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ROADS IN SALT MARSHES:
FLOODING, VEGETATION, AND SHARP-TAILED SPARROW HABITAT QUALITY IN TIDALLY RESTRICTED MARSHES

By

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B.A. University of California, Santa Cruz, 1997

A THESIS

Submitted in Partial Fulfillment of the

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(in Ecology and Environmental Science)

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The University of Maine

May, 2012

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Thesis Advisor: Dr. William E. Glanz

An Abstract of the Thesis Presented
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Even seemingly minor habitat modification may have negative consequences for tidal marsh inhabitants like the Saltmarsh Sparrow (*Ammodramus caudacutus*) and the salt-marsh subspecies of Nelson's Sparrow (*A. nelsoni subvirgatus*), collectively sharp-tailed sparrows. Roads and bridges that bisect marshes restrict tidal flow and alter natural hydrology. Their removal is currently under consideration by land managers. I investigated sharp-tailed sparrow habitat quality (habitat use by nesting females, nest flooding, and daily nest survival) on state and federal lands in two tidally restricted salt marshes and two unrestricted marshes in Maine. Two restricted areas were behind a single road with a wide bridge ≥25 m wide. A third restricted area was behind two roads, one with a 3-m wide culvert and a second road downriver with a 25-m wide bridge. On restricted rivers, flood frequency of available high-marsh habitat was reduced by 50% above the two-road restriction compared to areas located below restriction and above just one restriction. Use by nesting sparrows, however, was highest downriver, above one bridge-type restriction. Flood frequency of nests did not differ significantly between restricted and unrestricted areas or between low and high river reaches. Overall nest survival also did not differ between restricted and unrestricted systems, but effect of nest timing on nest survival did vary across restriction types. On low reaches (below restriction), it was important for sparrows to re-nest quickly after failure due to flooding (probability of nest survival decreased by ~35% for every day that clutch completion was delayed past peak high tide). Above tidal restrictions (one-road and two-road restrictions), nest survival was slightly better for nests that were initiated later after peak high tide (survival *increased* by ~10% for every day of delay). Precipitation increased flood frequency of available high-marsh habitat and was correlated with lower probability of nest survival (although not flood frequency at nests). These results suggest that on the restricted rivers in this study, areas above one bridge-type tidal restriction may be of higher quality to nesting sharp-tailed sparrows than areas located below restriction or the area located above the two-road restriction. The negative effect of precipitation on nest survival suggests sharp-tailed sparrows may be highly vulnerable to global climate change. In addition to rising sea levels, which are predicted to reduce sparrow nesting habitat, climate change is also expected to increase storm intensity and frequency in the Northeast, USA. In the face of changing climate and hydrology, managers should consider carefully before removing tidal restrictions such as those included in this study. Wide bridge-type tidal restriction did not appear to negatively affect high marsh flooding or sharp-tailed sparrow nesting, however wide culvert-type restriction may have had some negative impacts due to reduced flood frequency in the high marsh zone.

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LIST OF ABBREVIATIONS

AIC_c	Akaike's Information Criterion corrected for small sample size
ΔAIC_c	Difference in AIC_c between the best model the i^{th} model
CC	Timing of clutch completion relative to a lunar cycle
FLOOD	Flood frequency at a nest (habitat use analysis) or whether a nest flooded or did not flood during the observation interval (nest survival analysis)
GRASS	Cover of *Spartina patens* and *Juncus gerardii*
HT	Mean of the maximum tide heights during flood events for which a point was flooded (cm, tide height data from the NOAA Portland buoy)
MOUTH	Distance to the beginning of high-marsh habitat near the river's mouth (m)
PPT	Mean of the total precipitation during flood events for which a point was flooded (cm, precipitation data from NOAA weather station in Grey, ME)
R/A1	Location in a restricted system above one road (also known as a restricted, high one reach)
R/A2	Location in a restricted system above two roads (also known as a restricted, high two reach)
R/B	Location in a restricted system below roads (also known as a restricted, low reach)
RD	Distance to the nearest impermeable surface (road or parking lot)
REACH	River reach (low or high)
RIVER	River location (Nonesuch, Libby, Webhannet, or Ogunquit)
SD	Standard deviation
SDHT	Standard deviation of mean tide height (see HT above)

SDPPT	Standard deviation of mean precipitation (see PPT above)
SE	Standard error of the mean
SPAL	*Spartina alterniflora*
T	Treatment (unrestricted or restricted)
THATCH	Mean thatch depth
UNR/L	Location in an unrestricted system and on a low reach of the river
UNR/H	Location in an unrestricted system and on a high reach of the river
UTM	Universal Trans Mercator
w_i	Akaiki's weight of evidence in support of model *i*
YR	Year of data collection (2009 or 2010)

CHAPTER 1

EXECUTIVE SUMMARY

The Saltmarsh Sparrow (*Ammodramus caudacutus*) and the salt-marsh subspecies of Nelson's Sparrow (*A. nelsoni subvirgatus*), collectively sharp-tailed sparrows, are high conservation priorities throughout their ranges. Their populations have been adversely affected by extensive reduction and modification of high-marsh habitat, and it is likely that they will continue to be threatened by global climate change and sea level rise. Tidal restrictions are created by roads and bridges that bisect salt marshes, and severe tidal restrictions are known to have many negative impacts on salt-marsh ecosystems. They can diminish or completely prevent tidal flow across the road barrier. Sharp-tailed sparrows nest close to the ground in the high-marsh zone, and tidal restrictions have been seen to have positive consequences for nesting sharp-tailed sparrows because catastrophic nest flooding is reduced above restriction. However, tidal restrictions are also known to reduce cover of salt-marsh grasses that are used by nesting sharp-tailed sparrows. To date, only severe tidal restrictions (<1.5 m wide) have been studied. Wider tidal restrictions are more common, however, and there is a clear need for additional research on sharp-tailed sparrows in less severely restricted salt marshes. Here, I present results investigating the effects of moderate tidal restrictions on sharp-tailed sparrow habitat and nesting biology. The work was conducted in two tidally restricted salt-marsh systems managed by Rachel Carson National Wildlife Refuge, York County, Maine, and in two unrestricted systems managed by Maine Department of Inland Fisheries and Wildlife, Cumberland County, Maine. Two restrictions were created by a single road crossing the salt marsh and had wide bridges (25-47 m) spanning the river. A third restriction was created by a road that had a 3-m wide culvert spanning the river; this restriction was 800 m upriver from a wide bridge-type restriction also included in the study. Work was done during two breeding seasons, 25 May–7 Aug, 2009 and 2010. I describe tide height adjacent to each tidal restriction, flood frequency and vegetation patterns of available high-marsh habitat, and sharp-tailed sparrow habitat quality (habitat use by nesting females, flood frequency at nests, and nest survival) in tidally restricted and unrestricted systems.

I used paired tide gauges distributed on either side of each road and at similar distances upriver on unrestricted systems to describe tidal restriction above roads. I compared maximum tide height, timing of maximum tide, and rate of tidal draining during the falling tide (indicating pooling) between the tide gauge located below a road and the paired gauge located above the road.

Field crews conducted comprehensive nest surveys on each river every one-two weeks and monitored activity of found nests until final outcome was determined. I used iButtons to monitor flood frequency at random locations and at nests ($n = 440$ random points and 164 nests). I characterized vegetation within a 1-m^2 quadrat around each random and nest location. I used linear-mixed models to explore the effect of tidal restriction, distance upriver, and other parameters on flood frequency at random locations, vegetation at random locations, and flood frequency at nest locations. I used generalized linear-mixed models to explore differences between random locations (available high-marsh habitat) and used locations (nests). I used logistic-exposure models to explore effects of tidal restriction, distance upriver, and other parameters on daily nest survival. In order to account for the uniqueness of each river, I included river as a random intercept in the mixed models. All tide gauges and random points were located in high-marsh habitat, which is where sharp-tailed sparrows place their nests. I monitored four spring tide cycles (tides >3 m above mean low water) over the two years of study. It is these spring tide cycles that cause periodic and catastrophic nest failure for sharp-tailed sparrows.

The roads varied in degree of tidal restriction. Above one of the one-road restrictions (a 47-m wide bridge), there was no reduction in maximum tide height, no delay in peak tide, or any evidence of pooling during the falling tide. Above the second one-road restriction (a 25-m wide bridge), tide height was 1.7 cm lower, peak tide was 28 minutes delayed, and there was evidence of pooling during the falling tide. Above the two-road restriction (a 3-m wide culvert), tide height was 9.8 cm lower, peak tide was 20 minutes delayed, and there was evidence of pooling during the falling tide (Table 1.1).

iButtons monitored flooding at random locations throughout the high-marsh zone. They showed that flood frequency was significantly reduced at the highest river reaches above the two-road restriction (a 3-m wide culvert) compared to areas located below restriction or above one bridge-type restriction. In addition, points located above the culvert required significantly higher tides in order to flood. These patterns were not mirrored on unrestricted systems. There, flood frequency was significantly *greater* at high river reaches. In addition, I did not detect differences in the effect of tide height on flood frequency between low versus high river reaches (Table 1.1).

Vegetative composition was the same for all reaches of all rivers. In addition, relative cover of common salt-marsh species used by nesting sharp-tailed sparrows

(*Spartina alterniflora*, *S. patens*, and *Juncus gerardii*) was similar among all areas. I found that factors affecting frequency of occurrence for individual species were complicated. Nevertheless, tidal restrictions from this study did not appear to alter the composition of salt-marsh vegetation, and all areas were dominated by typical salt-marsh species.

Perhaps the clearest demonstration of differences in habitat quality was evidenced by habitat use from nesting female sparrows. In restricted systems, use was significantly greater at high river reaches located above one bridge-type tidal restriction (25-47 m wide). In unrestricted systems, I observed the opposite pattern, and use was significantly greater on *low* river reaches. Despite reduced flood frequency of high marsh habitat above the culvert-type restriction, I did not detect significant differences in nest flooding between restricted and unrestricted areas. I also did not detect significant differences in overall daily nest survival between restricted and unrestricted areas (Table 1.1).

Other factors did affect nest survival. Timing of clutch completion has been shown by other studies to be a strong predictor of nest survival, and nests that are initiated quickly after peak spring tide are more likely to succeed. Nests that are initiated too late risk being flooded by the next spring tide cycle. I observed this same pattern on low river reaches (below all tidal restrictions), but not on high reaches. Above tidal restriction (both bridge and culvert types), nests that delayed timing and were initiated later after peak spring tides were more likely to succeed (Table 1.1). This result has not been observed elsewhere and is interesting. It suggests that factors other than tidal flooding may be affecting sparrows that nest above moderate tidal restriction. Predation pressure is a possible cause, but this needs to be investigated further. Flooding was another factor affecting nest survival, and nests that flooded were less likely to survive.

Precipitation significantly increased flood frequency of high-marsh habitat, and the effect was the same regardless of restriction or river reach. Precipitation, however, did not appear to affect flooding at nests. Perhaps female sparrows were able to shelter their nests and keep them warm despite flooding from rain. Nevertheless, I did find that precipitation significantly reduced nest survival. While female sparrows may have been able to maintain nest temperature and mask flooding from precipitation, perhaps the wet weather compromised the nest or the female and caused nest failure. Precipitation may become increasingly important as global climate change models predict more frequent and severe storms in the future for the Northeast, USA. This will put sharp-tailed sparrows at risk from both sea level rise and increase rainfall.

Cumulatively, these results suggest that on the restricted systems studied here, wide bridge-type tidal restriction may be of less concern for high-marsh habitat conservation in terms of flood frequency and salt-marsh vegetation. Further, areas located above these restrictions may be of higher quality compared to areas located below restriction or above the culvert-type restriction, at least in terms of habitat use by nesting sharp-tailed sparrows. Because of reduced flood frequency, the wide culvert-type tidal restriction may be more of a concern for high-marsh conservation. It might be wise to continue monitoring this area for changes in salt-marsh vegetation and to investigate whether sedimentation and marsh accretion are on par with areas located below the restriction. Nesting sharp-tailed sparrows did not appear to be negatively or positively affected by this restriction. They did not preferentially nest above it, nor did sparrows nesting above it experience different nest survival compared to areas located below restriction or above one bridge-type restriction. Bear in mind, however, that the tidal restrictions studied here are a small sample of the variety of bridge and wide culvert-type restrictions found among salt-marsh systems. In some places, wide culverts may pose greater risks to nesting sharp-tailed sparrows.

Although sharp-tailed sparrows are species of conservation concern, their populations are notoriously difficult to track without extensive effort. We do know, however, that the high-marsh habitat required by nesting sparrows has been greatly reduced by human development and is further threatened by sea level rise. More research on common tidal restrictions like the wide culvert and bridges studied here would help land managers understand how to best conserve both salt-marsh ecosystems and sharp-tailed sparrows.

Table 1.1. Summary of results in restricted unrestricted areas. York and Cumberland Counties, Maine, 2009 and 2010.

Restricted		
Below road	• High-marsh flooding	Greater flooding compared to reach above two roads
	• Habitat use	Reduced use compared to reaches above one road; flood frequency had negative effect
	• Nest survival	Similar nest survival with reaches above one and two roads; timing had negative effect
Above 1 road	• Restriction type	47-m wide bridge, 25-m wide bridge (two replicates)
	• Tidal flow at tide gauges (comparison between below and above road gauges, 100 m apart)	First replicate: no reduction in tide height, no delay in timing of tide height and no pooling; second replicate: tide 1.7 cm lower above the road, 28 minute delay in timing of tide height, pooling above road on falling tide (2 min/cm slower draining of high marsh zone)
	• High-marsh flooding	Greater flooding compared to reaches above two roads
	• Habitat use	46% greater use compared to below road reaches; flood frequency had negative effect
	• Nest survival	Similar nest survival with reaches below and above two roads; timing had positive effect
Above 2 roads	• Restriction type	3-m wide culvert (one replicate)
	• tidal flow above at tide gauges	Tide height 9.2 cm lower above the road, 20 minute delay in timing of tide height, pooling above road on falling tide (5 cm/min slower draining of high marsh zone)
	• High-marsh flooding	50% less flooding compared to below road reaches; points here required higher tides compared to points located below roads in order to flood
	• Habitat use	Reduced use compared to reaches above one road; flood frequency had no effect on
	• Nest survival	Similar nest survival with reaches below and above two roads; timing had positive effect
Unrestricted		
Low	• High-marsh flooding	9% less flooding compared to high reaches
	• Habitat use	38% greater use compared to high reaches; flood frequency had negative effect
	• Nest survival	Similar nest survival with high reaches; timing had negative effect
High	• Tidal flow at tide gauges (comparison between gauges located 100 m apart)	No reduction in tide height, no delay in timing of high tide, no pooling
	• High-marsh flooding	Greater flooding compared to low reaches
	• Habitat use	Reduced use compared to low reaches; flood frequency had negative effect
	• Nest survival: similar nest survival with high reaches; timing had no effect	

CHAPTER 2

FLOODING AND VEGETATION OF HIGH-MARSH HABITAT

Introduction

Salt marshes are unique environments at the interface of marine and terrestrial habitats. Organisms like the sharp-tailed sparrow (*Ammodramus* sp.) that live in salt marshes must be able to negotiate hypersaline conditions as well as inundation from tidal flooding. Salt marshes are highly productive ecosystems and are thought to be driven primarily by bottom-up abiotic forces (Odum 1971). According to some estimates, they are some of the most valuable ecosystems on earth (Levin et al. 2001, Costanza et al. 1997). They are known to provide a variety of ecosystem services important to both human and wildlife populations. For example, salt marshes: (1) prevent and dampen coastal erosion by absorbing wave and storm energy, (2) are a global carbon sink that may help mitigate increasing levels of carbon dioxide, (3) provide habitat for young fish and invertebrates, (4) provide habitat for migrating, breeding and wintering bird populations, and (5) are home to unique and endemic species such as the sharp-tailed sparrow (Chmura et al. 2003, Greenberg et al. 2006, Costanza et al. 1997, Gedan et al. 2009). Some sources estimate that 40% of the world's population lives near a coast (UNEP 2006), and this juxtaposition underscores both the local importance of the ecosystem as well as the conservation challenges inherent in their proximity to human populations.

Salt marshes have historically been marginalized and exploited (Gedan et al. 2009). For example, water manipulation (diking and damming) have been used to drain marshes and change their hydrology. Agriculture (e.g. hay harvesting and grazing) have changed vegetative communities, and adjacent land use and development have polluted waterways. In addition, land reclamation has converted marshes into channelized harbors, airport runways and residential neighborhoods. Consequently, large portions of coastal wetlands have been lost (Lotze et al. 2006), and in New England alone, >80% have been destroyed (Teal 1986).

Tidal restrictions are a common impact from adjacent urban development and can have many detrimental effects on marsh ecosystems. Restrictions are created by roads and bridges that bisect salt marshes without allowing adequate tidal flow (undersized culverts are often to blame). Unfortunately, roads and bridges are a regular marsh feature in most North American salt marshes. In Connecticut and New Hampshire, for example, 10-20% of marshes are tidally restricted (USDA SCS 1994, Burdick et al. 1997). In Maine, 28% of marshes are restricted by narrow culverts (HRSC 2006, Crain et al. 2008). Deleterious effects resulting from road and bridge crossings include reduced flooding (tidal range, flood duration, and flood area are all reduced; Bertness and Ellison 1987, Burdick et al. 1997, Costa 2000, Boumans et al. 2002). In addition, marsh chemistry can be altered (e.g. reduced salinity accompanied by increased acidity; Roman et al. 1984, Burdick et al. 1997, Portnoy and Giblin 1997). These modifications can lead to vegetative and invertebrate changes, ultimately reducing biodiversity and productivity (Trombulak and Frissell 2000, Zedler et al. 2001, Mitchell et al. 2006). Typically, halophytic species decrease (e.g. *Spartina alterniflora*, *S. patens*, and *Salicornia europaea*), while weedy, brackish, and introduced species (e.g. *Typha angustifolia* and *Phragmites australis*) increase (Bertness and Ellison 1987, DiQuinzio et al. 2002, Roman et al. 2002).

Eutrophication can also occur following tidal restriction, and increased nutrient levels may promote excessive growth for some species (e.g. algae) at the expense of salt-marsh vegetation (Costa 1999). Perhaps the most serious effect of tidal restriction, however, is marsh subsidence. Following reduced tidal flow, marshes often fail to accrue enough new sediment to grow vertically and outpace sea-level rise (Burdick et al. 1997, Portnoy and Giblin 1997, Gedan et al. 2009). The result is a continual decrease of marsh elevation in areas above tidal restriction, which can further affect vegetation communities and complicate future tidal restoration (Gedan et al. 2009).

In light of current understanding of the importance of salt-marsh ecosystems, many land managers are actively restoring restriction-degraded wetlands (Barret et al. 2006) and seeking methods to encourage natural marsh hydrology, including road removal and culvert or bridge improvements (Mitchell et al. 2006, RCNWR and MDIFW pers. comm.). Studies have shown that restoration of tidal flow results in a rapid increase in salinity (Konisky et al. 2006). However, return of halophytic vegetation is complicated, and nekton and avian responses have been variable (Konisky et al. 2006). Thus far, research has focused on extremely severe tidal restrictions caused by culverts <1.5 m in diameter (e.g. Burdick et al. 1997, Portnoy and Giblin 1997, Boumans et al. 2002, DiQuinzio et al. 2002, Roman et al. 2002). Less severe restrictions may have negative consequences for flora and fauna, but have not yet been examined. Sharp-tailed sparrows, for example, are species of conservation concern that require high-marsh habitat in order to breed. In addition, they use salt-marsh grasses to build their nests and are extremely vulnerable to flooding of the high marsh. It has been suggested that sharp-tailed sparrows might benefit because flooding of their nests is reduced above severe restrictions (DiQuinzio et al. 2002). This has not been studied, however, in the context of moderate tidal restriction.

In this chapter, I will address the following objectives related to the effect of moderate tidal restriction (bridges ≥25 m wide and culverts 3 m wide) on sharp-tailed sparrow habitat: (1) describe tidal flow in high-marsh habitat adjacent to moderate restrictions, (2) investigate differences in flood frequency of high-marsh habitat between restricted and unrestricted areas, and (3) explore vegetation differences between restricted and unrestricted areas. Tidal restrictions are a serious concern for marsh health, and land managers require comprehensive information to enact appropriate restoration practices. Ultimately, these results will help identify which types of tidal restriction may be of more or less concern to salt-marsh habitats and sharp-tailed sparrow. They will add to other monitoring efforts currently underway that may be used to inform salt-marsh restoration.

Study Sites

Study sites included four rivers managed by Rachel Carson National Wildlife Refuge and Maine Department of Inland Fisheries and Wildlife in York and Cumberland Counties, ME. The Ogunquit (43.265380° N, -70.592190° W) and Webhannet Rivers (43.317450° N, -70.574290° W) are moderately restricted, while the Nonesuch (43.554040° N, -70.331720° W) and Libby Rivers (43.555690° N, -70.327030° W) are unrestricted in the reaches considered here. All four marshes are characterized by extensive high-marsh habitat, typically flooding only during spring tides >3 m above mean low water and dominated by *Spartina patens*. Mean tidal range is 2.6 m, and relative sea level rise was 2.3 mm annually between 1986 and 2003 (Fitzgerald et al. 1989, Goodman et al. 2007).

The Webhannet is a large back-barrier marsh, running south to north (~95 ha in area, ~3300 m in length). One tidal restriction is located at Mile Road ~2100 m upriver (straight distance from beginning of high-marsh habitat near the river's mouth). The bridge spanning the river at this location is 47 m wide (38% narrower than the width of the river, Figure 2.1). The Ogunquit is a smaller, narrower back-barrier marsh (~60 ha, ~3300 m), runs north to south, and is restricted by two roads that cross the marsh in the reaches considered here. One tidal restriction crosses the Ogunquit at Bourne Road ~1800 m upriver and has a 25-m wide bridge spanning the river (20% *wider* than the river's width, Figure 2.1). A second tidal restriction crosses the Ogunquit at Furbish Road ~2600 m upriver. This restriction has a 3-m wide culvert (170% narrower than river width, Figure 2.1) that does not have gates allowing water to flow at all times. Both the rivers are almost entirely tidal and have very little freshwater influence (Fitzgerald et al. 1984, Fitzgerald et al. 1989). The marshes are federally protected and are not open to public use. Both marshes have residential and other urban development surrounding 100% of their upland edges.

The lower reaches of the Nonesuch River is a fluvial marsh, running generally east to west (~45 ha in area, ~2600 m to the study area's upper boundary). The terminous of the Libby River is also a fluvial marsh, running generally south to north (~45 ha, ~2300 m to the study area's upper boundary). The Nonesuch and Libby marshes are both characterized by nontrivial riparian flow and thus have greater freshwater influence compared to the Webhannet and Ogunquit marshes (Goodman et al. 2007). Both rivers

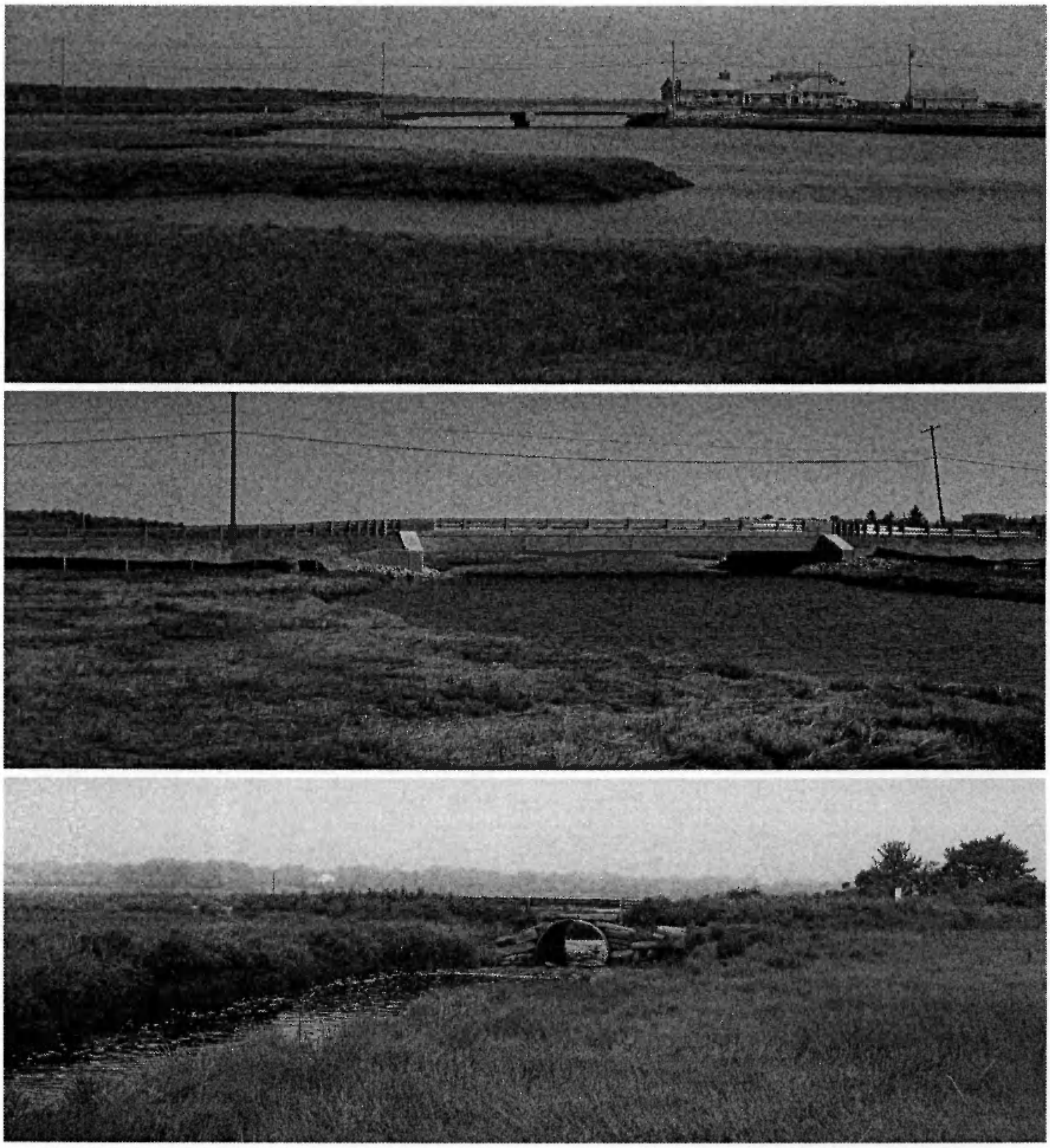

Figure 2.1. Photographs of the three tidal restrictions included in the study. York and Cumberland Counties, Maine, 2009 and 2010. The one-road restriction on the Webhannet River (top) had a 47-m wide bridge. The one-road restriction on the Ogunquit River (middle) had a 25-m wide bridge. The two-road restriction on the Ogunquit River (bottom) had a 3-m wide culvert.

empty into Scarborough Marsh at the mouth of the Scarborough River. The Nonesuch and Libby rivers are unrestricted in the reaches considered and were used as reference sites representing tidally unmodified systems. Protected by the state of Maine, the rivers are open to public use (e.g. fishing). Although unrestricted, they have residential development adjacent to ~50-75% of their upland edges.

Methods

I collected data during 25 May – 7 Aug, 2009 and 2010. I used a split-plot design set up with five treatment types over high and low reaches of each river: unrestricted/low, unrestricted/high, restricted/low (below restriction), restricted/high (above one restriction), and restricted/high (above two restrictions, Table 2.1). I defined low reaches as areas that were closer to the river mouth (on average < 1700 m upriver from beginning of high-marsh habitat) and below all roads. I defined high reaches as the areas that were further from the river mouth (on average > 2000 m upriver) and, on restricted rivers, also located above at least one road. I differentiated between reaches that were above one tidal restriction (on Webhannet and Ogunquit Rivers: "above 1") and the reach that was above two restrictions (Ogunquit River: "above 2"). I monitored tidal flooding across each reach during two spring tide cycles each year. For this study, I defined a spring tide cycle as the period of extreme high tides (>3 m above mean low water), which typically floods high-marsh habitat. These periods usually spanned 1-2 weeks per lunar calendar. I defined a tide event as a single extreme high tide. Usually, two tide events occurred per day, and I monitored many events per tide cycle.

Table 2.1. Characteristics of the four salt marshes included in the study. York and Cumberland Counties, Maine, 2009 and 2010. Distance of low vs. high reaches, size of reach, and number of study subplots are also shown. All subplots contained approx. 2.25 ha of high-marsh habitat.

Treatment	Reach[a]	Distance upriver (m)	Size (ha)	No. of subplots
Restricted				
• Webhannet	Low/Below (R/L)	0-2100	56	5
	High/Above 1 (R/A1)	2100-3300	38	5
• Ogunquit	Low/Below (R/L)	0-1800	23	5
	High/Above 1 (R/A1)	1800-2600	20	5
	High/Above 2 (R/A2)	2600-3300	18	5
Unrestricted				
• Nonesuch	Low (UNR/L)	0-1400	23	5
	High (UNR/H)	1800-2600	23	5
• Libby	Low (UNR/L)	0-1400	25	4
	High (UNR/H)	1400-2300	20	5

[a] R = restricted system, UNR = unrestricted system, L = low reach closer to the river's mouth and below all roads, H = high reach further from the river's mouth and below all roads, A1 = high reach and above one road (with a wide bridge), A2 = high reach and above two roads (road with a wide bridge followed by a road with a wide culvert)

Objective 2.1: Description of tidal flow adjacent to tidal restriction

Field methods. Each year, I deployed 18 vented tide gauges (Level Troll 500, InSitu Inc., Fort Collins, Colorado) across the study area (7 Jun – 31 Jul, 2009 and 1 Jun – 31 Jul, 2010). On the Webhannet and Ogunquit Rivers, I placed two gauges below each road and two above. On unrestricted rivers, I placed sets of gauges at comparable distances upriver (Table 2.2). I situated all gauges in high-marsh habitat, and each year they measured flooding throughout two spring tide cycles. Gauges hung 80-100 cm below ground and were supported by perforated PVC piping. Measurements were taken before and after setup to confirm that gauges had not moved during deployment. I placed gauges 40-150 m from restriction (on restricted rivers), ~25 m from the main channel edge, and ~100 m from adjacent gauges (Table 2.2). Each gauge recorded water height every five minutes (2009) or every 15 minutes (2010). I also measured relative elevation at each gauge (relative between the four gauges from each set). I corrected field measurements of water levels for gauge depth below ground and relative elevation. Corrected measurements therefore represent water height above mean marsh elevation.

Table 2.2. Layout of tide gauges across the four rivers included in the study. York and Cumberland Counties, Maine, 2009 and 2010.

River and Road	Gauge number: distance upriver (m)	Distance from road (m)[a]	Relative elevation (cm)
Webhannet			
• Mile Rd	1: 2000	100 below	0.00
	2: 2040	40 below	6.43
	3: 2080	40 above	1.53
	4: 2180	100 above	0.00
Ogunquit			
• Bourne Rd	1: 1650	150 below	0.00
	2: 1750	50 below	3.68
	3: 1850	50 above	6.13
	4: 1950	150 above	7.04
• Furbish Rd	1: 2450	150 below	11.28
	2: 2550	50 below	14.02
	3: 2650	50 above	0.00
	4: 2750	150 above	2.44
Nonesuch			
• *no road*	1: 1900	NA	6.77
	2: 2000	NA	0.00
	3: 2100[b]	NA	9.58
Libby			
• *no road*	1: 1400	NA	7.04
	2: 1500	NA	2.45
	3: 1600	NA	1.07
	4: 1700[c]	NA	0.00

[a]Gauges on restricted systems were 60-100 m apart while gauges on unrestricted systems were 100 m apart, [b]gauge operated during 2009 only, [b]gauge operated during 2010 only.

Statistical methods. I compared water level between paired gauges located immediately below versus immediately above each road (100 m separation between gauges). I looked at differences in maximum tide height during spring tide cycles, delay in timing of high tide (difference in timing of maximum tide height between gauges), and rate change of tide height (min/cm) during the falling tide. I used paired, one-tailed, Student *t*-tests to compare tide height, delay, and falling rate between below-road and above-road gauges on restricted systems and between adjacent gauges on unrestricted systems. I predicted that tide height would be lower above restriction and would be delayed in timing. On unrestricted systems, I predicted that tide height would not be lower at gauges located 100 m upriver and would not be delayed in timing. I predicted slower falling rates at above-road gauges compared to below-road gauges and used this as an indication of pooling above the road on the falling tide (Costa 2000). I report means ± SE and use $\alpha < 0.05$ to define significance. All analyses were conducted in R v.2.11.1 (R Development Core Team 2011).

Objective 2.2: Flood frequency in high-marsh habitat

Field methods. I used a stratified-random method to select 4-5 subplots per river per reach (Table 2.1). I used aerial maps overlaid with a UTM grid to randomly select plot vertices along a distance gradient starting at the beginning of high-marsh habitat near the river's mouth. Thus, survey effort was standardized on each river and reach according to distance upriver. Each subplot contained ~2.25 ha of high-marsh habitat. I modified some subplot boundaries to accommodate marsh channels, sloughs, and low-marsh or mudflat habitat.

I used temperature data loggers (Thermochron iButtons, Maxim, Sunnyvale, California, hereafter iButtons) to monitor flooding of high-marsh habitat throughout each reach. Each year, I located 8-12 random points on each subplot (18-22 total random locations per subplot). Points that fell in low-marsh habitat were replaced with new points in high-marsh habitat. I placed iButtons at each point, at the typical height of a sharp-tailed sparrow nest (10 cm high). Each iButton recorded temperature at 15-minute intervals during one entire spring tide cycle. In order to maximize coverage across the study sites, I rotated iButtons between subplots and monitored flooding at each subplot during one spring tide cycle per year. I also placed one iButton ~1.2 m high in the center of each subplot and recorded ambient temperature at 15 minute intervals throughout the study. I inspected temperature profiles from five random points per subplot per year (n = 440) and used temperature to infer when a point flooded. Each high tide event of the cycle was inspected in this way. I did not investigate possible flood events that might have occurred outside of a tide event. I also did not consider precipitation when assessing flood events. I used the following two methods to infer flooding at random points.

(1) During the night (1900 to 0700), I compared random–ambient temperature differences prior to high-marsh flooding vs. during high-marsh flooding. If the random–ambient temperature differences increased significantly, I categorized the random point as flooded for that tide event. At flooded points, random and ambient temperatures typically paralleled each other prior to flooding (mean difference ± SD: 0.3 ± 0.2° C), followed by a significant increase or decrease in random temperature during flooding (1.6 ± 0.6° C, $P < 0.01$). At non-flooded points, there was no significant difference between random–ambient differences before tide gauge flooding vs. after (prior mean: 0.3 ± 0.2° C, during mean: 0.4 ± 0.1° C, $P = 0.15$, Figure 2.2a).

(2) During the day (0700 to 1900) random and ambient temperatures and their differences tended to fluctuate greatly. When flooding occurred, however, there was less fluctuation, and temperature tended to remain constant. Thus, I measured temperature variability and compared variability prior to tide gauge flooding vs. during tide gauge flooding. I measured variability as the difference in temperature from one moment to the

next (i.e. between time t_i and time $t_{i-15min}$). If variability of random point temperature during high-marsh flooding was significantly less than it was prior to high-marsh flooding, I categorized the point as flooded for that event. At flooded points, mean variability prior to high-marsh flooding was 1.9 ± 0.6° C, and during high-marsh flooding it was 0.3 ± 0.3° C ($P < 0.01$). At non-flooded points, mean variability prior to flooding was 1.4 ± 0.5° C, during flooding it was 1.6 ± 0.1° C ($P = 0.57$, Figure 2.2b).

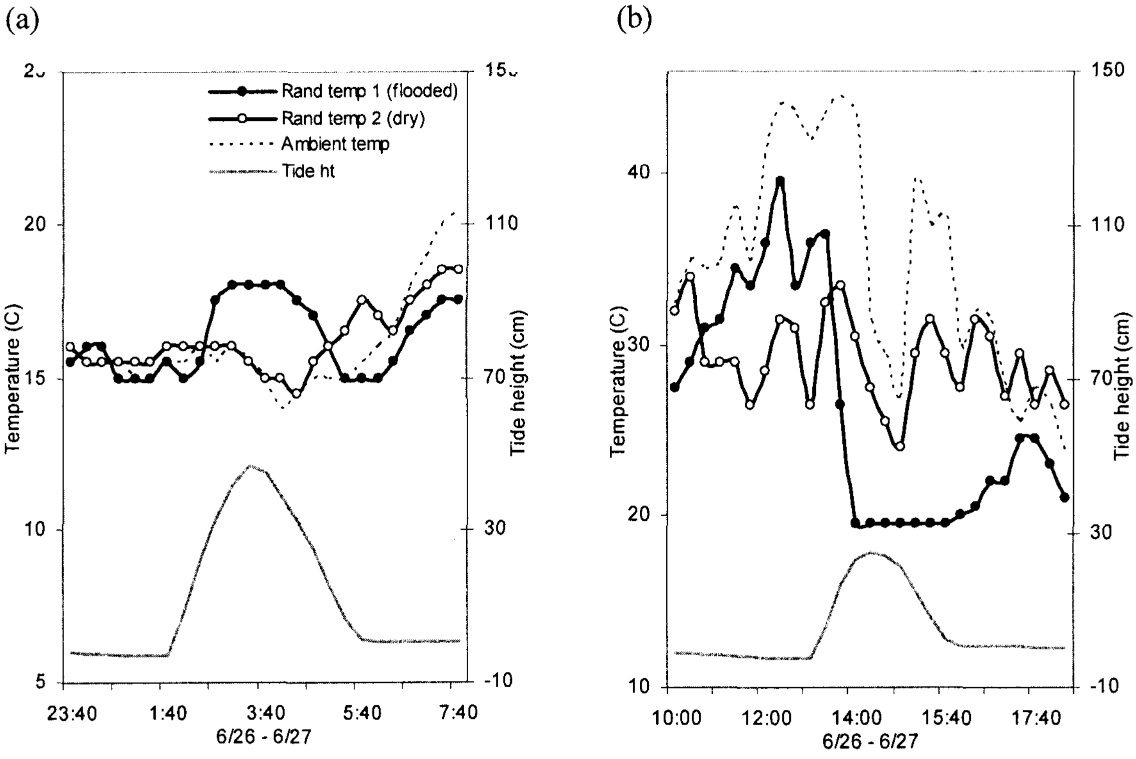

Figure 2.2. Examples of iButton temperature profiles used to infer when a point was flooded by a high tide event. York and Cumberland Counties, Maine, 2009 and 2010. (a) Typical night-time profile of a point that flooded vs. one that did not. (b) Typical day-time profile of a point that flooded vs. one that did not.

Due to variable weather conditions (e.g. wind and water temperature), I was unable to determine flood status for 57% of monitored flood events using these two methods (across all iButtons). In these cases, I extrapolated flood status from known flood events for a given point. For example, if I successfully determined that a point flooded during tides measuring 36 cm at the tide gauge, I assumed that the point also flooded during tides measuring >36 cm. Conversely, if a point did not flood during tides measuring 19 cm at the tide gauge, I assumed that the point also did not flood during tides measuring <19 cm.

Statistical methods. I calculated flood frequency at each point (frequency = number of flooded events ÷ total number of tide events monitored, $n = 440$ points) then logit transformed flood frequency using ln[frequency/(1-frequency)]. This enabled me to model flood frequency as a continuous variable while maintaining a 0-1 boundary. First, I compared mean flood frequency between unrestricted (UNR) and restricted treatments and between low and high reaches (reaches above 1 and 2 roads combined). Second, I looked at the restricted-only systems separately (i.e. Webhannet and Ogunquit) and compared means among three reaches: low (below road), above one road, and above two roads. I did this second comparison using only the restricted systems because unrestricted systems did not have a reach that was comparable to the restricted reach above two roads. In this way, I was able to investigate the effect of being above two roads.

Third, I modeled flood frequency in unrestricted and restricted systems using five main explanatory variables: treatment (T: unrestricted vs. restricted), reach (REACH: low vs. high), mean tide height of flooded events (HT: measured at NOAA Portland Buoy, 43.529856° N, -70.144325° W), mean precipitation of flooded events (PPT: measured at the nearest NOAA weather station with precipitation data, Grey, ME, 43.899986° N, -70.249995° W), and distance to the nearest impervious surface, defined here as any paved parking lot or road (RD, measured in ArcGIS). I predicted that the effect of HT would differ between low and high reaches and that this REACH×HT interaction effect would differ between restricted and unrestricted systems. Therefore, I included a T×REACH×HT interaction in the analysis. All nested interaction effects were also included in the analysis. I was also interested in whether impervious surfaces interacted with rainfall, creating runoff and increasing flooding. To examine this question, I included a RD×PPT interaction. Although this variable is course and might not capture some of the variation between impervious surfaces, I hoped that it would provide preliminary information that might be useful for future analyses. Rainfall was much heavier during 2009 so I included a PPT×YR interaction. I hypothesized 15 models *a priori* (not including a null model of constant variance, see Table 2.3) and used an information theoretic approach to compare multiple models (Burnham and Anderson 2002). I report Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c score between the best model with the lowest AIC_c and each i^{th} model (ΔAIC_c), and Akaike's weight of evidence (w_i).

Fourth, I modeled flood frequency on restricted-only marshes using REACH (below vs. above1 vs. above2), HT, PPT, and RD as explanatory variables. I included REACH×HT, RD×PPT, and PPT×YR interaction effects. I hypothesized 11 models *a priori* (see Table 2.5) and used the same information theoretic approach described above. This fourth step allowed me to investigate effects of being above a two-road restriction.

For all four analyses, I used linear mixed models with RIVER (Webhannet, Ogunquit, Nonesuch, or Libby) as a random intercept. Year (YR), distance upriver from the beginning of marsh habitat (MOUTH), standard deviation of mean tide HT (SDHT), and standard deviation of mean PPT (SDPPT) were used as covariates because they helped improve model fit. I evaluated model assumptions graphically for each global model and assessed spatial auto-correlation between model residuals using correlograms (0-200 m lag distances). I report means ±1 SE and interpret $\alpha < 0.05$ as significant. From model comparison analyses, I report parameter estimates and 95% confidence intervals from the best AIC models. I interpret 95% confidence intervals that do not overlap zero as significant. I conducted all analyses in R v.2.11.1 (R Development Core Team 2011).

Objective 2.3: Vegetation patterns in high-marsh habitat

Field methods. I characterized high-marsh vegetation within a 1-m^2 quadrat centered on each random point using a point-intercept method (Brower and Zar 1984, n = 335 points). I recorded every species that intercepted 10 evenly-spaced points along five, 1-m long, transects (50 points per quadrat). I used frequency of occurrence (total number of intercepted points ÷ 50) as an index of species cover. In addition, I measured thatch depth (dead grass from prior growing seasons still rooted in the ground) at one randomly chosen point per transect (five measurements per quadrat). All vegetation measurements were conducted towards the end of the growing season, Jul – Aug.

Statistical methods. I examined five dependent vegetation variables: mean thatch depth, cover of *Spartina alterniflora, S. patens, Juncus gerardii,* and salt-tolerant forbs (*Limonium nashii+Salicornia europaea*). I chose these variables because they are common high-marsh species (*S. patens* and *J. gerardii*), common low-marsh species (*S. alterniflora*), highly tolerant to hypersaline conditions (the forbs, Bertness and Ewanchuk 2002), and are used by nesting sharp-tailed sparrows (thatch, *S. alterniflora, S. patens,* and *J. gerardii*; Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008). I logtransformed thatch depth to meet model assumptions: ln(THATCH + 1). Cover variables were logit-transformed in order to model them as continuous variables while maintaining a 0-1 boundary: ln[frequency/(1-frequency)].

For each dependent variable, I constructed four linear mixed models with river as a random intercept and year as a covariate. First I compared means between unrestricted and restricted treatments and between low and high reaches. Second, I looked at the restricted-only systems and compared means among three reaches: low (below road), above one road, and above two roads. Third, I modeled vegetation from unrestricted and restricted systems using T, REACH (low vs. high), and flood frequency (FLOOD) as explanatory variables. I predicted that the effect of flooding would differ between low and high reaches and that this REACH×FLOOD interaction effect would differ between restricted and unrestricted systems. Thus, I included a T×REACH×FLOOD interaction and all nested interaction effects. Fourth, I modeled vegetation from restricted-only marshes using REACH (below vs. above1 vs. above2) and FLOOD as explanatory variables. I included a REACH×FLOOD interaction. For all four analyses, I used linear mixed models with RIVER as a random intercept and YR as a covariate.

I evaluated model assumptions graphically and assessed spatial auto-correlation between model residuals (correlograms, 0-200 m lag distances). Three variables showed evidence of residual spatial auto-correlation (*S. alterniflora, S. patens,* and *J. gerardii*). However, I continued the analyses with the understanding that additional variation remained unaccounted for by these models. I report means ± 1 SE, parameter estimates ± 1 SE and use $\alpha < 0.05$ to define significance. All analyses were conducted in R v.2.11.1 (R Development Core Team 2011).

Results

Objective 2.1: Description of tidal flow adjacent to tidal restriction

Above the 47-m wide one-road restriction on the Webhannet River, maximum tide height was not lower at the gauge located immediately above the road compared to the gauge located immediately below (above = 20.4 ± 1.6 cm, below = 19.7 ± 1.7 cm, t = -3.05, P = 0.99, Figure 2.3a). I did not detect a significant delay in timing of high tide above the road (above = 0.4 ± 0.7 min, below = 1.6 ± 0.6 min, t = 1.63, P = 0.11). Rate of falling tide was not slower above the road (above = 1.8 ± 0.04 min/cm, below = 2.1 ± 0.1 min/cm, t = 7.43, P = 0.99), indicating no pooling above the road during the falling tide.

Above the 25-m wide one-road restriction on the Ogunquit River, tide height was 1.7 cm lower above the road compared to the gauge below (above = 21.4 ± 1.6 cm, below = 23.1 ± 1.6 cm, t = 4.93, $P < 0.01$, Figure 2.3b). Timing of high tide was delayed above the road (above = 28.6 ± 1.0 min, below = 0.7 ± 0.4 min, t = 11.60, $P < 0.01$). Rate of falling tide was ~2 min/cm slower above the road, indicating pooling behind the road (above = 3.7 ± 0.1 min/cm, below = 1.9 ± 0.1 min/cm, t = -20.27, $P < 0.01$).

Above the 3-m wide two-road restriction on the Ogunquit River, tide height was 9.9 cm lower above the road compared to the gauge below (above = 16.6 ± 1.1 cm, below = 26.5 ±3.2 cm, t = 2.48, P = 0.02, Figure 2.3c), and timing of high tide was delayed (above = 20.4 ± 4.2 min, below = 2.5 ± 1.5 min, t = -3.37, $P < 0.01$). Rate of falling tide was 4.9 min/cm slower above the road (above = 8.1 ± 1.6 min/cm, below = 3.1 ± 0.3 min/cm, t = -2.80, P = 0.01).

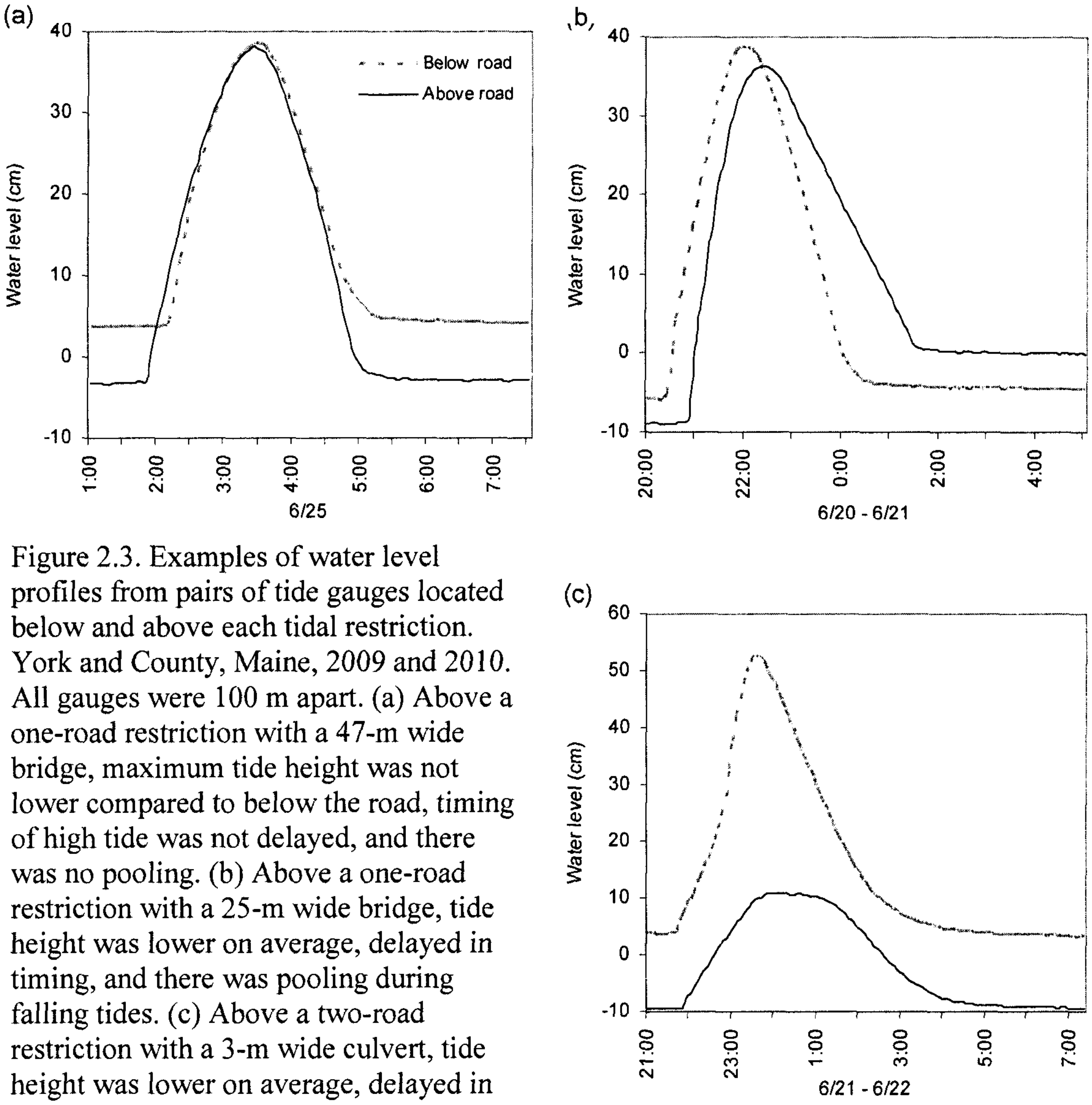

Figure 2.3. Examples of water level profiles from pairs of tide gauges located below and above each tidal restriction. York and County, Maine, 2009 and 2010. All gauges were 100 m apart. (a) Above a one-road restriction with a 47-m wide bridge, maximum tide height was not lower compared to below the road, timing of high tide was not delayed, and there was no pooling. (b) Above a one-road restriction with a 25-m wide bridge, tide height was lower on average, delayed in timing, and there was pooling during falling tides. (c) Above a two-road restriction with a 3-m wide culvert, tide height was lower on average, delayed in timing, and there was pooling during falling tides.

On the unrestricted Libby River, maximum tide height was not reduced at the upriver gauge compared to the one located 100 m downriver (upper gauge = 21.8 ± 13.5 cm, lower gauge = 19.2 ± 14.54 cm, t = -6.07, P = 0.99). I did not detect a significant delay in timing at the upriver gauge (upper gauge = 0.8 ± 8.3 min, lower gauge = 2.2 ± 5.7 min, t = 1.44, P = 0.16, Figure 2.4a). I did not detect a significant difference in rate of falling tide (upper gauge = 1.7 ± 0.4 min/cm, lower gauge = 1.6 ± 0.5 min/cm, $t = 0.93$, $P = 0.36$), indicating no pooling. On the unrestricted Nonesuch River, maximum tide height was not reduced at the upriver gauge (upper gauge = 28.35 ± 11.7 cm, lower gauge = 28.22 ± 11.7 cm, $t = 53.39$, $P = 0.99$, Figure 2.4b). I did not detect a significant delay in timing of high tide (upper gauge = 0.3 ± 7.0 min, lower gauge = 1.0 ± 3.8 cm, $t = -1.37$, $P = 0.18$). Nor was I able to detect evidence of pooling during the falling tide (upper gauge = 1.7 ± 0.6 min/cm, lower gauge = 1.8 ± 0.5, $t = 0.33$, $P = 0.74$).

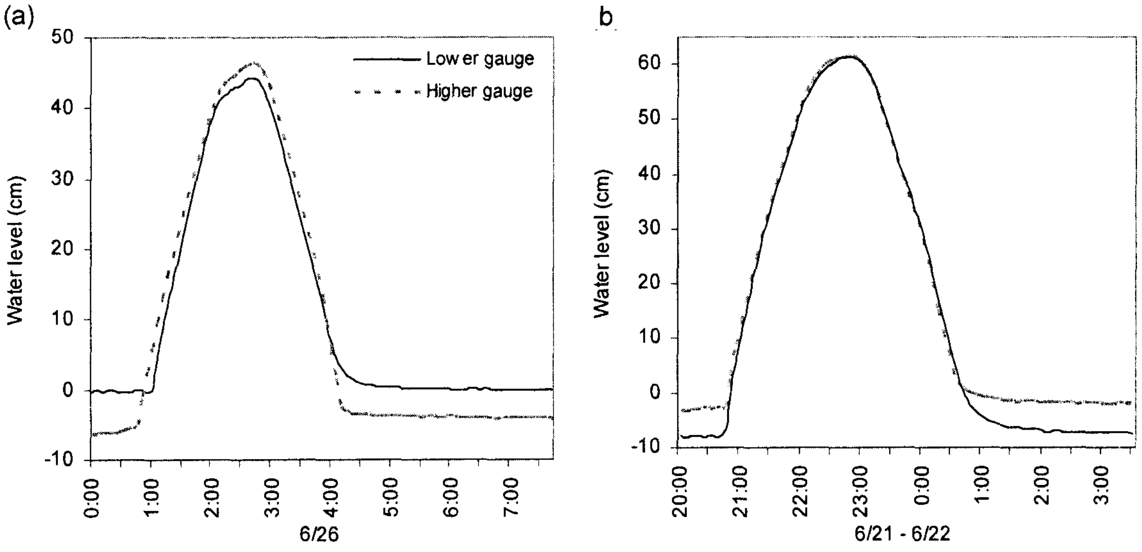

Figure 2.4. Examples of water level profiles from paired tide gauges located on unrestricted rivers. Cumberland County, Maine, 2009 and 2010. All gauges were 100 m apart. (a) Libby River tide height varied between gauges, but on average maximum tide height did not decrease for gauges located further upriver. Also, there was no significant delay in timing of high tide and no evidence of pooling at any gauge. (b) Nonesuch River tide height did not decrease for gauges located further upriver, nor was there a delay in timing between gauges or evidence of pooling.

Objective 2.2: Flood frequency in high-marsh habitat

Flooding patterns differed significantly between unrestricted and restricted systems ($t = -4.97$, $P < 0.01$; Figure 2.5a). In unrestricted systems, random points on low reaches flooded less frequently than points located on high reaches, whereas in restricted systems there was no difference in flood frequency between low and high reaches. When restricted-only systems were analyzed separately, significant differences were apparent: flood frequency did not differ significantly between points located below roads and points located above one road ($t = -1.71$, $P = 0.09$), but points located above two roads flooded less frequently than points further downriver ($t = -2.63$, $P < 0.01$, Figure 2.5a).

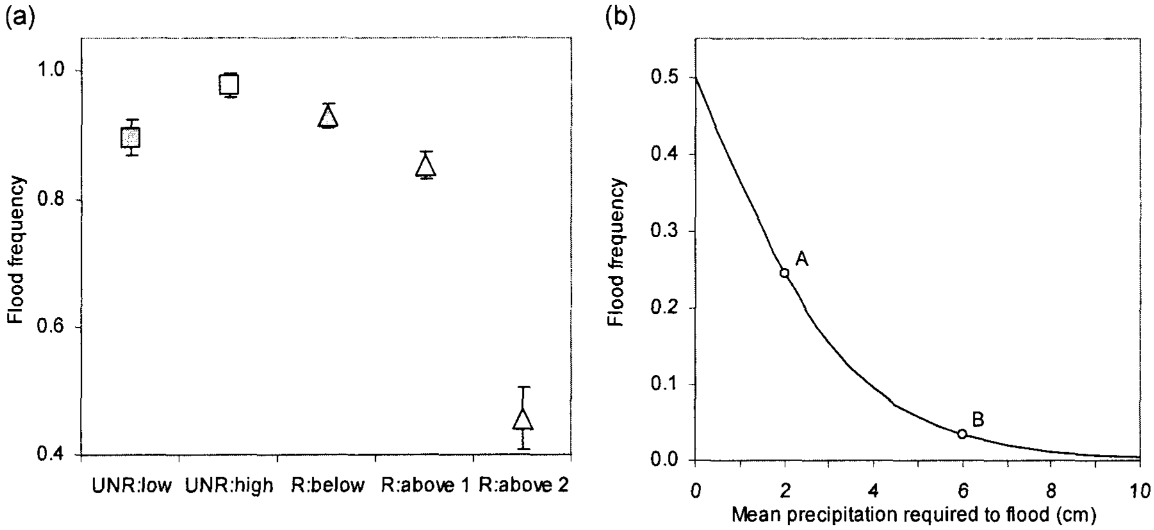

Figure 2.5. Mean flood frequency of available high-marsh habitat and effect of precipitation on flood frequency. York and Cumberland Counties, Maine, 2009 and 2010. (a) Flood frequency on unrestricted systems (squares) was significantly greater in high reaches vs. low. Flooding on restricted rivers (triangles) was equal between below road areas (low reach) and above one road, but it was significantly reduced above two roads. (b) At points that flooded 24% of the time (point A), rainfall needed to be ≥2 cm before flooding occurred. At points that flooded just 3% of the time (point B), rainfall needed to be ≥6 cm.

Model analysis of the combined unrestricted and restricted dataset found the full model to have the best support (ΔAIC_c of next best model = 210, Table 2.3). The full model contained all explanatory variables; however, of the variables of interest, only tide height and PPT×YR interactions had significant effects (Table 2.4, Figure 2.5b). The effect of tide height did not differ significantly between unrestricted and restricted systems or between low and high reaches (T×REACH×HT effect, Table 2.4). There was no evidence for increased flooding due to rain runoff next to impervious surfaces using the variable PPT×RD (Table 2.4).

Table 2.3. Model selection results from flood frequency analysis, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. Sixteen *a priori* models were hypothesized and compared using AIC_c. Also shown are number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
T×REACH×HT, RD×PPT, YR×PPT, MOUTH, SDHT, SDPPT	16	1256	0	1.0
T×REACH×HT, MOUTH, SDHT, YR	11	1466	210	0.0
T×REACH, REACH×HT, T×HT, MOUTH, SDHT, YR	10	1471	215	0.0
REACH, T×HT, MOUTH, SDHT, YR	8	1486	230	0.0
HT, T×REACH, MOUTH, SDHT, YR	8	1488	232	0.0
T, REACH×HT, MOUTH, SDHT, YR	8	1493	237	0.0
T, REACH, HT, MOUTH, SDHT, YR	7	1494	238	0.0
HT, MOUTH, SDHT, YR	5	1497	241	0.0
YR×PPT, MOUTH, SDPPT	6	1677	421	0.0
PPT, MOUTH, SDPPT, YR	5	1706	450	0.0
PPT, RD, MOUTH, SDPPT, YR	6	1709	453	0.0
RD×PPT, MOUTH, SDPPT, YR	7	1714	458	0.0
T×REACH, MOUTH, YR	6	1719	463	0.0
Constant	1	1727	471	0.0
T, REACH, MOUTH, YR	5	1740	484	0.0
MOUTH, YR	3	1743	487	0.0

[a] Models with interaction effects also included all nested interactions and main effects.

Table 2.4. Parameter estimates from the best AIC model of the flood analysis, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a]. Significant (95% CI ≠ zero) parameters of interest are outlined in grey.

Parameter	Estimate	SE	df	95% confidence interval
Intercept	121.40	7.29	422	107.11, 135.69
MOUTH[b]	0.00	0.00	422	-0.0001, 0.0004
YR (2010)[b]	-4.96	0.62	422	-6.17, -3.75
PPT	-0.56	0.37	422	-1.30, 0.17
RD	0.08	0.07	422	-0.07, 0.22
T (UNR)	12.28	6.01	2	-0.50, 24.06
REACH (L)	-0.80	6.17	422	-12.90, 11.30
HT	-36.42	2.08	422	-40.50, -32.34
SDPPT[b]	1.90	0.12	422	1.66, 2.14
SDHT[b]	-38.40	4.04	422	-46.32, -30.48
YR×PPT	-0.85	0.28	422	-1.39, -0.31
RD×PPT	-0.05	0.05	422	-0.14, 0.04
T×REACH	-14.65	9.13	422	-32.54, 3.25
T×HT	0.04	1.71	422	-3.32, 3.39
REACH×HT	0.33	1.99	422	-3.57, 4.23
T×REACH×HT	4.06	2.78	422	-1.38, 9.50

[a]Induced correlation of random effect = 0.67, [b]variable was used as a covariate.

Model analysis of the restricted-only dataset also found best support for the full model, (Table 2.5). Significant explanatory variables of interest were the REACH×HT interaction and PPT×YR interaction, (Table 2.6). For points located above two restrictions, higher tides were needed to achieve the same flood frequency as points located below roads; in areas above only one road, lower tides were able to achieve the same flood frequency as points located below roads (Figure 2.6a). There was no evidence for increased flooding due to rain runoff next to impervious surfaces using the PPT×RD variable (Table 2.6).

Table 2.5. Model selection results from flood frequency analysis, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. Eleven *a priori* models were hypothesized and compared using AIC_c. Also shown are number of model parameters (K), and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
REACH×HT, YR×PPT, RD×PPT, MOUTH, SDPPT, SDHT	14	661	0	1.0
REACH×HT, RD×PPT, MOUTH, YR, SDPPT, SDHT	13	685	24	0.0
REACH×HT, MOUTH, YR, SDHT	9	827	166	0.0
HT, MOUTH, YR, SDHT	5	834	173	0.0
REACH, HT, MOUTH, YR, SDHT	7	836	175	0.0
YR×PPT, MOUTH, SDPPT	6	962	301	0.0
PPT, YR, MOUTH, SDPPT	5	979	318	0.0
PPT, RD, MOUTH, YR, SDPPT	6	981	319	0.0
RD×PPT, MOUTH, YR, SDPPT	7	982	321	0.0
REACH, MOUTH, YR	5	985	324	0.0
Constant	1	1002	341	0.0
MOUTH, YR	3	1005	344	0.0

[a] Models with interaction effects also included all nested interactions and main effects.

Table 2.6. Parameter estimates from the best AIC model of the flood analysis, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	95% confidence interval
Intercept	127.15	9.73	235	108.07, 146.23
MOUTH[b]	0.00	0.00	235	-0.0001, 0.0006
YR (2010)[b]	-4.63	0.74	235	-6.08, -3.19
PPT	-0.60	0.45	235	-1.48, 0.29
RD	0.10	0.09	235	-0.08, 0.29
REACH (A1)	13.88	6.19	235	1.74, 26.02
REACH (A2)	-23.79	6.61	235	-36.74, -10.84
HT	-38.40	2.82	235	-43.93, -32.86
SDPPT[b]	2.22	0.15	235	1.93, 2.51
SDHT[b]	-38.73	5.01	235	-48.56, -28.90
YR×PPT	-1.58	0.30	235	-2.17, -0.99
RD×PPT	-0.02	0.06	235	-0.15, 0.10
REACH×HT (A1)	-4.54	2.00	235	-8.47, -0.62
REACH×HT (A2)	7.40	2.12	235	3.25, 11.56

[a] Induced correlation of random effect = 0.68, [b] variable was used as a covariate

Objective 2.3: Vegetation patterns in high-marsh habitat

In general, vegetation composition of high-marsh habitat was similar between unrestricted and restricted systems and between low and high reaches (Figure 2.6b).

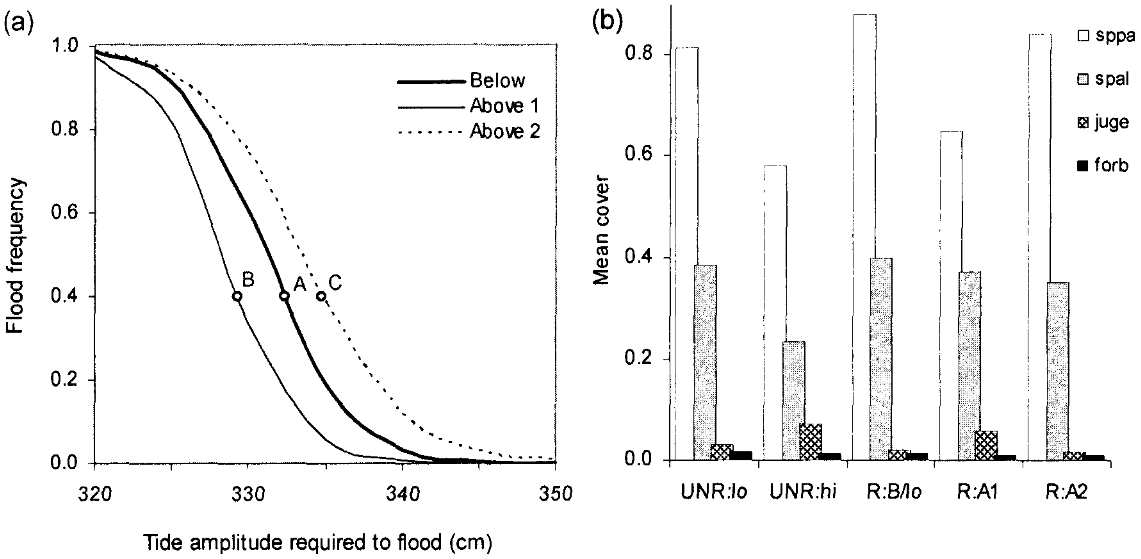

Figure 2.6. Effect of tide amplitude on flood frequency and vegetative composition of available high-marsh habitat. York and Cumberland Counties, Maine, 2009 and 2010. (a) It took higher tides to flood at the same rate in the area above two roads. For example, for points that flooded 40% of the time, tides needed to be ≥332 cm in order to flood areas below restriction (point A), ≥329 cm in order to flood above one road (point B), and ≥335 cm in order to flood above two roads (point C). (b) Composition and cover on of common salt-marsh plant species were similar among reaches. Species codes: forb = *Limonium nashii+Salicornia europaea*, spal = *Spartina alterniflora*, juge = *Juncus gerardii*, and sppa = *S. patens*.

Thatch depth. Thatch depth did not differ between unrestricted and restricted systems or between high and low reaches (t = 0.70, P = 0.49). Nor did it differ significantly among reaches that were below all, above one, or above two restrictions (below vs. A1: t = 1.42, P = 0.16; below vs. A2: t = -0.04, P = 0.97). In addition, modeling revealed no significant trends between thatch depth and any of the explanatory variables (Tables 2.7 and 2.8).

Table 2.7. Parameter estimates from thatch depth model analysis, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	t	P
Intercept	1.36	0.20	424	6.82	< 0.01
T (UNR)	0.05	0.49	2	0.10	0.93
REACH (L)	-0.47	0.45	424	-1.04	0.30
FLOOD	0.29	0.23	424	1.24	0.22
YR (2010)[b]	0.11	0.08	424	1.32	0.19
T×REACH	0.46	0.69	424	0.66	0.51
T×FLOOD	-0.07	0.55	424	-0.13	0.90
REACH×FLOOD	0.36	0.52	424	0.70	0.48
T×REACH×FLOOD	-0.31	0.80	424	-0.39	0.70

[a]Induced correlation of random effect < 0.001, [b]variable was used as a covariate

Table 2.8. Parameter estimates from thatch depth model analysis, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	t	P
Intercept	0.73	0.44	242	1.66	0.10
REACH (A1)	0.22	0.55	242	0.40	0.69
REACH (A2)	0.73	0.46	242	1.58	0.12
FLOOD	0.81	0.48	242	1.71	0.09
YR (2010)[b]	0.17	0.11	242	1.51	0.13
REACH×FLOOD (A1)	-0.03	0.63	242	-0.05	0.96
REACH×FLOOD (A2)	-0.97	0.59	242	-1.65	0.10

[a]Induced correlation of random effect = 0.02, [b]variable was used as a covariate.

Spartina alterniflora. Cover did not differ between unrestricted and restricted systems or between high and low reaches ($t = 1.07$, $P = 0.29$). Nor did it differ among reaches that were below all, above one, or above two restrictions (below vs. A1: $t = -0.26$,

$P = 0.78$, below vs. A2: $t = -0.41$, $P = 0.68$). Using the combined unrestricted and restricted dataset for model analysis, flood frequency had a complicated effect on *S. alterniflora* cover, which varied between unrestricted and restricted systems (T×FLOOD: $t = -2.13$, $P = 0.03$) and between high and low reaches (REACH×FLOOD: $t = -2.29$, $P = 0.02$, Table 2.9, Figure 2.7a). In the restricted-only models, flood frequency had a negative effect on *S. alterniflora* cover in areas located below and above one road ($t = -1.94$, $P = 0.05$). Above two roads, however, flooding had a positive effect (difference between below and A2: $t = 3.09$, $P < 0.01$, Table 2.10, Figure 2.7a).

Table 2.9. Parameter estimates from analysis of *Spartina alterniflora* cover, unrestricted and restricted systems combined. York and Cumberland Counties, Maine 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	-0.60	0.84	424	-0.72	0.47
T (UNR)	2.41	1.72	2	1.40	0.30
REACH (L)	3.30	1.41	424	2.33	0.02
FLOOD	0.39	0.74	424	0.53	0.60
YR (2010)[b]	-0.86	0.26	424	-3.29	< 0.01
T×REACH	-2.22	2.21	424	-1.01	0.32
T×FLOOD	-3.65	1.71	424	-2.13	0.03
REACH×FLOOD	-3.75	1.64	424	-2.29	0.02
T×REACH×FLOOD	2.64	2.55	424	1.03	0.30

[a]Induced correlation of random effect = 0.08, [b]variable was used as a covariate

Table 2.10. Parameter estimates from analysis of *Spartina alterniflora* cover, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	2.10	1.37	242	1.54	0.13
REACH (A1)	-0.78	1.78	242	-0.44	0.66
REACH (A2)	-4.27	1.52	242	-2.81	0.01
FLOOD	-2.95	1.52	242	-1.94	0.05
YR (2010)[b]	-0.40	0.37	242	-1.09	0.28
REACH×FLOOD (A1)	0.71	2.04	242	0.35	0.73
REACH×FLOOD (A2)	5.89	1.91	242	3.09	< 0.01

[a]Induced correlation of random effect = 0.00, [b]variable was used as a covariate.

Spartina patens. Cover did not differ between unrestricted and restricted systems (t = -0.83, P = 0.50), but it did differ between low and high reaches (t = 2.48, P = 0.01, Figure 2.7b). Looking at restricted-only systems, I found significantly less *S. patens* cover above one road but not above two (below vs. A1: t = -3.04, P < 0.01; below vs. A2: t = -0.58, P = 0.57, Figure 2.7b). From the combined unrestricted and restricted model analysis, flood frequency had a positive effect on *S. patens* cover in low reaches but a negative effect in high reaches (t = 2.18, P = 0.03, Table 2.11, Figure 2.8a). This pattern was the same regardless of restriction (T×REACH×FLOOD effect: t = -1.16, P = 0.25). In the restricted-only models, flood frequency did not have a significant effect on cover of *S. patens* in areas below and above one road (t = 1.65, P = 0.10). However, above two roads, flooding had a negative effect on *S. patens* cover (difference between below and A2: t = -2.22, P = 0.03, Table 2.12, Figure 2.8a).

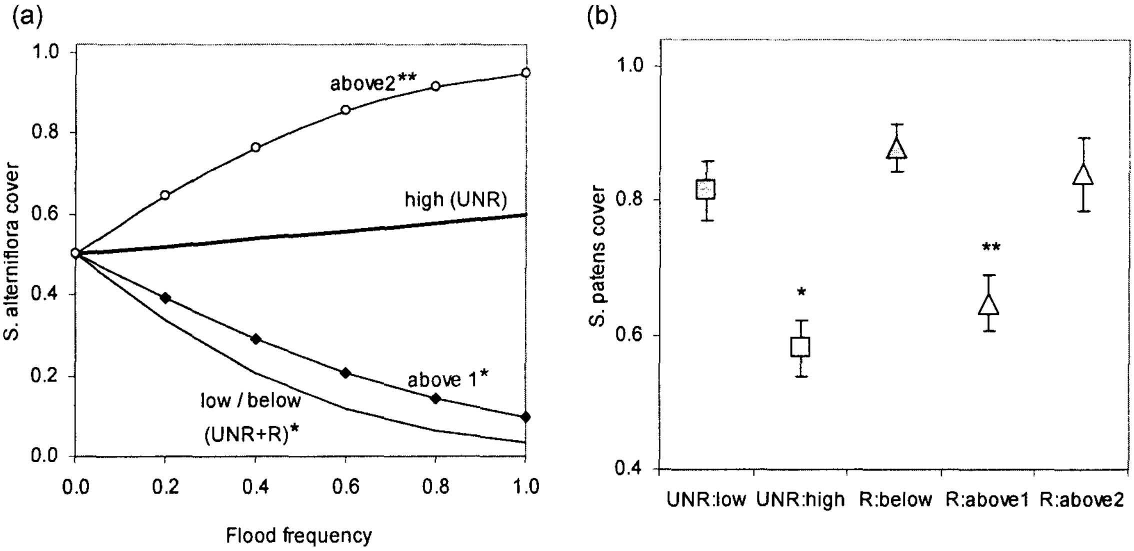

Figure 2.7. Effect of flood frequency on cover of *Spartina alterniflora* and mean cover of *S. patens* in unrestricted and restricted systems. York and Cumberland Counties, Maine, 2009 and 2010. (a) Flood frequency had a negative effect on *S. alterniflora* cover in low reaches of unrestricted systems, in areas below the roads on restricted systems (low reaches), and above one road in restricted systems. It had little effect on cover in high reaches of unrestricted systems. On restricted systems in the area above two roads, flooding had a positive effect on cover. (b) Cover of *S. patens* on unrestricted systems (squares) was significantly reduced in high reaches vs. low. Cover on restricted systems (triangles) was significantly less in areas above one road vs. areas below roads and the area above two roads.

Table 2.11. Parameter estimates from analysis of *Spartina patens* cover, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	1.55	0.86	424	1.81	0.07
T (UNR)	-1.22	1.96	2	-0.62	0.60
REACH (L)	-2.59	1.74	424	-1.48	0.14
FLOOD	-0.96	0.91	424	-1.05	0.29
YR (2010)[b]	-0.57	0.32	424	-1.76	0.08
T×REACH	3.18	2.72	424	1.17	0.24
T×FLOOD	0.95	2.11	424	0.45	0.65
REACH×FLOOD	4.41	2.02	424	2.18	0.03
T×REACH×FLOOD	-3.66	3.14	424	-1.16	0.25

[a]Induced correlation of random effect = 0.00, [b]variable was used as a covariate.

Table 2.12. Parameter estimates from analysis of *Spartina patens* cover, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
(Intercept)	-0.45	1.54	242	-0.29	0.77
REACH (A1)	-0.30	2.01	242	-0.15	0.88
REACH (A2)	3.12	1.71	242	1.83	0.07
FLOOD	2.82	1.71	242	1.65	0.10
YR (2010)[b]	-0.65	0.41	242	-1.57	0.12
REACH×FLOOD (A1)	-1.18	2.30	242	-0.51	0.61
REACH×FLOOD (A2)	-4.77	2.15	242	-2.22	0.03

[a]Induced correlation of random effect = 0.00, [b]variable was used as a covariate.

Juncus gerardii. Cover did not differ between unrestricted and restricted systems ($t = 0.83$, $P = 0.49$) but was significantly higher on high versus low reaches ($t = -2.19$, $P = 0.03$, Figure 2.8b). When restricted-only systems were compared, I found significantly more *J. gerardii* above one road compared to below ($t = 3.63$, $P < 0.01$), however, cover was similar between areas below restriction and above two restrictions ($t = -0.59$, $P = 0.56$, Figure 2.8b). From the combined unrestricted and restricted model analysis, flood frequency had a positive effect on *J. gerardii* cover ($t = 3.51$, $P < 0.01$, Table 2.13, Figure 2.9a), and this pattern was not significantly different between restriction or reach (T×REACH×FLOOD: $t = 1.83$, $P = 0.07$). In the restricted-only models, flood frequency had a positive effect on *J. gerardii* in areas above one road but no effect in areas below restriction or above two restrictions (below vs. A1: $t = 2.10$, $P = 0.04$; below vs. A2: $t = 0.85$, $P = 0.39$, Table 2.14, Figure 2.9a).

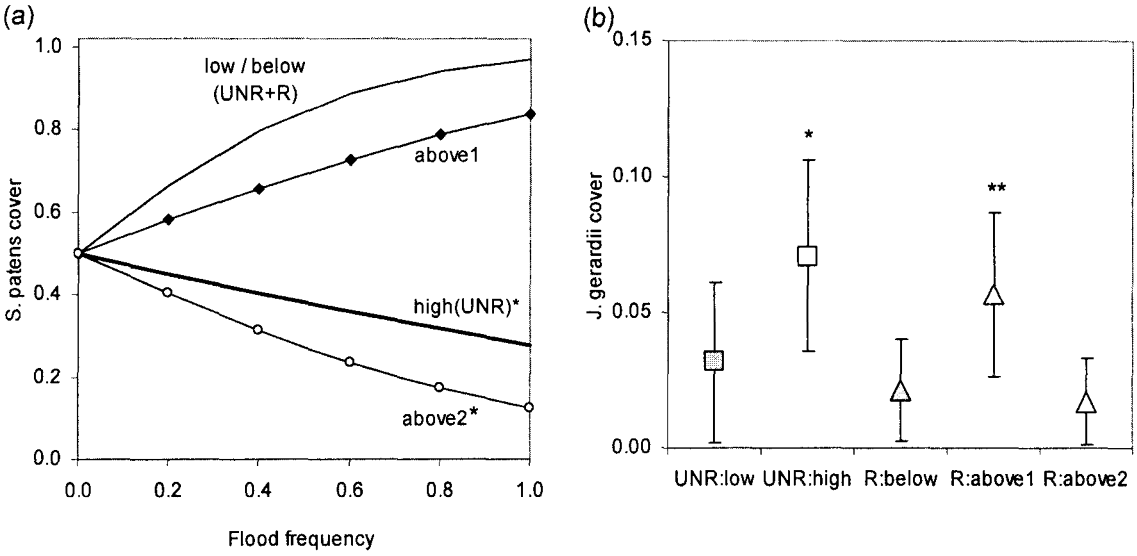

Figure 2.8. Effect of flood frequency on *Spartina patens* cover and mean cover or *Juncus gerardii* in unrestricted and restricted systems. York and Cumberland Counties, Maine, 2009 and 2010. (a) Flood frequency had a non-significant effect on cover of *S. patens* in low reaches of unrestricted systems, below roads on restricted systems, and above one road of restricted systems. It had a negative effect in high reaches of unrestricted systems and above two roads on restricted systems. (b) Cover of *J. gerardii* on unrestricted systems (squares) was significantly greater in high reaches vs. low. Cover on restricted systems (triangles) was significantly higher in areas above one road vs. areas below roads and the area above two roads.

Table 2.13. Parameter estimates from analysis of *Juncus gerardii* cover, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	-4.93	0.82	424	-6.00	< 0.01
T (UNR)	1.70	1.57	2	1.09	0.39
REACH (L)	1.30	1.20	424	1.08	0.28
FLOOD	2.21	0.63	424	3.51	< 0.01
YR (*2010*)[b]	-0.52	0.22	424	-2.36	0.02
T×REACH	-3.09	1.87	424	-1.65	0.10
T×FLOOD	-1.57	1.45	424	-1.09	0.28
REACH×FLOOD	-2.57	1.39	424	-1.85	0.07
T×REACH×FLOOD	3.96	2.17	424	1.83	0.07

[a]Induced correlation of random effect = 0.00, [b]variable was used as a covariate.

Table 2.14. Parameter estimates from analysis of *Juncus gerardii* cover, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	-3.63	1.04	242	-3.50	< 0.01
REACH (A1)	-1.59	1.29	242	-1.23	0.22
REACH (A2)	-0.91	1.08	242	-0.84	0.40
FLOOD	-0.32	1.12	242	-0.28	0.78
YR (2010)[b]	-0.59	0.26	242	-2.29	0.02
REACH×FLOOD (A1)	3.10	1.47	242	2.10	0.04
REACH×FLOOD (A2)	1.18	1.38	242	0.85	0.39

[a]Induced correlation of random effect = 0.00, [b]variable was used as a covariate.

Halophytic forbs (Limonium nashii+Salicornia europaea). Halophytic forbs were rare (mean frequency = 0.01 ± 0.53 per m^2), and cover did not differ between unrestricted and restricted systems ($t = -1.44$, $P = 0.15$). However, there was significantly more halophytic forb cover in low vs. high reaches ($t = 2.63$, $P = 0.01$, Figure 2.9b). When restricted-only systems were compared, there were significantly more halophytic forbs below roads compared to above one road ($t = -3.10$, $P < 0.01$) and above two roads ($t = -2.25$, $P = 0.03$, Figure 2.9b). Combined unrestricted and restricted model analysis did not reveal any effect of flood frequency on forb cover ($t = 0.60$, $P = 0.55$), and this did not differ across restriction or reach (T×REACH×FLOOD: $t = -0.79$, $P = 0.430$, Table 2.15). Results were similar in the restricted-only models, flood frequency was not significantly related to forb cover ($t = 1.37$, $P = 0.17$), and patterns did not differ between areas below vs. above one road ($t = -0.39$, $P = 0.69$) or below vs. above two roads ($t = -1.12$, $P = 0.27$, Table 2.16).

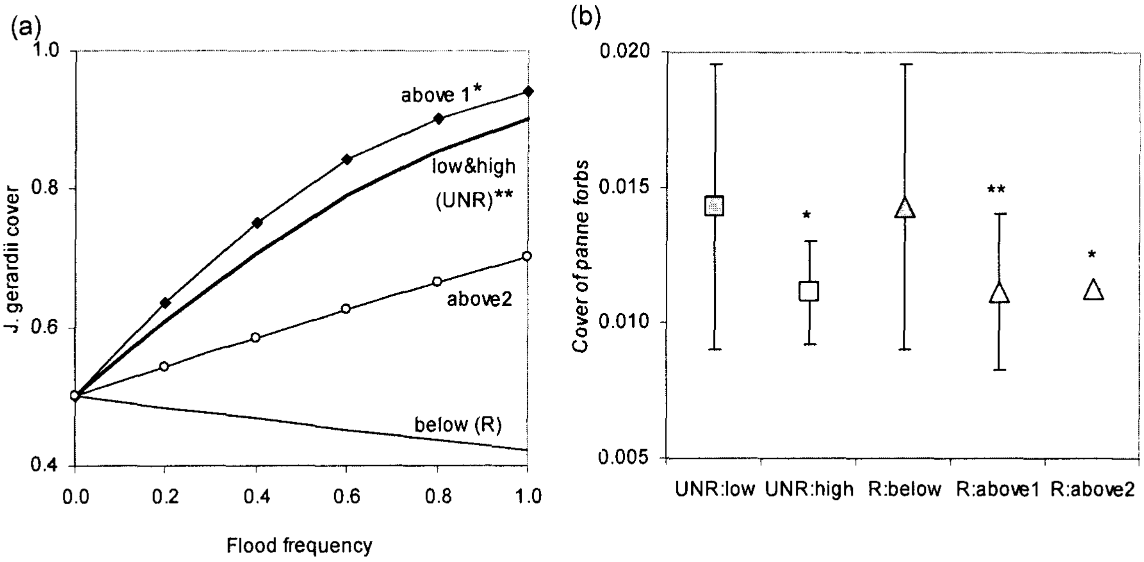

Figure 2.9. Effect of flood frequency on *Juncus gerardii* cover and mean cover of halophytic forbs (*Limonium nashii+Salicornia europaea*) in unrestricted and restricted systems. York and Cumberland Counties, Maine, 2009 and 2010. (a) Flood frequency had a positive effect on cover of *J. gerardii* in high and low reaches of unrestricted systems. On restricted systems, flooding also had a positive effect in areas located above one road, but it had little to no effect in areas located below roads and above two roads. (b) On unrestricted systems (squares), halophytic forb cover was significantly less on high reaches vs. low. On restricted rivers (triangles), cover was significantly less in areas above one and two roads compared to areas below roads.

Table 2.15. Parameter estimates from analysis of halophytic forb cover (*Limonium nashii+Salicornia europaea*), unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. River was used as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	-4.60	0.18	424	-25.16	< 0.01
T (UNR)	-0.18	0.43	2	-0.42	0.72
REACH (L)	-0.11	0.39	424	-0.28	0.78
FLOOD	0.12	0.20	424	0.60	0.55
YR (2010)[b]	0.01	0.07	424	0.10	0.92
T×REACH	0.36	0.61	424	0.59	0.56
T×FLOOD	0.56	0.47	424	1.19	0.24
REACH×FLOOD	0.42	0.45	424	0.92	0.36
T×REACH×FLOOD	-0.55	0.70	424	-0.79	0.43

[a]Induced correlation of random effect = 0.00, [b]variable was used as a covariate.

Table 2.16. Parameter estimates from analysis of halophytic forb cover (*Limonium nashii+Salicornia europaea*), restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. River was included as a random intercept[a].

Parameter	Estimate	SE	df	*t*	*P*
Intercept	-4.63	0.31	242	-14.85	< 0.01
REACH (A1)	-0.10	0.38	242	-0.26	0.80
REACH (A2)	0.13	0.32	242	0.41	0.68
FLOOD	0.45	0.33	242	1.37	0.17
YR (2010)[b]	0.00	0.08	242	-0.01	0.99
REACH×FLOOD (A1)	-0.17	0.43	242	-0.39	0.69
REACH×FLOOD (A2)	-0.45	0.41	242	-1.12	0.27

[a]Induced correlation of random effect < 0.001, [b]variable was used as a covariate.

Discussion

Objective 2.1: Description of tidal flow adjacent to tidal restriction

The one-road restriction on the Webhannet River (a 47-m wide bridge) did not restrict tidal flow according to any of the variables measured here. Maximum tide height in high-marsh habitat was not lowered by the restriction. There was no delay in timing of tide height, and there was no pooling above the road during falling tides. The one-road restriction on the Ogunquit River (a 25-m wide bridge) restricted tidal flow to a small degree. On average, maximum tide height was slightly reduced above the road and timing of high tide was delayed. There was also some evidence of pooling behind the road during falling tides. The two-road restriction on the Ogunquit River (a 3-m wide culvert) was more restrictive. Maximum tide height was reduced to a greater extent above the culvert compared to other tidal restrictions in the study (height reduced by 9.9), though timing of high tide was delayed behind both types of restriction (20.4 ± 4.2 min vs. 28.6 ± 1.0 min delay above two-road and one-road restrictions, respectively). There was also evidence that pooling during falling tides was greater above the culvert compared to the other tidal restrictions in the study (5.0 vs. 1.8 min/cm slower draining of high-marsh habitat above the two-road and one-road restrictions, respectively). Pooling behind roads has been observed from other tidal restrictions (Costa 2000). In contrast, the two unrestricted systems exhibited none of these effects. There were no consistent patterns of maximum tide height decreasing further upriver, no delays in timing of high tide between gauges, and no indication of pooling. These results are consistent with expectations for unrestricted rivers.

Previous studies have focused on extremely severe tidal restrictions where marine input was completely excluded from above-road reaches via culvert gates or where it was greatly reduced by small-sized culverts <1.5 m in diameter (Burdick et al. 1997, Boumans et al. 2002, Roman et al. 2002). Tidal restriction in these prior studies resulted in severely altered tidal hydrology and virtual absence of daily fluctuation. Although it is impossible to directly compare my results with previous studies because of differences in tide gauge methodology, my results shed some light on the effect of moderate tidal restriction in high-marsh habitat. Management implications here are broad because the wide culverts and bridges are ubiquitous and affect most salt-marsh systems. The 3-m wide culvert on the Ogunquit River had a relatively larger restricting effect compared to the wide bridges, and the reduction in tide height above the culvert (9.9 cm) was on par with the height of a sharp-tailed sparrow nest. Anecdotally, relative elevations taken at each of the tide gauges surrounding the culvert suggest the marsh might be subsiding above the culvert (elevation below = 12.7 cm, above = 1.2 cm, Table 2.2). However, only four elevation measurements were taken and further work is necessary to identify marsh subsidence.

Objective 2.2: Flood frequency in high-marsh habitat

Flooding across high-marsh habitat does not occur daily as it does in low-marsh habitats. Rather, it takes place only during spring tide cycles (usually 1-2 weeks per lunar cycle). I measure flood frequency in high-marsh habitat. Thus, high flood frequencies from this study do not reflect daily flooding. Rather they indicate flooding during most spring tide events, whereas low frequencies indicate flooding by only some spring tide events.

Flooding patterns were different on unrestricted vs. restricted systems. In unrestricted systems, high reaches flooded more often than low reaches. On restricted systems, however, the highest reach, above two roads, flooded the *least.* This may have been due to tidal restriction created by the 3-m wide culvert. However, the unrestricted rivers may be unique because they are fluvial and have larger watersheds compared to the restricted rivers. It is possible that watershed size effected high-marsh flooding and was responsible for the opposite patterns observed here. It is unclear why high reaches on unrestricted rivers would have flooded more often than reaches located closer to the mouth of the river, although local marsh topography may have been responsible. The low-reach marsh of the unrestricted Nonesuch and Libby Rivers contain more sloughs and channels (pers. obs.). In addition, the river is much wider on the lower reaches. The channels and wider river may absorb some of the high tide events and prevent water from reaching high-marsh habitat. Conversely, in the high reaches, the river is narrower and there are fewer channels (pers. obs.). .

On restricted systems, flood frequency was least affected by high tides in the reach above two roads. This is not surprising given the dampened tide height at the tide gauge located above the two-road restriction. It is also consistent with the above results of lower overall flood frequency above two roads. Interestingly, flood frequency was more affected by high tides in areas above one road compared to areas below all restriction. This is similar to patterns of overall flood frequency observed on unrestricted rivers and may be a factor of local marsh topography rather than restriction. The low reaches on the restricted systems (areas that were below all roads) had more channels and wider rivers compared to the upper reaches (pers. obs.), which may have helped absorb some of the rising tides.

On both unrestricted and restricted systems, precipitation increased high-marsh flooding. This may foretell more frequent flooding and greater freshwater influence in the future, as frequency and severity of storm events in New England are predicted to increase over the next few decades (Douglas and Fairbank 2011). This could have serious consequences for salt marshes since freshwater changes soil chemistry. Typical high-marsh species may begin to be outcompeted and replaced by brackish species (e.g. *Typha angustifolia*) or by brackish invasive species (e.g. *Phragmites australis*).

Objective 2.3: Vegetation patterns in high-marsh habitat

Vegetation patterns were highly variable among plant species, between restricted and unrestricted systems, and between high and low reaches. All reaches of all four marshes, however, had similar vegetative composition dominated by typical salt-marsh species. The common community structure may indicate that the restrictions I observed did not provide enough tidal restriction to greatly influence salt-marsh vegetation. Thus, although the two-road restriction on the Ogunquit River (the 3-m wide culvert) had a relatively larger restricting effect on tide height and flood frequency compared to the other restrictions, it did not cause obvious changes in vegetative species composition and cover. An alternate explanation is that the Ogunquit watershed is small, provides very little freshwater influence in general, and has high-marsh habitat that requires less tidal input. Tidal restriction, though present and significant, may not affect salt-marsh vegetation.

I related vegetative cover to flood frequency and tidal restriction because these plant species are known to tolerate varying degrees of salinity and might be indicators of altered hydrology resulting from tidal restriction. In addition, they are important species for nesting sharp-tailed sparrows. Resulting patterns between species cover and flood frequency were complicated and inconsistent with prior knowledge regarding salt tolerances. *Spartina alterniflora*, for instance, is largely a low-marsh plant that occurs in areas with daily tidal inundation (Bertness and Ewanchuk 2002, Crain et al. 2004, Bertness and Silliman 2008). Yet I found its occurrence to be *negatively* related to flood frequency. *S. patens*, on the other hand, is a typical high-marsh plant that cannot tolerate daily inundation (Bertness and Ewanchuk 2002, Crain et al. 2004, Bertness and Silliman 2008), and its cover *increased* in areas with higher flood frequency.

It is important to bear in mind that I measured flood frequency at the height of a sharp-tailed sparrow nest. It is possible that ground saturation from tidal flooding may have occurred at rates that are consistent with salt tolerances for these species. My scale of 10 cm above ground might be less relevant to salt-marsh vegetation than to nesting sharp-tailed sparrows. *S. alterniflora, S. patens, Juncus gerardii, Limonium nashii,* and *Salicornia europaea* have also been shown to respond strongly to competition (Bertness and Ewanchuk 2002, Crain et al. 2004, Bertness and Silliman 2008). Another potential explanation for these surprising results is that the scale at which I measured vegetation was too small to capture flood dynamics without confounding effects of species competition. For example, the negative relationship between *S. alterniflora* and flood frequency may be complicated by the fact that *S. alterniflora* is known to be outcompeted by *S. patens* (Bertness and Ewanchuk 2002), which was positively influenced by flood frequency in the same areas. Residual spatial auto-correlation observed with the *S. alterniflora, S. patens,* and *J. gerardii* models may indicate that my scale of measurement (1-m^2) was inadequate for detecting differences related to flood frequency. Alternatively, *S. alterniflora* is more salt-tolerant than *S. patens* (Bertness and Ewanchuk 2002, Crain et al. 2004, Bertness and Silliman 2008), and areas with low flood frequency may form hypersaline pools and panes through evaporation. Thus within the high marsh, areas that have less flooding may actually be more saline and hospitable to species like *S. alterniflora* than areas that receive more flooding.

The halophytic forb analysis (*L. nashii* and *Salicornia europaea*) did not have residual spatial auto-correlation. These forbs were fairly rare (mean frequency = 0.01 ± 0.53 per m^2), but they were more common in low reaches of all rivers, regardless of restriction. This did not appear to be influenced by flood frequency from spring tides. These forbs, like *S. alterniflora*, are more tolerant of saline conditions than other high-marsh species (Crain et al. 2004). Perhaps low reaches of these marshes had more locations that were hypersaline and more hospitable to these forbs. Halophytic forbs may also be more common where there has been disturbance from storms or ice scouring.

Perhaps low river reaches are more susceptible to disturbance, providing more area for these early colonizers.

These findings add new information to previous research regarding tidal restrictions, which focused on culverts <1.5 m wide and found tidal flow and high-marsh vegetation were clearly reduced above restriction (Bertness and Ellison 1987, Burdick et al. 1997, Costa 2000, Boumans et al. 2002, Roman et al. 2002). The large culvert and wide bridge-type tidal restriction studied here are much more common in salt marshes and results may have broad management implications. The large bridges did not appear to restrict spring high tide cycles very much, suggesting that tidal restrictions of this type might not be a large concern for high-marsh conservation. The 3-m wide culvert did appear to restrict tidal flow through reduced tide height and less frequent flooding of high-marsh habitat. Although vegetation composition was not greatly affected, reduced flood frequency above the culvert might impact sedimentation and might have negative effects on vegetation in the future. For this reason, it may be prudent to continue to monitor vegetation and elevation in the salt marsh above the culvert and in other marshes above similar tidal restrictions. This study focused solely on high-marsh habitat. Wide tidal restrictions may have greater negative effects on low-marsh habitat and on tidal flow within the river channel. Results here should not be construed to suggest that large culvert and wide bridge-type tidal restrictions do not affect tidal flooding outside of the high-marsh habitat.

CHAPTER 3

NELSON'S AND SALTMARSH SPARROW HABITAT QUALITY IN TIDALLY RESTICTED SALT MARSHES

Introduction

Salt marshes are unique environments at the interface between marine and terrestrial habitats. Intact marsh ecosystems are extremely valuable to both human and wildlife populations (Levin et al. 2001, Costanza et al. 1997), yet they have been subjected to extensive habitat loss and modification due to human activity (Hanson and Shriver 2006, Lotze et al. 2006, Gedan et al. 2009). For example, >80% of coastal wetlands in New England have been lost (Teal 1986). Tidal restrictions are created by roads and bridges that bisect salt marshes without allowing adequate tidal flow and are a common result of human development and urbanization. Restrictions can have many negative effects on salt-marsh ecosystems, including reduced tidal flow, reduced salinity, altered vegetative and invertebrate communities, eutrophication, and marsh subsidence (e.g., Burdick et al. 1997, Portnoy and Giblin 1997, Costa 1999 and 2000, Zedler et al. 2001, Roman et al. 2002, Mitchell et al. 2006, Gedan et al. 2009). Unfortunately, roads and bridges are a regular feature in New England marshes, and 28% of salt marshes in Maine are restricted by narrow culverts (HRSC 2006, Crain et al. 2008). In light of current understanding of the importance of salt-marsh ecosystems, many land managers are actively restoring restriction-degraded wetlands (Barret et al. 2006) and seeking alternatives to encourage natural marsh hydrology, including road removal and culvert or bridge improvement (Mitchell et al. 2006, RCNWR and MDIFW pers. comm.).

Saltmarsh Sparrows (*Ammodramus caudacutus*) and the salt-marsh subspecies of Nelson's Sparrow (*A. nelsoni subvirgatus*), collectively sharp-tailed sparrows, reside exclusively in salt marshes and are considered high conservation priorities (e.g., Carter et al 2000, MDIFW 2005, Atlantic Coast Joint Venture 2008, IUCN 2008). Because sharp-tailed sparrows nest close to the ground where tidal flooding causes >60% of nest failure (Greenlaw and Rising 1994, Gjerdrum et al. 2005, Shriver et al. 2007), they are particularly vulnerable to changes in hydrology. However, information regarding how tidal restrictions affect sharp-tailed sparrows is sparse or indirect. Research from Rhode Island suggests that Saltmarsh Sparrows nesting in severely restricted marshes may *benefit* from lack of tidal flow (greater habitat use, reduced nest flooding, and higher nest survival: DiQuinzio et al. 2002). However, other studies show that the grasses preferred by nesting females of both sharp-tailed sparrow species (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008) are *negatively* affected by severe tidal restriction (Burdick et al. 1997, Boumans et al. 2002, Roman et al. 2002). In addition, not all tidal restrictions are equal. Effects of extremely severe restriction caused by culverts <1.5 m in diameter have been well studied (e.g. Burdick et al. 1997, Portnoy and Giblin 1997, Boumans et al. 2002, DiQuinzio et al. 2002, Roman et al. 2002). However, many roads create less severe tidal restrictions (e.g. bridges >25 m wide) and have not yet been addressed in the literature. To effectively manage sharp-tailed sparrows, there is a clear need for additional research on nesting ecology in tidally restricted marshes, including consequences from a variety of restriction severities.

In the previous chapter, I found that flooding of high-marsh habitat from spring tide cycles was reduced behind a two-road restriction created by a 3-m wide culvert, while flooding was not reduced behind one-road restrictions created by bridges ≥25 m wide. In this chapter, I will examine sharp-tailed sparrow habitat quality surrounding these same tidal restrictions. According to Johnson (2007), density and reproductive parameters are some of the best ways to measure habitat quality. Because the available high-marsh habitat is not saturated and because sharp-tailed sparrows are not territorial, nest density might be a good indication of habitat preference and selection (Fretwell and Lucas 1970, Johnson 2007). However, habitat selection may not accurately reflect habitat quality (Van Horne 1983, Johnson 2007). Therefore, I will also investigate nest survival and nest flooding (the primary cause of nest failure). My objectives are: (1) to characterize differences in habitat use by nesting sharp-tailed sparrows, (2) to examine patterns of nest flooding, and (3) to characterize differences in nest survival in restricted and unrestricted areas. Ultimately, these results will help identify which types of tidal restriction may be of more or less concern for breeding populations of sharp-tailed sparrows and may help guide restoration efforts while minimizing negative impacts to these species of conservation concern.

Study Species

The Saltmarsh Sparrow is a salt-marsh specialist limited to a narrow margin of fragmented habitat along the Atlantic coast. Ninety percent of its breeding range is in the northeastern USA (Greenlaw and Rising 1994). They have strong site fidelity, often returning to the same marsh to breed year after year (DiQuinzio et al. 2001 and 2002). They usually occur in larger, less isolated marshes (Benoit and Askins 2002, Shriver et al. 2004). The Nelson's Sparrow has a wider range and breeds in a variety of wetland habitats, including fresh water, brackish, and salt marsh (Shriver et al. 2011). The two species breed sympatrically between Parker River, MA and Weskeag River, ME (Hodgman et al. 2002).

Before 1995, Saltmarsh and Nelson's Sparrows were considered a single species by the American Ornithologists' Union (AOU 1995), and although there are behavioral and morphological differences between *A. caudacutus* and *A. nelsoni subvirgatus* (Shriver et al. 2005 and 2007), the two species are similar in many respects and readily hybridize (Walsh et al. 2011). In addition, both species nest in grass in the high-marsh zone, build nests 5-30 cm from the ground, and are periodically vulnerable to catastrophic nest failure due to spring high tide cycles (Greenlaw and Rising 1994, Shriver et al. 2007, Shriver et al. 2011). Thus, it is reasonable for them to be managed jointly where they co-occur, and here they are treated together as a single sharp-tailed sparrow group.

Sharp-tailed sparrows are non-territorial and have an opportunistic mating system that is often described as "scramble polygamy" (Greenlaw and Rising 1994). Males provide no parental care and leave nest building, incubation, and provisioning of young to females (Greenlaw and Rising 1994). Females have been shown to have 1-2 undefended core areas within a larger home range while males typically roam throughout large home ranges in pursuit of foraging and mating opportunities (Shriver et al. 2010). This system leads to high rates of promiscuity (Hall et al. 2010). Saltmarsh Sparrows and the *subvirgatus* subspecies of Nelson's Sparrow nest in the high-marsh zone where extremely high spring tides periodically flood (Greenlaw and Rising 1994). Nests are built close to the ground, and nest survival is therefore greatly dependent on frequency and timing of tidal flooding (Gjerdrum et al. 2005, Shriver et al. 2007, Bayard and Elphick 2011). Both species seem to prefer nest sites at slightly higher elevation, with greater cover of salt meadow hay (*Spartina patens*) and black grass (*Juncus gerardii*; Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008). Usually, nests are also supported by a layer of thatch (dead grass from previous growing seasons) and often have a thatch covering or roof (Greenlaw and Rising 1994, Gjerdrum et al. 2005, Humphreys et al. 2007, Shriver et al. 2007).

Hybrids from the two species have been shown to be more similar genetically and morphologically to Saltmarsh Sparrows than to Nelson's Sparrows, suggesting asymmetrical hybridization (Shriver et al. 2005). Within the hybrid zone, interesting behavioral differences between the two species have been observed. For example, Saltmarsh Sparrow males never guard mates while Nelson's Sparrows sometimes guard mates for up to 48 hours (Shriver et al. 2007). In addition, Saltmarsh Sparrows appear to be better adapted to nesting in tidal habitat because they quickly renest within ~3 days of nest flooding from spring high tides and are better able to successfully fledge young before the next series of spring high tides (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008). Nelson's Sparrows, however, take longer to re-nest and consequently are less successful (Shriver et al. 2007).

Study Sites

Study sites included four rivers managed by Rachel Carson National Wildlife Refuge and Maine Department of Inland Fisheries and Wildlife, York and Cumberland Counties, Maine. The Ogunquit (43.265380° N, -70.592190° W) and Webhannet Rivers

(43.317450° N, -70.574290° W) are restricted marsh systems (see Chapter 2), while the Nonesuch (43.554040° N, -70.331720° W) and Libby Rivers (43.555690° N, -70.32703° W) are unrestricted. All four marshes are characterized by extensive high-marsh habitat dominated by *S. patens*. Mean tidal range is 2.6 m, and relative sea-level rise was 2.3 mm annually between 1986 and 2003 (Fitzgerald et al. 1989, Goodman et al. 2007). Low-marsh habitat floods diurnally while high-marsh habitat typically floods only during spring tides >3 m above mean low water.

The Webhannet (~95 ha in area, ~3300 m in length) has one tidal restriction at Mile Road ~2100 m upriver (straight distance from beginning of high-marsh habitat near the river's mouth). The bridge spanning the river at Mile Road is 47 m wide (see Figure 2.1 and Table 2.1). The Ogunquit (~60 ha, ~3300 m) has one tidal restriction at Bourne Road, ~1800 m upriver (bridge = 25 m wide), and one restriction at Furbish Road, ~2600 m upriver (culvert = 3 m wide, see Figure 2.1 and Table 2.1). Both rivers are almost entirely tidal and have very little freshwater influence (Fitzgerald et al. 1984, Fitzgerald et al. 1989). The marshes are federally protected and the high-marsh habitat is not open to public use. However, both are surrounded on all sides by extensive residential and other urban development. The Nonesuch (~45 ha in area, ~2600 m to the study area's upper boundary) and Libby Rivers (~45 ha, ~2300 m to the study area's upper boundary) are unrestricted in the reaches considered here and were used as reference sites representing tidally unmodified systems (see Chapter 2). Both are fluvial marshes and have greater freshwater influence compared to the Webhannet and Ogunquit (Goodman et al. 2007). They are protected by the state of Maine and are open to public use (e.g. fishing and boating). Although unrestricted, they have residential development adjacent to ~50-75% of their perimeter.

Methods

Field methods. I collected data during 25 May – 7 Aug, 2009 and 2010, using a split-plot design with five treatment types over the high and low reaches of each river: unrestricted/low, unrestricted/high, restricted/low (below restriction), restricted/high (above one restriction), and restricted/high (above two restrictions, see Table 2.1). I defined low reaches as the areas that were closer to the river mouth (on average < 1700 m upriver from the beginning of high-marsh habitat) and below all roads. I defined high reaches as the areas that were further from the river mouth (on average > 2000 m upriver) and, on restricted rivers, also located above at least one road. I differentiated between reaches that were above one tidal restriction (on Webhannet and Ogunquit Rivers: "above 1") and the reach that was above two restrictions (Ogunquit River: "above 2"). I defined a spring tide cycle as a period of extreme high tides flooding the high-marsh zone (>3 m above mean low water). Spring tide cycles usually spanned 1-2 weeks per lunar calendar, and I monitored two cycles during each year of the study. I defined a tide event as a single extreme high tide. Usually, two tide events occurred per day, and I monitored many events per tide cycle.

I used a stratified-random method to select 4-5 subplots per river per reach (see Table 2.1). I used aerial maps overlaid with a UTM grid to randomly select subplot vertices along a distance gradient starting at the beginning of high-marsh habitat near the river's mouth. Thus, survey effort was standardized on each river and reach according to distance upriver (see Table 2.1). Each subplot contained ~2.25 ha of high-marsh habitat. I modified some subplot boundaries in order to accommodate marsh channels, sloughs, and low-marsh or mudflat habitat.

Two to four people exhaustively surveyed each subplot for nests once every two weeks (2009) or once per week (2010). We attempted to locate every active nest within the subplots using behavioral cues and systematic searches (Martin and Geupel 1993). Nests were revisited and monitored every 1-4 days for evidence of hatching, fledging, flooding, predation, and abandonment. General nest activity and nest flooding were also monitored with temperature data loggers (Thermochron iButtons, Maxim, Sunnyvale, California, hereafter iButtons). One iButton (16x6 mm) was placed inside each nest among eggs and/or young using a bobby pin attachment (Bayard and Elphick 2011; mean iButton height = 9.3 cm, SD = 4.0 cm). iButtons were placed during incubation or nestling stages and none were rejected by the female with this attachment method. iButtons recorded temperature at 15-minute intervals for all possible flood events that occurred during observation of the nest. Sometimes, during the course of travel between subplots, we found nests outside subplot boundaries. We monitored these nests as well, and I used them in nest survival analysis where location inside a subplot was not a factor.

Each year, I characterized available high-marsh habitat at 8-12 randomly located points per subplot (total of 18-22 points per subplot). I replaced points that happened to fall in low-marsh habitat with new ones. I monitored flooding at random locations using iButtons placed at about the same height as a sharp-tailed sparrow nest (10 cm above ground). Each iButton recorded temperature at 15-minute intervals during an entire spring tide cycle. In order to maximize coverage across the study sites, I rotated iButtons between subplots and monitored flooding at each subplot during one spring tide cycle per year. I also placed one iButton ~1.2 m high in the center of each subplot and recorded ambient temperature at 15-minute intervals throughout the study.

I characterized vegetation within 1-m^2 quadrats at nest and random locations using a point-intercept method (Brower and Zar 1984). I recorded every species intercepting 10 evenly-spaced points along five, 1-m long, transects (50 points per quadrat). I used frequency of occurrence (total number of intercepted points ÷ 50) as an index of species cover. In addition, I measured thatch depth (dead grass from prior growing seasons still rooted in the ground) at one randomly chosen point per transect (five measurements per quadrat). I conducted all vegetation measurements towards the end of the growing season, Jul – Aug.

Objective 3.1: Patterns of habitat use by nesting sparrows

Statistical methods. I used five random points per subplot per year (total of 10 unique points per plot) to represent the spectrum of available high-marsh habitat (n = 435). To represent the used habitat, I only included nests that were found inside subplots and had complete vegetation and flood information (n = 156). To identify when flooding occurred for each point and nest, I inspected temperature profiles of iButtons. At nests, flooding was defined as a precipitous drop in nest temperature corresponding with a tide event high enough to flood the high-marsh habitat (Gjerdrum et al. 2008, Bayard and Elphick 2011). I did not investigate possible flooding outside of high tide events that did not flood the high-marsh habitat, and I did not consider precipitation when examining temperature profiles. See Chapter 2 for methods used to identify when tide events flooded random points.

Because the number of random points was almost three times greater than the number of nests, I split the random points into two separate datasets of roughly equal sizes and analyzed each set separately against the same 156 nest locations. To maintain the stratified balance among marshes and across distances upriver, I randomly assigned (without replacement) approximately equal number of points from each subplot and year to be in dataset 1; the remaining points were assigned to dataset 2. Thus, dataset 1 had 156 nests (used points) plus 218 random (available points), while dataset 2 had the same 156 nests plus 217 different random points. The two datasets provided statistical replicates, results of which were later averaged and summarized together.

I used generalized linear mixed models with a binomial distribution to investigate habitat use by nesting sparrows. River (RIVER: Webhannet, Ogunquit, Nonesuch, or Libby) was used as a random intercept and year (YR) as a covariate. First, I compared means between unrestricted (UNR) and restricted treatments and between low and high reaches (reaches above one and two roads combined). Second, I looked at the restricted-only systems separately (i.e. Webhannet and Ogunquit) and compared means among the three reaches: low (below road), above one road, and above two roads. I did this second comparison using only the restricted systems because unrestricted systems did not have a reach that was comparable to the restricted reach above two roads. In this way, I was able to investigate the effect of being above two roads. I used Akaike's Information Criterion corrected for small sample size (AIC_c) and Akaike's weight of evidence (w_i) to model average results from dataset 1 and dataset 2 (Burnham and Anderson 2002). Results and inferences were ultimately based on model averages.

Third, I examined the effect of several explanatory variables on probability of habitat use at unrestricted and restricted systems. Explanatory variables were treatment (T: unrestricted vs. restricted), reach (REACH: low vs. high), flood frequency (FLOOD: proportion of monitored tide events that flooded the point), thatch depth (THATCH, cm), *Spartina alterniflora* cover (SPAL), and cover of *S. patens*+*J. gerardii* (GRASS). I was interested in whether habitat use would be better predicted by restriction, flood frequency, or vegetation variables that have previously been shown to be important (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008). I predicted that the effect of flooding would differ between low and high reaches and that this REACH×FLOOD interaction effect would differ between restricted and unrestricted systems. Thus, I included a T×REACH×FLOOD interaction as well as all nested interaction effects. I hypothesized 19 models *a priori* (not including a null model of constant variance, see Table 3.1) and used an information theoretic approach to compare candidate models within dataset 1 and dataset 2 separately (Burnham and Anderson 2002). For each dataset, I report AIC_c, difference in AIC_c score between the best model with the lowest AIC_c and each i^{th} model (ΔAIC_c), and w_i.

Fourth, I modeled habitat use from restricted-only systems using REACH (below vs. above 1 vs. above 2), FLOOD, THATCH, SPAL, and GRASS. In order to investigate whether the effects of these variables varied among reaches, I included REACH×FLOOD, REACH×THATCH, REACH×SPAL, and REACH×GRASS interactions. This fourth step allowed me to investigate effects of being above a two-road restriction. I hypothesized 16 models *a priori* and used the same information theoretic approach described above (Table see 3.3).

For the third and fourth analyses, there was not a clearly superior model (several models in each dataset had $\Delta AIC_c < 4$). Therefore, I used AIC_c and w_i values to model average parameter estimates using models with $\Delta AIC_c < 10$ from datasets 1 and 2 (Burnham and Anderson 2002). Results and inferences were ultimately based on model averages. All analyses passed Hosmer-Lemeshow's Goodness of Fit test and met model assumptions (UNR/restricted dataset 1 global model: $\chi^2_2 = 2.94$, $P = 0.23$; UNR/restricted dataset 2 global model: $\chi^2_2 = 2.50$, $P = 0.29$; restricted-only dataset 1 global model: $\chi^2_1 = 0.22$, $P = 0.64$; restricted-only dataset 2 global model: $\chi^2_1 = 0.60$, $P = 0.44$; Hosmer and Lemeshow 2000). I also found no evidence of residual spatial auto-correlation (assessed graphically for each global model using correlograms with 0-200 m lag distances). I report means ±1 SE and interpret $\alpha < 0.05$ as significant. From model comparison analyses, I report model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals. I interpret 95% confidence intervals that do not overlap zero as significant. All analyses were conducted in R v.2.11.1 (R Development Core Team 2011).

Objective 3.2: Flooding patterns at nests

Statistical methods. I used linear mixed models with RIVER as a random intercept to examine flood frequency at nests. I used only nests that were found within subplot boundaries and that had been monitored for flooding via iButtons ($n = 164$). I calculated flood frequency as described above then logit-transformed flood frequency using ln[frequency/(1-frequency)]. This enabled me to model flood frequency as a continuous variable while maintaining a 0-1 boundary. First, I compared means between unrestricted and restricted treatments and between low and high reaches (above 1 and above 2-road reaches combined). Second, I looked at the restricted-only systems separately and compared means among three reaches: low (below road), above one road, and above two roads. By focusing on restricted systems only, I was able to investigate the effect of being above two roads.

Third, I modeled flood frequency on unrestricted and restricted systems using five main explanatory variables: T, REACH (low vs. high), mean tide height of flooded events (HT: measured at NOAA Portland Buoy, 43.529856° N, -70.144325° W), mean precipitation of flooded events (PPT: measured at the nearest NOAA weather station with precipitation data, Grey, ME, 43.899986° N, -70.249995° W), and distance to the nearest impervious surface, defined here as any paved parking lot or road (RD, measured in ArcGIS). I predicted that the effect of HT would differ between low and high reaches and that this REACH×HT interaction effect would differ between restricted and unrestricted systems. Therefore, I included a T×REACH×HT interaction in the analysis. All nested interaction effects were also included in the analysis. I was also interested in whether impervious surfaces interacted with rainfall, creating runoff and increasing flooding. To examine this question, I included a RD×PPT interaction. Although this variable was course and might not capture some of the variation between impervious surfaces, I hoped that it would provide preliminary information that might be useful for further analysis. Rainfall was much heavier during 2009 so I also included a PPT×YR interaction. I hypothesized 15 models *a priori* (see Table 3.5) and used an information theoretic approach to compare and model average candidate models having $\Delta AIC_c < 10$ (Burnham and Anderson 2002). Fourth, I modeled flood frequency on restricted-only systems using REACH (below vs. above1 vs. above2), HT, PPT, and RD as explanatory variables. I included REACH×HT, RD×PPT, and YR×PPT interaction effects. I hypothesized 11 models *a priori* and used the same information theoretic approach described above (Table see 3.7). This fourth step allowed me to investigate effects of being above a two-road restriction.

For all four analyses, YR, distance upriver from the beginning of marsh habitat (MOUTH), standard deviation of mean tide HT (SDHT), and standard deviation of mean PPT (SDPPT) were used as covariates because they helped improve model fit. Model assumptions were assessed graphically for the global models. Spatial auto-correlation between model residuals was also assessed graphically using correlograms with 0-200 m lag distances. I report means ±1 SE and interpret $\alpha < 0.05$ as significant. From model comparison analyses, I report model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals. I interpret 95% confidence intervals that do not overlap zero as significant. All analyses were conducted in R v.2.11.1 (R Development Core Team 2011).

Objective 3.3: Patterns of nest survival

Statistical methods. I used all nests (inside and outside subplot boundaries) that had iButton flood information, known clutch completion date, and complete vegetation information ($n = 160$). Date of clutch completion was either indirectly observed (nests found during egg laying, assuming one egg was laid per day) or back calculated from estimated hatch date (assuming an 11-day incubation and 9-day nestling period, LAC unpubl. data). I estimated hatch date from nestling age and development (Greenlaw and Rising 1994). I did not include nests that were found after clutch completion and never hatched because date of clutch completion could not be estimated. I converted date of clutch completion to a lunar calendar corresponding to spring high tide cycles. During this study, spring high tides occurred around the new moon. Thus, I used the new moon as day 1 of the lunar calendar.

I used logistic-exposure models to examine nest survival (Shaffer 2004). I included year (YR) as a covariate. First, I compared daily nest survival between unrestricted and restricted treatments and between low and high reaches. Second, for restricted-only systems, I compared survival between the three reaches: low (below road), above one road, and above two roads. By focusing on restricted systems only, I was able to investigate the effect of being above two roads. Third, I examined the effect of several explanatory variables on probability of daily nest survival in unrestricted and restricted systems. Explanatory variables were T, REACH (low vs. high), whether the nest flooded during the observation interval (FLOOD: yes vs. no), total precipitation during the observation interval (PPT: measured at NOAA weather station in Grey, ME), timing of clutch completion (CC), THATCH, and GRASS. I was interested in whether flooding, precipitation, timing, or vegetation variables would better predict nest survival. I predicted that flooding and timing effects would differ between low and high reaches and that these REACH×FLOOD and REACH×CC effects would differ between treatments. Thus, I included T×REACH×FLOOD and T×REACH×CC interactions as well as all nested interaction effects. Because rainfall was greater in 2009, I included a PPT×YR interaction. I hypothesized 21 models *a priori* (see Table 3.9) and used an information theoretic approach to compare and model average candidate models as described above in Objective 2 (Burnham and Anderson 2002). Results and inferences were ultimately based on model averages. Fourth, I modeled daily nest survival in restricted-only systems using REACH (below vs. above 1 vs. above 2), FLOOD, PPT, CC, THATCH, and GRASS. To investigate whether the effects of these variables varied among reaches, I included REACH×FLOOD, REACH×CC, REACH×THATCH, and REACH×GRASS interactions. The PPT×YR interaction was also included. I hypothesized 19 models *a priori* and used the same information theoretic approach described above (see Table 3.11).

All analyses passed Hosmer-Lemeshow's Goodness of Fit Test and met model assumptions (UNR/restricted global model: $\chi^2_1 = 1.28$, $P = 0.26$; restricted-only global model: $\chi^2_1 = 1.90$, $P = 0.17$; Hosmer and Lemeshow 2000). I also found no evidence of residual spatial auto-correlation (assessed graphically for each global model using correlograms with 0-200 m lag distances). I report means ±1 SE and interpret $\alpha < 0.05$ as significant. From model comparison analyses, I report model-averaged parameter estimates, unconditional standard errors, and 95% confidence intervals. I interpret 95% confidence intervals that do not overlap zero as significant. All analyses were conducted in R v.2.11.1 (R Development Core Team 2011).

Results

We found 315 active sharp-tailed sparrow nests (Table 3.1) and placed iButtons in 219. In unrestricted systems, 63% were from Saltmarsh Sparrows, 12% from Nelson's, and 25% were unidentified sharp-tailed nests. In restricted systems, 70% were from Saltmarsh Sparrows, 2% from Nelson's, and 28% were unidentified. Nest density varied among marshes and within marshes. On unrestricted systems, density ranged from 0 to 3.6 nests/ha (summarized by subplot). On restricted systems, nest density ranged from 0 to 6.2 nests/ha. Flooding was a common occurrence for most nests with 88% flooding at least once and 53% flooding more than once (Figure 3.1a). In addition, flooding caused 88% of nest failures. Predation was attributed to only 10% of failures, and abandonment by the female was attributed to 2% (Table 3.1).

Table 3.1. Summary of sharp-tailed sparrow nest results (nest locations, percent that successfully fledged at least one young, and proportion of failure due to various causes). York and Cumberland Counties, Maine, 2009 and 2010.

Location	Total nests[a]	Plot[b]	Flood + clutch completion[c]	Percent Success[d]	Failure due to flood[e]	Failure due to predation[f]	Failure due to desertion[g]
Unrestricted / low							
Libby	19	14	7	29	0.60	0.40	0
Nonesuch	68	46	24	46	0.92	0.08	0
Unrestricted / high							
Libby	25	19	12	25	0.78	0.22	0
Nonesuch	23	16	12	17	1.00	0	0
Restricted / below							
Webhannet	22	8	16	44	0.78	0.11	0.11
Ogunquit	24	18	14	50	1.00	0	0
Restricted / above 1							
Webhannet	53	35	29	41	0.76	0.24	0
Ogunquit	48	42	27	07	0.96	0	0.04
Restricted / above 2							
Ogunquit	33	28	18	17	0.93	0.07	0
Total	315	226	160	31	0.88	0.10	0.02

[a]Total number of active sparrow nests found during the project, [b]number of active nests found inside subplot boundaries, [c]number of active nests having complete flood and clutch completion information (nests used for survival analysis), [d]percent of nests used for survival analysis that fledged at least one young, [e]proportion of failed nests (from survival analysis) that failed due to flooding, [f]proportion of failed nests (from survival analysis) that failed due to predation, [g]proportion of failed nests (from survival analysis) that failed due to desertion by the adult female.

Objective 3.1: Patterns of habitat use by nesting sparrows

Probability of use was significantly different between unrestricted and restricted systems. Low reaches of unrestricted systems had higher used by nesting sparrows, while in restricted systems, use was highest in high reaches ($z = 3.07$, $P < 0.01$; Figure 3.1b). Separate analysis of restricted-only systems found that use was greatest above one road ($z = 3.08$, $P < 0.01$; Figure 3.1b).

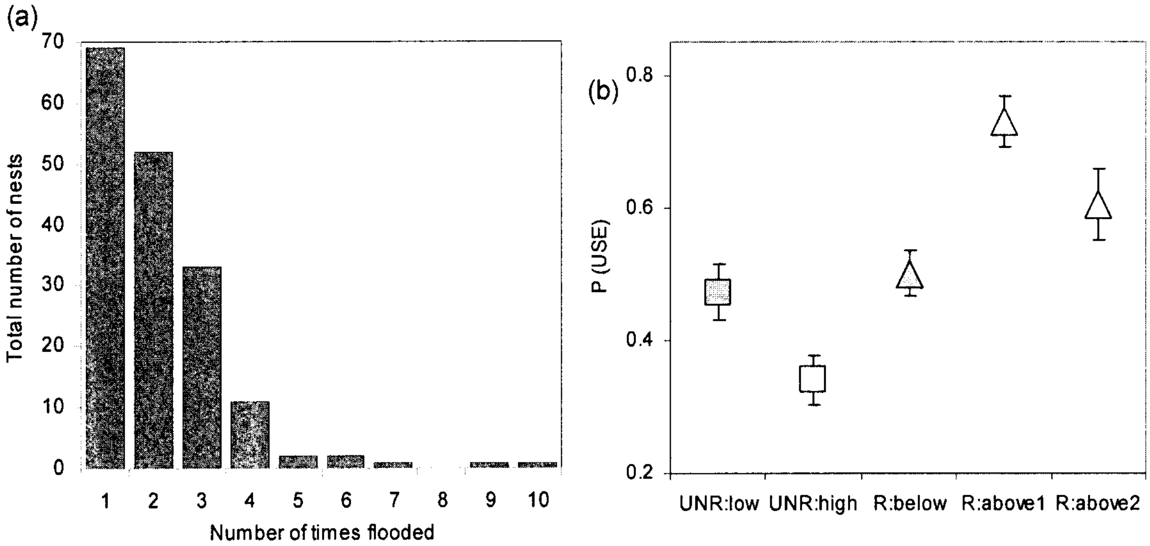

Figure 3.1. General flooding frequency of nests and mean habitat use by nesting sparrows in unrestricted and restricted systems. York and Cumberland Counties, Maine, 2009 and 2010. (a) Most nests flooded at least 1-2 times, but seven nests flooded at least five times. (b) Use was significantly higher on low reaches of unrestricted systems. On restricted systems, however, use was highest on high reaches above one road.

Model analysis of the combined unrestricted and restricted dataset 1 and dataset 2 found four competitive models had $\Delta AIC_c < 10$ (collectively accounting for >99.9% of the weight of support, Table 3.2). Each of the four models contained all main effects and various combinations of interaction effects. Model averaging between these four models from datasets 1 and 2 found significant effects from FLOOD, THATCH, SPAL, and GRASS (Table 3.3, Figure 3.2). The effect of flooding on probability of habitat use did not differ significantly between unrestricted and restricted systems or between high and low reaches (Table 3.3).

Table 3.2. Model selection results from the analysis of habitat use by nesting sparrows, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. Nineteen *a priori* models were hypothesized and compared using AIC_c. Also shown, number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
Dataset 1[b]				
YR, GRASS, SPAL, THATCH, REACH×FLOOD	**8**	**331**	**0.0**	**0.65**
YR, GRASS, SPAL, THATCH, T×REACH×FLOOD	**12**	**334**	**2.6**	**0.17**
YR, GRASS, SPAL, THATCH, T×FLOOD	**8**	**334**	**2.9**	**0.16**
YR, T, REACH, FLOOD, GRASS, SPAL, THATCH	**8**	**339**	**7.5**	**0.02**
YR, GRASS, SPAL, THATCH	5	361	30	0.00
YR, THATCH	3	370	39	0.00
YR, GRASS, SPAL	4	443	112	0.00
YR, GRASS	3	458	127	0.00
YR, T×REACH×FLOOD	9	478	147	0.00
YR, REACH×FLOOD	5	480	149	0.00
YR, T×REACH, REACH×FLOOD, T×FLOOD	8	482	150	0.00
YR, T×FLOOD	5	488	157	0.00
YR, REACH, FLOOD	4	489	157	0.00
YR, FLOOD	3	488	157	0.00
YR, T, FLOOD	4	490	159	0.00
YR, SPAL	3	508	176	0.00
YR, T×REACH	5	509	178	0.00
constant	1	512	181	0.00
YR	2	514	183	0.00
YR, T, REACH	4	517	186	0.00

[a] Models with interaction effects also included all nested interactions and main effects, [b] the random points were separated into two datasets and analysis was conducted once for each dataset (see text for more details).

Table 3.2. Continued.

Model[a]	K	AIC_c	ΔAIC_c	w_i
Dataset 2[b]				
YR, GRASS, SPAL, THATCH, REACH×FLOOD	**8**	**351**	**0.0**	**0.36**
YR, GRASS, SPAL, THATCH, T×FLOOD	**8**	**352**	**0.2**	**0.32**
YR, T, REACH, FLOOD, GRASS, SPAL, THATCH	**8**	**352**	**0.4**	**0.29**
YR, GRASS, SPAL, THATCH, T×REACH×FLOOD	**12**	**356**	**4.8**	**0.03**
YR, GRASS, SPAL, THATCH	5	370	19	0.00
YR, THATCH	3	380	29	0.00
YR, GRASS, SPAL	4	448	97	0.00
YR, GRASS	3	461	110	0.00
YR, REACH×FLOOD	5	486	135	0.00
YR, T×REACH, REACH×FLOOD, T×FLOOD	8	488	137	0.00
YR, T×REACH×FLOOD	9	488	137	0.00
YR, REACH, FLOOD	4	489	137	0.00
YR, FLOOD	3	490	138	0.00
YR, T, FLOOD	4	491	140	0.00
YR, T×FLOOD	5	493	142	0.00
YR, T×REACH	5	508	157	0.00
YR, SPAL	3	508	157	0.00
constant	1	511	159	0.00
YR	2	513	161	0.00

[a] Models with interaction effects also included all nested interactions and main effects, [b] the random points were separated into two datasets and analysis was conducted once for each dataset (see text for more details).

Table 3.3. Model-averaged parameter estimates and unconditional standard errors from the best models in the habitat use analysis ($\Delta AIC_c < 10$), unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010.

Parameter	Estimate	SE	95% Confidence interval
Intercept	-4.07	0.98	-6.00, -2.14
YR (2010)	0.48	0.30	-0.11, 1.07
GRASS	2.08	0.76	0.59, 3.57
SPAL	1.06	0.45	0.17, 1.95
THATCH	0.32	0.04	0.23, 0.40
T (UNR)	0.34	1.21	-2.03, 2.71
REACH (L)	0.99	1.28	-1.51, 3.50
FLOOD	-1.94	0.76	-3.44, -0.44
T×REACH	-3.67	2.43	-8.44. 1.10
T×FLOOD	-0.68	2.03	-4.66, 3.29
REACH×FLOOD	-2.06	1.66	-5.32, 1.20
T×REACH×FLOOD	4.60	2.71	-0.72, 9.91

Model analysis of the restricted-only dataset 1 and dataset 2 ranked that the same two models as best. Though only one and two models, respectively, met the cutoff to be included in model averaging (ΔAIC_c <10, Table 3.4). Model averaging found significant effects from REACH×FLOOD, THATCH, and REACH×GRASS (Table 3.5). Flood frequency had a negative effect on probability of habitat use in areas located below roads and above one road, but above two roads the effect was not significant (Table 3.5, Figure 3.2a). In areas above just one road, points that had greater cover of *S. patens* and *J. gerardii* were more likely to be used by nesting sparrows. However, in areas located below roads and in the area above two roads, I did not find a significant difference in grass cover between used and random points (Figure 3.2b).

Table 3.4. Model selection results from the analysis of habitat use by nesting sparrows, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. Sixteen *a priori* models were hypothesized and compared using AIC_c. Also shown are number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
Dataset 1[b]				
YR, REACH×FLOOD, REACH×GRASS, REACH×SPAL, REACH×THATCH	**16**	**193**	**0.0**	**1.00**
YR, REACH, FLOOD, GRASS, SPAL, THATCH	9	206	13	0.00
YR, GRASS, SPAL, THATCH	5	211	18	0.00
YR, THATCH	3	213	20	0.00
YR, REACH×GRASS, REACH×SPAL, REACH×THATCH	13	216	22	0.00
YR, REACH, THATCH	5	217	24	0.00
YR, REACH×THATCH	7	219	26	0.00
YR, REACH×GRASS	7	263	70	0.00
YR, REACH, GRASS	5	266	73	0.00
YR, REACH×FLOOD	7	277	83	0.00
YR, REACH, FLOOD	5	292	99	0.00
YR, REACH. SPAL	5	293	100	0.00
YR, REACH•SPAL	7	296	102	0.00
YR, REACH	4	299	106	0.00
YR, FLOOD	3	299	106	0.00
constant	1	303	110	0.00
YR	2	305	112	0.00
Dataset 2[b]				
YR, REACH, FLOOD, GRASS, SPAL, THATCH	**9**	**200**	**0.0**	**0.96**
YR, REACH×FLOOD, REACH×GRASS, REACH×SPAL, REACH×THATCH	**16**	**206**	**6.2**	**0.04**
YR, GRASS, SPAL, THATCH	5	213	13	0.00
YR, THATCH	3	221	21	0.00
YR, REACH×GRASS, REACH×SPAL, REACH×THATCH	13	224	24	0.00
YR, REACH, THATCH	5	223	23	0.00
YR, REACH×THATCH	7	224	24	0.00
YR, REACH, GRASS	5	274	74	0.00
YR, REACH×GRASS	7	276	77	0.00
YR, REACH×FLOOD	7	279	79	0.00
YR, REACH, FLOOD	5	286	86	0.00
YR, REACH, SPAL	5	289	89	0.00
YR, REACH•SPAL	7	293	93	0.00

[a]Models with interaction effects also included all nested interactions and main effects, [b]the random points were separated into two datasets and the analysis was conducted once for each dataset (see text for more details).

Table 3.4. Continued.

Model[a]	K	AIC_c	ΔAIC_c	w_i
Dataset 2[b]				
YR, FLOOD	3	294	94	0.00
YR, REACH	4	299	99	0.00
constant	1	303	103	0.00
YR	2	305	105	0.00

[a]Models with interaction effects also included all nested interactions and main effects, [b]the random points were separated into two datasets and the analysis was conducted once for each dataset (see text for more details).

Table 3.5. Model-averaged parameter estimates and unconditional standard errors from the best models in the habitat use analysis ($\Delta AIC_c < 10$), restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010.

Parameter	Estimate	SE	95% Confidence interval
Intercept	-2.64	2.36	-7.27, 1.98
YR (2010)	1.25	0.69	-0.11, 2.61
GRASS	1.58	1.36	-1.10, 4.25
SPAL	0.95	1.36	-1.71, 3.62
THATCH	0.39	0.11	0.17, 0.62
REACH (A1)	-2.51	3.45	-9.26, 4.25
REACH (A2)	-3.01	3.75	-10.36, 4.35
FLOOD	-4.65	2.22	-9.00, -0.30
REACH×GRASS (A1)	5.80	2.62	0.68, 10.93
REACH×GRASS (A2)	-1.83	3.55	-8.79, 5.13
REACH×SPAL (A1)	2.57	1.46	-0.29, 5.43
REACH×SPAL (A2)	2.38	2.17	-1.87, 6.63
REACH×THATCH (A1)	-0.27	0.15	-0.57, 0.04
REACH×THATCH (A2)	0.10	0.25	-0.40, 0.59
REACH×FLOOD (A1)	2.10	2.15	-2.12, 6.31
REACH×FLOOD (A2)	7.75	2.52	2.81, 12.70

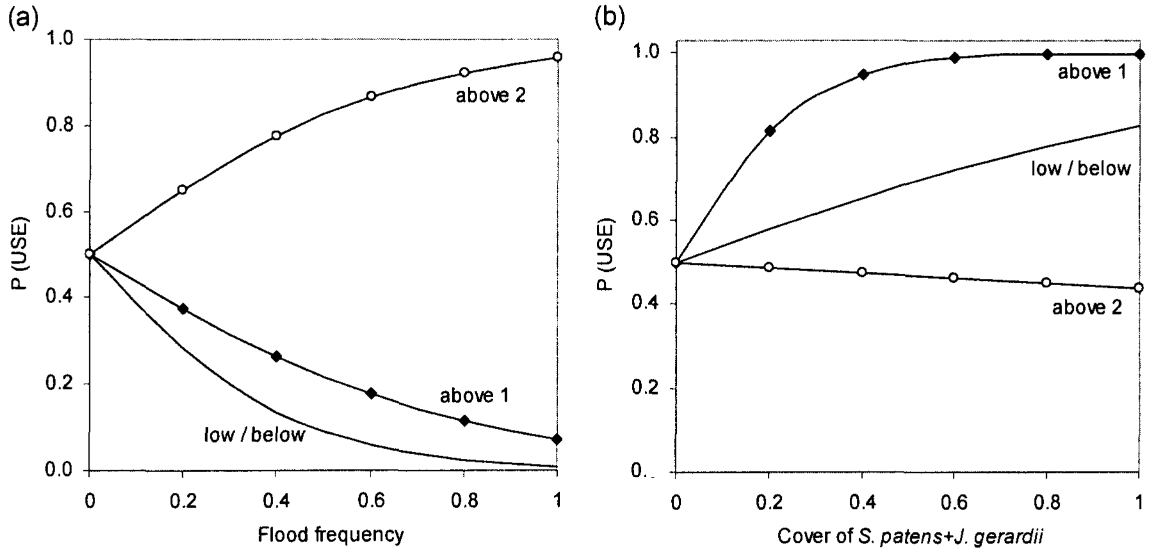

Figure 3.2. Effect of flood frequency and grass cover on habitat use. York and Cumberland Counties, Maine, 2009 and 2010. (a) Flood frequency had a negative effect on habitat use in all low reaches (unrestricted and restricted systems) and above one road on restricted systems. Above two roads, however, no significant effect was detected. (b) Above one road in the restricted systems, there was a positive relationship between cover of *S. patens* and *J. gerardii* and habitat use. Areas located below all roads and above two roads, no significant effect was detected.

Objective 3.2: Flooding patterns at nests

I did not find a significant difference in flood frequency between nests placed in unrestricted vs. restricted systems ($z = 1.31$, $P = 0.24$) or between low and high reaches ($z = -1.33$, $P = 0.18$). In addition, when restricted-only systems were analyzed separately, there were no differences in frequency of nest flooding among areas located below roads, above one road, or above two roads ($z = 0.85$, $P = 0.40$).

Model analysis of the combined unrestricted and restricted dataset found three competitive models with ΔAIC_c <10 (Table 3.6). None of these models contained the T×REACH×HT, T×HT, or REACH×HT interaction effects. Nor were the PPT×YR or RD×PPT interaction effects included. Model averaging found only tide HT to have a significant effect on flood frequency, such that nests with higher flood frequencies were flooded by a greater range of tide heights (Table 3.7).

Table 3.6. Model selection results from the analysis of nest flood frequency, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. Fifteen *a priori* models were hypothesized and compared using AIC$_c$. Also shown are number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC$_c$	ΔAIC$_c$	w_i
HT, T×REACH, MOUTH, SDHT, YR	**8**	**604**	**0.0**	**0.41**
T, REACH, HT, MOUTH, SDHT, YR	**7**	**604**	**0.1**	**0.40**
HT, MOUTH, SDHT, YR	**5**	**605**	**1.5**	**0.19**
T, REACH×HT, MOUTH, SDHT, YR	8	615	12	0.00
REACH, T×HT, MOUTH, SDHT, YR	8	616	13	0.00
T×REACH, REACH×HT, T×HT, MOUTH, SDHT, YR	10	628	24	0.00
T×REACH×HT, MOUTH, SDHT, YR	11	639	35	0.00
T×REACH×HT, YR×PPT, RD×PPT, MOUTH, SDHT, SDPPT	16	655	51	0.00
T×REACH, MOUTH, YR	6	671	67	0.00
T, REACH, MOUTH, YR	5	671	68	0.00
constant	1	673	69	0.00
MOUTH, YR	3	675	71	0.00
PPT, MOUTH, SDPPT, YR	5	678	74	0.00
YR×PPT, MOUTH, SDPPT	6	680	76	0.00
PPT, RD, MOUTH, SDPPT, YR	6	682	79	0.00
RD×PPT, MOUTH, SDPPT, YR	7	686	83	0.00

[a] Models with interaction effects also included all nested interactions and main effects.

Model analysis of the restricted-only dataset found two competitive models with ΔAIC$_c$ <10 (Table 3.8). The REACH×HT interaction was not included in either of these models. Similar to the above combined unrestricted and restricted analysis, model averaging found only tide HT to have a significant effect on flood frequency (Table 3.9).

Table 3.7. Model-averaged parameter estimates and unconditional standard errors from the best models in the nest flood analysis ($\Delta AIC_c < 10$), unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010.

Parameter	Estimate	SE	95% Confidence interval
Intercept	1.12	0.83	-0.50, 2.75
MOUTH	-0.0003	0.0003	-0.001, 0.000
SDHT	7.40	2.02	3.44, 11.35
YR (2010)	0.81	0.21	0.39, 1.22
HT	-0.010	0.001	-0.012, -0.007
T (UNR)	0.46	0.66	-0.83, 1.75
REACH (L)	-0.70	0.53	-1.74, 0.33
T×REACH	-0.68	0.49	-1.64, 0.29

Table 3.8. Model selection results from the analysis of nest flood frequency, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. Twelve *a priori* models were hypothesized and compared using AIC_c. Also shown are number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
HT, MOUTH, YR, SDHT	**5**	**375**	**0.0**	**0.76**
REACH, HT, MOUTH, YR, SDHT	**7**	**377**	**2.3**	**0.24**
REACH×HT, MOUTH, YR, SDHT	9	399	24	0.00
constant	1	406	31	0.00
PPT, MOUTH, YR, SDHT	5	408	33	0.00
MOUTH, YR	3	410	35	0.00
YR×PPT, MOUTH, SDPPT	6	410	36	0.00
REACH, MOUTH, YR	5	410	36	0.00
PPT, RD, MOUTH, YR, SDPPT	6	410	36	0.00
REACH×HT, YR×PPT, RD×PPT, MOUTH, SDPPT, SDHT	14	413	38	0.00
REACH×HT, RD×PPT, MOUTH, YR, SDPPT, SDHT	13	414	39	0.00
RD×PPT, MOUTH, YR, SDPPT	7	416	41	0.00
HT, MOUTH, YR, SDHT	5	375	0.0	0.76

[a] Models with interaction effects also included all nested interactions and main effects.

Table 3.9. Model-averaged parameter estimates and unconditional standard errors from the best models in the nest flood analysis ($\Delta AIC_c < 10$), restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010.

Parameter	Estimate	SE	95% Confidence interval
Intercept	0.45	0.61	-0.74, 1.63
MOUTH	-0.0002	0.0003	-0.001, 0.000
SDHT	8.25	2.67	3.01, 13.50
YR (2010)	1.10	0.29	0.53, 1.66
HT	-0.009	0.002	-0.012, -0.006
REACH (A1)	1.74	4.22	-6.53, 10.01
REACH (A2)	1.78	4.77	-7.58, 11.14

Objective 3.3: Patterns of nest survival

I found no difference in daily nest survival between unrestricted and restricted systems ($z = -0.95$, $P = 0.34$) or between low and high reaches ($z = 0.96$, $P = 0.34$). In addition, when I analyzed restricted-only systems separately, I found no differences in nest survival among areas located below roads, above one road, or above two roads ($z = -0.70$, $P = 0.49$).

Model analysis of the combined unrestricted and restricted dataset found three competitive models with $\Delta AIC_c < 10$ (Table 3.10). Two of these models contained the T×REACH×FLOOD and T×REACH×CC interactions, while the third contained only main effects. Precipitation was included in all three models, and vegetation variables were in two models. Model averaging found significant effects from PPT, FLOOD, and REACH×CC (Table 3.11). Daily nest survival was reduced when the nest flooded (Figure 3.3a) and when there was more rain during the observation interval (Figure 3.3b). On low reaches, nest survival was highest for clutches completed shortly after the new moon; but on high reaches, timing of clutch completion did not have a significant effect on nest survival (Figure 3.4).

Table 3.10. Model selection results from the nest survival analysis, unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010. Twenty-one *a priori* models were hypothesized and compared using AIC_c. Also shown are number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
YR×PPT, T×REACH×CC, T×REACH×FLOOD	**15**	**391**	**0.0**	**0.58**
YR, THATCH, GRASS, PPT, CC, FLOOD, T, REACH	**9**	**392**	**0.9**	**0.37**
THATCH, GRASS, YR×PPT, T×REACH×CC, T×REACH×FLOOD	**17**	**396**	**4.8**	**0.05**
YR, REACH, FLOOD	4	404	13	0.00
YR×PPT, T×REACH, REACH×CC, T×CC, T×FLOOD, REACH×FLOOD	11	405	14	0.00
YR, REACH×FLOOD	5	405	14	0.00
YR, T×REACH×CC, T×REACH×FLOOD	13	407	16	0.00
YR, T×REACH, REACH×FLOOD, T×FLOOD	8	409	18	0.00
YR, T×REACH×FLOOD	9	411	20	0.00
YR×PPT	4	486	95	0.00
YR, PPT	3	498	107	0.00
YR, REACH×CC	5	550	159	0.00
YR, REACH, CC	4	552	161	0.00
YR, T×REACH, REACH×CC, T×CC	8	555	164	0.00
YR, T×REACH×CC, T×REACH×FLOOD	9	556	165	0.00
YR	2	563	172	0.00
YR, T, REACH	4	563	172	0.00
YR, THATCH	3	564	173	0.00
YR, T×REACH	5	565	174	0.00
YR, GRASS	3	565	174	0.00
YR, THATCH, GRASS	4	566	175	0.00
constant	1	568	177	0.00

[a]Models with interaction effects also included all nested interactions and main effects.

Table 3.11. Model-averaged parameter estimates and unconditional standard errors from the best models in the nest survival analysis ($\Delta AIC_c < 10$), unrestricted and restricted systems combined. York and Cumberland Counties, Maine, 2009 and 2010.

Parameter	Estimate	SE	95% Confidence interval
Intercept	4.13	0.71	2.73, 5.52
YR (2010)	1.11	0.37	0.38, 1.83
GRASS	0.34	0.85	-1.32, 2.00
THATCH	0.01	0.03	-0.05, 0.07
PPT	-0.24	0.07	-0.38, -0.09
T (UNR)	0.07	0.82	-1.53, 1.67
REACH (L)	3.63	3.31	-2.86, 10.12
FLOOD	-2.39	0.39	-3.15, -1.63
CC	-0.04	0.03	-0.09, 0.02
YR×PPT	-0.23	0.16	-0.55, 0.09
T×REACH	-3.78	2.82	-9.30, 1.74
T×FLOOD	-0.96	0.90	-2.74, 0.81
REACH×FLOOD	-1.21	1.01	-3.19, 0.77
T×REACH×FLOOD	1.26	1.53	-1.73, 4.26
T×CC	0.04	0.06	-0.08, 0.15
REACH×CC	-0.38	0.14	-0.66, -.01
T×REACH×CC	0.25	0.16	-0.07, 0.57

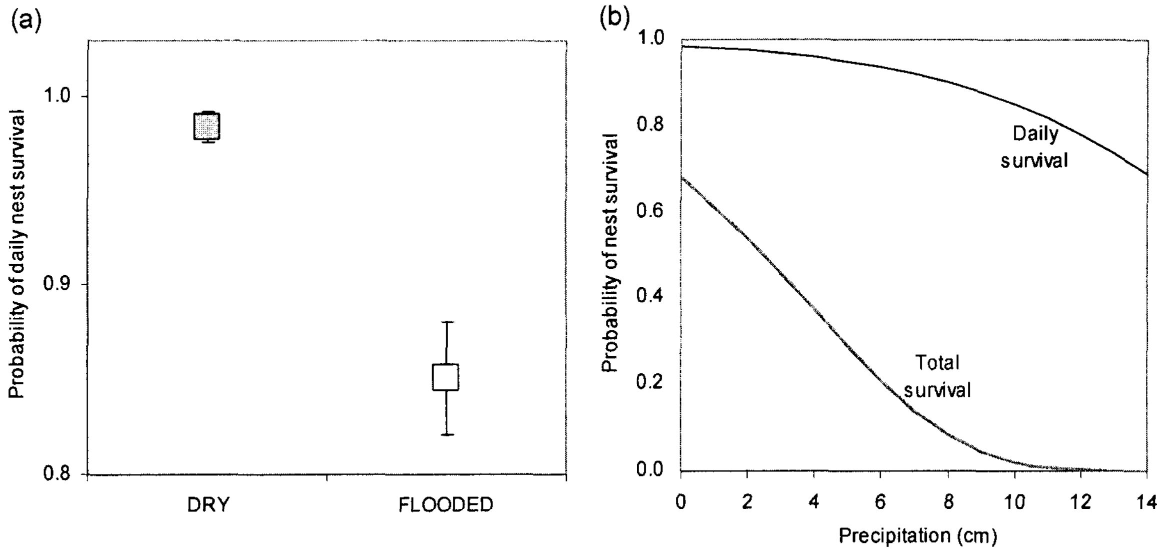

Figure 3.3. Effect of flooding and precipitation on nest survival. York and Cumberland Counties, Maine, 2009 and 2010. (a) Flooding had a negative effect on daily nest survival (total nest survival = $[\text{daily survival}]^{24}$; total survival for dry nests = 0.68, flooded nests = 0.02). (b) Rainfall had a negative effect on probability of daily nest survival, and this effect did not differ between unrestricted and restricted systems or among reaches.

Model analysis of the restricted-only dataset found four competitive models with $\Delta AIC_c < 10$ (Table 3.12). The REACH×FLOOD and REACH×CC interactions were included in two of these models, while their main effects were included in all four models. Precipitation was included in all four models, and vegetation variables were included in two models. Model averaging found significant effects from PPT, FLOOD, REACH×CC, and REACH×THATCH (Table 3.13). Timing of clutch completion had a negative effect in areas located below roads but a slight *positive* effect in areas located above one and two roads (Figure 3.4). Thatch depth had a *negative* effect on probability of daily nest survival, but only in the area above two roads, while elsewhere there was no significant relationship between nest survival and thatch depth.

Table 3.12. Model selection results from the nest survival analysis, restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010. Nineteen *a priori* models were hypothesized and compared using AIC_C. Also shown are number of model parameters (K) and Akaiki's weight (w_i).

Model[a]	K	AIC_c	ΔAIC_c	w_i
YR×PPT, REACH×CC, REACH×FLOOD	**12**	**285**	**0.0**	**0.63**
YR, REACH, CC, PPT, FLOOD	**7**	**287**	**2.0**	**0.23**
YR, REACH, CC, PPT, FLOOD, THATCH, GRASS	**9**	**288**	**3.1**	**0.13**
YR×PPT, REACH×CC, REACH×FLOOD, REACH×THATCH, REACH×GRASS	**18**	**293**	**8.7**	**0.01**
YR, REACH×CC, REACH×FLOOD	10	296	11	0.00
YR, REACH, FLOOD	5	296	12	0.00
YR, REACH×FLOOD	7	300	15	0.00
YR×PPT	4	334	50	0.00
YR, PPT	3	346	61	0.00
YR, REACH×CC	7	381	96	0.00
YR, REACH, CC	5	383	98	0.00
YR	2	383	98	0.00
Constant	1	385	100	0.00
YR, REACH	4	386	102	0.00
YR, REACH, THATCH	5	386	102	0.00
YR, REACH×THATCH	7	387	102	0.00
YR, REACH, GRASS	5	387	102	0.00
YR, REACH, THATCH, GRASS	6	388	103	0.00
YR, REACH×GRASS	7	391	106	0.00
YR, REACH×THATCH, REACH×GRASS	10	392	108	0.00

[a] Models with interaction effects also included all nested interactions and main effects.

Table 3.13. Model-averaged parameter estimates and unconditional standard errors from the best models in the nest survival analysis ($\Delta AIC_c < 10$), restricted systems only. York and Cumberland Counties, Maine, 2009 and 2010.

Parameter	Estimate	SE	95% Confidence interval
Intercept	7.71	3.02	1.80, 13.62
YR (2010)	1.13	0.46	0.22, 2.04
GRASS	0.75	1.01	-1.24, 2.73
THATCH	0.08	0.06	-0.03, 0.19
PPT	-0.22	0.10	-0.41, -0.03
REACH (A1)	-3.49	3.20	-9.76, 2.78
REACH (A2)	-4.30	3.76	-11.66, 3.06
FLOOD	-3.06	0.92	-4.88, -1.25
CC	-0.28	0.21	-0.68, 0.13
YR×PPT	-0.39	0.19	-0.75, -0.02
REACH×FLOOD (A1)	1.18	1.04	-0.86, 3.22
REACH×FLOOD (A2)	1.51	1.14	-0.73, 3.75
REACH×CC (A1)	0.36	0.14	0.08, 0.64
REACH×CC (A2)	0.41	0.15	0.11, 0.71
REACH×GRASS (A1)	-0.36	2.73	-5.71, 5.00
REACH×GRASS (A2)	2.17	2.48	-2.68, 7.02
REACH×THATCH (A1)	-0.19	0.15	-0.48, 0.11
REACH×THATCH (A2)	-0.32	0.16	-0.64, 0.00

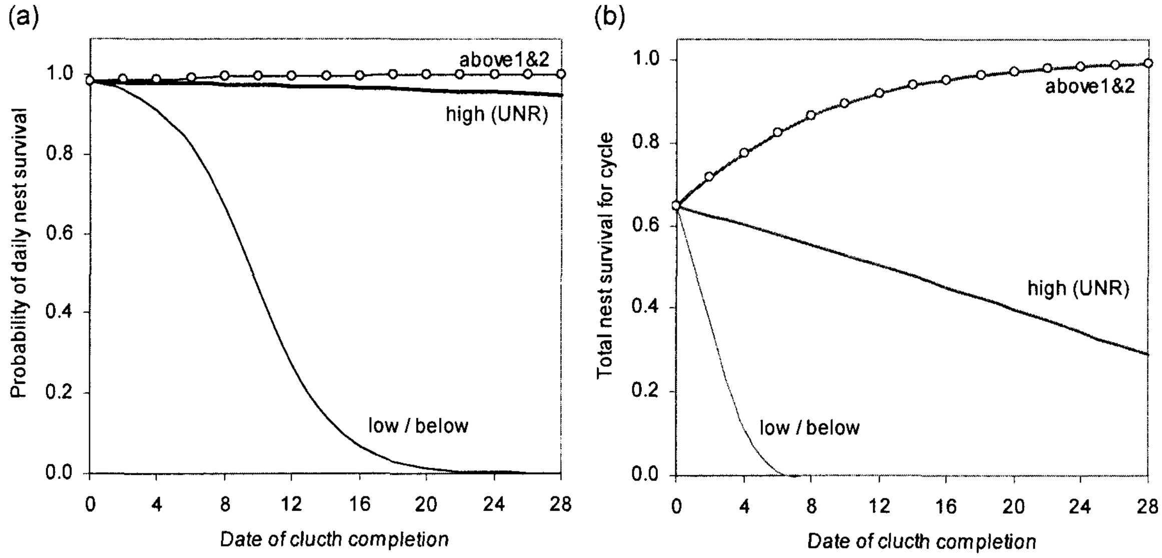

Figure 3.4. Effect of timing of clutch completion on nest survival (day 1 = new moon of lunar cycle). York and Cumberland Counties, Maine, 2009 and 2010. (a) Effect on daily nest survival. In low reaches of all rivers, probability of daily nest survival decreased quickly for each day that clutch completion was delayed past the new moon (corresponding to timing of spring high tides). In high reaches of unrestricted systems, timing did not have a significant effect, while in high reaches of restricted systems above one and two roads, timing had a small positive effect. (b) Effect on total nest survival for a 24-day nesting cycle (total nest survival = [daily survival]^{24}).

Discussion

Objective 3.1: Patterns of habitat use by nesting sharp-tailed sparrows

Although flooding of available high-marsh habitat was reduced by 50% in the area above two roads, and although flooding was responsible for 88% of nest failure, sharp-tailed sparrows did not preferentially nest there. Instead, in restricted systems, they selected high reaches that were located above one moderate restriction. Conversely, in unrestricted systems, sparrows selected low reaches of the marsh where flooding of available habitat was significantly less. Although flooding is the main factor affecting nest survival and Saltmarsh Sparrows have been evolving in tidal habitat for ~600,000 years (Rising and Avise 1993), results here suggest that they may not consistently choose marshes based on likelihood of flooding. This is also suggested by other studies that found that Saltmarsh Sparrow nesting strategy was to avoid flooding temporally rather than spatially (i.e. by elevation, Gjerdrum et al. 2005, Shriver et al. 2007).

Nevertheless, at the scale of an individual point, flood frequency appeared to have a negative effect on probability of habitat use. This is complicated, however, by the fact that random (unused) points were monitored during one entire spring tide cycle, while most nests were monitored for only a fraction of a cycle. Thus all random points experienced ≥10 flood events while most nests experienced 1-3 flood events before failing or fledging. Flood frequency at nest locations may have been higher if all possible flood events had been monitored. The diminished effect of flooding on probability of habitat use in the area located above two roads may be due to the fact that overall flooding of available habitat was reduced in that area.

The positive relationship between habitat use, thatch depth, and cover of *S. patens* and *J. gerardii* has been shown in other studies at other locations (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008) and appears to be a common behavioral trait of Saltmarsh Sparrows and the *subvirgatus* subspecies of Nelson's Sparrow. However, DiQuinzio et al. (2002) found that Saltmarsh Sparrows in severely restricted marshes nested in patches of short-form *Phragmites australis*. In the severely restricted area above two roads in this study, I found no relationship between *S. patens*, *J. gerardii*, and sharp-tailed sparrow habitat use. Perhaps this reflects the flexibility of the sparrows and their ability to use any grasses that are available.

Objective 3.2: Flooding patterns at nests

Although there were differences in flooding of the available habitat between restricted and unrestricted rivers and between low and high reaches (Chapter 2), I found no differences in flooding of nests. This may be due to complications discussed above and the possibility that nest locations would have flooded more often had their observations not been truncated by nest failure or fledging. The strong relationship between tide height and nest flood frequency was mirrored in flooding of the available habitat (Chapter 2). For available habitat on restricted rivers, this relationship varied among reaches, and it took higher tides to flood the area above two roads (Figure 2.6). For nesting sparrows, however, tide height had an equally strong effect on flooding regardless of reach or restriction. Alternatively, nest placement may have ameliorated the differences in flood frequency of nests among the different reaches and restriction treatments.

Interestingly, I did not find a relationship between precipitation and nest flooding. However, precipitation did affect flood frequency of the available high-marsh habitat (Chapter 2). It may be difficult to detect the effect of precipitation on flooding at nests with methods I used here. Tide height had a strong effect on flooding, and I predicted that precipitation would have a lesser, additive effect. However, perhaps sparrows were able to shelter their nests during rainstorms and keep them warm, despite being flooded from rain. This might have prevented my ability to detect flooding due to precipitation. Random points were not sheltered in this way.

Objective 3.3: Patterns of nest survival

Flooding had a negative effect on nest survival, and probability of daily nest survival decreased by 90% when a nest flooded. Most nests flooded at least once during my observation of them, and many nests flooded more than once. In fact, flood frequency was probably underestimated because monitoring of some nests began after onset of incubation, and some flooding may have occurred before iButton placement. The high rate of flooding is supported by every study of Saltmarsh Sparrow nest survival (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008a and 2008b) with the noted exception of DiQuinzio et al. 2002. In a severely restricted marsh with extremely limited tidal flow, they found predation to be a leading cause of nest failure. However, once tidal flow was reinstated, flooding caused >90% of failures. In this study, even the more severely restricted area above two roads exhibited typical patterns of nest failure (93% due to flooding and 7% due to predation). This suggests a more natural tidal regime was operating above the two-road restriction in this study compared to that seen in the DiQuinzio et al. (2002) study.

Although precipitation did not appear to affect frequency of nest flooding, it did have a negative effect on probability of daily nest survival. Nest survival decreased by 20% for every 1-cm increase in precipitation. Rainfall might be stressful to both nesting females and young chicks in the nest, particularly heavy or prolonged rainfall. Perhaps precipitation acted synergistically with tidal flooding and reduced the ability of a nest to survive flooding. Regardless of the possible mechanism, this result is interesting and may warrant further investigation as frequency and severity of storm events are predicted to increase in the Northeast, USA (Douglas et al. 2011).

Nest timing may be the primary determinant of nest survival for sharp-tailed sparrows (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008). However, results here suggest that timing may be less important for nests located on higher reaches upriver and above tidal restriction. In low reaches of restricted and unrestricted systems, daily nest survival decreased by ~34% for every day that clutch completion was delayed past the new moon. Sparrows that initiated nests shortly after the new moon also coincided with the ending of a spring tide cycle. The next spring tide cycle began ~25 days later. This window was just long enough for sharp-tailed sparrows to lay and incubate eggs and rear and fledge young (~24-day nesting cycle) before risking nest failure due to flooding from extremely high tides. Conversely, on higher river reaches of unrestricted systems, timing did not have a significant effect on nest survival. Above one and two roads in restricted systems, I found a small, but significant, *positive* effect from timing of clutch completion. Nest survival increased by ~10% for every day that clutch completion was delayed past the new moon. This trend has not been observed at other locations and may reflect some unique characteristics of the Webhannet and Ogunquit salt marshes. Or, it may be an effect from the tidal restrictions. A reasonable theory is that predation and timing of predation played a larger role in survival of nests located above tidal restriction. This may have been the case; however, data presented here do not suggest support to this theory because few nests failed due to predation in all reaches of the rivers, regardless of restriction (Table 3.1). Nevertheless, it is possible that predation played a role, but because of low sample size the effect was not apparent. These results suggest that there may be a cost to rapidly re-nesting after failure from flooding. This cost may be due to poor timing coinciding with predator activity, less energy put into nest construction (e.g. thinner nests), or less energy put into eggs. Sparrows nesting above one and two tidal restrictions might be responding to different selection pressures compared to reaches located further downriver or compared to other salt-marsh systems. More research on sharp-tailed sparrow nesting biology in tidally restricted systems would help elucidate the effect of restrictions on nest timing and nest survival.

Management implications

Land managers and municipalities need comprehensive information to implement appropriate restoration practices and conserve salt-marsh species like sharp-tailed sparrows. Previous studies have shown that tidal restrictions are a serious concern for marsh conservation (e.g., Burdick et al. 1997, Portnoy and Giblin 1997, Costa 1999 and 2000, Zedler et al. 2001, Roman et al. 2002, Mitchell et al. 2006, Gedan et al. 2009). However, those studies were focused on restrictions created by narrow culverts <1.5 m wide. Here, I examined wider tidal restrictions (3-47 m wide) and placed their effects in the context of nesting sharp-tailed sparrows. Results from this study have broad management implications because wider restrictions are more common and affect most salt-marsh systems in New England.

Results from this study demonstrate that not all tidal restrictions are equal or necessarily detrimental, particularly regarding high-marsh flooding and nesting sharp-tailed sparrows. Wide bridges (≥ 25 m) may be of less concern for conservation of high-marsh habitat as flood frequency was not reduced above them. In addition, more sharp-tailed sparrows nested above these bridges compared to adjacent areas located below tidal restriction or above the two-road culvert-type restriction (although daily nest survival was similar across all areas). The two-road tidal restriction in this study, created by a wide culvert (3 m), appeared to pose more of a concern for salt-marsh conservation. This area experienced less frequent flooding, and although salt-marsh vegetation was not greatly different in this area, the reduced flooding could hinder continued sediment accretion and may cause problems in the future. It would be prudent to continue monitoring vegetation and elevation in this area and at similarly restricted locations. If the culvert should be widened, results from this study suggest that nesting sharp-tailed sparrows on the Ogunquit River would not be greatly affected. Sparrows did not appear to preferentially nest above this restriction, and nest survival was not improved above it. Nevertheless, it is important to bear in mind that salt-marsh systems differ in many characteristics, including watershed size and surrounding anthropogenic development. In some cases, wide culverts may pose greater risks to nesting sharp-tailed sparrows than was found in this particular catchment.

It is interesting that nest timing relative to peak spring tides appeared to affect sparrows nesting above restriction differently from what has been found in other systems (Gjerdrum et al. 2005, Shriver et al. 2007, Gjerdrum et al. 2008). In unrestricted areas, rapid re-nesting was an important determinant of successful nesting, however above tidal restriction, nest survival was slightly higher for nests that delayed clutch completion. This suggests that while tidal flooding was the dominant selection pressure in unrestricted areas, there may have been additional pressures on sparrows nesting above tidal restriction.

Precipitation was correlated with higher flood frequency of the available habitat and with lower nest survival. This suggests that sharp-tailed sparrows may be highly vulnerable to climate change, which is expected to bring greater frequency of large storm events to the Northeast, USA (Douglas et al 2011). Sharp-tailed sparrow population size and trends are not well understood. We do know, however, that high-marsh habitat has been disappearing for over a century due to human use and development, and impending sea level rise will likely make matters worse. Studies like this are important for sharp-tailed sparrow conservation, and more research on these common types of tidal restrictions would help land managers understand how to best conserve salt-marsh ecosystems while minimizing impacts to sharp-tailed sparrows and other salt-marsh nesting species. In addition, much could be learned from comparative studies done before and after tidal restoration and would help inform management of salt marshes and sharp-tailed sparrows in the future.

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