbances. Due to its importance in natural ecological systems, fire is used worldwide as a tool to achieve many types of habitat management goals (Bond and Van Wilgen 1996). An important topic in conservation biology is the maintenance and enhancement of rare species. Understanding how fire affects plant demographics is necessary for effective management of many species of special concern. Fire can have variable effects on different plant life history stages (Schemske et al. 1994; Lesica 1999; Quintana-Ascencio et al. 2003). An individual's response to a fire event is not only dependent on the frequency at which the disturbance occurs (Menges and Quintana-Ascencio 2004) but also on the timing (Brewer and Platt 1994, Hiers et al. 2000) relative to events in the life cycle.

Population models provide a way to determine how fire affects individual vital rates and how these vital rates subsequently contribute to changes in overall population growth (Caswell 2001). Many population models that investigate the response of an organism to fire are constrained by a number of factors. Often, due to limited sampling intensity, the number of populations or individuals is small and/or the sampling period is short (Menges 2000). In many studies the effects of fire are restricted to a single burn event or a small number of burned populations. Finally, the importance of both frequency and timing (days since fire) of burn is seldom compared. Without data on

many populations over a large number of unique burn events the inferences made concerning a species response to fire via altered population growth trajectory may be misleading.

Recent advances in population demography and modeling allow for the examination of the effects of fire on a continuous time scale while linking multiple populations to determine the response at the species level. New methodologies provide the foundation to improve analysis of demographic data. Multi-state recapture models with dead recoveries allow survival and transition probabilities to be modeled while accounting for undetected individuals (White et al. 2002). This is beneficial when all marked individuals cannot be found at every census because they occupy a complex habitat, are inconspicuous, or distributed over a large area that includes multiple populations. The additional information derived from dead recoveries can be used to enhance the precision of these estimates (Barker and Kavalieris 2001). When these corrected demographic rates are combined with an experimental manipulation, such as prescribed burning, the results can be analyzed in a Life Table Response Experiment (LTRE) (Hoffmann 1999; Emery and Gross 2005).

The principal goal of a LTRE analysis is to determine how a treatment alters demographic parameters such as reproduction and survival and how observed changes affect population growth. In regression-based LTREs, population growth rate is modeled as a continuous response to a continuous treatment variable (Caswell 1996). Measurement the actual range of possible treatment values, rather than choosing discrete values, may provide more accurate and realistic insights into underlying ecological processes. Regression-based LTREs have been used to determine the effects of pollutant

concentration on demography of *Daphnia* (Caswell, 1996) and a mysid (*Americamysis bahia*; Raimondo and McKenney 2005). To date this methodology has been used in a controlled laboratory setting but has not been applied to data from natural systems.

In fire-dependent communities environmental characteristics such as vegetation cover and nutrient availability are related to the time since last burn. This relationship may be especially important for species subjected to frequent fires. Although the disturbance event is distinct and readily recorded, changes to a community may be gradual and continuous, resetting with each subsequent disturbance event. The ability to model continuous change with a continuous variable allows for greater understanding of the relationship between the rate of change in a variable of interest with the magnitude of its effects. Regression-based LTRE models offer a way to study the effects of both frequency and season of burn (days since fire) as a single continuous variable, number of days since last burn.

The combination of frequency and season of fire in a single variable, number of days since last burn, allows for the examination of how a species is affected on a time scale that is relevant to important demographic stages and in relation to a species' phenology. In plants, for example, we can learn how a fire event at the seed, seedling or flowering adult stage causes changes in population growth that may be either immediate or delayed in time. This information is vital for making informed management decisions. This knowledge is especially important in threatened and endangered species whose protection is legally mandated.

Pinguicula ionantha

Pinguicula ionantha (Lentibulariaceae) is a federally listed carnivorous plant found only in the lower Apalachicola River Basin (United States Fish and Wildlife Service 1994). The distribution of *Pinguicula ionantha* is restricted to a unique habitat known as herb bogs or savannahs in the Gulf Coastal Plain habitat of Franklin, Gulf, Wakulla, Liberty, and Bay counties, Florida (Wunderlin 2003). Although there is limited information on some aspects of *P. ionantha* biology (Godfrey and Stripling 1961, United States Fish and Wildlife Service 1994), no demographic information is available. Information on recruitment, growth and survival is necessary for conservation efforts to be effective for this rare plant. The longleaf pine (*Pinus palustris*) savannah habitat, where *P. ionantha* occurs, is defined as a fire-dependent community. *Pinguicula ionantha* occurs in herb bog habitats embedded in longleaf pine savannahs.

Prescribed burns are a common management tool in this ecosystem yet no information on the influence of fire on *P. ionantha* is available. The upland longleaf pine ecosystem of the southeastern Coastal Plain is considered to have had naturally-occurring lightning-initiated fires every 1-3 years (Myers and White 1987). This longleaf pine ecosystem includes habitats that cover a range of hydrologic regimes from xeric upland sites to wetland bogs that are inundated for months out of the year (Platt et al. 2006). The effects of fire frequency and timing on the demography of plants occupying upland sites have received more attention than have plants occupying wetland bog systems (but see Brewer 2001). Natural fires are predicted to have occurred primarily during the early lightning season (May – June) before the onset of flooding (Platt et al. 2006).

Information on the fire frequency and season that benefits *P. ionantha* are necessary to make management recommendations in this wetland habitat.

The goals of this study are to 1) determine the population growth or decline of federally threatened *Pinguicula ionantha* throughout its range; 2) to model the effects of fire on the population growth rate of this species and; 3) to determine the relative contributions of individual growth and fecundity to population growth, including the effect of fire on these contributions. This information is the basis for creating management recommendations that maximize population growth for this rare species.

METHODS

Study Sites

This study was conducted in the western portion of the Apalachicola National forest and the Tate's Hell state forest (Fig. 1). Within this area herb bogs exist where gradually sloping land intersects the water table. Areas where seepage occurs over a wide area are referred to as savannas (Myers and Ewel 1990). These habitats are located between an upslope longleaf pine flatwoods and lower wetter cypress and bay swamps. *Pinguicula ionantha* is typically found on the lower edge of the herb bog savannah habitat along the cypress bay swamp / herb bog boundary. This boundary has water close to or above the soil surface for the majority of the year except for the spring and the fall (Kindell 1997). These treeless areas are dominated by graminoides such as *Aristida beyrichiana*, *Rhynchospora chapmanii*, *Rhynchospora plumosa*.

Population Demography

An in vitro seed germination trial was conducted from seeds collected in June of 2005 from four populations that were not included in the main study. The Trial was initiated in June 2005. A total of 2,000 seeds were placed in 20 culture vessels. Seeds were sterilized for 10 minutes in 6% by volume household bleach solution with the addition of two drops of Tween 20[®]. One hundred seeds were placed on 1/5 strength Murashige & Skoog (MS) media containing nutrients and salts (Adams et al. 1979) with the addition of 2 g Gelrite[®] per liter and addition of two ml liter Plant Preservative Mixture (PPM). The PH of media was adjusted to 5.4. Cultures were monitored once a month for seed germination.

In June 2005 15 30.48 X 25.4 cm paired plots were established in areas with exposed bare ground at two *P. ionantha* populations that served as seed source for the germination trials but that were not used in our demography study. In each pair of plots, one plot had 200 local seeds added and the other paired plot served as a control to monitor the background rate of germination. Plots were monitored monthly for the first five months (June through October) and then twice yearly during the scheduled population censuses.

In April 2004 a total of fifteen *Pinguicula ionantha* populations, 12 in the Apalachicola National Forest and three in the Tate's Hell State Forest were selected based on burn history and scheduled upcoming burn dates. *Pinguicula Ionantha* seeds are thought to have short dispersal distance (United States Fish and Wildlife Service 1994) and so populations were considered distinct if the distance between them was greater than 1km. Populations on different management units were on different burn

cycles but all populations were on a four year burn rotation. Each population was surveyed during flowering (March – April) and numbered pin flags were placed next to individuals as they were found. Individuals were not marked if they were within 1m of an existing flag individual. The individual marked by each flag served as the center point for establishment of 0.5m diameter plots. A minimum of 20% of each population was sampled. All individuals within a plot were given a unique identification number by placing an aluminum tree tag anchored in the ground with an aluminum fence-post tie next to the plant. Within each plot plant diameter, total number of flowers and fruits, and recruitment of seedlings was monitored. All individuals within plots were numbered and monitored for the duration of the study. Yearly population censuses were conducted in April from 2004 to 2006. A second census took place in October/November of each year to estimate seedling survival.

Determination of size classes

Plants were divided into three size classes (Fig. 2). Small-diameter plants (S) were classified as those individuals below the flowering threshold of less than 35mm in diameter. The medium-diameter size class (M) consisted of plants with diameters greater than 35mm but less than 85mm. The large-diameter (L) size class was defined as individuals greater than or equal to 85mm in diameter. The medium and large size classes differ in their fecundity. Plants in the large size class produced an average of three times the number of flowers as plants in the medium size class (Fig.3). The average number of seeds per flower was determined by counting seeds from 10 capsules from each of the medium and large size classes.

Mark recapture

Multi-state mark-recapture models with live encounters and dead recoveries were used to estimate annual survival and transition probabilities. This method implements maximum likelihood to accurately estimate survival (S), transition (Ψ), recapture (P), and recovery (r) probabilities. The use of mark-recapture models allows for the inclusion of individuals that were unable to be recaptured at every census. To accurately estimate survival and transition rates among classes the probability that an individual failed to be re-sighted in a given census period must also be estimated.

Multi-state mark-recapture models with live encounters and dead recoveries (Barker et al. 2005) are a combination of the multi-state models (Brownie et al. 1993, Schwartz et al. 1993) and the joint live-recapture/dead-recovery model of Burnham (1993). Multi-state models allow for the estimation of transitions between states. These states can be geographical location such as breeding grounds (Hestbeck et al. 1991, Fletcher et al. 2002, Tallmon et al. 2003) or a physical state such as reproductive and even unobservable states (Sandercock et al. 2000, Kendall and Nichols 2002, Bradshaw et al. 2003, Kéry and Gregg 2004, Kéry et al. 2005). The inclusion of dead recovery information from the joint model increases the precision of parameter estimates (Barker and Kavalieris 2001).

Traditionally, mark-recapture models including dead recovery information have been used for mobile organisms occupying complex habitats that are harvested or hunted. Recoveries often happen between or after recapture census intervals when fishermen and

hunters return tags. Although *P. ionantha* is a non-mobile organism it occupies a complex habitat making it difficult to locate every marked individual at every census. Flooding, dense groundcover growth and substrate movement made it difficult to locate all individuals at each census.

Encounter histories were developed for plants discovered and then subsequently encountered for three censuses. A plant with three capture occasions and three life stages S, M, L conditioned on the period of first discovery can be written as:

$$\text{Pr (S0M0L0| first discovered in year one as small)} = S_1^S \psi_1^{SM} P_2^B S_2^M \psi_2^{ML} P_3^L$$

$$\text{Pr (S000M0| first discovered in year one as small)} = S_1^S \left[\psi_1^{SS} (1 - P_2^S) (S_2^S \psi_2^{MM} P_3^M) + \psi_1^{MM} (1 - P_2^M) (S_2^S \psi_2^{SM} P_3^M) \right]$$

$$\text{Pr (L00100| first discovered as large in year one)} = S_1^L \left[\psi_2^{LM} (1 - P_2^M) r_2^M + \psi_2^{LL} (1 - P_2^L) r_2^L \right]$$

Where S_i^x is the survival probability of an individual in state x from time i to i+1, ψ_i^{xs} is the probability that an individual in state x at time i will transition to state s at time i+1, P_i^x is the detection probability of an individual in the x state at time i, and r_i^x is the probability that a marked individual in state x dies in the interval i to i+1 and its tag is located.

The above encounter histories are comprised of three pairs of observations per plant. Each pair of observations represents a potential live-encounter followed by a recovery event. In the first encounter history, the individual is first discovered as a small individual at time one, encountered as a medium sized individual at time two, and encountered as a large individual at time three. In the second capture history the individual was discovered in time one as a small individual but not encountered in time

two and encountered as M in time three. The probability in the brackets includes the uncertainty of the plant's state in the second encounter occasion. In the last history the individual was first discovered in time one as L, not encountered on time two and then found dead during the second recovery period.

Program Mark (White and Burnham 1999) was used to obtain parameter estimates for the multi-state likelihood function using the simulated annealing algorithm (Lebreton and Pradel 2002, Barker et al. 2005). The assumptions of this model are: 1) individuals within an identical state have an equal probability of survival, transition, and detection, from time i to $i+1$; 2) all individuals make the transition between census periods at the same time; 3) survival from i to $i+1$ does not depend on a individuals state at $i+1$; 4) tags are read correctly and do not affect transition probabilities. In addition, in the current study, if a tag was recovered in time $i+1$ without its associated individual it was assumed that the individual was dead and that death occurred in the interval between i and $i+1$. This assumption is possible because *P. ionantha* was not observed to exhibit a dormant state. Therefore, if a tag was located without its associated individual at time $i+1$ it was certain that the plant was dead and that death occurred sometime within the previous census interval. During the course of this study there were only four instances out of 2638 marked individuals over three capture occasions in which the tag was recovered and the associated plant was mistakenly identified as dead. To test for variation in survival and transition probabilities between groups and years the most general model $S_{gxt} \psi_{gxt}$ was compared to models in which parameters were constrained across time, group or both. The best model was chosen based on the QAIC criteria of Burnham and Anderson (1998).

Because there were only three capture occasions in this study, estimates of overdispersion were calculated from the single state CJS model rather than the multi-state model (Lebreton and Pradel 2002). A parametric bootstrap was applied to the global model in which all parameters were fully group and time-dependent. The mean deviance was calculated from 1000 bootstrap replicates. The deviance of the global model was divided by the mean boot strap deviance to yield estimates of the overdispersion factor c . This estimate was used to calculate quasilielihoods for model comparison (Burnham and Anderson 1998).

Matrix models

Annual Size-based transition matrices were constructed for each population for the 2004-2006 census period based of the life cycle graph in Figure 3. Multi-state mark-recapture models were used to estimate the matrix transition probabilities. Because seeds germinate the year they are produced and germinates have the ability to reach the medium size class within their first year the contribution of M and L size classes to S and M was calculated as the fertility times the proportion of recruits. The yearly population specific fertility (F) of the M and L size classes were calculated as $F = (\text{average number fruits}) \times (\text{average number seeds}) \times (\text{seed germination rate}) \times (\text{recruit survival}) \times (\text{proportion small recruits})$ or $\times (\text{proportion medium recruits})$.

Life Table Response Experiment (LTRE)

To determine which stages of the life cycle are affected by fire and how these effects translate to changes in population growth a Life Table Response Experiment (LTRE) was performed (Hoffmann 1999, Emery and Gross 2005, Jacquemyn et al.

2005). In this evaluation, LTREs were used to determine the effects of days since burn on *P. ionantha* vital rates. LTREs are a retrospective approach that can be used to decompose the effects of a treatment on population growth rate and determine which demographic rates are responsible for the observed changes (Caswell 2001). In the current study we implemented a regression-based approach (Caswell 1996, Raimondo and McKenney 2005). Much like traditional regression techniques, in regression design LTREs the response (population growth rate) is explained by a continuous predictor variable. This approach was the best use of available data. It allowed for the treatment of time since fire as a continuous variable rather than combining all populations burned between 1 and 365 days prior to a census as a single category, 365-730 days as a second category, etc. Therefore the effects of days since last fire could be assessed at a continuous scale.

For each annual population matrix the population growth rate (λ) was calculated as the dominant right eigenvalue for each of two census periods. The days since last fire were determined from each April 1st census. The population growth rate was regressed on days since fire and fitted using Least Squares regression in SAS 9.1.

The sensitivity of λ to each matrix element a_{ij} was calculated. The sensitivity measures the slope of the relationship between λ and each matrix element. It measures the change in population growth rate that would result from a small change in a_{ij} while keeping all other elements of the matrix constant. The sensitivity was calculated as

$$S_{ij} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_i}{\langle vw \rangle} \quad [1]$$

w is the stable age distribution calculated as the right eigenvector of the matrix and v is the reproductive value calculated as the left eigenvector.

A LTRE based on the regression decomposition technique following (Caswell 1996) was used to decompose the treatment effects on λ for each population at each census period. The effect of days since last fire on population growth rate is decomposed into contributions by each of the vital rates using

$$\frac{d\lambda}{dx} = \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}(x)} \frac{\partial a_{ij}(x)}{\partial x} \quad [2]$$

The first term $\partial \lambda / \partial a_{ij}(x)$ is the sensitivity (s_{ij}) of λ to each matrix element a_{ij} as calculated in equation 1. The second term in equation 2, $\partial a_{ij}(x) / \partial x$, measures the rate of change of the element a_{ij} to changes in the treatment effect at level x , and is the vital rate sensitivity. The strength and direction of the functional relationship of a_{ij} to x was estimated using locally weighted regression (Loess; Hastie and Tibshirani 1999).

Loess regression is a semi-parametric technique. At each observation (x_0) in the dataset the nearest neighbors (k) are found constituting a neighborhood. Each of the observations within this neighborhood is assigned a weight based on the distance from x_0 . A linear weighted least squares fit is then calculated within this neighborhood. This process is repeated for each predictor value and neighborhood. The choice of the size k minimizing the mean square error was determined using local cross-validation from a range of 0.2 to 0.8 (Ruppert et al. 2003).

Because elements of the matrix best describing the *P. ionantha* life cycle are a combination of lower level rates, the following parameterization was used to decompose the effects of x on λ :

$$\begin{bmatrix} S_{11} & F_2 * P_1 + R_{21} & F_3 * P_1 \\ G_{21} & F_2 * P_2 + S_{22} & F_3 * P_2 + R_{32} \\ 0 & G_{32} & S_{33} \end{bmatrix}$$

F is fertility, G is growth, S is stasis, R is size-class regression, P_1 is the proportion of small recruits and P_2 is the proportion of medium recruits. The regression decomposition of lower-level parameters (Caswell 1996) to the effect of days since last fire on λ is given as

$$\frac{d\lambda}{dx} = \sum \frac{\partial z_k(x)}{\partial x} \sum_{i,j} \frac{\partial \lambda}{\partial a_{ij}} \frac{\partial a_{ij}}{\partial z_k} \quad [3]$$

Where $\partial z_k(x)/\partial x$ is the functional relationship of the lower-level rate to changes in days since last fire as determined by the Loess regression. $\partial \lambda / \partial a_{ij}$ is the sensitivity of lambda to changes in the a_{ij} element and $\partial a_{ij} / \partial z_k$ is the partial derivative of each matrix element with respect to the underlying rate z_k .

RESULTS

Seed germination trials

Seed germination was low in both control and experimental (seed added) plots. A total of eight germinates occurred in the seeded plots. Five were found in the August census and the remaining germinates were found by the November census. No new germinates were found after November and all germinates but one survived for the remainder of the study.

One germinate was found within the control plot. Seed germination in the in vitro germination trials was higher than that of the field plots. A total of 18 cultures were included in the 2005 in vitro germination trial. Two of the cultures became contaminated with mold and were therefore excluded. There was a total of 47 germinates out of 1,800 seeds (2.6%) observed in the 18 cultures. Germination started in August and continued through January.

A total of 2638 individuals were marked during the 2004-2006 census period of which 2313 were included in the analysis (Table 1). Three of the 15 populations were removed from the analysis (Table 1). The three sites were excluded because 1) one was located near a river and all but two individual died following Hurricane Francis (Sept. 2005), possibly due to salt intrusion during the storm, 2) population demographics appeared to have been negatively impacted as the result of a road widening project on one sight and, 3) heavy flooding and lack of access prevented data collection the second spring flowering census for the final site.

Mark-recapture models

The overdispersion factor \hat{c} was estimated to be 2.3 from the single state CJS model. The fully parameterized model in which survival and transition probabilities varied across both time and group (populations) had the highest support (Table 2). The next best model $S_{gxt}\Psi_t$ has considerably less support, $\Delta QAIC = 5.55$. Given the set of candidate models under consideration the time- and group-dependent model was 18.8 times likeley to be the best model than the model in which transition probabilities were constrained to be equal across group (Burnham and Anderson 2002). Survival and transition estimates from the group- and time-dependent model were used to estimate the parameter values for the matrices used in the LTRE analysis.

LTRE analysis

The regression of population growth rate shows a non-linear relationship to days since last fire (Figure 4). A cubic model explained approximately 57% of the variation in lambda ($R^2=0.57$, $P=.006$). The third order term was included since it was found to be significant to the model ($P=.0025$). There was an initial increase in λ from 51 to 436 days since last fire. This increase was followed by a decrease which showed signs of slowing between 913 and 1355 days since last fire.

The Loess regression indicated that the effects of days since last fire on the vital rates fertility (F), growth (G), stasis (S), and size-class regression (R) varied (Figure 5). The relationship of fertility with time of both the M and L size classes was positive from 51 to 416 days. This initial increase was followed by strong decrease in fertility occurring between 436 and 786 days after a burn. The effects remained negative but

constant after 801 days. The growth response to days since last fire was dependent on size class. Medium individuals showed positive effects from 51 to 416 days followed by negative effects between 436 – 918 days. The relationship remained negative but slowed after 913 days. The positive effects on growth in the small size class occurred between 51 and 645 days lasting longer than the medium size class. Negative effects then followed which showed no signs of slowing as did the M size class.

The relationship between stasis and days since fire was positive for the small and large size classes up to 645 days. After 786 days, this relationship was negative for the small and medium size classes was negative due to the increase in regression. There is a decrease in size class regression of both the M and L size classes from 51-646 days. This decrease continues for the L size class but becomes positive for the medium size class from 786 days on.

The contributions of the changes in vital rates (F, G, S, and R) to population growth rate is shown in Figure 6. The L size class made the largest fertility contributions to population growth between 84 and 416 days. This was followed by a negative contribution between 436-786 days. The largest growth contributions were made by the medium size class and occurred between 85 and 335 days.

Contributions summed over size classes (Figure 7) indicated that fertility and growth made the largest positive contributions to λ between 85-416 days. The largest negative contribution to population growth occurred between 436-786 days. The contributions summed over size classes and vital rates are shown in Figure 8.

DISCUSSION

This study successfully used multi-state mark-recapture with dead recovery models to estimate survival and transition probabilities of a rare plant. This likelihood based method has the advantage of estimating recapture rates and assessing the fit of competing models. This methodology successfully estimated the transition probabilities for a model that was both time and group (population) dependent. This precision is necessary in order to determine the effects of fire on populations burned at different times and forms the basis for the comparison of life table responses after a burn event.

The use of regression LTREs allowed for the estimation of the effect of fire on the demographic parameters and the contribution of these parameters to population growth rate. The use of the continuous variable, days-since-last fire, aided in the detection of demographic responses that occur over a short time period. *Pinguicula ionantha* was found to respond positively to burn events from 51 to 430 days post fire but then respond negatively for 800 to 1247 days post fire. The use of mark recapture methodologies and regression LTREs in this study provided conclusive data that fire plays a critical role in the population demographics of *P. ionantha*. In fact, days since fire explained 57% of the variation in population growth rate for this species.

There is little argument that natural fire disturbance has played an important role in shaping flora diversity in the southeastern United States (Platt 1999). Today, however, with humans controlling the fire regime it is important to determine how fire frequency and timing affects species abundance and phenology in order to aid in management decisions. The diversity of habitats and plant species found within this area make a one-

size-fits-all approach unrealistic. The Apalachicola river basin covers 2,400 square miles in the Florida panhandle. This relatively limited area is made up of a diverse mosaic of 16 recognized habitats based mainly on plant community change due to elevation and hydrology. Estimates for fire return intervals for upland longleaf pine habitats of the southeastern United States range from to 1-3 years (Myers and White 1987) but return intervals for wetland sites are unknown.

In order to determine the effects of fire interval in the herb bog/savannah habitat, this study focused on the population dynamics of a rare endemic plant, *Pinguicula ionantha*. To date, only one other study has investigated population level effects of fire on a plant species occupying a similar habitat (Brewer 2001). Studying the pitcher plant, *Sarracenia alata* in Mississippi, Brewer (2001) found that fire intervals greater 3 years reduced population growth rates. In this study, I found that *P. ionantha* demography is tightly linked with fire disturbance. Regression data shows that without frequent (1-3 yr) burns populations begin to decline. The herb bog/savannah habitats of *Sarracenia* and *Pinguicula* species are frequently flooded and little information was available on the frequency and dynamics of fire in these wetland areas. These data support that bog areas, similar to their upland counterparts, had a frequent fire return interval. The recent historic fire suppression may have played an important role in these species decline prior to the introduction of prescribed fire as a management tool.

Demographic contributions

Overall, our data show that on the four year fire interval generally prescribed by Apalachicola National Forest, *P. ionantha* populations are increasing. This positive

population growth is due to the contributions of fecundity and growth directly influenced by post fire events. Unlike bog-inhabiting species such as *Drosera capillaris* and *Utricularia spp.* (Brewer 2001) no persistent seed bank buffers *P. ionantha* populations between-fire return intervals. No indication of a seed bank was found for the species in vitro or in situ seed experiments in the current study. Due to the lack of seed bank, the increased fecundities shortly following a burn event drive population growth for this species. *Pinguicula ionantha* showed a positive rate of increase up until 430 days following a burn. These positive contributions were followed by a sharp decrease in fertility contributions between 430 and 800 days following a fire event.

Timing of the burn event had an influence on fecundity contributions. Dormant-season burns occurring December-February did not have high fecundity rates the year of the fire. Increased population growth rates associated with increased fertility were not realized until the following year (430 days since burn). This slow response supports our data as to the lack of a *P. ionantha* seed bank. Since there are no viable seeds remaining, recruitment on dormant season burns must wait until that year's seed crop has matured. In contrast, growing season burns (June-July) had a positive contribution to population growth rate the year of a burn. Although these fertility contributions were decreasing by the following year, population growth rate was still estimated to be positive the second year. The highest lambda values found in our study were between 2.09 and 2.4. These values were found for population burned in May of that year or in January/February the year prior. This study did not include any April burns but burns during this time may have a negative impact that year due to the loss of flowers which may result. Many plant species in fire dependent systems show positive seedling response to fire (Whelan 1985,

Carrington and Keeley 1999). An increase in seedling establishment following fire was also found in the bog species, *Drosera capillaris* and *Sarracenia alata* (Brewer 1999a Brewer 1999b). However these studies looked only at winter burns.

Post-fire growth of the medium size class made the second largest fire-mediated contribution to population growth. These contributions occur almost simultaneously with observed fecundity increases. Fires increase the growth rate of fire tolerant plants by reducing competition (Barker and Williamson 1988). This response most likely represents a real increase in growth not a reallocation of resources (Brewer 1999a) because *P. ionantha* does not have an extensive below ground storage as does *S. alata*

Management implications

Federally threatened species like *P. ionantha* have governmentally mandated conservation goals. In order to meet these goals, ANF and Tate's Hell have limited number of feasible and economical management tools; the most important of which is prescribed fire. Luckily, *P. ionantha* responds strongly and positively to prescribed fire.

Within the protected areas of ANF and Tate's Hell State Forest, the four year prescribed fire program currently in place is able to maintain populations without any management changes. This research also indicates that that if specific management goals require more frequent burning, *P. ionantha* populations will persist and possibly increase at a faster rate. In addition, the timing of a burn (season) will not have a negative impact on population growth. Finally, this study only investigated *P. ionantha* response to days since last fire on the four year interval in which these populations were currently

managed. If longer fire return intervals are initiated, it is possible that the decline in population growth will be more severe than seen in this study.

If *P. ionantha* is being managed correctly for population conservation, will this species be removed from the threatened species list? The rarity of *P. ionantha* populations is not due to the effects of management on this species but rather due to the rarity of its herb bog habitat. *Pinguicula ionantha* primarily occupies the wettest edge of the herb bog/savannah habitat. Field observations suggest that this edge may be particularly vulnerable to rapid encroachment by woody shrubs. For the conservation and potential expansion of this habitat, more frequent, growing season burns may be necessary. Growing season burns may play an important role by top killing shrubs and stopping encroachment in upland longleaf pine habitat (Waldrop et al. 1992). However, because these herb habitats are seasonally flooded fire timing may be more crucial.

Many rare plant species, besides *P. ionantha*, are restricted to the herb bog/savannah habitat of the Apalachicola river basin. It is estimated that between 85 and 98% of herb bog/savannah habitats have been lost (Folkerts 1982) due to a variety of factors including draining, conversion into farm ponds, urbanization, road construction (United States Fish and Wildlife Service 2004). Within this rare habitat twenty-five plant species are monitored by the Florida Natural Areas Inventory (Kindell 1997). These habitats are home to many federally and state listed plant species including *Calapogon multiflorus* (Orchidaceae), *Harperocallis flava* (Liliaceae), and *Scutellaria floridana* (Lamiaceae). Today, the ANF and Tate's Hell are the torchbearers for the preservation of these few remaining areas of herb bog/savannah habitat. The conservation and

monitoring of this habitat's response to fire will be imperative to the success of both *P. ionantha* and its associated rare plant species for future generations.

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FNAI site	# individuals	# .5m diam plots	not used in study
1	128	6	XX
5	94	17	XX
6	144	12	
21	188	17	
22	189	13	
29	206	15	
30	141	18	
31	253	27	
34	79	10	
37	151	15	
38	59	8	
39	580	14	
40	149	18	
47	103	13	X
60	174	19	

Table 1. Populations used in study, XX = both census years not used, X = one census year not used.

Model	K	QAIC	Δ QAIC	w
$S_{gxt} \Psi_{gxt}$	214	2678.90	0	0.941
$S_{gxt} \Psi_t$	117	2684.43	5.55	0.058
$S_{gxt} \Psi_g$	167	2707.67	28.77	0
$S_t \Psi_{gxt}$	91	4023.94	1345.03	0
$S_g \Psi_{gxt}$	184	7530.2	4851.34	0

Table 2. Summary of the five models for *P. ionantha*. The analysis of time and group variation in survival and transition rate was assessed by constraining S and Ψ of the most general model $S_{gxt} \Psi_{gxt}$ to be equal across group or time. K= number of estimable parameters, QAIC = Quasi Akaike information criteria, Δ QAIC = difference of models QAIC and the QAIC of the top model, w = Akaike weights.



FIG. 1. Range of *Pinguicula ionantha* and location of populations used in the current study.

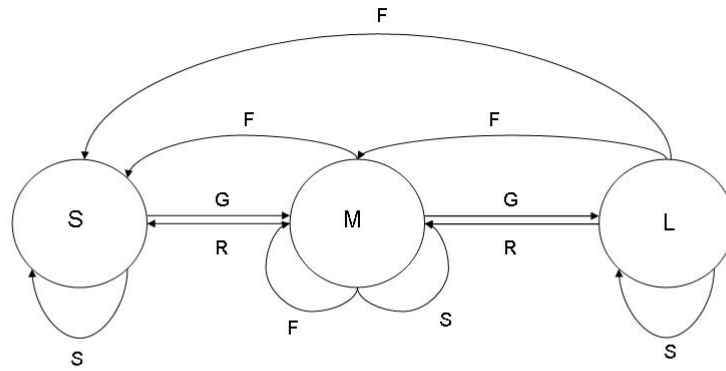


FIG. 2. Life cycle diagram for *Pinguicula ionantha*. The size classes are defined as $35 \geq$ (S), $35 < (M) \leq 85$, and $85 < (L)$ mm in diameter. Arrows indicate transitions between three stage classes. Transitions observed include fertility (F), growth (G), stasis (S), and regression (R).

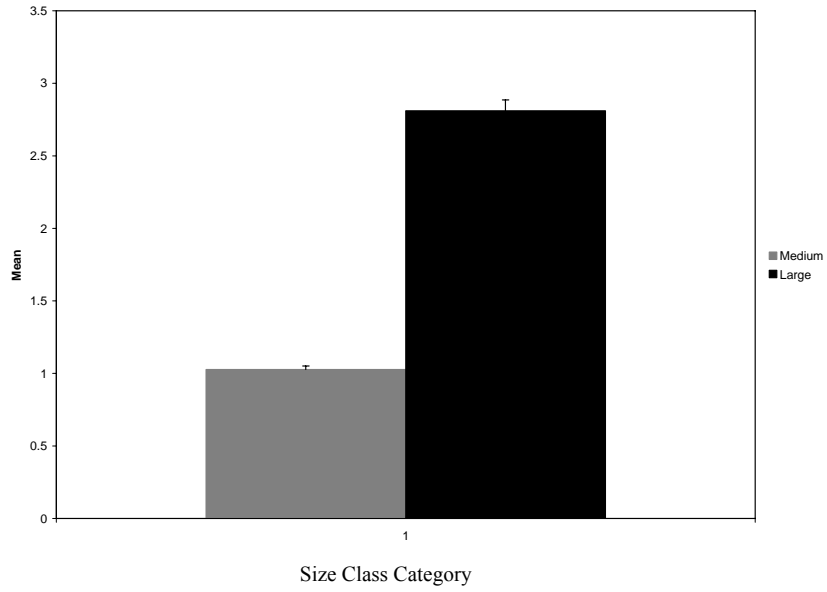


FIG. 3. Mean number of flowers for medium and large size classes shown with standard errors.

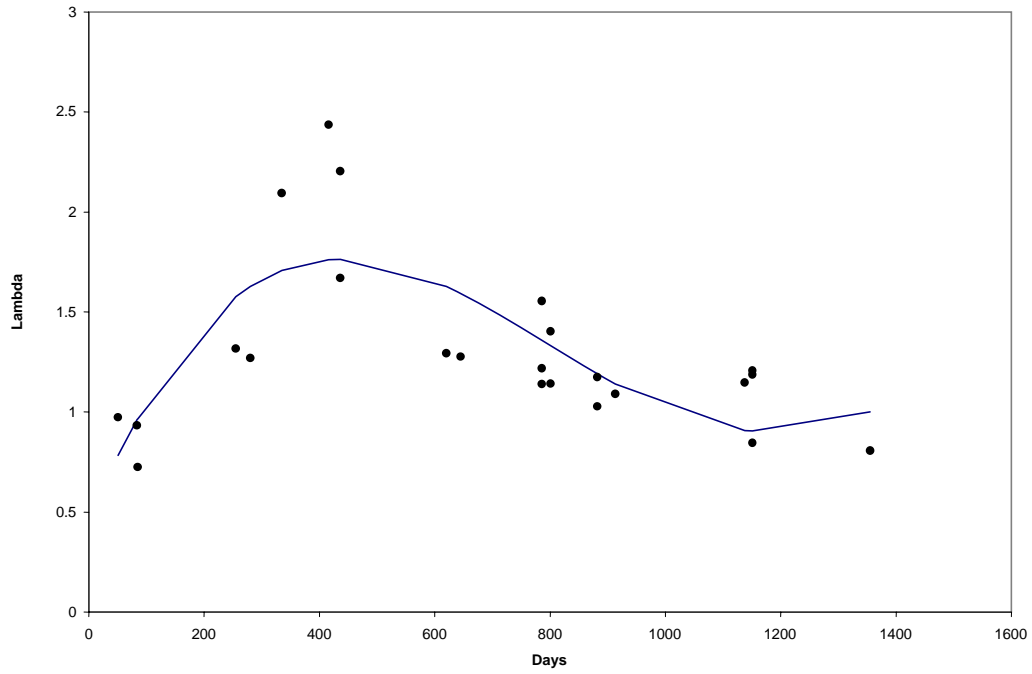
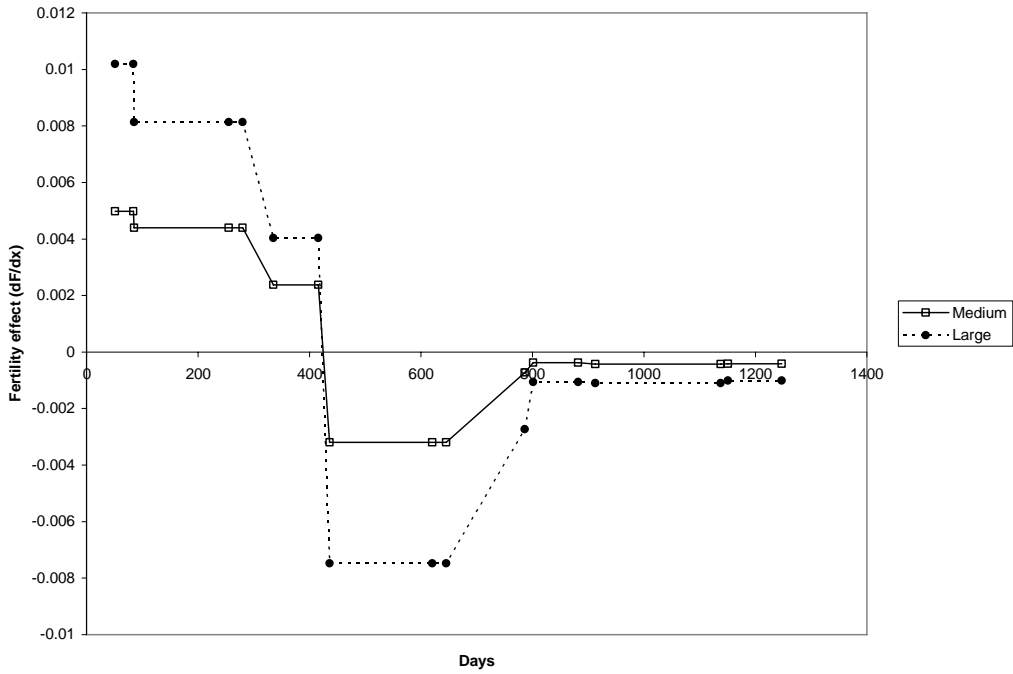


FIG. 4. Population growth rate (λ) as a function of number of days since last fire for *Pinguicula ionantha* ($R^2 = 0.57$, $P = 0.006$).

a.



b.

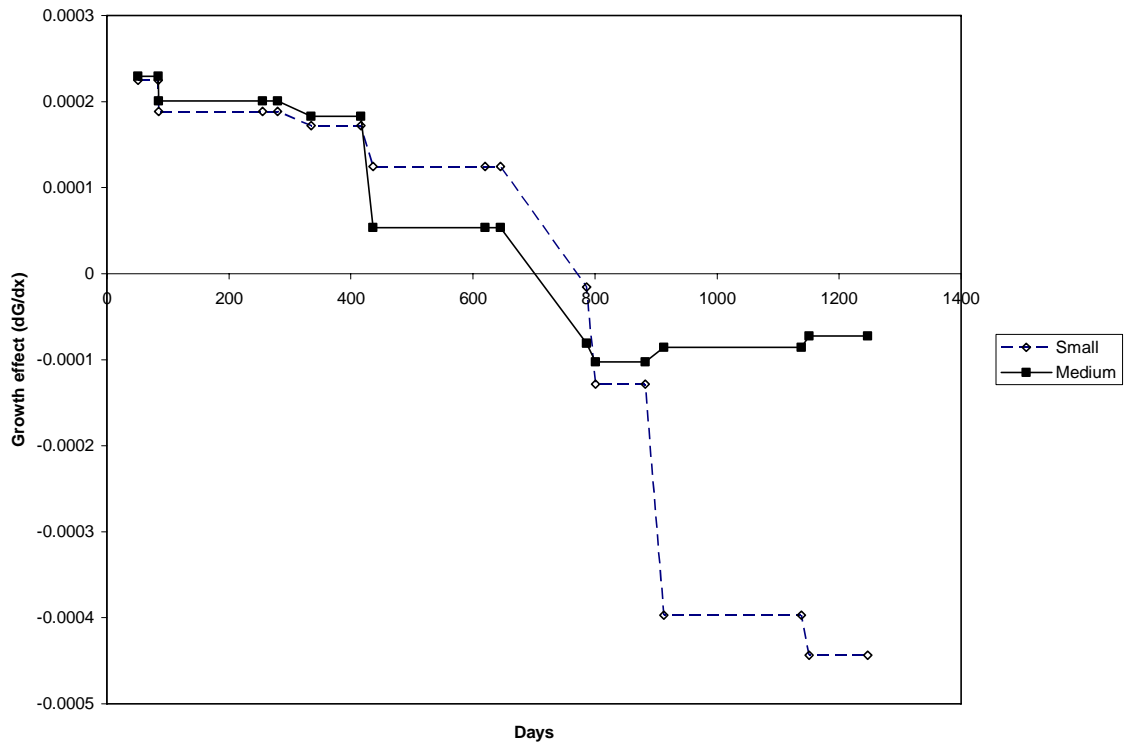
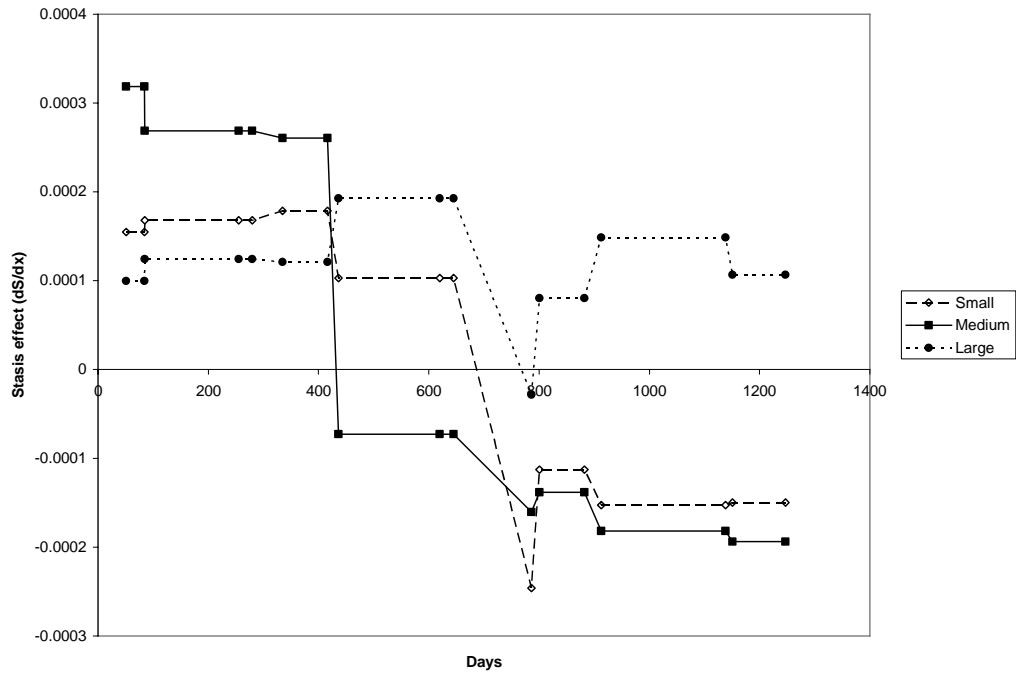


FIG. 5. The effects of number of days since last fire on size specific (a) fertility, (b) growth, (c) stasis, (d) regression estimated from the slope of the Loess regression.

c.



d.

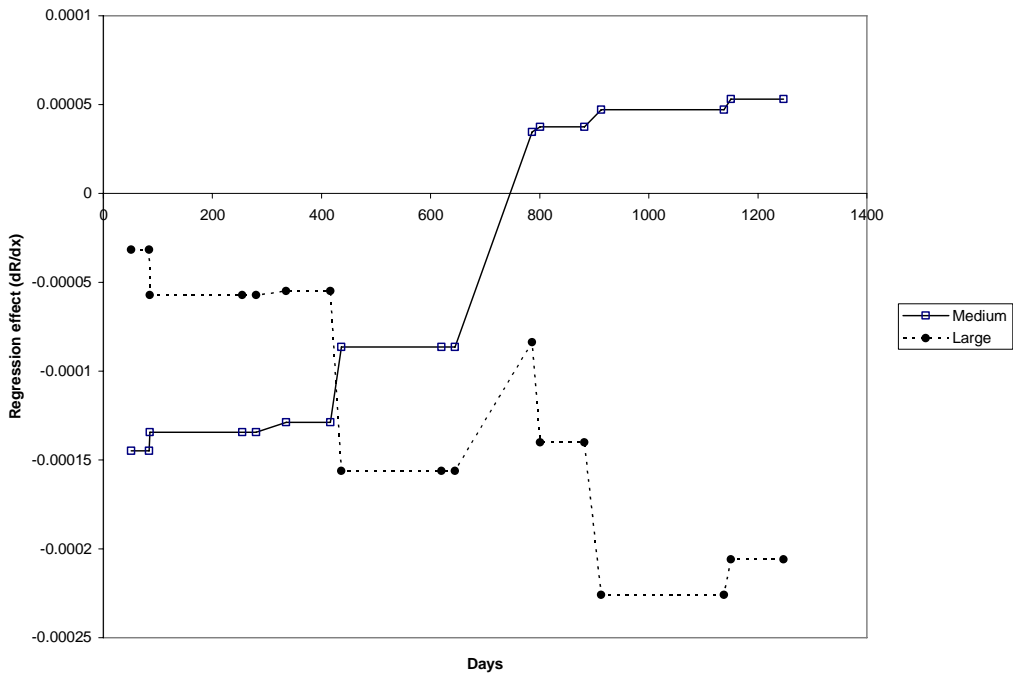
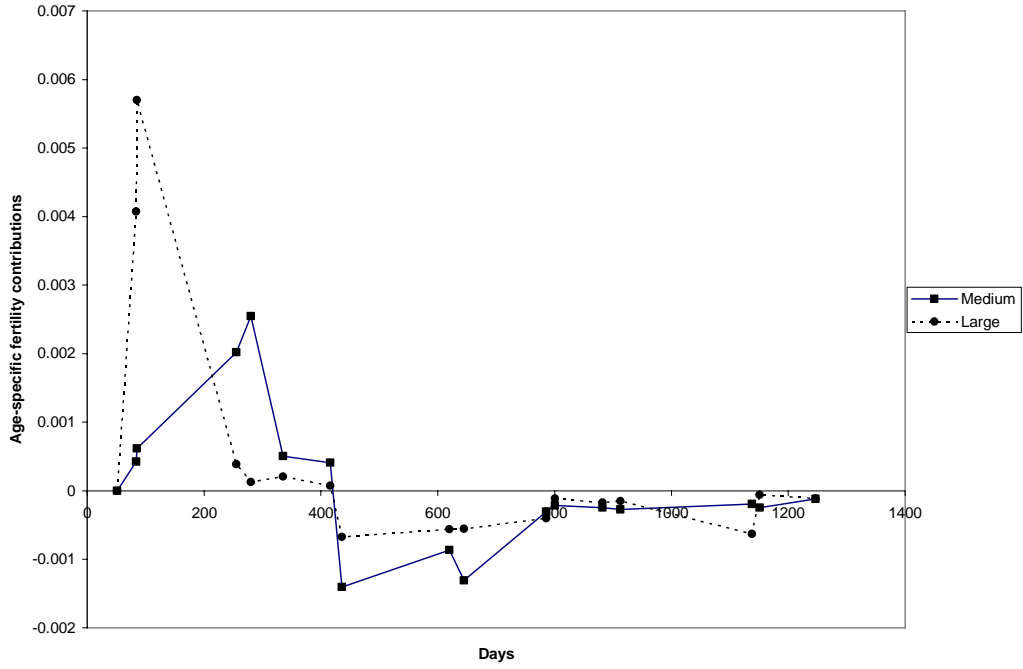


FIG. 5. The effects of number of days since last fire on size specific (a) fertility, (b) growth, (c) stasis, (d) regression estimated from the slope of the Loess regression.

a.



b.

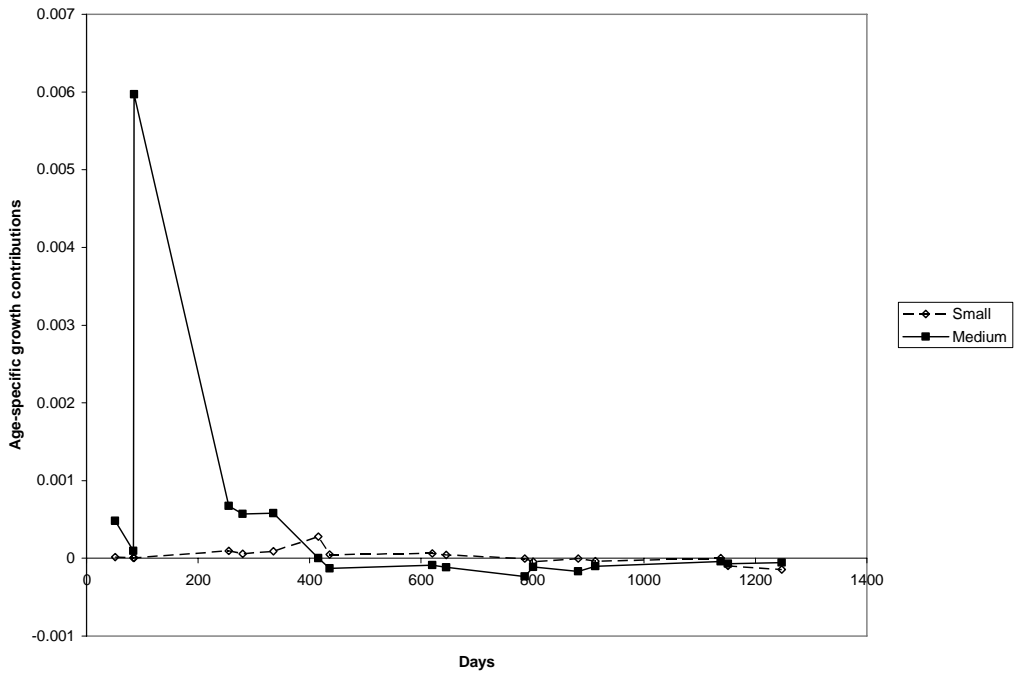
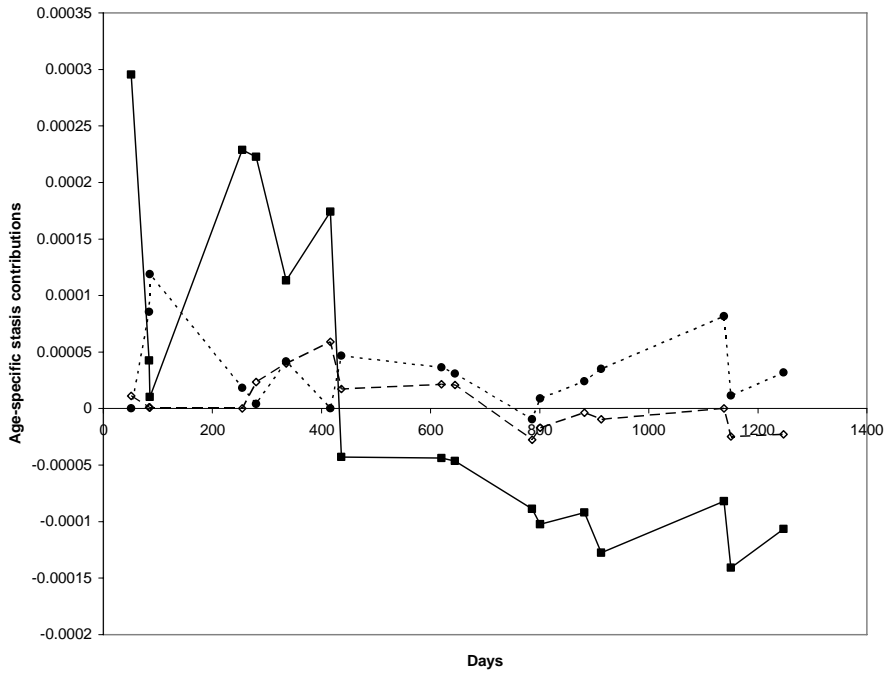


FIG. 6. Contributions of age specific effects on (a) fertility, (b) growth, (c) stasis, (d) regression to lambda from number of days since last fire.

c.



d.

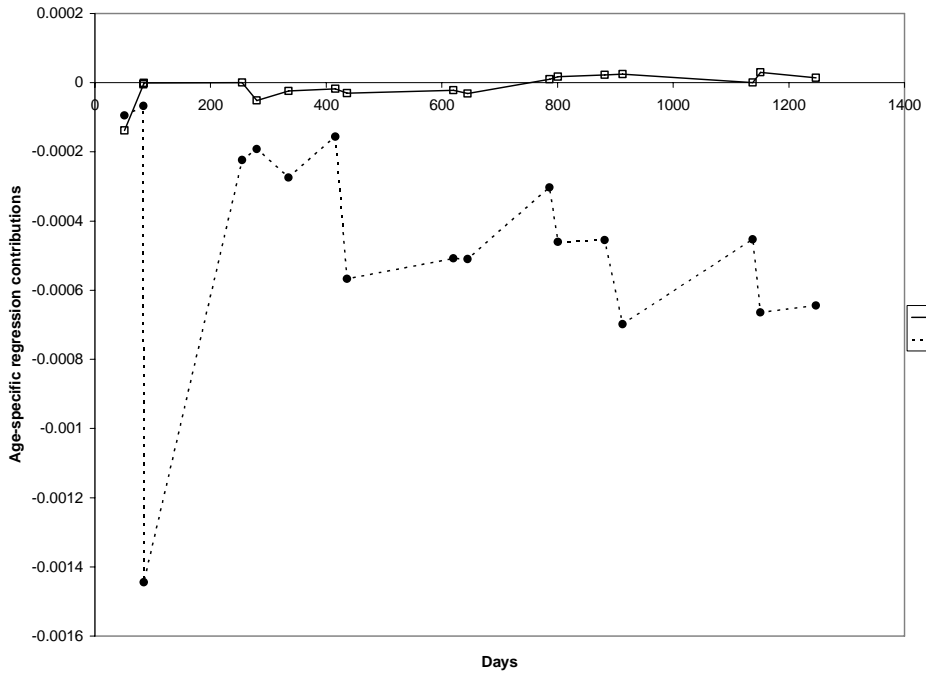


FIG. 6 Cont. Contributions of age specific effects on (a) fertility, (b) growth, (c) stasis, (d) regression to lambda from number of days since last fire.

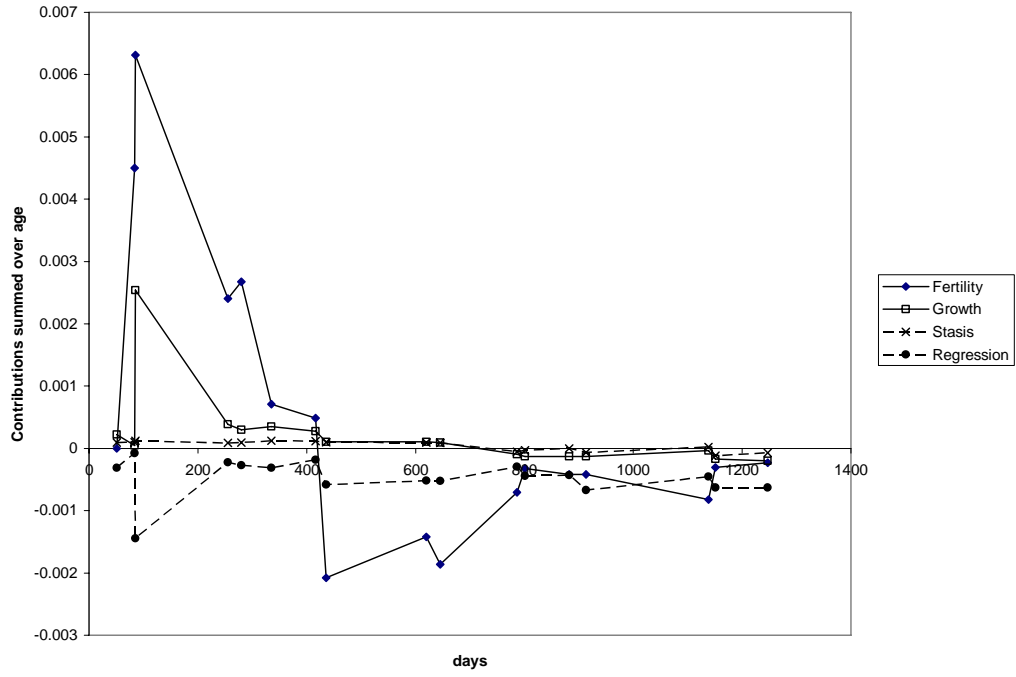


FIG. 7. Contributions of fertility, growth, stasis, regression to the effect of days since last fire to lambda summed over age.

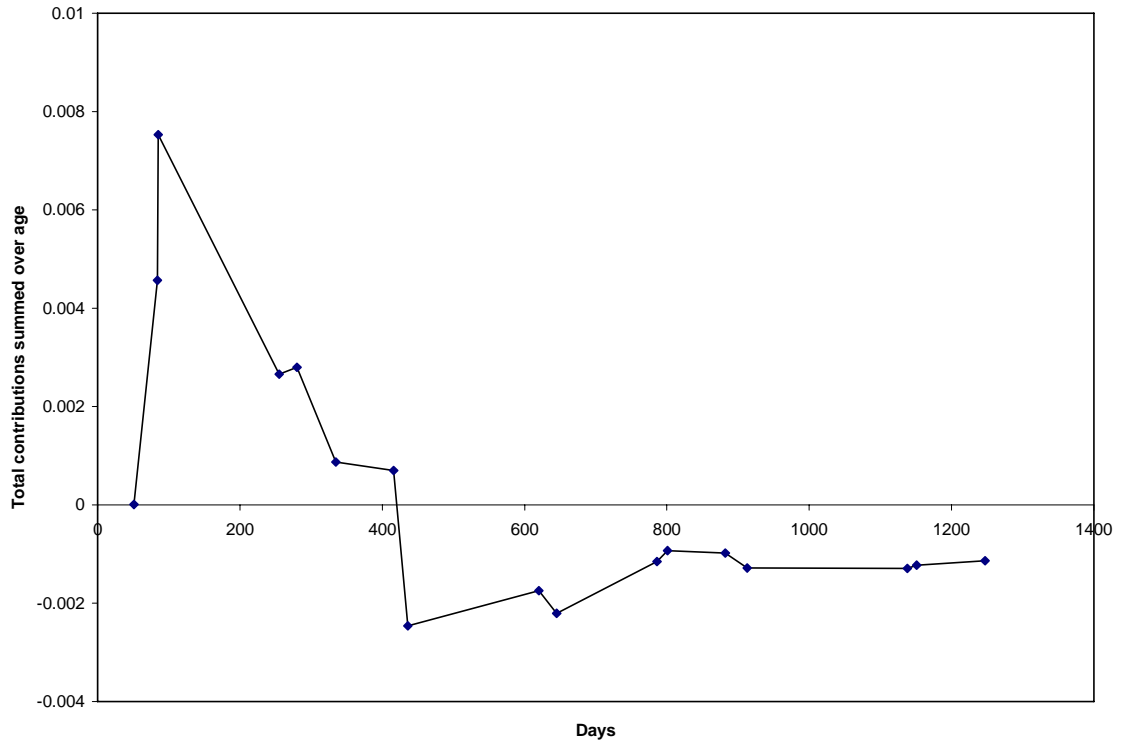


Fig. 8 Age integrated contributions summed over fertility, survival, stasis, and regression to the effect of number of days since last fire to lambda.

Site	Time	S ₁₁	F ₂	P ₁	R ₂₁	F ₃	G ₂₁	P ₂	S ₂₂	R ₃₂	G ₃₂	S ₃₃
6*	1	0.000	0.163	0.000	0.000	0.299	0.000	1.000	0.500	0.083	0.500	0.750
6*	2	0.000	0.000	0.889	0.125	12.600	1.000	0.111	0.500	0.600	0.375	0.300
21	1	0.200	0.088	0.533	0.000	0.551	0.500	0.467	0.702	0.190	0.277	0.690
21	2	0.000	0.224	0.820	0.016	0.764	1.000	0.180	0.871	0.391	0.081	0.565
22	1	0.434	0.637	0.566	0.044	2.286	0.000	0.538	0.803	0.417	0.102	0.333
22	2	0.329	0.466	0.940	0.026	1.638	0.439	0.060	0.714	0.500	0.260	0.300
29	1	0.327	0.469	0.566	0.052	1.441	0.440	0.434	0.874	0.615	0.030	0.154
29	2	0.413	0.280	0.842	0.034	1.595	0.537	0.158	0.786	0.500	0.180	0.250
30	1	0.125	0.304	0.448	0.030	0.957	0.615	0.552	0.837	0.301	0.070	0.599
30	2	0.135	0.084	0.923	0.134	0.386	0.559	0.077	0.630	0.213	0.045	0.287
31	1	0.248	0.345	0.102	0.075	1.025	0.348	0.898	0.407	0.148	0.518	0.824
31	2	0.184	0.294	0.733	0.037	0.969	0.703	0.267	0.805	0.472	0.076	0.449
34	1	0.000	0.045	0.000	0.074	0.197	1.000	0.000	0.852	0.525	0.000	0.225
34	2	0.000	6.264	0.933	0.037	0.000	0.500	0.067	0.812	0.000	0.151	1.000
37	1	0.135	0.085	0.875	0.068	0.291	0.047	0.125	0.523	0.077	0.184	0.716
37	2	0.000	0.147	0.971	0.281	0.700	0.067	0.029	0.428	0.332	0.010	0.518
38	1	0.000	0.768	0.370	0.000	2.125	0.617	0.630	0.778	0.556	0.111	0.222
38	2	0.286	0.265	0.200	0.031	0.255	0.714	0.800	0.750	0.167	0.125	0.667
39	1	0.195	1.565	0.771	0.012	6.360	0.632	0.229	0.571	0.231	0.417	0.695
39	2	0.408	0.975	0.728	0.080	1.461	0.368	0.272	0.791	0.404	0.040	0.533
40	1	0.288	0.077	0.409	0.000	0.753	0.517	0.591	0.811	0.348	0.135	0.435
40	2	0.337	0.018	0.500	0.038	0.033	0.168	0.500	0.627	0.037	0.217	0.889
47	1	0.204	0.433	0.917	0.000	1.041	0.225	0.083	0.632	0.667	0.087	0.333
60	1	0.100	0.147	0.182	0.000	0.663	0.800	0.818	0.810	0.282	0.119	0.667
60	2	0.500	0.129	0.897	0.060	0.386	0.250	0.103	0.771	0.213	0.112	0.735

Appendix 1. Matrix elements of population study sites for two time periods. Time 1 is from April 2004- April 2005; Time 2 is from April 2005-April 2006. Twelve sites are located in the Apalachicola National Forest. One site (indicated by *) is located in Tate's Hell State Forest.