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Jesse Cunningham

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POND-BREEDING AMPHIBIAN SPECIES DISTRIBUTIONS
IN A BEAVER-MODIFIED LANDSCAPE,
ACADIA NATIONAL PARK,
MOUNT DESERT ISLAND,
MAINE

By

Jesse Cunningham

B.A. Middlebury College, 1995

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

December, 2003

Advisory Committee:

Aram J.K. Calhoun, Assistant Professor of Wetland Ecology, Co-Advisor

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Thesis Co-Advisors: Dr. Aram J.K. Calhoun and Dr. William E. Glanz

An Abstract of the Thesis Presented
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In order to maintain pond-breeding amphibian species richness, it is important to understand how both natural and anthropogenic disturbances affect species assemblages and individual species distributions both at the scale of individual ponds and at a larger landscape scale. The goal of this project was to investigate what characteristics of ponds and the surrounding wetland landscape were most effective in predicting pond-breeding species richness and the individual occurrence of wood frog (*Rana sylvatica*), bullfrog (*Rana catesbeiana*) and pickerel frog (*Rana palustris*) breeding sites in a beaver-modified landscape and how this landscape has changed over time. The wetland landscape of Acadia National Park was historically modified by the natural disturbance

cycles of beaver (*Castor canadensis*), and since their reintroduction to the island in 1921, beaver have played a large role in creating and maintaining palustrine wetlands. In 2000 and 2001, I studied pond-breeding amphibian assemblages at 71 palustrine wetlands in Acadia National Park, Mount Desert Island, Maine. I determined breeding presence of 7 amphibian species and quantified 15 variables describing local pond conditions and characteristics of the wetland landscape. I developed *a priori* models to predict sites with high amphibian species and used model selection with Akaike's Information Criterion (AIC) to identify important variables. Single species models were also developed to predict wood frog, bullfrog and pickerel frogs breeding presence. The variables for wetland connectivity by stream corridors and the presence of beaver disturbance were the most effective variables to predict sites with high amphibian richness. Wood frog breeding was best predicted by local scale variables describing temporary, fishless wetlands and the absence of active beaver disturbance. Abandoned beaver sites provided wood frog breeding habitat (70%) in a similar proportion to that found in non-beaver-influenced sites (79%). In contrast, bullfrog breeding presence was limited to active beaver wetlands with fish and permanent water, and 80% of breeding sites were large (≥ 2 ha in size). Pickerel frog breeding site selection was predicted best by the connectivity of sites in the landscape by stream corridors. Models including the presence of beaver disturbance, greater wetland perimeter and greater depth were included in the confidence set of pickerel frog models but showed considerably less support. Analysis of historic aerial photographs showed an 89% increase in the total number of ponded wetlands available in the landscape between the years of 1944 and 1997. Beaver colonization generally converted forested wetlands and riparian areas to open water and

emergent wetlands. Temporal colonization of beaver wetlands favored large sites low in the watersheds and sites that were impounded later were generally smaller, higher in the watershed, and more likely to be abandoned. These results suggest that beaver have not only increased the number of available breeding sites in the landscape for pond-breeding amphibians, but the resulting mosaic of active and abandoned beaver wetlands also provides suitable breeding habitat for species with differing habitat requirements.

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1. PREDICTORS OF POND-BREEDING AMPHIBIAN SPECIES OCCURRENCE AND RICHNESS IN A BEAVER-MODIFIED LANDSCAPE

Introduction

Distributions of pond-breeding amphibian species may shift naturally over time in response to changes both within ponds and in the landscape surrounding breeding ponds (Pechmann et al. 1991, Alford and Richards 1999, Skelly et al. 1999, Skelly 2001). If we are to develop effective conservation strategies, we must understand how amphibian species and populations respond to natural, as well as anthropogenic, perturbations at both pond and landscape scales. Recent research in North America has investigated the relative importance of local and landscape-scale variables in predicting amphibian species richness in agricultural, urban and developing landscapes (Richter and Azous 1995, Hecnar and M'Closkey 1998, Kolozsvary and Swihart 1999, Lehtinen et al. 1999, Findlay et al. 2001, Guerry and Hunter 2002). Similar multiple-scale studies are absent from regions where direct anthropogenic disturbance, in the form of habitat loss and fragmentation, is minimal. North American beaver (*Castor canadensis*) are capable of widespread natural disturbance of wetlands (Muller-Schwarze and Sun 2003), yet their effects on patterns of pond-breeding amphibian distribution and species richness have received little attention.

The effect of beaver on the landscape, and their ability to drastically modify stream and wetland habitat, is well documented (Naiman et al. 1988, Hammerson 1994, Muller-Schwarze and Sun 2003). Beaver activity varies spatially and temporally, thereby

creating a shifting mosaic of wetlands and an increase in wetland heterogeneity at the landscape scale (Naiman et al. 1986, Remillard et al. 1987, Naiman et al. 1988, Snodgrass 1997). Studies assessing the spatial and temporal dynamics of beaver disturbance on plant community composition and structure, and on the distribution and community structure of a variety of animal taxa (including fish, birds, reptiles, mammals, and aquatic invertebrates) have been conducted (McDowell and Naiman 1986, Remillard et al. 1987, Dubuc et al. 1990, Brown et al. 1996, McCall et al. 1996, Snodgrass and Meffe 1998). However, studies examining relationships between beaver activity and amphibian species richness and distribution have been limited, and have not shown strong relationships. Studies in Oregon and South Carolina found no significant difference in amphibian species richness or diversity between beaver-occupied and unoccupied stream reaches, or between new and old beaver ponds (Suzuki 1992, Russell et al. 1999).

Hydroperiod is a major determinant in structuring amphibian communities, with longer hydroperiod wetlands supporting more diverse amphibian populations (Wellborn et al. 1996, Snodgrass et al. 2000). Since beaver manipulate hydrology and increase the occurrence of longer-hydroperiod wetlands, it seems likely that the presence of beaver disturbance would result in sites with high amphibian species richness. Although local-scale variables, such as hydroperiod, may be of primary importance in determining breeding presence of amphibian species, it is unclear how the overall landscape in a beaver-modified wetland mosaic may contribute to species diversity and individual species distribution. Studies that address only amphibian species richness may not take into account the varying life histories of individual pond-breeding species. For example, wood frogs (*Rana sylvatica*) are known to breed primarily in temporary, fishless wetlands

(Hunter et al. 1999). Adults and juveniles are terrestrial, spending most of the year in adjacent uplands, seasonal pools, and forested wetlands where they forage and overwinter. In contrast, bullfrogs (*Rana catesbeiana*) require permanent wetlands to accommodate a 2 to 3 year larval development period (Hunter et al. 1999). Adults are primarily aquatic in nature and require deep ponds to overwinter successfully. In addition to being influenced by local variables at breeding sites, some species may require a wetland landscape that provides additional habitat or resources for foraging or overwintering (Dunning et al. 1992). For example, Northern leopard frogs (*Rana pipiens*) require shallow water bodies with open canopies for breeding (Werner and Glennemeier 1999), grassy meadows or wetlands for summer foraging and permanent lakes or streams for overwintering habitat (see Pope et al. 2000). Pickerel frogs (*Rana palustris*), a closely related species, frequent stream corridors, lake and pond shores and other wet areas during the summer (Gibbs 1998, Hunter et al. 1999), and breeding populations of this species may be influenced by the availability of suitable wetland foraging habitat in the surrounding landscape.

To assess the relative importance of local and landscape-scale variables in determining amphibian species richness and occurrence in a beaver-modified landscape, we studied pond-breeding amphibian assemblages in freshwater wetlands in Acadia National Park (ANP), Mount Desert Island, Maine, USA. The history of beaver in ANP is well documented and the Park has not lost significant amounts of habitat due to direct anthropogenic disturbance. This study investigated the relative importance of local (pond) and landscape-scale wetland characteristics, particularly those affected by or related to beaver disturbance, on pond-breeding amphibian species distributions and

species richness in wetlands. We developed habitat models to predict (1) sites with high amphibian species richness, and (2) the individual occurrence of 3 species (wood frogs, bullfrogs and pickerel frogs) chosen to represent a range of hydroperiod preferences and life history strategies.

Methods

Study Area

We studied 71 wetlands in Acadia National Park, Mount Desert Island, Maine, USA in 2000 and 2001 (Figure 1.1). Mount Desert Island is located along the central coast of Maine (44° 20' N, 68° 15' W) and is connected to the mainland by a short roadway bridge. Acadia National Park covers nearly half of the 281 km² area of the island (Patterson et al. 1983). The study area is at the transition zone between spruce-fir forests to the north and northeastern hardwood forests to the south (Davis 1966). Coniferous forests are dominated by white spruce (*Picea glauca*), red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*). Deciduous forests are characterized by birch (*Betula* spp.), aspen (*Populus* spp.), maple (*Acer* spp.), American beech (*Fagus grandifolia*) and red oak (*Quercus rubra*). Mixed coniferous-deciduous forests are common. The climate is moist (mean annual precipitation of 106 cm) and cool (-8.2°C and 17.8°C mean annual winter and summer temperatures, National Oceanic and Atmospheric Administration, 1990-2001).

The terrain is a rugged, glacially carved landscape consisting of alternating north-south oriented ridges and u-shaped valleys. Watersheds are generally short in length (<5 km from headwaters to ocean). Acadia National Park contains approximately 12,840 hectares (20% by area) of wetland. Palustrine wetlands (vegetated freshwater wetlands

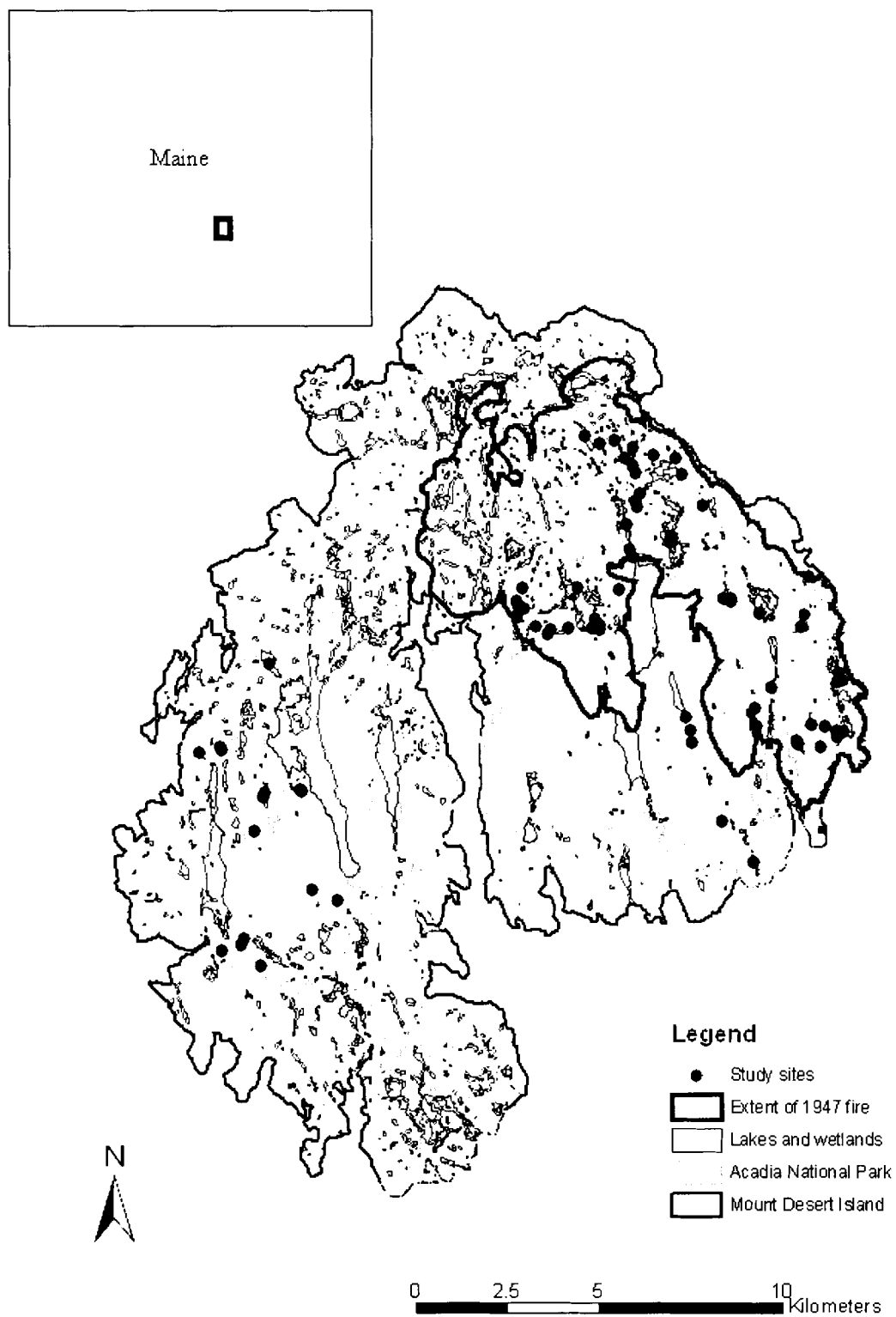


Figure 1.1. Location of amphibian study sites in Acadia National Park, Mount Desert Island, Maine.

<8 ha in size and <2 m maximum depth at low water, Cowardin et al. 1979) comprise 32% of the total wetland area and over 40% of the 9,000 wetland units represented by National Wetlands Inventory (NWI) maps (Calhoun et al. 1994).

Beaver, although historically present on Mount Desert Island, were extirpated due to trapping in the 19th century (Bailey 1925). Reintroductions began with four individuals in 1921 and population numbers likely remained low prior to a large fire in 1947, which burned 6,800 ha on the eastern side of the island (Bailey 1925, Baird 1964, Patterson 1983). The resulting change in forest composition, particularly the dominance of early successional species preferred by beaver, such as aspen (*Populus* spp.) and birch (*Betula* spp.), created favorable conditions for beaver population expansion. Beaver populations reached a peak in the late 1970s (approximately 300 individuals)(Muller-Schwarze 1979) and have since decreased in number. Recent surveys estimate that beaver populations have stabilized at about 100 individuals (B. Connery, Acadia National Park, personal communication). While present throughout the island, beaver-created wetlands (both active and abandoned) continue to be much more prevalent on the eastern side of the island (Muller-Schwarze 1979, JMC personal observation).

Study Species

Eleven pond-breeding amphibian species (8 anuran and 3 salamander species) have been reported historically on Mount Desert Island (Manville 1939, Davis 1958, Coman 1987, Hunter et al. 1999; Table 1.1). While gray treefrogs (*Hyla versicolor*) and northern leopard frogs (*Rana pipiens*) have been noted in the past (Manville 1939, Davis 1958, Coman 1987), there have been no recent confirmed reports of their presence on Mount Desert Island (MDI) (B. Connery, ANP, personal communication). American

Table 1.1. Pond-breeding amphibian species historically reported for Mount Desert Island, Maine (Manville 1939, Davis 1958, Coman 1987, Hunter et al. 1999).

Common Name	Species Name	Status ^a
Spotted salamander	<i>Ambystoma maculatum</i>	C
Eastern newt	<i>Notophthalmus viridescens</i>	C
Spring peeper	<i>Pseudacris crucifer</i>	C
Bullfrog	<i>Rana catesbeiana</i>	C
Green frog	<i>Rana clamitans</i>	C
Pickerel frog	<i>Rana palustris</i>	C
Wood frog	<i>Rana sylvatica</i>	C
American toad	<i>Bufo americanus</i>	L
Four-toed salamander	<i>Hemidactylium scutatum</i>	L
Gray treefrog	<i>Hyla versicolor</i>	U
Northern leopard frog	<i>Rana pipiens</i>	U

^a C=common, L=limited distribution or limited knowledge of distribution, U=unknown (presumed not present, no recent documented reports).

toads (*Bufo americanus*) have a limited range in the southwest corner of MDI, and little is known about the distribution of four-toed salamanders (*Hemidactylium scutatum*) (Hunter et al. 1999). Our survey methods were not designed to include specialized searches for four-toed salamanders, but recent surveys have documented their presence throughout ANP (R. Chalmers, unpublished data). The remaining 7 species- Eastern newts (*Notophthalmus viridescens*), spotted salamanders (*Ambystoma maculatum*), spring peepers (*Pseudacris crucifer*), green frogs (*Rana clamitans*), wood frogs, pickerel frogs, and bullfrogs- are pond-breeding species commonly found in ANP.

Site Selection

Seventy-one palustrine wetlands within Acadia National Park were selected as study sites in 1999. An NWI data layer in a Geographic Information System (GIS) was used to identify all mapped palustrine wetlands and to obtain area measurements for wetland polygons. A stratified random design was used to select sites based on 4 categories of wetland area (<0.5 ha, 0.5-2 ha, 2-4 ha and 4-8 ha). Additional small vernal pool sites not detected on NWI maps (n=10) were located and selected with the assistance of ANP personnel. The non-random selection of these additional sites was justified by an effort to eliminate an inherent size bias that might result by selection based solely on NWI maps, which do not adequately represent small sites (< 0.4 ha, Calhoun et al. 1994), and to increase our sample of temporary hydroperiod sites. Although site selection was not stratified for dominant vegetation class or hydroperiod, our selection procedure yielded a suite of sites representative of the available range of these variables.

Amphibian Surveys

We used a combination of methods to maximize the detection of pond-breeding amphibian species with a wide range of breeding strategies and chronology. Egg mass surveys, call surveys, larval sampling and visual encounters were used to establish amphibian presence at all sites in 2000, and all methods were repeated in 2001.

We conducted egg mass surveys at all sites in April to document the breeding presence of wood frogs (*Rana sylvatica*) and spotted salamanders (*Ambystoma maculatum*)(Crouch and Paton 2000). We waded the perimeter of each site (up to one meter in depth) and identified and counted all visible egg masses. Surveys were only done when visibility was not affected negatively by wind or rain. All egg mass surveys were completed within the approximate 3-week window of wood frog egg development and overlapped with spotted salamander breeding.

We conducted anuran call surveys once per month at all sites in May, June, and July, to correspond with the expected breeding times of all potential anuran species (except wood frogs). Call survey methods followed the standardized protocol of the North American Amphibian Monitoring Program (Weir 2001). A 5-minute listening period at each site was preceded by a 1-minute waiting period. At sites in the largest size category, two 5-minute listening periods were used (1 at each end) to increase detection of species that are less abundant or that may call underwater (e.g., pickerel frogs). We used call surveys primarily to increase the detection of species with unknown or uncertain status (e.g., gray treefrogs and leopard frogs) or limited distribution on the island (e.g., American toads)(Table 1.1).

We used larval surveys to detect the breeding presence of all potential pond-breeding amphibian species. Although larval surveys can be problematic for assessing relative abundance, due to inconsistent efforts among sampling personnel and differences in catchability and microhabitat use among species, they are an effective method for establishing amphibian species breeding presence (Shaffer et al. 1994). Due to differences in the life history strategies of the studied species, larval sampling was the only method we used that could potentially document the breeding presence of all species.

We used dipnet sampling to capture larval amphibians. This method is easily implemented to survey a large number of sites and provides an active approach to sampling various microhabitats and the opportunity to capture both fast-moving and cryptic species (Shaffer et al. 1994, Fellers and Freel 1995, Thoms et al. 1997). The entire perimeter of each wetland (up to 1 m in depth) was sampled once in both June and July 2000 and 2001. This sampling schedule overlapped with the larval stages of all expected pond-breeding amphibians. Rapid sweeps, of approximately 1 m in length along the top of the substrate, with a D-shaped dipnet were taken at a minimum interval of every 5 m. Dipnet sweeps alternated between shallow and deep (< 1 m) habitats. All microhabitats were sampled in proportion to their occurrence to account for the microhabitat specialization of many amphibian larvae (Shaffer et al. 1994). Total sampling time was proportional to the size of the wetland.

In addition to the standardized survey methods described above, opportunistic visual observations were also recorded to document species presence during routine visits to sites. Visual encounters provided additional data to augment the egg, call, and larval

surveys and were especially useful in identifying non-breeding wetland use by adult and sub-adult anurans.

Site Characterization

We characterized surveyed sites by biotic and abiotic variables expected or hypothesized to affect amphibian distributions at the local (pond) or landscape scale (Table 1.2). We classified active beaver sites by the presence of active lodges, recent evidence of dam repair or construction, cut trees, and sightings of beaver. Abandoned sites were characterized by the presence of dams that were not actively maintained and, as a result, generally tended to impound less water.

Minnow trapping efforts in 1999 documented the presence of fish at study sites (Kolozsvary 2003). Additional sightings or captures of fish, during the course of amphibian larval sampling in 2000 and 2001, were used to confirm the data from 1999. We assumed that the presence of fish would exclude predation sensitive species (e.g. wood frogs, Hopey and Petranka 1994). Therefore, we did not distinguish between predatory and non-predatory fish in our analysis.

Water depth gauges were installed at the deepest point at each research site in March 2000. Maximum depth was recorded at spring high water and levels were checked at least once every 2 weeks from April-August. Maximum depth was not measured at sites >2m in depth; a fixed value of 200cm was assigned to these sites. Drying date was noted for sites that dried completely during the field season to determine site hydroperiod. A binary model variable was coded for those sites that dried completely at least once in either 2000 or 2001.

Table 1.2. Definition and scale of model variables recorded for each amphibian survey site ($n=71$)

Variables	Scale	Description
BEAVER	Local	Presence of beaver disturbance
ACTIVE	Local	Presence of current beaver activity
FISH	Local	Presence of fish
DEPTH	Local	Maximum depth (cm) at spring high water
DRY	Local	Presence of complete drying in at least one year (2000 and/or 2001)
WCLASS	Local	# of NWI wetland classes flooded (as determined by field surveys)
AREA	Local	Flooded wetland area (ha), measured from NWI polygons
PER	Local	Perimeter to area ratio ($\text{perimeter} / \sqrt{\text{area}}$)
ELEV	Landscape	Elevation (m), measured from Digital Elevation Model
WSHED	Landscape	Watershed position (low or high), distance of site from watershed outlet divided by distance to top of watershed
NEAR	Landscape	Distance (m) to nearest non-forested wetland on NWI maps
100	Landscape	Proportion (%) of palustrine and lacustrine wetlands within 100m
1000	Landscape	Proportion (%) of palustrine and lacustrine wetlands within 1000m
CONN	Landscape	Presence of stream corridor (inlet or outlet) connecting to other wetlands in watershed
FIRE	Landscape	Present within area of 1947 fire

Wetland vegetation structure was classified during mid-summer according to the Cowardin et al. (1979) classification system. Each wetland was classified at two scales: an overall classification corresponding to the scale at which NWI maps are classified and a finer scale to describe smaller patches within a wetland, which may include important microhabitats for amphibian refuge or egg deposition. Fine scale classification included patches comprising 5% or greater of the wetland by area and occasionally included smaller patches in temporary sites with little vegetation. The total number of inundated NWI classes present at each site provided a coarse index of wetland complexity.

We quantified additional spatial and landscape variables with a Geographic Information System (ArcGIS 8.1, Environmental Systems Research Inc., 2002). GIS data including a Digital Elevation Model (DEM) and watershed, fire and NWI map coverages were acquired from ANP. Sites that were not present on digital NWI maps were mapped with a Trimble Pro XR GPS unit. GPS files were corrected using base station files, cleaned and exported as ARC/INFO files.

Area and perimeter measurements were taken from NWI polygons corresponding to the area of standing water at each site at spring high water. Perimeter was divided by the square root of the area to provide an area-adjusted measure of edge habitat. Elevation was determined from a 1:24,000 DEM. We assessed relative watershed position for each site using the ArcGIS distance tool and the watershed coverage. Based on the distance from the base of the watershed, we classified sites as low ($<1/2$ distance) or high ($>1/2$) in the watershed. Nearest neighbor wetland was measured as the shortest distance between the study site and the nearest non-forested palustrine wetland. Forested wetlands were excluded from the nearest neighbor measurement because the presence of

standing water suitable for amphibian breeding was uncertain at these sites. The proportion of wetland area (all mapped palustrine and lacustrine wetlands) in the surrounding landscape was measured at two scales (100 m and 1000m). Wetland connectivity was coded as a binary variable based on the presence of a stream inlet and/or outlet connecting the site to other wetlands in the watershed. A GIS coverage delineating the extent of the 1947 fire was used to assign a binary value to describe whether a site was located within the burned area.

Data Analysis

The data from all survey methods were combined to determine amphibian species assemblages at all sites. We combined data from 2000 and 2001, assuming that any between-year differences were due to a lack of detection rather than an actual change in assemblage. For each species at each site a value was given to indicate absence (or lack of detection), non-breeding presence (present but no detected breeding), or breeding presence. The presence of eggs or larvae was used to indicate breeding presence at a site. The presence of calling anurans was not considered evidence of breeding; calling species for which no larvae were found at a site were considered non-breeding species. Visual encounters of adult or sub-adult amphibians were also considered evidence of non-breeding wetland use. The analyses presented in this study are based on amphibian species breeding presence, unless otherwise noted.

We developed and tested *a priori* models using model selection with Akaike's Information Criteria (AIC, Burnham and Anderson 2002) to predict 1) sites with high amphibian species richness and 2) bullfrog, wood frog and pickerel frog breeding sites. We used AIC model selection because it allowed us to compare the weight of evidence

for multiple competing hypotheses rather than selecting a single best model.

Additionally, it is more conservative and less prone, than many traditional data analysis methods, to producing spurious results (Anderson et al. 2001).

We limited our analyses to include 15 predictor variables (Table 1.2) that represent local pond conditions and landscape-scale wetland characteristics in a beaver-modified wetland landscape. We tested for significant correlations ($p < 0.01$) among model variables using a Spearman's rank-correlation test (SYSTAT 10.2.01, Systat Software Inc., 2002). Since many local-scale variables (e.g. hydroperiod, depth) were directly manipulated by beaver disturbance, we recognized that significant correlations were likely to exist among predictor variables. However, retaining these variables allowed us to test their relative predictive ability. We tested each model variable individually, to assess how they performed in the absence of other variables, and additional simple models (of 2-5 variables) were created based on hypotheses generated from field observations, natural history knowledge and potential competing hypotheses from the scientific literature.

We used logistic regression (Hosmer and Lemeshow 2000) to develop quantitative models. Appropriate logistic regression models were run in SYSTAT to predict species richness ($n=32$), and wood frog ($n=30$), bullfrog ($n=32$) and pickerel frog ($n=32$) breeding ($n = \text{\#of models considered}$). To quantify species richness models with logistic regression, it was necessary to split the species richness data into two categories (high and low) and convert the counts to a binary response variable. Species richness counts ranged from 1 to 6 species per site (Figure 1.2). The fit of the global model,

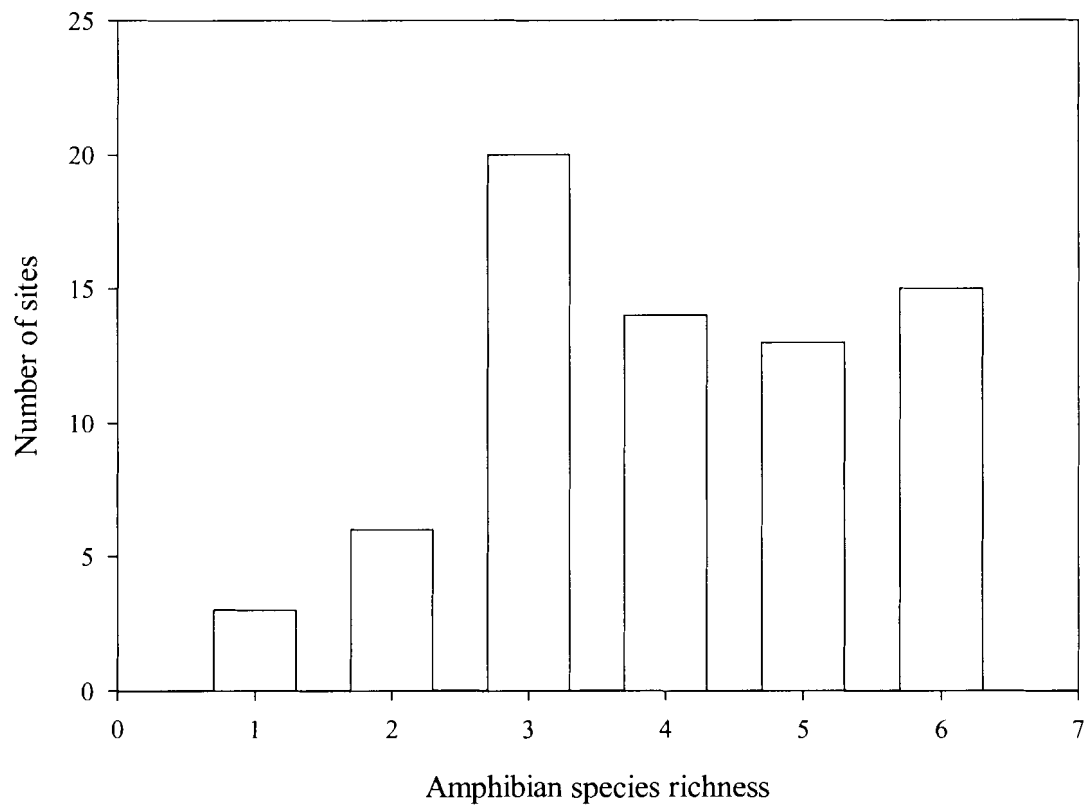


Figure 1.2. Distribution of pond-breeding amphibian species richness values at survey sites in Acadia National Park ($n=71$).

containing all 15 variables (Table 1.2), was tested for the two possible richness cutoffs that produced the most equal sample sizes in the binary dependent variable [0-3=low (n=29) and 4-6=high (n=42), or 0-4=low (n=43) and 5 and 6 =high (n=28), Figure 1.2]. A variance inflation factor (\hat{c}), estimated from the goodness-of-fit chi-square statistic divided by the degrees of freedom, was calculated individually for the global model for each of the two dependent variables (Burnham and Anderson 2002). A variance inflation factor is estimated to account for the overdispersion that is common when modeling count data. An estimated overdispersion factor of $1 \leq \hat{c} \leq 4$ generally indicates adequate model structure to describe the variation in the data. The variance inflation factor was lower ($\hat{c} = 1.81$ vs. 3.39) in the latter case (0-4=low, 5 and 6=high) indicating a better global model fit; therefore, we present the results using these categories. Species models were also quantified with logistic regression, using breeding presence as a binary dependent variable. Variance inflation factors were estimated separately for wood frog ($\hat{c} = 3.31$), bullfrog ($\hat{c} = 3.85$), and pickerel frog ($\hat{c} = 1.88$) global models.

We used a small sample correction of AIC for overdispersed count data (QAIC_C, Burnham and Anderson 2002), including a variance inflation factor, to rank the ability of the competing models to fit the data. AIC model selection is based on a principle of parsimony that penalizes models for each additional parameter. To prevent overfitting of the model, QAIC further penalizes more complex models through the use of the variance inflation factor and an additional parameter for the estimation of the variance inflation factor.

Model selection uncertainty is presented with Akaike weights (w_i), which represent the likelihood of the model given the data and are dependent on the set of tested

models (Burnham and Anderson 2002). Our results are presented as confidence sets of the best-ranked models. Species richness models are presented in a 95% confidence set, and single species models are presented in 90% confidence sets to further limit the number of considered models. Confidence sets are based on the combined likelihood of the Akaike weights and may be interpreted as posterior probabilities that a given model is the best model. Variables that contribute to the selected best models are defined as those whose parameter estimates have a 95% confidence interval that does not include 0. The relative importance of each predictor variable is determined by the sum of the Akaike weights across all of the models where that variable occurs.

Results

Amphibian Surveys

We documented 7 pond-breeding amphibian species at 71 study sites from April through August of 2000 and 2001 (Table 1.3). Spotted salamanders bred in 69 of the 71 surveyed wetlands; spring peepers (n=63) and green frogs (n=52) were also widespread breeders. Wood frogs (n=42) and Eastern newts (n=29) were common but more restricted in their breeding site selection. Pickerel frogs (n=21) and bullfrogs (n=10) bred in the fewest number of sites but were widespread in their use of additional study sites for non-breeding activity (n=37 and 40, respectively), thereby exhibiting a cumulative species presence that more closely resembles that of the most frequent breeders. Although our analyses are based only on the breeding presence of amphibian species, non-breeding wetland use is presented here to show the extent to which some species used additional wetlands for non-breeding purposes (e.g., as travel corridors or foraging sites). We observed single American toads at two sites, but no breeding activity was

Table 1.3. Amphibian breeding and non-breeding presence at wetland study sites
(*n*=71)

Species	Common name	Breeding	Non-breeding	Absent
<i>Ambystoma maculatum</i>	Spotted salamander	69	0	2
<i>Notophthalmus viridescens</i>	Eastern newt	29	11	31
<i>Pseudacris crucifer</i>	Spring peeper	63	2	6
<i>Rana catesbeiana</i>	Bullfrog	10	40	21
<i>Rana clamitans</i>	Green frog	52	15	4
<i>Rana palustris</i>	Pickerel frog	21	37	13
<i>Rana sylvatica</i>	Wood frog	42	6	23

documented; therefore, this species was not included in our analysis. We observed no evidence of Northern leopard frogs or gray treefrogs.

Breeding species richness counts ranged from 1 to 6 species (median=4.0, 25% ile=3, 75% ile=5; Figure 1.2). Wood frogs and bullfrogs never co-occurred, supporting our selection of these species as indicators of contrasting responses to hydroperiod and/or additional variables. Species richness was highest in wetlands with medium (dried 1 of 2 years) to long (did not dry) hydroperiod. For sites that either did not dry or only dried in 2001 (lowest recorded annual precipitation 1895-2001, NOAA), 77% (36/47) had high species richness (>4 species), whereas only 24% (6/25) of sites that dried both years had high species richness. Although species richness appeared to be greater in wetlands with medium to long hydroperiod, no consistent patterns of species turnover along the hydroperiod gradient were observed. Breeding wood frogs and spotted salamanders (species assumed to prefer short hydroperiod wetlands) occurred at wetlands representing the entire hydrologic gradient. For example, spotted salamander breeding occurred in nearly every site (69/71, Table 1.3) and wood frog breeding occurred frequently (with species adapted to longer hydroperiod) in the most species-rich sites [87% (13/15) of sites with 6 species].

The 3 focal species showed varying responses to beaver disturbance (Figure 1.3). Wood frog breeding presence was highest in non-beaver-influenced wetlands (79% of such sites). Although few active beaver sites supported wood frog breeding, the proportion of sites where wood frog breeding occurred was similar in abandoned beaver (70%) and non-beaver influenced wetlands (79%). The combined frequency of wood frog breeding in abandoned and non-beaver wetlands accounted for 93% of observed

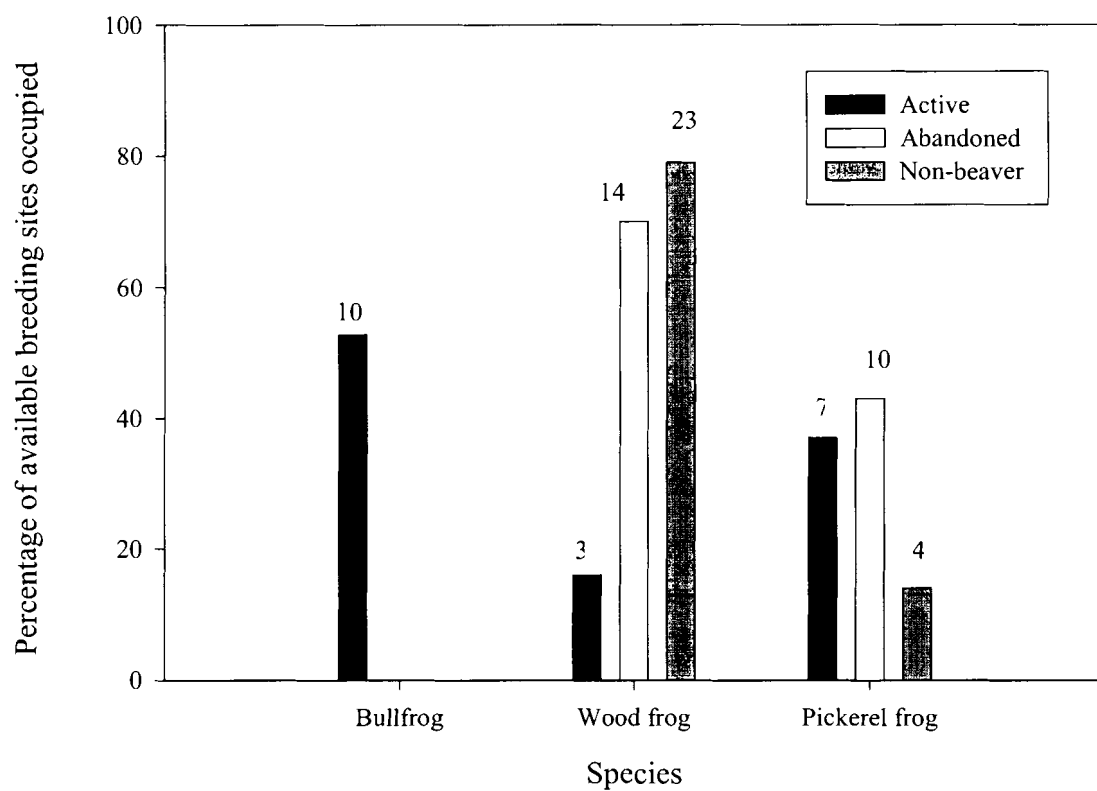


Figure 1.3. Patterns of amphibian species breeding in relation to beaver disturbance. Bars indicate the percentage of sites occupied within a given disturbance category. Number of breeding sites within each category is noted above the bars.

occurrences. Bullfrogs showed the most distinct pattern of occurrence relative to beaver disturbance, with breeding populations occurring only in active beaver wetlands.

However, the active presence of beaver disturbance alone does not fully explain patterns of bullfrog breeding population distribution, since only 53% of active beaver sites were occupied. Pickerel frog breeding distribution was also associated with beaver presence, with 81% of documented breeding in active (37%) or abandoned (43%) beaver sites.

Local and Landscape Characteristics

Local and landscape variable characteristics are described in Tables 1.4 and 1.5. Spearman rank correlations revealed significant relationships ($p < 0.01$), particularly among local scale variables related to beaver disturbance (Table 1.6). The variables for active beaver sites (ACTIVE), fish (FISH), area (AREA), wetland complexity (WETCLASS), maximum depth (MAXDEPTH) and pond permanence (DRY) were all intercorrelated. The single highest significant correlation was between the variables for wetland connectivity and the presence of beaver activity ($r_s = 0.887$, $p < 0.01$). Additional landscape variables showed fewer significant correlations; however, higher watershed position (WSHED) was correlated with an increase in elevation (ELEV, $r_s = 0.515$, $p < 0.01$) and a decrease in area-adjusted perimeter (PER, $r_s = -0.387$, $p < 0.01$). The proportion of wetland area within 100m (100) was negatively correlated with the distance to the nearest non-forested wetland (NEAR, $r_s = -0.509$, $p < 0.01$).

Table 1.4. Descriptive statistics of local- and landscape-scale variables for pond-breeding amphibian survey sites ($n=71$).

Variable ^a	Mean	SE	Median	25 th %ile	75 th %ile	Min	Max
ELEV (mAMSL) ^b	59.89	3.33	57.00	42.00	76.50	5.00	140.00
AREA (ha)	1.09	0.27	0.30	0.08	0.90	0.01	8.42
PER (m / $\sqrt{m^2}$)	4.63	0.11	4.25	3.94	5.10	3.65	7.14
NEAR (m)	125.99	14.01	90.00	42.50	170.00	5.00	740.00
WET100 (%)	17.84	2.70	9.20	0.00	25.58	0.00	87.40
WET1000 (%)	11.46	0.89	9.99	6.68	13.33	0.58	35.96
DEPTH (m)	106.01	6.52	92.00	65.00	150.00	35.00	200.00 ^c
WCLASS (count) ^d	2.27	0.11	2.00	2.00	3.00	1.00	4.00

^a Variable codes defined in Table 1.2.

^b mAMSL= meters above mean sea level.

^c Sites >200cm in depth ($n=13$) were assigned a fixed value of 200cm.

^d Measured as a count.

Table 1.5. Frequency of occurrence of binomial local and landscape-scale variables for pond-breeding amphibian survey sites ($n=71$).

Variable ^a	Present	Absent
BEAVER	42	29
ACTIVE	19	52
FIRE	52	19
FISH	20	51
DRY	46	25
WSHED_low ^b	19	0
WSEHD_high ^b	52	0
CONN	46	25

^a Variable codes defined in Table 1.2.

^b Watershed position (WSHED) was coded 0=low, 1=high

Table 1.6 Spearman rank correlation coefficients among local and landscape-scale variables for amphibian survey sites in Acadia National Park (n=71).

Variable ^a	1 ^b	2	3	4	5	6	7	8	9	10	11	12	13	14
1 BEAVER	1.000													
2 ACTIVE	0.502*	1.000												
3 FIRE	0.210	0.150	1.000											
4 FISH	0.393*	0.753*	0.096	1.000										
5 DRY	-0.313*	-0.753*	0.154	-0.653*	1.000									
6 ELEV	0.067	-0.183	0.161	-0.246	0.201	1.000								
7 WSHED	-0.312*	-0.475*	-0.116	-0.445*	0.336*	0.431*	1.000							
8 AREA	0.614*	0.647*	0.270	0.565*	-0.544*	0.007	-0.330*	1.000						
9 PER	0.190	0.278	0.085	0.122	-0.210	-0.381*	-0.369*	0.314*	1.000					
10 WCLASS	0.369*	0.607*	0.193	0.493*	-0.500*	-0.084	-0.248	0.747*	0.390*	1.000				
11 NEAR	-0.179	-0.281	-0.473*	-0.213	0.191	-0.033	0.189	-0.237	-0.024	-0.178	1.000			
12 WET100	0.291	0.179	0.440*	0.156	-0.051	-0.121	-0.363*	0.260	0.220	0.203	-0.509*	1.000		
13 WET1000	0.013	0.004	0.281	0.079	0.173	0.091	0.033	0.054	0.107	0.187	-0.251	0.147	1.000	
14 CONN	0.887*	0.446*	0.087	0.462*	-0.420*	0.019	-0.238	0.662*	0.210	0.441*	-0.053	0.228	-0.088	1.000
15 DEPTH	0.458*	0.650*	0.103	0.646*	-0.700*	-0.076	-0.350*	0.638*	0.209	0.675*	-0.245	0.185	0.013	0.583*

^a Variable codes defined in Table 1.2.

^b Correlation coefficient and significance *p<0.01.

Model Selection

The best model for predicting high species richness was a single variable model for wetland connectivity ($\beta=2.71, CI= 1.12, 4.29$) (Table 1.7). Additional models that include connectivity (CONN) have variables with 95% confidence intervals that include 0 and therefore do not add any extra information. The strength of a single variable (CONN) is such that the top 5 models may be interpreted as essentially the same model, and the combined likelihood of the models with CONN, given the available data, is high ($w_i=0.81$). Models including the presence of beaver activity (BEAVER) account for the additional models in the confidence set ($w_i=0.14$). Models with a Δ_i value of 0-2 have substantial support and may be considered valid models. Given that the single variable model for BEAVER has $\Delta_i=2.05$ there is good reason to consider it as a potentially useful predictive variable as well, although with this data set, connectivity appears to be a better predictor of high amphibian species richness. Also, it should be noted that the variables for beaver presence (BEAVER) and connectivity (CONN) are highly correlated ($r_s=0.887, p<0.01$; Table 1.6) and may not represent truly independent variables as beaver activity tends to expand along existing stream courses (Naiman et al. 1986, Muller-Schwarze and Sun 2003)

Table 1.7. Confidence set (95%) of models to predict pond-breeding amphibian species richness at wetlands in Acadia National Park, Maine.

Models ^a	β^b	$\log(L)$	K	QAIC _c	Δ_i^c	w_i^d
CONNECT	+	-38.46	4	51.03	0.00	0.23
CONNECT + FIRE	+	-36.76	5	51.47	0.44	0.18
CONNECT + NEAR	+	-37.26	5	52.02	0.99	0.14
CONNECT + 100	+	-37.49	5	52.27	1.24	0.12
CONNECT + ELEV	+	-37.90	5	52.72	1.70	0.10
BEAVER	+	-40.32	4	53.07	2.05	0.08
BEAVER + FIRE	+	-39.39	5	54.37	3.34	0.04
CONNECT +100 + PER	+	-37.24	6	54.39	3.36	0.04
BEAVER + WSHED + ELEV	+	-39.33	6	56.69	5.66	0.01
BEAVER + ACTIVE + WSHED	+	-40.03	6	57.46	6.43	0.01

^a Variables in bold are ones for which 95% confidence intervals do not include 0.

^b Indicates whether the parameter estimates for variables in bold were positive or negative.

^c AIC differences (Δ_i) represent the difference between the selected best model and each subsequent model.

^d Akaike weights (w_i) represent the likelihood of the model given the data.

The top-ranked models for wood frog breeding show a predictable preference for temporary (DRY, $\beta = 2.80$, CI= 1.56, 4.04) and fishless pools (FISH, $\beta = -2.91$, CI=-1.50, -4.33), as single variable models describing local habitat characteristics, followed closely by a model that combines both variables (Table 1.8). Other equally plausible models ($\Delta_i < 2$) include a model that combines temporary sites with a high watershed position (DRY, $\beta = 2.559$, CI=1.27, 3.85; WSHED, $\beta = 1.477$, CI= 0.069, 2.89) and a negative response to active beaver sites (ACTIVE, $\beta = -2.77$, CI=-4.18, -1.37). Isolated sites [CONN (-)] and sites with a lower maximum depth [DEPTH (-)] might also provide some predictive power with additional data sets. The combined Akaike weights for variables in the confidence set models with 95% confidence intervals that do not overlap 0 are: DRY ($w_i = 0.57$), FISH ($w_i = 0.24$), ACTIVE ($w_i = 0.15$), WSHED ($w_i = 0.12$) and DEPTH ($w_i = 0.04$).

Table 1.8. Confidence set (90%) of models to predict wood frog breeding presence at wetlands in Acadia National Park, Maine.

Models ^a	β^b	$\log(L)$	K	QAIC _c	Δ_i^c	w_i^d
DRY	+	-35.25	4	29.92	0.00	0.17
FISH	-	-36.28	4	30.54	0.62	0.12
DRY+FISH	+,-	-32.59	5	30.63	0.71	0.12
DRY+WSHED	+,+	-33.00	5	30.88	0.96	0.10
ACTIVE	-	-37.53	4	31.30	1.38	0.08
DRY+CONN	+	-34.20	5	31.61	1.69	0.07
ACTIVE+DRY	+	-34.32	5	31.68	1.76	0.07
DEPTH	-	-39.90	4	32.73	2.81	0.04
ACTIVE+WSHED	-	-36.30	5	32.87	2.95	0.04
ACTIVE+DRY+FISH	+	-32.57	6	33.01	3.09	0.04
BEAVER+ACTIVE	-	-37.21	5	33.42	3.50	0.03
WSHED	+	-42.19	4	34.12	4.20	0.02
CONN	-	-42.70	4	34.43	4.51	0.02

^a Variables in bold are ones for which 95% confidence intervals do not include 0.

^b Indicates whether the parameter estimates for variables in bold were positive or negative.

^c AIC differences (Δ_i) represent the difference between the selected best model and each subsequent model.

^d Akaike weights (w_i) represent the likelihood of the model given the data.

Quantifying bullfrog models with logistic regression was problematic because bullfrog breeding was only found in one of the two categories for several of the binary variables. These zero occurrences made it difficult to estimate meaningful parameter values and variances with logistic regression. However, patterns of breeding presence can be illustrated without the use of a model selection procedure. Bullfrog breeding in our study was closely tied to active beaver sites (Figure 1.2) and local variables correlated with active beaver activity (Table 1.6). All documented bullfrog breeding sites (n=10) were active beaver sites that did not dry and contained fish. All bullfrog-occupied sites had a maximum depth greater than 150 cm, and 70% had a maximum depth of ≥ 200 cm. Bullfrogs appeared to prefer larger wetlands with 80% (8/10) of breeding ponds ≥ 2 ha in size and a 67% (8/12) occupancy of all sites > 2 ha in size. In contrast, bullfrogs had a 3% (2/59) occupancy of sites < 2 ha in size.

Pickerel frog breeding was best predicted by the landscape variable describing wetland connectivity (Table 1.9). The best model was a single-variable model for wetland connectivity (CONN, $\beta = 2.916$, CI= 0.80, 5.04), and connectivity was the dominant variable in the top 9 models (no other variables had confidence intervals that did not include 0). The combined weight of these models is high ($w_i = 0.83$). Models including beaver disturbance (BEAVER), wetland perimeter (PER) and maximum depth (DEPTH) were included in the confidence set (Table 1.9) but had considerably less support ($\Delta_i = 4-7$).

Table 1.9. Confidence set (90%) of models to predict pickerel frog breeding presence in Acadia National Park, Maine.

Models ^a	β^b	$\log(L)$	K	QAIC _c	Δ_i^c	w_i^d
CONN	+	-35.69	4	46.53	0.00	0.21
CONN+PER	+	-34.61	5	47.70	1.17	0.12
BEAVER+CONN	+	-34.79	5	47.90	1.36	0.11
CONN+ELEV	+	-34.89	5	48.00	1.46	0.10
CONN+1000	+	-34.95	5	48.06	1.53	0.10
CONN+DEPTH	+	-35.51	5	48.66	2.12	0.07
BEAVER+CONN+PER	+	-33.63	6	49.05	2.51	0.06
BEAVER+CONN+1000	+	-34.34	6	49.80	3.27	0.04
BEAVER+CONN+PER+1000	+	-33.16	7	51.01	4.48	0.02
BEAVER	+	-39.98	4	51.09	4.56	0.02
DEPTH	+	-40.31	4	51.44	4.91	0.02
BEAVER+PER	+	-38.56	5	51.89	5.36	0.01
PER	+	-41.02	4	52.19	5.66	0.01

^a Variables in bold are ones for which 95% confidence intervals do not include 0.

^b Indicates whether the parameter estimates for variables in bold were positive or negative.

^c AIC differences (Δ_i) represent the difference between the selected best model and each subsequent model.

^d Akaike weights (w_i) represent the likelihood of the model given the data.

Discussion

Species Richness Models

Our results suggest that beaver disturbance may be important in maintaining a diversity of wetland habitats for pond-breeding amphibians in forested landscapes in the northeastern US. Connectivity by stream corridors was the best predictor of high amphibian species richness; connections through linear stream corridors provide favorable conditions for amphibian movement by maintaining moist microclimates and herbaceous cover (Reh and Seitz 1990, Gibbs 1998). Beaver may play a crucial role in enhancing connectivity by reducing the distance between suitable sites. A 68% decrease in median inter-wetland distance due to beaver disturbance has been documented in a Maine watershed with a beaver recolonization history similar to that of Acadia National Park (Lisle 1994).

Beaver activity is dependent on having stream corridors (connectivity) in which beaver may build dams to create or modify wetlands. Many of the wetlands we surveyed would not exist or would not provide suitable breeding habitat for pond-breeding amphibian species without the influence of beaver. Since beaver reintroduction on Mount Desert Island, the number of open water wetlands, which represent potential breeding sites, has increased by 89% on the eastern side of the island (Chapter 2). Beaver disturbance has directly created suitable habitat at a local (pond) scale for increased amphibian species richness in ANP. Furthermore, the proximity and connectivity of these sites in the landscape is likely to increase the probability that suitable sites will be colonized by amphibians and that populations will be maintained (Fahrig and Merriam 1985).

Our findings contrast with previous studies where significant differences in amphibian species richness in relation to beaver disturbance were not found (Suzuki 1992, Russell et al. 1999). Study design may partially explain differences in our results. For example, rather than comparing impounded and unimpounded stream reaches, we observed beaver-modified and unmodified palustrine wetlands. In doing this, we did not sample streams or consider the potential contribution of stream salamanders in determining amphibian species richness; a conversion of habitat from small, free-flowing streams to lentic ponds would tend to exclude these species. Only one stream salamander species (Northern two-lined salamander, *Eurycea bislineata*) is commonly found in ANP (Hunter et al. 1999). Although beaver impoundments may serve to fragment populations, two-lined salamander populations can be abundant in unimpounded reaches of streams as well as in streams without beaver disturbance (M. Bank, University of Maine, personal communication). Furthermore, our methods were designed to document amphibian breeding presence. Suzuki (1992) and Russell et al. (1999) did not distinguish between breeding and non-breeding amphibian presence. While landscape complementation (Dunning et al. 1992), in the form of non-breeding use of wetlands, appears to be important for some species (Pope et al. 2000), we asked which habitat and wetland landscape characteristics were most suitable for predicting breeding site use by pond-breeding amphibian species. Indeed, had we included non-breeding presence (particularly for bullfrogs, green frogs, and pickerel frogs) in our analyses, species assemblages would have been more similar among sites and differences between beaver and non-beaver sites would have been difficult to detect (see Table 1.3). Additionally, regional variation in landscape configuration and the extent of beaver disturbance, as well

as natural history differences in the potential pool of amphibian species, may also contribute to observed differences between our study and previous studies.

Single-species Models

Our results for 3 species with varying life history strategies indicate that beaver-modified landscapes maintain suitable habitat for all of these species. Active beaver sites provided conditions at a local scale to favor species, such as bullfrogs, that are primarily aquatic and require permanent wetlands to complete their life cycle. While bullfrogs do not directly require the presence of beaver, active beaver sites are indicative of the necessary hydrological conditions for this species. In addition to maintaining a greater depth and permanent hydroperiod at individual sites, beaver have directly increased the size and number of potential breeding sites in the landscape for bullfrogs. An analysis of historical aerial photos showed that several bullfrog breeding sites did not exist as ponded wetlands in 1944, before the 1947 fire and subsequent beaver recolonization (Chapter 2).

Because of their highly aquatic nature, bullfrogs had a breeding distribution that was tightly linked to local pond conditions. However, the large number of sites with non-breeding individuals ($n=40$) (Table 1.3), particularly sub-adults, suggests that bullfrogs may show patterns of landscape supplementation, where they rely on additional wetlands in the landscape to maintain higher populations (Dunning et al. 1992). Although our results show the importance of local variables in determining breeding presence of bullfrogs, the role of other wetlands in the landscape may prove important in maintaining population abundance and should be investigated further.

Temporal changes in abandoned beaver wetlands allowed for wood frog breeding by providing variable hydroperiod conditions and an absence of fish predators. Increased

presence of fish and invertebrate predators in permanent wetlands often excludes amphibian species, such as wood frogs, with larvae that do not possess behavioral or chemical adaptations to avoid predation. Bullfrog tadpoles are unpalatable to fish, and may actually require fish to suppress invertebrate predators in order to successfully exploit wetlands at the permanent end of the hydroperiod gradient (Kruse and Francis 1977, Werner and McPeck 1994). In contrast, wood frogs are highly vulnerable to fish predation and have active larvae that rely on rapid development and early metamorphosis to utilize short-hydroperiod wetlands with few predators (Skelly 1999).

Abandoned beaver wetlands were most often found higher in watersheds (Chapter 2). We believe that a high watershed position, coupled with barriers to dispersal in the form of beaver dams, excludes fish from dispersing to these sites. Additionally, due to their landscape position, and lack of maintained dams, abandoned beaver sites provide a favorable hydroperiod regime for wood frog breeding. Of the 16 abandoned beaver sites where wood frog breeding occurred, only 3 dried in 2000 and 13 (81%) dried in 2001 (a dry year), indicating that many of these sites do not dry every year, but may dry periodically. Even in a dry year (2001, driest year on record, 1895-2001), the earliest of these sites to dry was not until July 31st, creating a consistent hydroperiod length to ensure successful wood frog metamorphosis (Paton and Crouch 2002).

As the permanence of wetlands increases, so too does the suite of potential predators (Wellborn et al. 1996), which may serve as a tradeoff in determining overall reproductive success at abandoned beaver sites. Wood frog egg mass numbers suggest that, despite increased predation by invertebrate predators in long-hydroperiod or permanent fishless beaver sites, wood frogs may be highly successful in these sites.

Anecdotal, the study site with the highest number of wood frog egg masses was a permanent, fishless beaver site. Additional research is needed to determine if the reproductive success (survival to metamorphosis) of wood frogs differs between isolated, temporary wetlands and abandoned beaver flowages.

The wetland landscape may play a larger role in determining breeding site selection for pickerel frogs than for wood frogs or bullfrogs. Wetland connectivity by stream corridors was the best predictor of pickerel frog breeding. The proximity of streams and connectivity to other wetland patches for foraging is likely to provide non-breeding habitat for this species. Pope et al. (2000) used Northern leopard frogs, a closely related species, as a study species that exhibits landscape complementation: they must have different patches in the landscape to fulfill their resource needs for breeding, foraging, and hibernation. Landscape complementation occurs when necessary patches are located in close proximity and, as a result, a given site is able to support larger populations (Dunning et al. 1992). Pickerel frogs are ecologically similar to leopard frogs in their use of multiple habitats and are often found around wetland edges or in intermittent stream corridors in the summer (Gibbs et al. 1998, Hunter et al. 1999). The proximity of streams, and connectivity to other wetland patches for foraging, is likely to provide a form of landscape complementation or supplementation [populations benefit by having supplemental resources in other patches available nearby (Dunning et al. 1992)] for this species.

Pickerel frogs breeding patterns suggested a preference for breeding in beaver-modified wetlands. Beaver create a heterogeneous mosaic of wetlands in the landscape connected by stream corridors (Remillard et al. 1987, Naiman et al. 1988), and this

mosaic is likely to increase the quality and proximity of additional habitat for pickerel frogs. Temporal change in abandoned beaver wetlands results in what are commonly referred to as beaver meadows, emergent wetlands that may have been previously flooded or may be flooded temporarily during the year, thereby killing trees and promoting the growth of graminoids. These beaver meadows provide excellent foraging habitat for pickerel frogs, and remaining pools may either provide suitable breeding habitat or are connected by stream corridors to additional breeding sites in the landscape.

Although pickerel frog breeding populations appear to be responding to the landscape, local pond conditions will be important in determining breeding site selection. Pope et al. (2000) found that wetland perimeter and available spawning habitat for leopard frogs were positively correlated and that the amount of spawning habitat at a site was a significant contributor in explaining leopard frog abundance. Our results suggest that wetland perimeter may also be a useful predictor of pickerel frog breeding (Table 1.9). Pickerel frogs could be selecting sites with greater wetland perimeter for increased potential oviposition habitat or for the larger foraging area that these sites would provide.

Conclusions

In order to conserve pond-breeding amphibian species richness and populations, a diversity of wetlands with regard to hydroperiod, as well as connectivity of sites in the landscape, must be maintained (Semlitsch 2000, Snodgrass et al. 2000). As beaver recolonize areas of their former range, they are increasing the available number of wetlands and decreasing inter-wetland distance, which enhances wetland connectivity in the landscape (Naiman et al. 1986, Remillard et al. 1987, Lisle 1994, Chapter 2). This study highlights the importance of beaver in creating and connecting suitable breeding

sites for amphibians. Additionally, our results indicate that in areas where beaver populations are allowed to occur with minimal management, a spatial and temporal mosaic of active and abandoned beaver wetlands with a variety of hydroperiods results (Chapter 2). The hydroperiod range available in beaver-modified wetlands supports a diversity of pond-breeding amphibian species adapted to a range of hydroperiods, from temporary ponds to permanent wetlands. In addition, a beaver-modified wetland landscape also provides additional non-breeding wetland habitat for species that likely derive benefits from this habitat for hibernation or foraging.

As amphibian populations in human-dominated landscapes are faced with increased habitat fragmentation and degradation, the natural disturbance regime in beaver-modified landscapes and the return of beaver to areas of their former range may increase both the quantity and diversity of habitat for pond-breeding amphibians. Although our data suggest that wetland connectivity and beaver disturbance may be important for maintaining pond-breeding amphibian species richness in northern forested landscapes, we caution against assuming that isolated wetlands are less valuable (see Semlitsch and Bodie 1998). Isolated wetlands provide unique (often temporary and fishless) wetland habitat that supports species that may not exist in other wetlands, or may persist in lower abundances. Further research is necessary to understand more fully not only the spatial and temporal effects of beaver disturbance on amphibian species richness and occurrence, but also the reproductive success and population dynamics of individual species in beaver-modified landscapes and how these patterns may vary regionally.

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2. PATTERNS OF BEAVER COLONIZATION AND WETLAND CHANGE IN ACADIA NATIONAL PARK: IMPLICATIONS FOR POND-BREEDING AMPHIBIAN SPECIES DISTRIBUTIONS

Introduction

Beaver (*Castor canadensis* Kuhl) were historically widespread and abundant throughout North America but were locally extirpated in many areas due to trapping (Ruedemann and Schoonmaker 1938, Jenkins and Busher 1979, Naiman et al. 1988). Beaver are known ecosystem engineers, impounding streams to create and modify wetlands (Jones et. al 1994). Beaver dams retain sediments, modify nutrient flow, and change riparian areas to wetland basins; the results of these changes in the landscape affect geomorphology and can persist for centuries in the absence of beaver (Ruedemann and Schoonmaker 1938, Ives 1942, Naiman et al. 1986). With reduced trapping during the 20th century, beaver returned, or were reintroduced, to many areas within their former range and actively recolonized available habitat (Naiman et al. 1988, Johnston and Naiman 1990a, Lisle 1994). In the presence of beaver, a shifting mosaic of wetlands in the landscape is created, which changes temporally due to colonization and abandonment of individual wetland patches in response to natural disturbances (e.g. fire), food resources, disease, and predation (Remillard et al. 1987, Naiman et al. 1988).

The importance of beaver wetlands and the effect of beaver on both game and non-game wildlife species have been studied for a variety of taxa (McDowell and Naiman 1986, Dubuc et al. 1990, Suzuki 1992, Brown et al. 1996, McCall et al. 1996, Snodgrass and Meffe 1998, Russell et al. 1999). Studies have investigated patterns of

amphibian species richness or occurrence in relation to beaver disturbance (Suzuki 1992, Russell et al. 1999, Chapter 1), but no research has looked at how colonization and abandonment of wetlands by beaver may affect amphibian assemblages and distributions over time. Field research on an order of decades would be necessary to directly study changes in amphibian assemblages in relation to beaver colonization and abandonment. However, examining changes in wetland types and distributions in the landscape over time, coupled with knowledge of amphibian habitat preferences, could provide useful insight into potential past and future amphibian species distributions and population trends. Beaver wetlands are easily identified on aerial photographs and long-term investigations of beaver colonization and landscape changes due to wetland creation and modification by beaver are made possible by interpreting historical aerial photographs (Howard and Larson 1985, Remillard et al. 1987, Johnston and Naiman 1990a, Lisle 1994).

We used aerial photographs to study wetland creation and modification by beaver at Acadia National Park, Mount Desert Island, Maine between 1944 and 1997, a period of beaver population expansion following reintroduction in 1921 and a major fire event in 1947 (Muller-Schwarze 1979). The goal of our research was to investigate how the overall landscape, and individual beaver-influenced wetland sites, changed during this time period, and what implications these changes could have for pond-breeding amphibian species. Our specific objectives were: 1) to quantify the change in the number of ponded wetlands in the landscape and 2) to quantify patterns of beaver colonization and wetland change (hydrology and vegetation structure) in beaver-modified wetlands with current amphibian assemblage data.

Methods

Study Area

Mount Desert Island (MDI) is located along the central coast of Maine, USA (44° 20' N, 68° 15' W), and is connected to the mainland by a causeway. Acadia National Park covers nearly half of the 281 km² area of the island (Patterson et al. 1983). The study area is in the transition zone between spruce-fir forests to the north and east and northeastern hardwood forests to the south and west (Davis 1966). Coniferous forests are dominated by white spruce (*Picea glauca*), red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*). Deciduous forests are characterized by birch (*Betula* spp.), aspen (*Populus* spp.), maple (*Acer* spp.), American beech (*Fagus grandifolia*) and red oak (*Quercus rubra*). Mixed coniferous/ deciduous forests are common. The climate is moist (mean annual precipitation of 106 cm) and cool (-8.2°C mean annual winter temperature and 17.8°C mean annual summer temperature, National Oceanic and Atmospheric Administration, 1990-2001)

The terrain is a rugged, glacially carved landscape consisting of alternating north-south oriented ridges and u-shaped valleys. Watersheds are generally short in length (<5 km from headwaters to ocean) and range in elevation from sea level to 466 m. The study area contains approximately 12,840 hectares (20% by area) of wetland, with freshwater wetlands comprising 42% of the total wetland area and over 40% of the 9,000 wetland units represented by National Wetlands Inventory (NWI) maps (Calhoun et al. 1994). Beaver are a known agent of freshwater wetland creation and modification on MDI (Muller-Schwarze 1979, Calhoun et al. 1994).

Beaver, although historically present, were extirpated from MDI in the 19th century due to trapping (Bailey 1925). Reintroductions began with four individuals in 1921 and population numbers likely remained low prior to an extensive fire that burned 6,800 ha on the eastern side of the island in 1947 (Bailey 1925, Baird 1964, Patterson et al. 1983). The resulting change in forest composition, particularly the dominance of early successional species preferred by beaver, such as aspen (*Populus* spp.) and birch (*Betula* spp.), created favorable conditions for beaver population expansion. Beaver populations reached a peak in the late 1970s (approximately 300 individuals), with over 95% of the population inhabiting the eastern side of the island (Muller-Schwarze 1979), and have since decreased in number. Recent surveys estimate that the beaver population has stabilized at about 100 individuals (B. Connery, Acadia National Park, personal communication). The long-term effect of the 1947 fire on forest composition is still evident as stands of aspen and birch trees are common on the eastern side of the island (Figure 2.1).

Quantifying Landscape Change

We obtained 6 sets of aerial photographs, ranging from 1944 to 1997, from Acadia National Park (Table 2.1). The time series studied spans from a set before the 1947 fire, and the subsequent expansion of beaver populations, to a recent set (1997) that most closely represents present conditions. To estimate the change in the suitability of the landscape for pond-breeding amphibian species, we counted and compared the number of visible open water or flooded wetlands in 1944 and 1997. The area in which wetlands were counted covers the entire large eastern unit of Acadia National Park and adjacent areas, including both burned and unburned areas (Figure 2.1). All wetlands that were

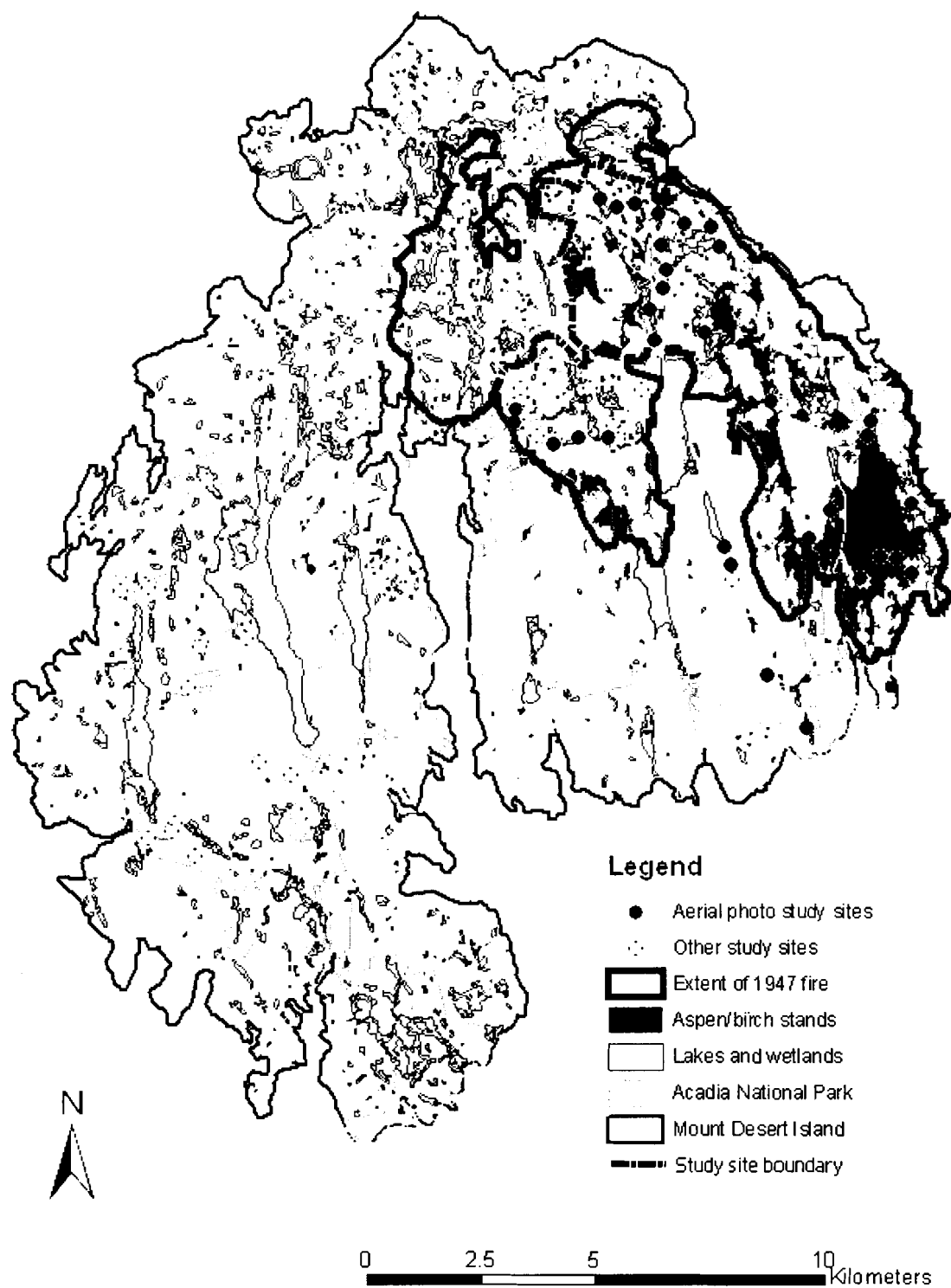


Figure 2.1. Location of aerial photo study sites in Acadia National Park, Maine. The entire area to the south and east of the study site boundary was included in the wetland landscape analysis.

visibly flooded, and would therefore provide potential breeding sites for pond-breeding amphibians, were counted in the 1944 photographs. Counts were repeated for the same area in the 1997 photographs. The difference between these two numbers was used as an index of wetland landscape change over the observed time period.

Table 2.1. Aerial photographs used to determine beaver colonization patterns in Acadia National Park, Mt. Desert Island, Maine.

Year	Scale	Film type	Commissioning Agency
1944	1:15,000	Black and white	National Oceanic Service
1953	1:833	Black and white	U.S. Navy
1970	1:20,000	Black and white	U.S Geological Survey
1979	1:9,000	Color infrared	J.W. Sewall Co.
1985	1:9,000	Black and white	U.S. Fish and Wildlife Service
1997	1:15,840	Color infrared	J.W. Sewall Co.

Beaver Colonization and Wetland Change

The locations of beaver-modified wetland sites with current amphibian species assemblage data (n=33) were identified in aerial photographs for each of six time periods (1944, 1953, 1970, 1979, 1985, 1997; Figure 2.1, Table 2.1). We considered only primary beaver colony sites, defined as those with evidence of past or present lodge construction. Study sites, which represented a range of vegetation types, were compared in the field with current (1997) aerial photographs to match air photo signatures with ground conditions. We stereoscopically interpreted photographs (3X magnification) to determine the proportion of each wetland vegetation class as defined by Cowardin et al. (1979). We used a transparent grid with 2 mm x 2mm squares to estimate wetland class proportions. Wetland classes were identified simply as open water (OW), emergent (EM), scrub/shrub (SS) or forested (FO). The total proportion of impounded area (area with visible standing water) and the presence of beaver dams and lodges were recorded

for each observation. Due to limited access to aerial photographs and differences in photo scale, proportions, rather than actual areas, were used to quantify trends in beaver wetlands. Independent measurements by a second trained observer on a subset of 10 sites resulted in proportion estimates that were generally (>80%) within 2% of those of the initial observer, and in no case did estimates vary by more than 5%, indicating that the method was repeatable.

Current wetland areas were obtained from GIS coverages of NWI maps. We quantified relative watershed position for each site using the ArcGIS distance tool and a GIS watershed layer obtained from ANP. Based on the distance from the base of the watershed, we classified sites as low (<1/3 distance) medium (1/3-2/3) or high (>2/3) in the watershed. We performed all statistical tests with SYSTAT (SYSTAT 10.2.01).

Results

Landscape Change

The number of visibly flooded wetland units in the study area increased from 73 in 1944 to 138 in 1997, resulting in an 89% increase in potential available breeding sites for pond-breeding amphibians. Evidence of beaver activity, in the form of dams and lodges, was evident throughout the study area in the 1997 photographs.

Beaver Colonization and Wetland Change

Of the beaver colony sites studied (n=33), 27% (n=9) existed as ponded wetlands or contained some portion of standing water in 1944. One site showed evidence of an active beaver colony, one site was an abandoned beaver wetland and the remaining 7 sites contained natural or human-created ponds without interpretable evidence of past or present beaver colonization.

Widespread colonization of new sites after the 1947 fire was not immediate; only 3 study sites, all within 1 km of existing beaver colonies, were newly colonized by 1953 (Figure 2.2). Temporal colonization of new sites paralleled the increase in the beaver population to its peak in 1979 (Figure 2.3). Additional colonization after 1979 was minimal, suggesting that much of the available habitat in the landscape had been exploited (Figures 2.2 and 2.3).

Beaver colonized existing ponded wetlands and wetlands low in the watershed earlier in the study period. By 1970, 6 of the previously ponded sites were colonized and the additional 3 previously ponded sites were colonized by 1979. Sites lower in the watershed were generally colonized first (Figure 2.4). All sites in the lowest watershed category were colonized by 1970. In 1970 beaver activity was greatest in the mid-watershed sites and present at sites higher in the watershed. Sites colonized after 1970 were primarily located high in the watershed with limited new colonization of mid-watershed sites.

The mean area of sites in the lowest watershed category was significantly larger than for sites found higher in the watershed (Figure 2.5, Kruskal-Wallis test statistic = 8.33, 2 df, $p=0.016$). The mean area of impounded wetlands showed a decreasing trend with both time and higher watershed position (Figure 2.6). The mean area (\pm SE) of sites colonized at each time period was: 1953, 2.020 ± 1.283 ; 1970, 2.155 ± 0.587 ; 1979, 1.429 ± 0.299 ; 1985, 0.371 ± 0.243 . The large variability in the area of sites colonized by 1953 was influenced by a small sample size ($n=3$) and one small site. Mean area of newly-colonized wetlands is not provided for 1944 and 1997; these years had only single observations.

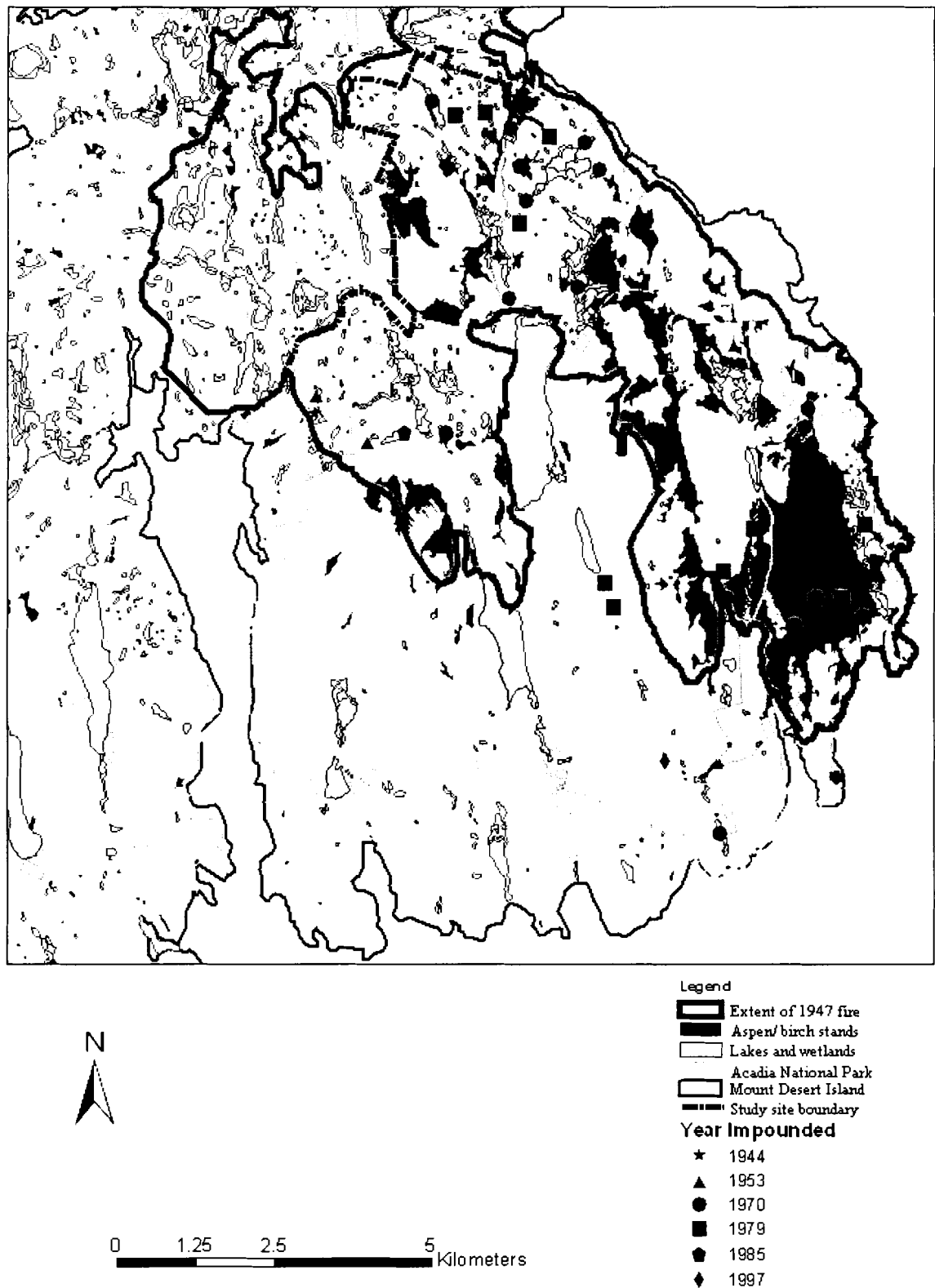


Figure 2.2. Spatial and temporal distribution of beaver impoundment at aerial photo study sites, Acadia National Park, Mount Desert Island, Maine.

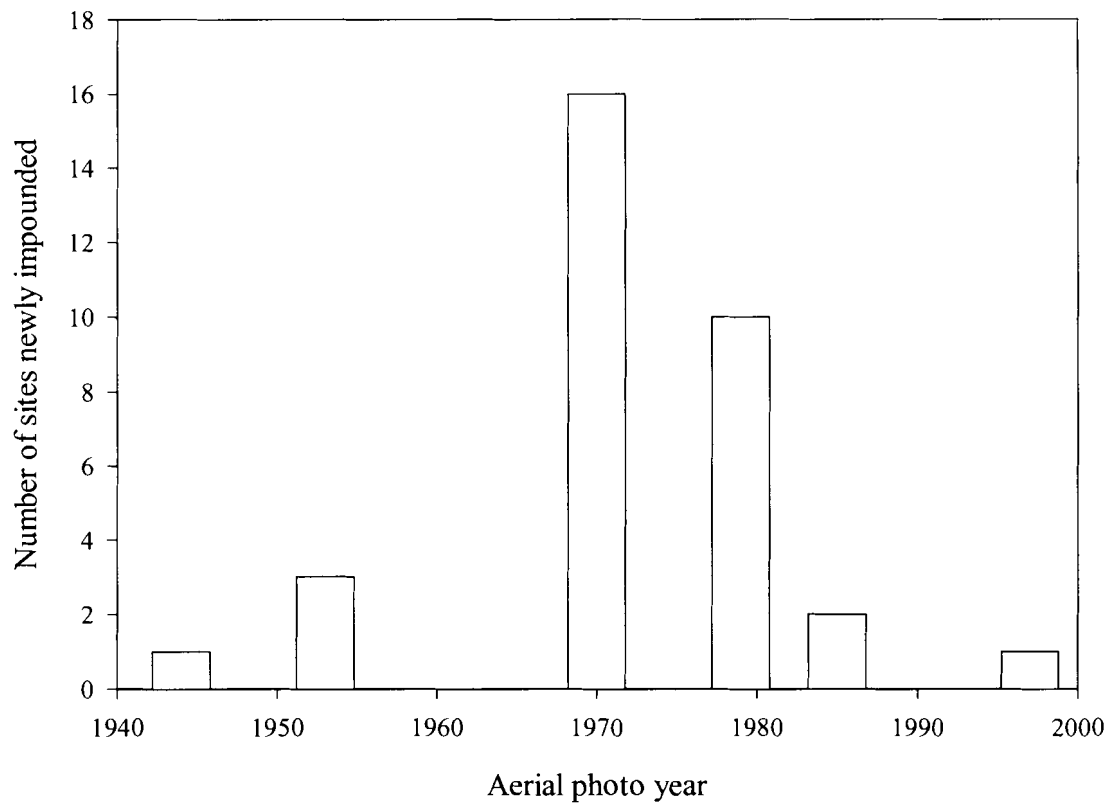


Figure 2.3. Number of newly impounded study sites observed at each aerial photo interval. Aerial photo years are 1944, 1953, 1970, 1979, 1985, and 1997.

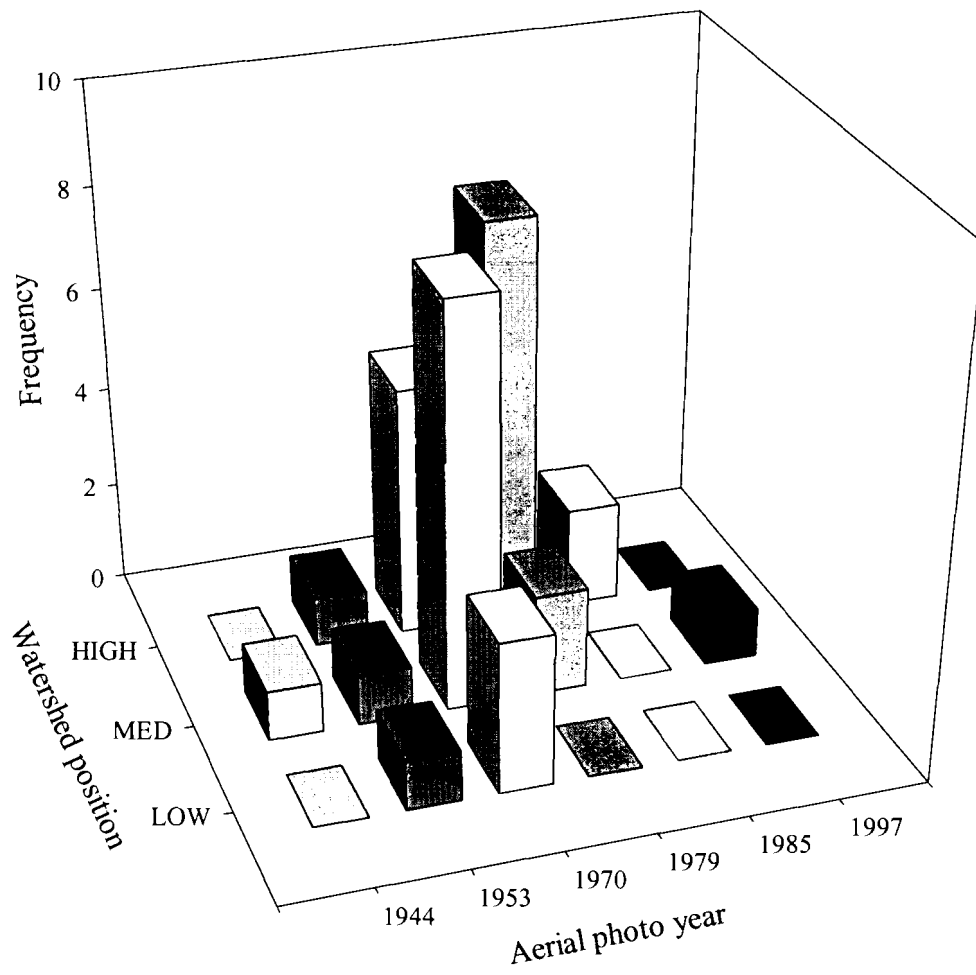


Figure 2.4. Number of sites newly colonized in each watershed position at each aerial photograph interval. Beaver colonization shows a trend from early colonization of sites low in the watershed to later colonization of sites high in the watershed.

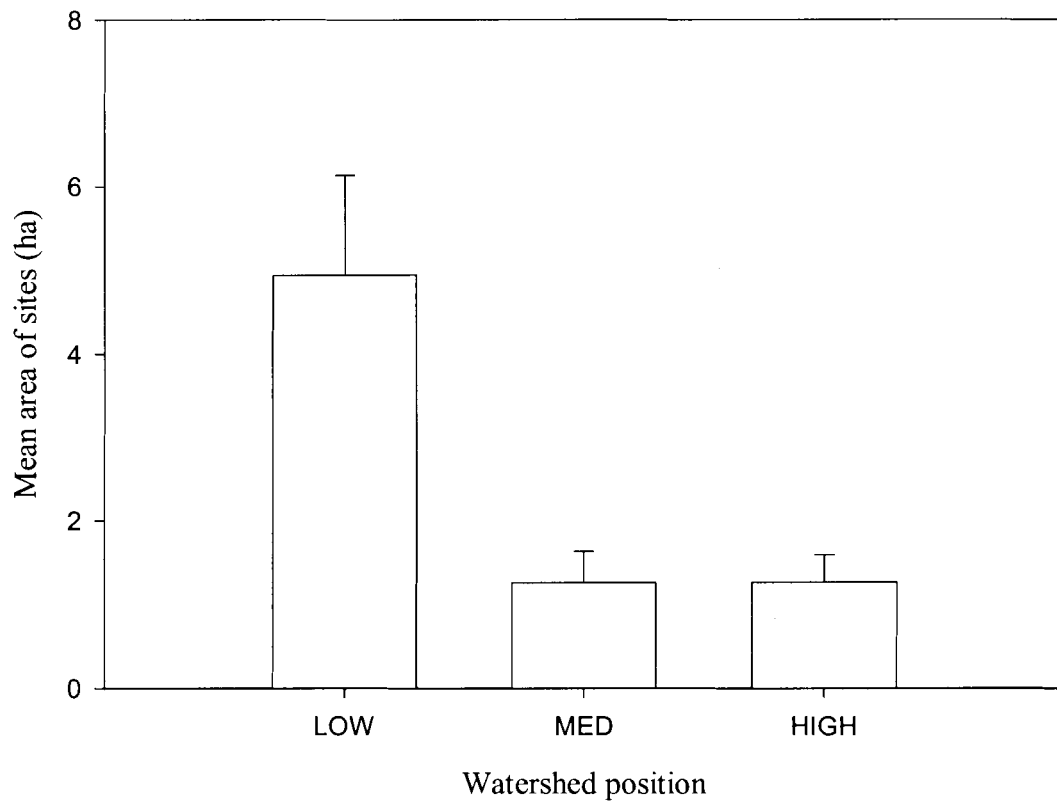


Figure 2.5. Mean area of sites (ha) by watershed position. Error bars indicate standard errors of the means. Sites lowest in the watersheds were significantly larger than those found higher in the watershed.

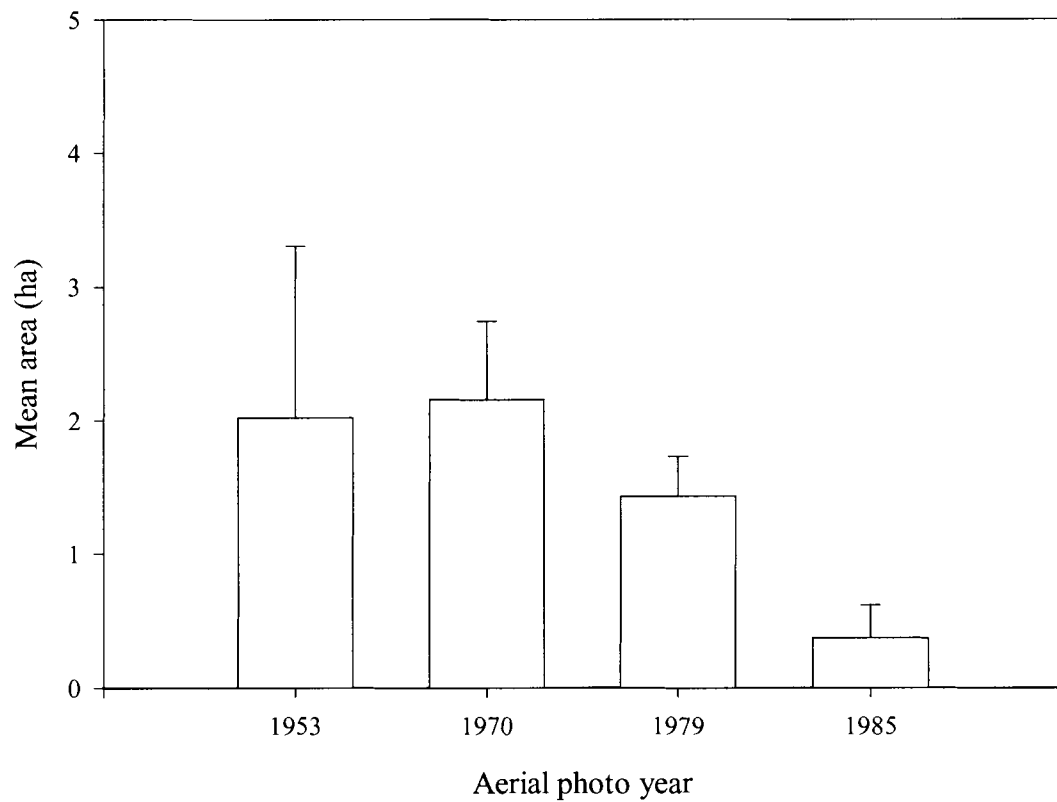


Figure 2.6. Mean area (ha) of newly impounded sites by aerial photo year. Mean area shows a decreasing trend over time. Data from 1944 and 1997 aerial photos were excluded because they represent only single observations.

Abandonment of sites by beaver appeared to be related to watershed position; sites in the highest watershed category showed a strong trend toward being abandoned by the end of the study period (Figure 2.7; $\chi^2 = 3.640$, 1 df, $p=0.056$). Abandoned sites were smaller in area than active sites (t-test = -2.809, df=31, $p=0.009$). The probability that a site would be abandoned by 2000 increased the later the site was initially colonized (Figure 2.8). All sites colonized after 1979 were abandoned before 2000.

The creation of beaver flowages between 1944 and 1997 increased the percentage of impounded wetland area and resulted in a general conversion of forested wetlands to earlier stages of wetland succession, particularly open water and herbaceous wetlands. Mean impounded area at study wetlands increased significantly from 10% in 1944 to 61% in 1997 ($t=-8.244$, df=32, $p<0.001$; Figure 2.9). The change in hydrology, as indicated by an increase in impounded area, was accompanied by significant increases in mean open water (OW; $t=-6.022$, df=32, $p<0.001$) and emergent (EM; $t=-4.545$, df=32, $p<0.001$) wetland class percentages and a decrease ($t=8.590$, df=32, $p<0.001$) in the mean percentage of site area dominated by forested (FO) wetland classes (Figure 2.9). The mean percentage of shrub/scrub (SS) wetland classes did not change significantly ($t=0.406$, df=32, $p=0.688$). All wetlands that were subsequently abandoned by beaver still retained open water and herbaceous wetland components through 1997.

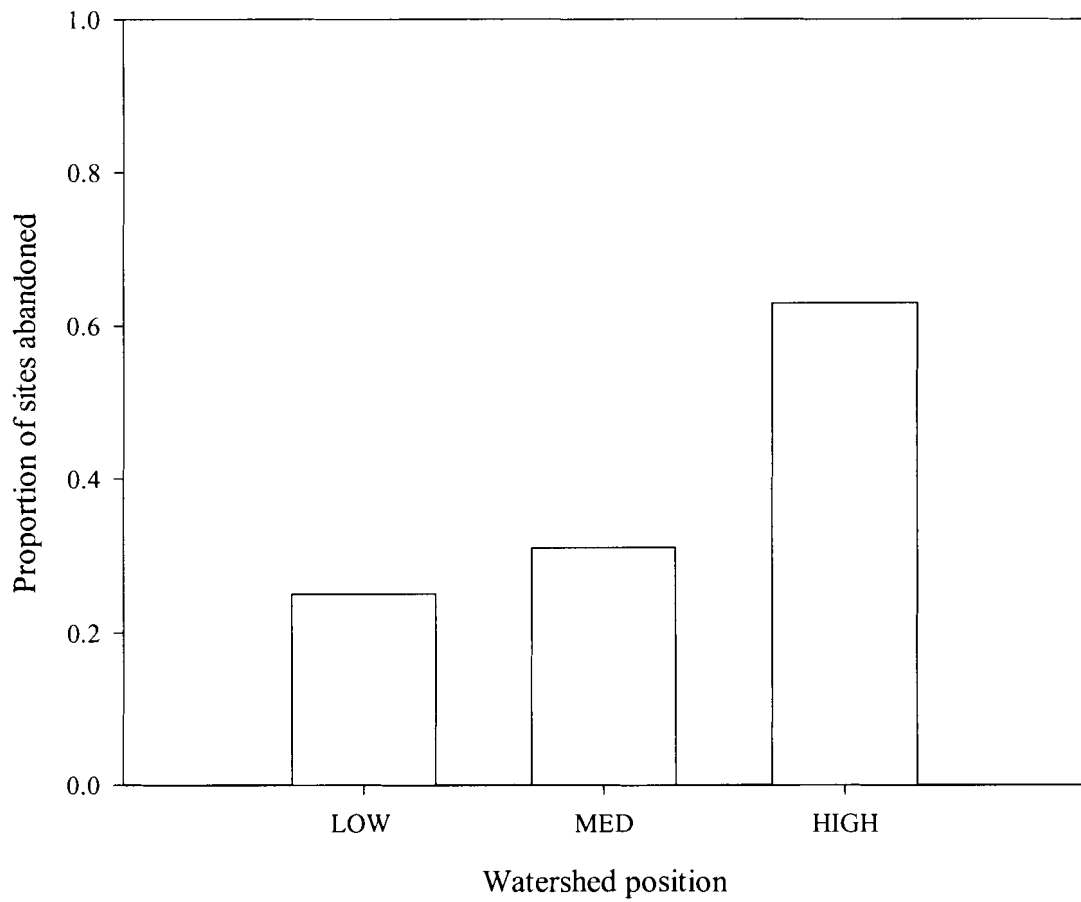


Figure 2.7. Proportion of sites currently (2000) abandoned by watershed position. A higher proportion of sites high in the watershed were abandoned than those found lower in the watershed. Abandonment was determined by field surveys in 2000.

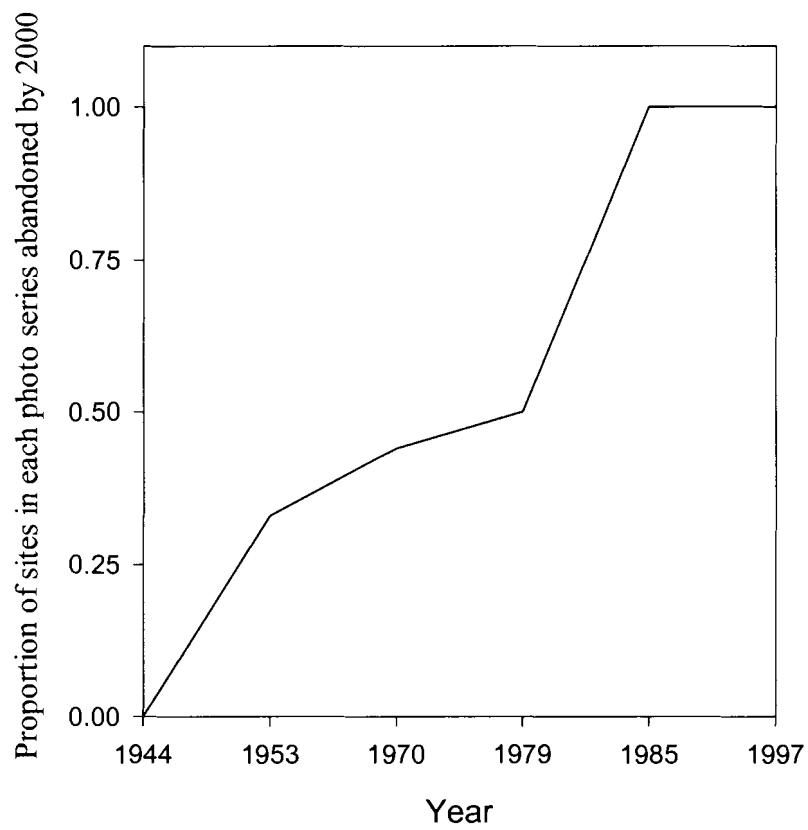


Figure 2.8. Proportion of sites in each photo series currently (2000) abandoned. The likelihood of abandonment increases the later a site was initially colonized. Abandonment was determined by field surveys in 2000.

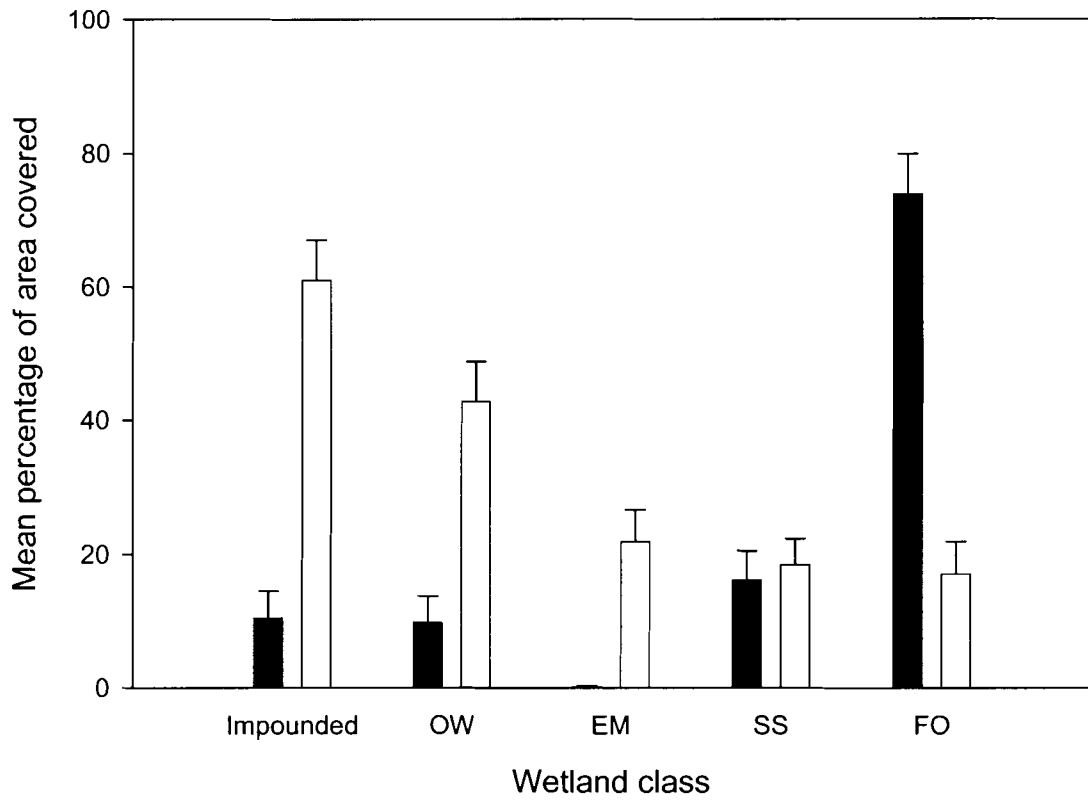


Figure 2.9. Change in mean percentage area of wetland impounded and wetland class composition in study sites from 1944 (black bars) to 1997 (gray bars). Impounded area refers to the total area with visible standing water regardless of wetland class. OW=open water, EM=emergent vegetation, SS=Scrub/shrub, FO=forested. Mean impounded area and mean open water and emergent wetland area increased significantly from 1944-1997. Mean area covered by forested wetland classes decreased significantly.

Discussion

Return of Beaver to the Landscape

The 1947 fire on Mount Desert Island undoubtedly facilitated the return of beaver to Acadia National Park. The beaver population increased from an initial reintroduction of 4 individuals in 1921, to an estimated population of nearly 300 individuals in 1979 (Muller-Schwarze 1979). The effect of the fire on forest composition is still evident today, with many deciduous, mixed, and aspen/birch forests (Figure 2.1; Patterson et al. 1983). In contrast, unburned areas are dominated by spruce-fir coniferous forests. Since aspen, birch and other early successional tree species are a favored food source for beaver (Jenkins 1979, Johnston and Naiman 1990b, Fryxell and Doucet 1993), forest regeneration in the burned area provided an abundant food supply that would favor beaver population growth.

Beaver Colonization Patterns

Beaver colonized pre-existing ponds previous to, and early in, the study period. Although beaver are most known for foraging on the inner bark of small diameter early successional tree species, beaver will forage preferentially on aquatic macrophytes, particularly during the summer months (Bradt 1938, Svendsen 1980). In large wetlands with abundant resources, a beaver colony might be sustained almost exclusively by resources found within the pond (Howard and Larson 1985). Colonization of these sites represents less effort in dam construction and a food supply with a greater longevity, particularly in the absence of abundant preferred tree species.

Lisle (1994) traced beaver colonization patterns in a watershed in Maine and concluded that the long-term absence of beaver in the watershed allowed for succession

of wetlands to a shrub or forested state. Rather than creating new wetlands, beaver recolonization from 1939-1991 at this site resulted in a conversion of forested and shrub wetlands to open water and herbaceous wetlands. Our results corroborate those findings, indicating that beaver were recolonizing wetlands that were likely historically created and/or modified by beaver. At least 42% of newly created beaver flowages in our study were colonized from obvious existing wetland basins. These basins were flat areas in otherwise steep watersheds where sediments had been previously deposited and are likely the direct result of beaver activity prior to their local extinction. Many of the additional riparian areas that were impounded may have been forested wetland basins as well; however, we were unable to distinguish distinct basins due to small size and/or dense tree cover at these sites.

Beaver in Acadia National Park showed patterns of colonization from 1944-1997 similar to those reported previously in Maine from 1939-1991 (Lisle 1994) and in Minnesota from 1940-1986 (Johnston and Naiman 1990); in all cases large sites were impounded earlier in the study period. Lisle (1994) also described a pattern of colonization that was related to the perimeter/ dam ratio; sites in which a small dam could impound a large amount of water were colonized first. Large sites provide convenient access to a greater area of potential food, both within and outside of the wetland. These patterns of colonization indicate a selection for higher quality sites initially and smaller, less-desirable sites either when food resources are exploited at more desirable sites, or when populations expand to the point where only marginal habitat is available (Howard and Larson 1985, Johnston and Naiman 1990).

Johnston and Naiman (1990) concluded that a reduced rate of new site colonization over time was constrained by geomorphology rather than by a decrease in beaver population. Presumably, in this case, beaver had exhausted potential sites in the landscape. The mountainous topography of Mount Desert Island with steep, high gradient watersheds limits suitable sites for potential beaver colonization (Baird 1964), and our data suggest that beaver population expansion on MDI was also constrained by geomorphology. Very few sites were colonized after 1979, despite the fact that beaver populations were deemed to be at or near their carrying capacity at this time (Muller-Schwarze 1979). The estimated rate of beaver population growth from 1964-1978 was 2.4%, suggesting that populations were stabilizing, most likely due to the decreasing availability of suitable habitat. Estimates of beaver colonized sites in 1979 deemed 19% as optimal, 27% as adequate, 42% as marginal and 11% as sub-optimal based on available food supplies. With greater than 50% of the sites classified as marginal or poorer, it is no surprise that we found smaller sites that were colonized later were more likely to be abandoned. Our study site sample appears to be representative of the reported distribution of available habitat quality, since close to 50% (16/33) of our study sites were abandoned by 1997.

Beaver activity showed a general trend from early colonization of larger sites low in the watershed to smaller sites high in the watershed. Small sites high in the watershed would not only provide less access to food resources, resulting in decreased longevity, but would also prove more difficult for beaver to maintain adequate water levels for protection and storage of winter food supplies (Howard and Larson 1985). Watersheds in Acadia National Park are generally short and steep with many ephemeral and intermittent

streams in the higher reaches, which would provide limited additional inflow after the spring rains and snowmelt runoff (Baird 1964, JMC personal observation). Lisle (1994) observed that some drainages were not colonized in a stair-step fashion; that dispersal occurred in both an upstream and downstream direction. Because the area measurements of mid-watershed and high watershed sites were not significantly different in our study (Figure 2.5), it is likely that some of our watersheds were colonized in a non-linear fashion; however, there was still a clear trend toward upstream movement of colonization over time. High watershed sites were also much more likely to be abandoned (Figure 2.7), indicating that they were less suitable sites.

Implications for Pond-breeding Amphibians

We studied beaver colonization and wetland change patterns in the context of potential habitat for pond-breeding amphibian species. Available habitat increased by 89% during the time of the study period, which corresponds with the return of beaver to the landscape. Beaver created flooded wetland patches in the landscape and maintained these patches to the potential benefit of pond-breeding amphibian species. Beaver colonization not only increases the number of ponded wetland patches in the landscape, but also decreases inter-wetland distance (Lisle 1994). Assuming that beaver-created or modified wetlands provide suitable habitat, increased habitat availability and connectivity should benefit all pond-breeding amphibian species. A concurrent study of amphibian species distributions found that beaver activity and connectivity of wetlands were useful predictors of high species richness for pond-breeding amphibians in Acadia National Park (Chapter 1). Increased species richness in beaver wetlands is likely a direct result of

beaver creating suitable habitat, and may be enhanced further by the connectivity of these sites in the landscape.

The rapid expansion of the beaver population in Acadia National Park in response to abundant food and habitat resources has resulted in a spatial and temporal mosaic of wetlands that was not available for amphibian breeding prior to beaver recolonization. This mosaic is the result of a beaver population that grew to its limit spatially, exploited marginal habitats, and has since decreased to a population that is likely to be more sustainable. Temporal changes in abandoned beaver wetlands and wetlands that are infrequently disturbed by beaver further increase wetland heterogeneity in the landscape.

Wetland heterogeneity in the landscape is important to provide a range of possible sites for pond-breeding amphibian species with differing habitat preferences. For example, bullfrogs (*Rana catesbeiana*) were found to breed only within large, deep sites with fish that were created or modified and maintained by beaver (Chapter 1). Such conditions are necessary to support the 2-3 year larval period of bullfrogs. Abandoned beaver wetlands maintained a fishless pond environment, due to a high watershed position and periodic drying, that favored wood frog (*Rana sylvatica*) breeding (Chapter 1). Wood frogs and bullfrogs never co-occurred due to their mutually exclusive requirements for successful breeding, however, the presence of beaver in the landscape has increased the overall availability of habitat for both of these species (Chapter 1).

Conclusions

The return of beaver to Acadia National Park has re-established a natural disturbance regime that contributes to increased landscape heterogeneity. Rapid, widespread colonization of the landscape was made possible by a fire disturbance that

increased the availability of preferred early successional tree species. Wetland succession in beaver-disturbed landscapes follows non-linear, multidirectional pathways due to varying levels of beaver disturbance (Remillard et al. 1987). Cycles of beaver colonization and abandonment had an estimated return interval of 10-30 years in one study, and although some sites succeeded to shrub/scrub wetlands, in no instance did wetlands progress to a forested state (Remillard et. al 1987). If this is the case in Acadia National Park, the current wetland landscape could be maintained for some time. However, if in the absence of large-scale disturbance on the landscape (e.g. fire), beaver populations do not continue to expand and colonize marginal sites, we may see a return of some of these sites to a forested state. The loss of these small, open-canopy sites would reduce the number of suitable wood frog breeding sites in the landscape and might also affect populations of other pond-breeding amphibian species (Chapter 1, Skelly et al. 1999, 2002, Halverson et al. 2003). Large sites with permanent beaver colonies and a stable water level and hydroperiod may not be as likely to experience large shifts in amphibian assemblages over time. However, sites that are periodically disturbed by beaver, and therefore more dynamic, could show substantial changes in amphibian species composition. Further research is needed to understand more fully how amphibian assemblages change in relation to patterns of beaver disturbance over time.

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