

**LIFE HISTORY DIVERGENCE & TIDAL SALT MARSH
ADAPTATIONS OF THE COASTAL PLAIN SWAMP SPARROW**

Brian J. Olsen

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Jeffrey R. Walters, Chair
Russell G. Greenberg
Marcella J. Kelly
James A. Parkhurst
John B. Phillips

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ABSTRACT

Adaptation to local environments via natural selection is a powerful mechanism for population divergence and likely one of the primary causes of speciation. To understand how specific habitats shape local adaptation, it is helpful to study closely-related populations from widely differing ecosystems that have not had sufficient time to diverge by genetic drift. Throughout the following chapters I examine the distribution of morphological, behavioral, and reproductive phenotypes within and between two subspecies of the swamp sparrow. These two populations, the tidal salt marsh endemic *Melospiza georgiana nigrescens* and the nominant inland subspecies, *M. g. georgiana* were incompletely isolated from each other following the retreat of the Wisconsin glaciation. Since that time the increased nest predation, temperature, season length, salinity and tidal flow of the coastal marshes relative to inland wetlands has resulted in a number of adaptations among coastal sparrows due to natural selection, sexual selection, and phenotypic plasticity. Specifically I examine the habitat preferences of the coastal plain swamp sparrow, the difference in clutch size between the two subspecies, the rates of extrapair fertilization relative to male quality, the ecosystem-specific interactions between natural and sexual selection on plumage badges, and the role of conspecific attraction in nest placement. The environmental differences of the tidal salt marsh have played strong roles in the local adaptation and divergence of coastal plain swamp sparrows from their freshwater ancestors. Many of these divergent mechanisms may be similar among other tidal marsh endemics, although some (especially those related to sexual selection) may be specific to the swamp sparrow. In general, however, we see that the added environmental challenges of tidal ecosystems strongly alter selection regimes on a terrestrial vertebrate inhabiting this dynamic ecotone. The swamp sparrow system can further increase our understanding of how the interplay between environmental resources, sexual selection, and natural selection affects the local adaptations leading to evolutionary divergence.

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CHAPTER I:

AN INTRODUCTION TO SWAMP SPARROW DIVERGENCE

TIDAL SALT MARSHES AS CRUCIBLES OF DIVERGENCE

For over two centuries (Lamarck 1801; Darwin 1859; Wallace 1889), biologists have attempted to explain the diversity of life as a result of environmental forces. Convergent patterns among diverse taxa in similar habitats (Keast 1972; Gill 1995; Grenier and Greenberg 2005; Greenberg and Maldonado 2006) suggest that certain behavioral, demographic, morphological, or physiological traits may be shaped by specific environmental attributes, and hence adapted to those environments. Such convergent patterns have generated a number of classic evolutionary “rules” that implicate the role of abiotic and environmental effects on species diversification (e.g. temperature: Bergmann 1847; Allen 1877; Rapoport 1982; Stevens 1989; humidity: Gloger 1833; Beebe 1907; seasonal fluctuation: Ashmole 1963). Undoubtedly environmental characteristics have played a large role in shaping the life histories of bird species (e.g. Martin 1995; Martin and Badyaev 1996; Martin et al. 2006).

With their widely fluctuating abiotic conditions, tidal salt marshes represent an ideal system in which to study local adaptation and incipient speciation. The saline waters and flooding periodicity of tidal salt marshes produce a harsh physical environment, and few species have been able to colonize this ecotone between marine and terrestrial environments (Greenberg et al. 2006a). As a result, tidal salt marshes possess relatively low levels of plant, herbivore, and vertebrate diversity (Odum 1988; Greenberg et al. 2006a), despite the ecosystem’s higher than average productivity (Adam 1990). Endemism in North American tidal salt marshes, however, is relatively high, providing examples where environmental factors may have encouraged species divergence repeatedly (Greenberg et al. 2006a; Greenberg and Maldonado 2006). To better understand these processes, I investigated two subspecies of the swamp sparrow: the nominate inland *Melospiza georgiana georgiana* (Latham 1790) and the tidal-salt-

marsh endemic, *M. g. nigrescens* (Bond and Stewart 1951). Differences between these two subspecies parallel similar differences among inland and tidal marsh endemics from a wide variety of vertebrates (Greenberg and Droege 1990; Grenier and Greenberg 2005; Greenberg and Maldonado 2006), making the swamp sparrow system a logical place to investigate the effects of the tidal salt marsh specifically, and environmental attributes in general, on diversification and speciation.

The scattered inland and coastal wetlands that arose in abundance following the last retreat of the North American glacial sheet in the late Pleistocene (Colman and Mixon 1988; Greenberg et al. 2006a; Malamud-Roam et al. 2006), offered a wide array of challenges to existing species. The swamp sparrow, a North American wetland specialist, likely colonized newly emergent, tidal salt marshes from small, scattered, wetland refugia south of the glacial boundary during this post-Pleistocene period (Greenberg et al. 1998). Populations of sparrows inhabiting these tidal marshes today are morphologically distinct from other swamp sparrow subspecies (Greenberg and Droege 1990). Outwardly, with its relatively homogenous and low vegetation, the tidal salt marsh appears similar to many inland, freshwater marshes. Yet there are marked differences between the inland (*M. g. georgiana* and *M. g. ericrypta*) and the coastal plain subspecies of the swamp sparrow, which may be adaptations to the underlying differences between these two habitats (Odum 1988). In the following chapters I will compare the selective pressures of both inland and coastal habitats on the demography, morphology, and behavior of two swamp sparrow subspecies to understand how environmental attributes of the tidal salt marsh have shaped the divergence of these two subspecies.

ADAPTATIONS TO WETLAND SYSTEMS BY AVIAN FAUNA

Behavioral Adaptations

A variety of life history and behavioral traits are shared among many wetland endemics (Table 1.1). Polygamy, for example, is most common among passerines in species that occupy habitats with little vertical heterogeneity (Verner and Willson 1966; Willson 1966; Verner and Willson 1969), and has evolved repeatedly in marsh-nesting blackbirds

(Searcy et al. 1999; Johnson and Lanyon 2000). Additionally, the spatial heterogeneity of wetland habitat quality has led to locally denser bird populations than in nearby upland sites (Orians 1980; Greenberg 1988b; McDonald and Greenberg 1991; Picman et al. 1993), possibly increasing both agonistic interactions and territorial trespass rates (Greenberg 1988b; McDonald and Greenberg 1991; Searcy and Yasukawa 1995; Johnson and Lanyon 2000). Furthermore, spatial heterogeneity may have facilitated the evolution of colonial or semi-colonial nesting schemes in marsh Icterids and Emberizids (Tompa 1964; Orians 1966; Ellis 1980; Orians 1980; Picman et al. 2002). Close proximity resulting from such strategies may have increased the risk of nest predation, a well-cited cost of colonial nesting (Møller 1987; Møller and Birkhead 1993a). This may favor group nest defense, another common behavioral trait of marsh species (Stefanski and Falls 1972; Picman et al. 1988; Post 1998; Picman et al. 2002).

Marsh-nesting females also share common behavioral adaptations. Of the 17 recorded species where females give specific calls associated with departure from or arrival to the nest (hereafter “nest-departure calls”), 15 are associated with dense marshy, grassy, or shrubby habitats (McDonald and Greenberg 1991). The adaptation appears to have evolved at least three times (in European warblers, North American Icterids, and Emberizid finches: McDonald and Greenberg 1991) and apparently benefits the females by either reducing harassment from territorial males or increasing mate vigilance while the nest is untended (Beletsky and Orians 1985; Yasukawa 1989; McDonald and Greenberg 1991). The combination of high territorial aggression among marsh nesting males and the poor visibility of marsh systems favors inter-sexual acoustic signals to avoid unnecessary harassment from mistaken identification (McDonald and Greenberg 1991).

Morphological Adaptations

Increased sexual dimorphism appears to have evolved independently in several marsh-nesting species as a morphological adaptation to marsh life (Greenberg 1988a; Johnson and Lanyon 2000). Strong selection pressure for visually assessed, sexually dimorphic signals has been linked to increases in male-male aggression (Studd and Robertson 1985; Tanaka 1996; Johnson and Lanyon 2000) and the benefits of such a signal appear to

outweigh the presumed cost of increased predation in many marsh systems (Endler 1978; Endler and Houde 1995). High population densities may select for visual over auditory systems because of the gross increase in competitive noise from close territories (Post and Greenlaw 1975). Regardless of the mechanism, density appears to be a key cause of this adaptation, as blackbirds and sparrows that nest in lower densities in similar habitats have not evolved similar signals (e.g. Brewer's blackbird, *Euphagus cyanocephalus*, in savannahs: Johnson and Lanyon 2000; and *Ammodramus* sparrows in grasslands and salt marshes: Post and Greenlaw 1975). Both the sexual dimorphism and high nesting densities of swamp sparrows are unique among closely related genera and a rarity among all Emberizid sparrows (Greenberg 1988a).

ADAPTATIONS TO SALINE TIDAL WETLANDS BY AVIAN FAUNA

Although avian species that breed in salt-marsh ecosystems share many of the characteristics that make inland marsh birds ecologically competitive, they also possess a variety of morphological attributes not found among their freshwater counterparts (Table 1.2). Presumably, these differences are related to environmental attributes unique to tidal salt marshes. Many of the estuarine Emberizid sparrows have larger bills than their inland cohorts (Grenier and Greenberg 2005). Examples include the coastal plain swamp sparrow (Greenberg and Droege 1990), the seaside sparrow (*Ammodramus maritimus*), the saltmarsh sharp-tailed sparrow (*Ammodramus caudacutus*: Murray 1969), the Suisun Bay song sparrow (*Melospiza melodia maxillaris*: Marshall 1948), and the salt-marsh savannah sparrow (*Passerculus sandwichensis beldgingi*: Ridgeway 1901). Although this trait is not universal, there exists no species of tidally restricted sparrow with a *smaller* bill than its closest inland relative (Greenberg and Droege 1990). The convergence in bill morphology is likely related to shifts in dietary or foraging preferences tied to community and ecosystem characteristics.

Tidal species are also typically grayer or blacker and less red or brown overall compared to their inland counterparts, a condition that has been dubbed salt-marsh melanism (Greenberg and Droege 1990). This condition has been recorded in a number of avian subspecies, including the coastal plain swamp sparrow (Greenberg and Droege

1990), four song sparrow subspecies (Grinnell 1909; Marshall 1948; Nolan 1968), all of the seaside sparrow subspecies, two subspecies of sharp-tailed sparrow (Greenberg and Droege 1990), four marsh wren subspecies (*Cistothorus palustris*: Phillips 1986), and the clapper rail (*Rallus longirostris*: Greenberg and Droege 1990). Melanism has also been recorded numerous times in diurnal small mammal populations along both coasts of North America (e.g. Grinnell 1913; Von Bloeker 1932; Thaeler 1961; Wood et al. 1982). As the shift to eumelanic (gray to black) versus phaeomelanic (buff to rusty) pigments in birds occurs so often among phylogenetically distinct species, environmental selection is probably intense (Greenberg et al. 1998). Von Bloeker (1932) suggested that the pattern was related to the background color of estuarine muds, a theory supported in part by the presence of salt-marsh melanism in only diurnal small mammals. Water with high levels of NaCl has relatively low oxygen levels, a condition which causes soil irons to be reduced through anaerobic action into gray or black iron sulfides instead of the rusty iron oxides present in freshwater horizons. Predation against these two backdrops may produce enough selective pressure to cause evolution among a variety of diurnally active taxa (Greenberg et al. 1998).

Alternatively, melanic pigments have been shown to resist wear by feather-eating parasites (Burt and Ichida 2004; Goldstein et al. 2004), which may explain the increase in melanic plumage among birds in humid environments (Gloger's Rule: Gloger 1833) and with increased temperatures (Gloger 1833; Burt and Ichida 1999; Muza et al. 2000), like the conditions found at wetlands in the lower elevations associated with tidal marsh. In fact, feather-eating bacteria counts on coastal plain swamp sparrows greatly exceeds those found among inland swamp sparrows (E.H. Burt, in prep).

Another clear example of the effect of environmental attributes on species divergence is the ability of salt-marsh sparrows to drink saline water when closely related species are unable to do so. These adaptations involve kidney structure and function which allow salt adapted species to conserve water and concentrate salt in waste fluids and have been demonstrated in salt-marsh song sparrows (Basham and Mewaldt 1987), salt-marsh savannah sparrows (Cade and Bartholomew 1959), saltmarsh sharp-tailed sparrows, and seaside sparrows (Poulson 1969).

PHYLOGENETIC DIVERGENCE OF TIDAL MARSH ENDEMIC

The shared attributes of salt-marsh vertebrates indicate a strong influence of the ecosystem on species divergence. Further supporting this claim, time since estimated salt marsh colonization is correlated with both the degree of the development of many of these shared traits and the amount of genetic divergence from sister species as measured by neutral markers (Greenberg et al. 2006a). The coastal plain swamp sparrow has a low degree of divergence from the inland subspecies in both bill size and plumage color compared to other tidal marsh endemics. Likewise, despite the relative geographic isolation between the coastal plain swamp sparrow and its inland relatives during the breeding season, there is no obvious genetic differentiation based on mitochondrial, microsatellite, or nuclear DNA (Balaban 1988; Greenberg et al. 1998, *in prep*). The two subspecies possess distinctly different morphologies, however, which follow many of the patterns mentioned earlier (Greenberg and Droege 1990). Furthermore, *M. g. nigrescens* reared in the laboratory maintain the distinct traits of their group (Greenberg and Droege 1990), suggesting that the differences are indeed genetic (Beebe 1907; James 1982; Zink and Remsen 1986). Given this, it is clear that selective pressures in tidal ecosystems are sufficiently strong to cause rapid genetic divergence with either continued gene flow or following a recent split where selection on adaptable traits has outpaced the presumably fast-evolving markers used in genetic tests (Haavie et al. 2000). As most of the current habitat of the swamp sparrows was covered by glaciers 10,000 to 15,000 years ago or formed by subsequent glacial melt (Flint 1947; Greenberg et al. 1998), it is not surprising that neutral markers show no divergence. What is surprising is that such a recent isolation has allowed a number of recorded morphological, behavioral, and demographic differences to arise.

STUDY DESIGN

The recent divergence, incomplete morphological adaptation, and presence of a nearby inland relative make the coastal plain swamp sparrow system ideal for

investigations into the effect of the tidal salt marsh on adaptation and incipient speciation. In the chapters to follow, I approach study of this effect in three ways:

1. Identify known differences between inland and coastal populations and test for the effects of known environmental differences
2. Identify known environmental differences and test for additional, unreported divergence between the two subspecies.
3. Compare the influence of within-site and between-site environmental variance on the distribution of sparrow phenotypes.

The following chapters will investigate five topics from these two perspectives:

II. Habitat preferences in the coastal plain swamp sparrow

Inland subspecies occupy a wide variety of vegetated wetlands from cedar swamps to cranberry bogs, sphagnum and sedge fens, cattail marsh, and beaver impoundments (Mowbray 1997). Previous studies on *M. g. georgiana* have found three primary requirements for swamp sparrow habitat: standing water, dense vegetative cover, and tall perches for song posts (Reinert and Golet 1979; Greenberg 1988b, 1992; Mowbray 1997). Coastal populations are unable to key in on standing water alone, since water level is tied to tidal fluctuations that change both daily and seasonally. Given this known environmental differences, the second chapter investigates how habitat preferences may be operating in this fundamentally different ecotype.

III. Clutch size divergence

The third chapter tests for ecological explanations of the published difference in clutch size between inland and coastal birds (Greenberg and Droege 1990).

IV. Extra-pair mating

Given the higher productivity of tidal salt marshes (Adam 1990) and the periodic unavailability of resources due to tidal influx, one would expect that changes in resource spatial structure may affect the evolution of coastal mating systems (Orians 1980; Beletsky 1996). The fourth chapter looks for divergence in the extra-pair mating system of coastal versus inland birds as a result of this known environmental difference, using known variation in nesting synchrony, and territory size and density both within and between populations.

V. *Sexual versus natural selection*

Given the recorded plumage divergence in coastal plain swamp sparrows (Greenberg and Droege 1990) and similar convergent patterns among other tidal marsh vertebrates (Greenberg and Droege 1990; Greenberg and Maldonado 2006), it is reasonable to presume that natural selection exerts a strong force on pigment production. The crown of the swamp sparrow, however, is sexually dimorphic (Greenberg 1988a) and male crowns are likely under sexual selection. The fifth chapter investigates the possible conflicting selection processes exerted by natural and sexual selection on male crown color using the large variability in male crown color within and between the populations.

VI. *Nest site selection*

In swamp sparrows nest placement represents a secondary site selection within the territory (the primary site selection) by females. As in other cases of site selection, conspecific attraction may play a role. Given the differences in marsh resources between coastal and inland sites and the resulting effects on territory establishment, territory density, territorial aggression, mating system, and the relative benefits of group nest defense, the sixth chapter investigates whether females of either subspecies base nest site selection on the location of high quality habitat, neighboring male proximity, or the nesting activity of neighboring females.

FURTHER BACKGROUND

Natural History (Mowbray 1997)

The swamp sparrow was first described by John Latham in 1790 and currently has three recognized subspecies: *Melospiza georgiana georgiana* (Latham 1790), *M. g. ericrypta* (Oberholser 1938), and *M. g. nigrescens* (Bond and Stewart 1951). Of these only *M. g. nigrescens* is associated with brackish waters. The swamp sparrow is a sister species to the Lincoln's sparrow (*M. lincolnii*), and both share the song sparrow as their basal taxon (Zink 1982; Zink and Blackwell 1996; Patten and Fugate 1998).

Because of its ties to wetlands, swamp sparrows are associated with historic glacial processes. The species occurs only sporadically south of the Wisconsin glacial maximum, and even tidal habitats along the Delaware and Chesapeake Bays were formed

during eustatic sea-level rise during the late Pleistocene (Greenberg et al. 1998). The *M. g. nigrescens* populations are dispersed in an arm of tidal marsh that extends south from the Hudson River Valley along the Atlantic seaboard and into the Delaware and Chesapeake Bays. These coastal populations are separated by a gap of nearly 120km through the piedmont of Maryland and Pennsylvania from the nearest inland populations (Greenberg and Droege 1990). The only significant area of contact between *M. g. nigrescens* and *M. g. georgiana* is in northern New Jersey (Greenberg et al. 1998).

Swamp sparrows are primarily monogamous and migratory, breeding throughout the northeastern and north-central United States and southern Canadian provinces. Both inland subspecies winter in wet areas in the southeastern United States, including both inland wetlands and tidal salt marshes along the Gulf of Mexico and Atlantic Ocean (Mowbray 1997). The coastal swamp sparrow subspecies (possibly in its entirety) winters in a band of tidal salt marsh along the North Carolina Coast, perhaps reaching as far north as coastal Virginia (R. Greenberg, unpub. data).

During the spring males appear on the breeding grounds to set up territories before female arrival. Males set-up territories with song, chases, flight displays, “growl” notes, and occasionally physical contact, although territories are maintained mostly through song later in the season. Some researchers have reported territorial aggression by females early in the season (Ellis 1980). Territories are usually all-purpose, although instances of communal feeding grounds in undefended areas have been reported (Ellis 1980). Adults feed on a wide variety of foods, from seeds and fruits to aquatic and terrestrial arthropods, although they are generally more insectivorous than other Emberizids. As in most songbirds, young are feed mainly arthropods. Foraging occurs almost entirely near standing water or on saturated soils. In search of macroinvertebrates, adults wade or hang from low vegetation, picking arthropods off the water’s surface, submerging to turn over debris, or gleaning directly off vegetation. Their small size assists in maneuvering in and around dense vegetation (Mowbray 1997).

Females chose nest sites and are principally responsible for nest construction, although males rarely assist by bringing materials to the site. Eggs are laid one per day and incubation begins upon clutch completion. Only females incubate, and they utter a distinctive nest-departure call upon flying from the nest. Nest-departure calls are used

left often on the return trip, however, as females often arrive through the undergrowth rather than with sustained flight. Eggs hatch in 11-14 days and nestlings are provisioned by both parents. Young fledge in 9-12 days after hatching and are tended by both parents for a few days to more than a week afterwards, although the male typically spends more time with the fledglings at this time. Neighboring birds respond to distress cries by adults or young. Nests are predated by a wide array of mammals, birds, and reptiles. Adults will mob potential predators, although they are also preyed on by a variety of raptors and mammals themselves.

Study Areas

Melospiza georgiana nigrescens

I investigated the coastal subspecies on two plots (Fig. 1.1). The first ('Gate': Fig. 1.2) was established during the summer of 2002 and investigation were conducted from 1 May to 31 August for four summers (2002-2005). The second ('Bridge': Fig 1.3) was established during the summer of 2003 and investigations there occurred through three summers (2003-2005). Both plots are on Delaware State Game Lands along the Smyrna River in Short's Landing, Kent County, Delaware and experience both daily tides and oceanic surges during storm events. The center of the Gate and Bridge plots were straight-line distances of 2.8km and 3.3km from the Delaware Bay, respectively. Salinities (as measured with a salinity refractometer in standing water across both plots at multiple tidal stages throughout the summer months) ranged from 1 to 15 parts per thousand (‰) and the marshes were dominated by a mix of grass (*Spartina patens*, *S. alterniflora*, and *S. cynosuroides*), sedge (*Schoenoplectus americanus*), reed (*Phragmites australis*), and shrub (*Iva frutescens* and *Baccharis halimifolia*) species. Other birds that bred in both plots include Virginia rail (*Rallus limicola*), clapper rail, red-winged blackbird (*Agelaius phoeniceus*), seaside sparrow, common yellowthroat (*Geothlypis trichas*), and marsh wren.

Both study plots receive largely unrestricted tidal flows, although the Bridge plot possesses signs of six old ditches that have largely collapsed and are intersected by natural tidal guts and muskrat tunnels at multiple points. The Bridge plot is bordered on

the east by a seventh, intact ditch that parallels Delaware State Route 9, on the west by a tidal tributary of the Smyrna River, on the north by the river itself, and on the south by a ~15m strip of secondary forest separating the marsh from old-field habitat (seen as actively mowed hay-field in Fig. 1.3). Three, shallow (<10 cm) ponds are contained within the plot and typically receive tidal inputs during new and full moon tides. Muskrat trapping occurs rarely on the Bridge plot, and muskrat lodges, feeding platforms, and ditches are present in high abundance (Fig. 1.3).

The Gate plot is trapped heavily and thus possesses much lower concentrations of muskrat activity. This plot has not been ditched but its upland border follows a dirt road with two culverts allowing upland water from two freshwater wetland impoundments to flow into the plot. A secondary forest and an open field mowed annually by the Delaware Division of Fish and Wildlife complete the upland boundary. It is bordered on the northwest and northeast by additional, unaltered, tidal salt marsh and on the south by a ~20m strip of secondary forest separating the marsh from un-irrigated agricultural fields, which alternated annually between corn and soy bean crops throughout the study period. Delaware State Route 9 runs near the western edge of the plot.

Both plots are reportedly burned in roughly 4-5 year cycles (W. Lehman, pers. comm.), although no physical evidence of prior burning (e.g. scorched shrub stems or tree trunks found within or along the border of the marsh) was found on the Bridge plot. The Gate plot was last burned prior to the year 2000 and was not burned during the length of this study. Both plots were marked in 20m intervals with 1.5m aluminum tension bar.

Melospiza georgiana georgiana

I investigated the inland subspecies on two study plots on the Allegheny Plateau in Garret County, Maryland (Fig. 1.4) from 1 May until the cessation of breeding activity in 2004 and 2005. Both wetlands were stream-fed, sphagnum-peat fens dominated by sedge (*Carex* sp.), shrubs (*Ilex mucronata*, *Alnus incana*, *Viburnum* sp., *Hypericum prolificum*, *Vaccinium angustifolium*), cattail (*Typha latifolia*), sporadic trees (*Picea mariana*, *Amelanchier laevis*, *Acer rubrum*), and a mixed herbaceous ground cover (*Sphagnum* sp.,

Rubus sp., *Vaccinium macrocarpon*, *Symplocarpus foetidus*, *Thelypteris thelypteroides*, *Drosera* sp.). Both wetlands are the source of first order tributaries that drain north and make up the headwaters of the North Branch of the Casselman River. Other birds that breed at both plots include golden-winged warblers (*Vermivora chrysoptera*), song sparrows, rose-breasted grosbeaks (*Pheucticus ludovicianus*), common yellowthroat (*Geothlypis trichas*), northern waterthrush (*Seiurus noveboracensis*), Wilson's snipe (*Gallinago delicata*), and American black duck (*Anas rubripes*). Both plots were marked at 20m intervals with 2.5cm x 2.5cm x 1.5m wooden stakes.

The Glades plot (Fig. 1.5) covers the majority of the largest peat deposition in Maryland (Fenwick and Boone 1984). The north end of the 55ha fen was extensively mined for peat until the 1980's, resulting in a large pond that borders the fen's downstream edge. The Glades harbor 19 species listed as species of conservation concern (S1-S3) by the state of Maryland. The southern, intact section of the Glades is currently owned by the Nature Conservancy and possesses no points of public access. On all upstream edges the Glades is bordered by secondary forest, late-successional old-field, or white pine (*Pinus strobus*) plantation. There is a large complex of haying fields downstream from the plot which includes breeding red-winged blackbirds (*Agelaius phoeniceus*), bobolink (*Dolichonyx oryzivorus*), and vesper (*Pooecetes gramineus*) and savannah sparrows.

The Cunningham Swamp plot (Fig. 1.6) covers the southern edge of Cunningham swamp, which is a privately owned wetland dominated by sphagnum-alder thicket throughout much of its 54ha extent. The wetland is fed by a stream running out of the dammed Cunningham Lake (8ha), a public recreational spot which is commonly used for fishing, boating and swimming in the summer and includes numerous public access points and a 4H summer camp. The plot is more open than the swamp in general and possesses more cattail and evergreen trees than does the Glades plot. The southern, upland edge borders late-successional old-field and secondary forest and alder thicket along its downstream edge. On the east of the plot is a large wet meadow dominated by grasses and sandier soils than those found within the swamp. The sphagnum and peat layers are much shallower in this plot than at the Glades, often less than half a meter in depth.

FIGURES

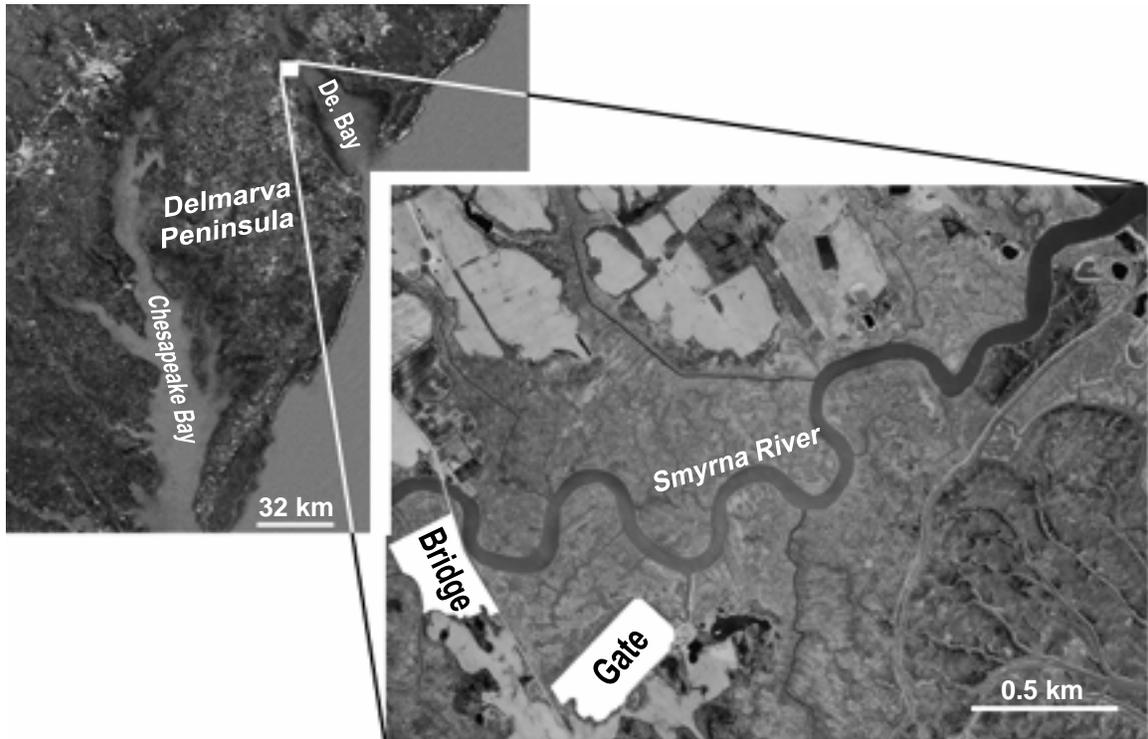


Figure. 1.1. Coastal Plots

Photos depicting the relative locations of two study plots (white polygons) situated in Short's Landing, Kent County, Delaware in tidal salt marsh along the Delaware Bay.



Figure 1.2. Gate Plot

Aerial photograph showing the boundary (white line) of the 'Gate' plot in Short's Landing, Kent County, Delaware.



Figure 1.3. Bridge Plot

Aerial photograph showing the boundary (white line) of the 'Bridge' plot in Short's Landing, Kent County, Delaware.

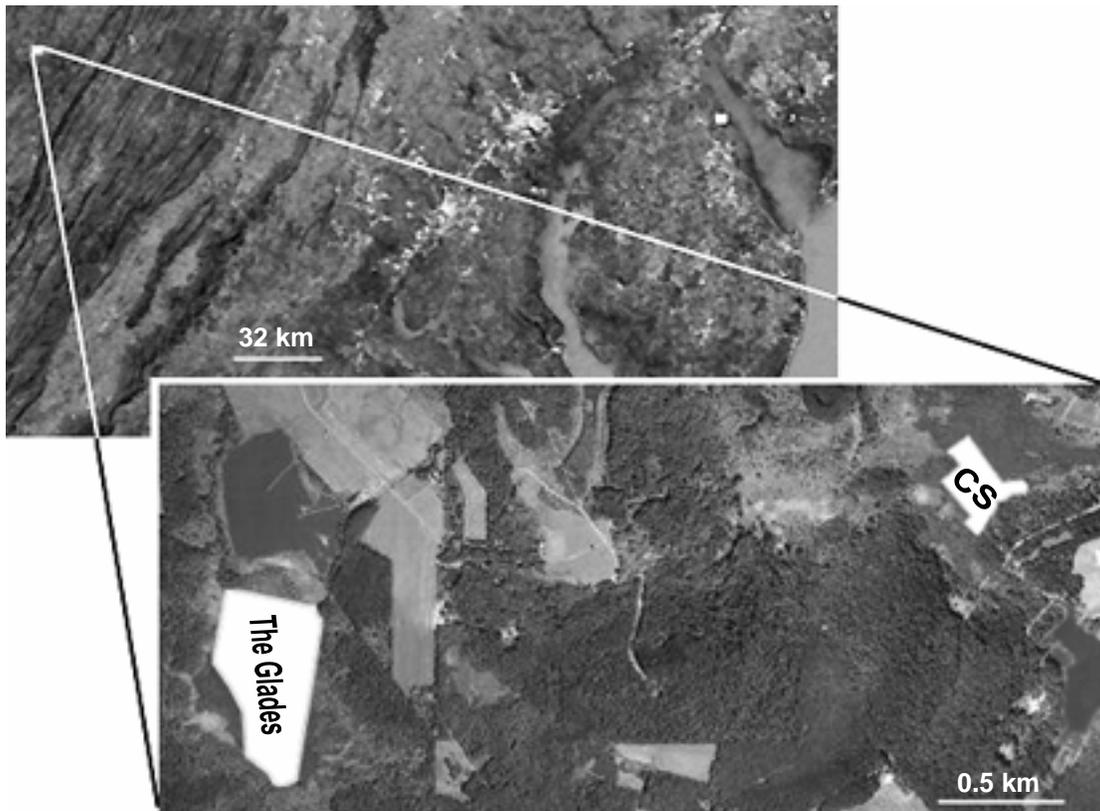


Figure 1.4. Inland Plots

Photos depicting the relative positions of the Glades and Cunningham Swamp (CS) plots (represented by white polygons) near Bittinger, Garrett County, Maryland. Both the inland and coastal field sites are indicated with a white square on the upper image.



Figure 1.5. The Glades Plot

Aerial photograph showing the boundary (white line) of the Glades plot near Bittinger, Garrett County, Maryland.

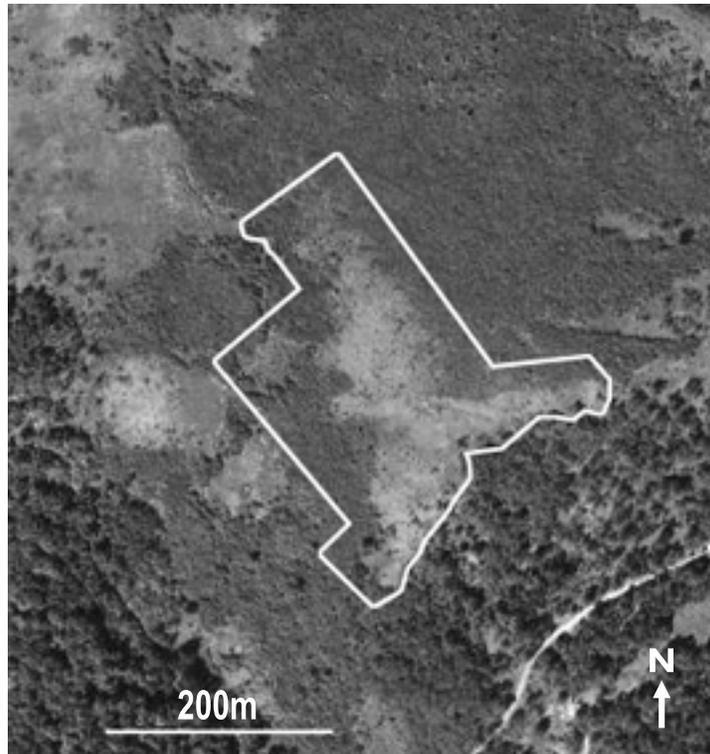


Figure 1.6. Cunningham Swamp Plot

Aerial photograph showing the boundary (white line) of the Cunningham Swamp plot near Bittinger, Garrett County, Maryland.

TABLES

Table 1.1. Avian adaptations to wetlands.

The listed adaptations are generally more common in wetland specialists than their nearest upland relatives.

Adaptation	Source
Polygamy	Verner and Willson 1966; Willson 1966; Verner and Willson 1969; Searcy et al. 1999; Johnson and Lanyon 2000
Increased population density	Orians 1980; Greenberg 1988b; McDonald and Greenberg 1991; Picman et al. 1993
Increased territorial aggression and trespass rates	Greenberg 1988b; McDonald and Greenberg 1991; Searcy and Yasukawa 1995; Johnson and Lanyon 2000
Colonial or semi-colonial nesting	Tompa 1964; Orians 1966; Ellis 1980; Orians 1980; Picman et al. 2002
Group nest defense	Stefanski and Falls 1972; Picman et al. 1988; Post 1998; Picman et al. 2002
Nest-associated female calls	Ellis 1980; Beletsky and Orians 1985; Yasukawa 1989; McDonald and Greenberg 1991
Sexual dichromatism	Greenberg 1988a; Johnson and Lanyon 2000; Post and Greenlaw 1975

Table 1.2. Avian adaptations to tidal, saline wetlands.

The listed adaptations are more common in tidal salt marsh specialists than their nearest inland relatives.

Adaptation	Source
Large bill size	Ridgeway 1901; Marshall 1948; Murray 1969; Greenberg and Droege 1990; Grenier and Greenberg 2005
Salt-marsh melanism	Grinnell 1909, 1913; Von Bloeker 1932; Marshall 1948; Thaeler 1961; Nolan 1968; Wood et al. 1982; Phillips 1986; Greenberg and Droege 1990
Kidney physiology	Cade and Bartholomew 1959; Poulson 1969; Basham and Mewaldt 1987

CHAPTER II:
HABITAT SELECTION IN A MONOGAMOUS PASSERINE:
ASSESSING SCALE AND GENDER INTERACTIONS THROUGH
INDIVIDUAL QUALITY

ABSTRACT

The basis for habitat selection has been a central issue in ecology. While many studies investigate responses to particular habitat features, research increasingly shows that different sexes may respond to their environment at different scales. Because individuals compete within sexes, individual quality must also be considered in assessing preferred habitat. In this study, we analyzed the distribution of high quality coastal plain swamp sparrows (*Melospiza georgiana nigrescens*) with respect to habitat features that predicted reproductive success, specifically fledging success and nestling growth rate. We found that each sex selected territories differently by responding to habitat at differing scales. Nest success was predicted by the presence of dense Olney three-square (*Schoenoplectus americanus*) or big cordgrass (*Spartina cynosuroides*) near initial nesting attempts, while nestling growth rate was predicted by the salinity of water across the territory. High quality males (defined by crown patch size) were associated with larger territories with intermediate values of territorial salinity and high sedge-grass cover around initial nest sites. Female condition, on the other hand, was associated with male crown patch size and nest-site scale variables but was not associated with territorial salinity. High quality males thus maximize nest success and nestling growth through direct selection of habitat, while females achieve the same results through indirect selection on male quality and direct association with nest-site scale habitat. Our results illustrate the methodological benefits of using individual quality to assess habitat preference and the importance of both sex and scale in even socially monogamous systems.

INTRODUCTION

The ecological literature is awash with habitat association studies, including investigations of habitat selection, use, and quality (Cody 1985; Jones 2001; Gottschalk et al. 2005). Increasingly, it has become clear that habitat associations operate at multiple scales, and different mechanisms may govern habitat selection within each scale (Bock 1987; Sodhi et al. 1999; Luck 2002).

Apart from scale considerations, males and females may respond differently to habitat features during settlement. Furthermore, sex/scale interactions may lead to sexes selecting different habitat features at different scales. Although these interactions may be intuitive in polygamous species where each sex uses the landscape in an explicitly different way (Badyaev et al. 1996; Miller et al. 1999), few studies have investigated such processes within socially monogamous pairs during the breeding season (Sedgwick and Knopf 1992). Knowledge of such interactions is crucial when selecting which features to measure when determining habitat suitability. Typically, studies have examined display areas (Morrison and Meslow 1983; Knopf et al. 1990; Beck and George 2000), nesting sites (Holway 1991; Steele 1993; Goodman et al. 2005), foraging areas (Matsuoka et al. 1997; Roth et al. 2004; Wasserberg et al. 2005), or roosting sites (Kilpatrick et al. 1988; Chamberlain et al. 2000; Miller et al. 2003) to determine habitat associations. These different measures, however, may represent the needs of only a specific sex, thereby resulting in biased conclusions about habitat relationships for the entire population (Collins 1981; Sedgwick and Knopf 1992).

Defining habitat availability is yet another problem. Most habitat preference studies use correlations between a species' distribution and specific habitat features, comparing used-versus-unused or used-versus-available habitats. Determining which unused habitat should be included in the analysis, however, is difficult and has evoked criticism in the past (Johnson 1980; Jones 2001). An alternative approach to determine habitat preferences is to compare the density (Fretwell and Lucas 1970; Fretwell 1972) and quality of individuals (Fretwell and Lucas 1970; Sergio and Newton 2003; Norris et al. 2004) occupying different habitats within the area actually used by a population. In this study we use individual quality to determine which habitat features are the most

contested, assuming that individuals of the highest quality will occupy the most desired sites. Under this method the designation of available habitat is less problematic because it is restricted to habitat that is actually occupied, albeit by individuals of varying social dominance. Thus, although preferred habitat identified by this method may be at a smaller scale than more commonly used techniques, there is little doubt that all habitat considered is fully available to at least the highest quality individuals. This assumption is especially safe in migratory songbird systems where arrival time and quality are correlated.

Site fidelity, however, may limit the expression of habitat preferences to dispersing individuals (Beletsky and Orians 1987; DiQuinzio et al. 2001; Ward and Weatherhead 2005). The quality of site faithful birds may be unrelated to the quality of their territories in years subsequent to settlement, as habitat features in a given area may shift away from preferred features or the quality of a territory holder may change. Within areas that match a species' habitat preferences, however, continued competitive pressure from dispersing individuals assures that only high quality individuals maintain high-quality, preferred territories (Hyman et al. 2004). To understand habitat preference we therefore used competitive pressure (the inverse of territory size) as our measure of preference strength for males (controlling for individual quality with plumage badge). For females we tested for habitat variables that predicted individual quality (controlling for date of measure), assuming that intra-specific competition for established males would result in high quality females on preferred territories.

Despite being shaped by sex, scale, individual quality, and site fidelity, an individual's selection of specific habitat is ultimately determined by the effects of habitat features on survival and reproduction. In species exhibiting parental care, the quality of foraging locations (provisioning and growth rate) and the ability to avoid predation until offspring fledge (nest success) are two important endpoints. The habitat features that affect these measures may not be spatially correlated, and a variety of strategies likely exist to maximize both endpoints, strategies that may vary with sex and scale (Lima and Dill 1990; Brown and Kotler 2004).

We investigated the habitat selection of male and female coastal plain swamp sparrows (CPSS), *Melospiza georgiana nigrescens*, based on key, individual attributes

measured at two different scales. Specifically, we used nest success and nestling growth to define habitat quality and examined which habitat features predicted both these measures and the competitive success (male territory size controlling for male plumage badge) and quality (female body condition) of the individuals that settled there.

CPSS are tidal, brackish-marsh endemics that breed primarily in *Spartina* marshes along the Mid-Atlantic States within a specific zone of salinity (Beadell et al. 2003). They are socially monogamous and males defend small (0.23 ± 0.07 ha), all-purpose, breeding season territories, which are established before female arrival from the wintering grounds (Mowbray 1997). This system is ideal for habitat investigations, as the occurrence of discrete plant assemblages and a simple vegetative structure allows for relatively simple habitat relationships (Bertness et al. 2002).

METHODS

Study Site & Habitat Measurements

All investigations occurred on two ~15 ha plots within Delaware State Game Lands, in tidal marsh dominated by several species of *Spartina* near Woodland Beach, Delaware. The vegetation in these plots consists of discrete habitat patches along a salinity gradient known to be within CPSS tolerance (<15 ‰; Beadell et al. 2003). Major vegetation zones include shrub-grass patches (*Iva frutescens* and *Spartina patens*), sedge-grass mixes (*Schoenoplectus americanus* and *Spartina patens*), tall grass beds (*Spartina cynosuroides*), low marsh grasses (*Spartina alterniflora*), and invasive reeds (*Phragmites australis*). Over our three years of study (2002-2004) we monitored 111 territories for which both members of the territorial pair were banded with unique color combinations. Of these 111 territories, 79 produced initial nesting attempts for which all habitat measures were gathered. To control for one key aspect of habitat quality heterogeneity, we equalized song-post density by placing artificial song-posts (1.5m aluminum stakes) across the marsh every 20m in a grid. Stakes were taller than the mean vegetation height at the beginning of the breeding season and were used heavily by males throughout the season. We measured the percentages of vegetative and water/mud (a single category due to tidal shifts) cover in 5m-radius circles centered on each stake (Table 2.1), and

standing water salinity and maximum and minimum water depth within one meter of each stake. The three water measurements were gathered within one hour of high tide and salinity was measured with a refractometer in parts per thousand (‰) at a random point within 1m. The 5m radius allowed for a much finer resolution estimate of ground cover than the standard 0.04 ha circles used by many habitat studies (James 1971; Noon 1981; Sedgwick and Knopf 1992) without compromising the percentage of the study area sampled. It also lessened the probability that measured habitat fell outside of a given territory. We also measured ground cover type and water variables around the locations of initial nesting attempts. We used initial attempts because they are more likely to influence the settlement of individuals (and hence habitat preference) than later nest-sites.

Habitat Correlates of Quality

Having partially controlled for song-post heterogeneity prior to territorial establishment, we identified nest-site quality, foraging-area quality, and mate quality as additional influences on settlement. For investigations of foraging-area quality, we averaged cover type and water variables around all stakes found within each territory, as adults typically forage in multiple vegetation zones and at multiple sites across their territory. For nest-site quality, we used only the 5m-radius (0.008 ha) circle immediately surrounding the initial nest (a 29 fold difference in scale on average).

We defined nest-site quality binomially, with high quality sites fledging young and low quality sites failing to do so. To determine foraging area quality, we assumed that nestlings raised on food gathered from high-quality foraging grounds would gain mass faster than those raised in poorer areas. We therefore used the slope of the nestling growth curve for each territory as a proxy for foraging-area quality. We weighed all surviving nestlings younger than eight days post-hatch (to prevent early fledging) every three days with a digital scale to the nearest hundredth of a gram, resulting in data with a variety of ages from multiple broods for each territory. The slope of nestling growth was calculated by plotting all chick weights for each territory against a logistic growth curve via the method described by Ricklefs (1967).

Only initial nesting attempts were used for nest-site habitat measurements as the first nest represents the initial selection by a female. Nestling growth, however, was

calculated over the entire season. We did this for two reasons. First, initial nesting attempts did not always hatch young, and limiting our data set to the initial attempt or the initial attempt that succeeded in hatched chicks would have severely limited our sample size. Second, using all nesting attempts (four nesting attempts are not uncommon in our population) resulted in a mean measure of the foraging quality of a territory for the entire season, a measure that is much less likely to be affected by short-term weather events than a measure based on a single nesting attempt. Ultimately, selection for habitat preferences at the scale of the territory is more likely to be based on such seasonal averages.

Measures of Individual Quality

Female quality was defined by the body mass to size ratio, using the weight of each individual at the first capture of the season (typically before or within three weeks of territorial establishment) divided by the length of the tarsus. This measure reflects the energetic costs inflicted upon an individual during migration and the non-breeding season, and represents the relative caloric stores available for intra-individual territorial competition (Marra et al. 1998; Sillett et al. 2000; Studds and Marra 2005). Male quality was assessed indirectly by territory size, controlling for the extent of rust-colored feathers in the crown. The rusty crown patch is acquired directly before the breeding season and lost after, and it is likely a plumage badge reflecting male quality (Mulder and Magrath 1994; Örnborg et al. 2002; McGraw et al. 2003). Furthermore, male crown patch size is correlated with behavioral variables related to territorial defense within our population (Chapter 5). All captured bird crowns were categorized on a scale of one to four (1 = no rusty feathers, 2 < 50% rusty feathers, 3 > 50% rusty feathers, and 4 = 100% rusty crown). All males in our study population received a crown score of two or higher. Territory size was calculated using minimum convex polygons whose vertexes were defined by male song posts.

Statistical Analysis

All statistical analyses were computed in SAS 9.1.3 (SAS Institute 2005). Given the large amount of habitat variables we measured (Table 2.1) and the correlative nature of

vegetative and water characteristics within tidal salt marshes (Bertness et al. 2002), we used principal components analysis (PCA) to assess the multivariate nature of habitat heterogeneity. PCA was conducted at each scale separately, as correlations between measures may differ at different scales. Additionally, some measures (sal, min, max, tal: Table 2.1) were not measured at nests in all years and so were precluded from analysis at the smaller scale to conserve sample size. *A posteriori* analysis examined the effects of important territory-scale variables on the smaller, complete set of nest measurements. All principal components with eigenvalues greater than 1.0 were accepted for analysis (Sharma 1996).

Correlations between habitat principal components and nestling growth curves were explored using multiple linear regression (after testing for normality and homogeneity of variance). Model selection was based on Mallows' Cp. Following the designation of the best performing model(s), single effect models (using all variables with significant Pearson's correlation coefficients at $P < 0.001$) were run *a posteriori* to determine whether the performance of the successful principal components was simply a result of a single heavily weighted variable (Sharma 1996). In instances where the more simple, single-variable model explained more variation than the resulting principal component, single-variable models were used for further analysis.

Correlations between habitat principal components and initial nest success were investigated using multivariate logistic regression. Model selection was stepwise with addition and elimination alpha levels set *a priori* to 0.15. Single-variable models were tested *a posteriori* upon designation of the best performing principal component models similarly to the nestling growth curve analyses.

The best performing models of both nest-site (small scale) and foraging-area (large scale) quality were tested with male crown (two indicator variables representing the three classes) as predictors of territory size using multiple linear regression and Mallows' Cp as a model selector. Likewise, nest-site quality, foraging-area quality, territory size, and male crown were tested as predictors of female quality, controlling for the date of female measure (as female condition is influenced by date). All means are presented with 95% confidence intervals.

RESULTS

Predictors of Quality

PCA for habitat measurements at the territory-scale resulted in seven principal components with eigenvalues greater than 1.0, accounting for 78% of the variation in the original 16-variable dataset (Table 2.2). Of the 111 territories, 54 produced chicks that survived until the first weighing. Of those, 28 produced multiple broods that were weighed, or produced chicks that survived through multiple weighings. The fifth Principal Component (PC5) alone was the best, albeit insignificant, predictor of nestling growth ($F_{1,26} = 1.2$, $n = 28$, $r^2 = 0.046$, $P = 0.28$). *A posteriori* analysis on the heavily weighted components of PC5 (Table 2.2) revealed that salinity alone was a better model than PC5 ($F_{1,26} = 6.2$, $r^2 = 0.19$, $n = 28$, $P = 0.02$) with low salinity associated with faster nestling growth (Fig. 2.1).

PCA for measurements at the nest-site scale produced six principal components, which explained 73% of the variation in the original 11-variable dataset (Table 2.3). The second Principle Component (PC2) was the best predictor of nest success and was negatively correlated with success ($\chi^2_1 = 3.8$, $n = 79$, $P = 0.05$; Fig. 2.2). PC2 describes a shrub-grass mixture (*Iva frutescens* and *Spartina patens*) that is common along the edge of the high marsh and is negatively correlated with sedge and tall grasses (*Schoenoplectus americanus* and *Spartina cynosuroides*) found further along the tidal gradient (Table 2.3). High nest success was associated with more of the sedge and tall grass and less of the shrub-grass mixture. *Spartina patens* cover within 5m performed the next best ($\chi^2_1 = 2.6$, $n = 86$, $P = 0.11$) and was negatively associated with nest success. Analysis on the smaller, complete data set showed that salinity near the nest was not related to success ($\chi^2_1 = 0.21$, $n = 49$, $P = 0.65$).

Predictors of High Quality Individuals

Having determined that salinity predicts overall territory (foraging habitat) quality and that the sedge-grass vegetation type (PC2) predicts nest-site scale quality, we then tested whether the settlement of high-quality individuals was based on a single factor or a

combination of factors. We captured 30 males and 37 females for which we also obtained information about their respective territories, nest sites, and mates.

To determine male habitat preferences, territory size was log-transformed to meet assumptions of normality. Male crown type, territory-scale quality, and nest-site scale quality together produced the best predictor of territory size ($F_{5, 24} = 5.8$, $r^2 = 0.55$, $P = 0.001$: Fig. 2.3). The relationship between territory size and both measures of quality were quadratic, and both the linear (territory scale: $t_1 = -2.1$, $P = 0.05$; nest-site scale: $t_1 = -2.5$, $P = 0.02$) and squared terms (territory scale: $t_1 = 3.0$, $P = 0.006$; nest-site scale: $t_1 = 3.4$, $P = 0.002$) were significant components of the final model (Figs. 2.4, 2.5).

With female preference, on the other hand, nest-site quality, log territory size, and male crown produced the best model when banding date was controlled ($F_{4, 32} = 10.4$, $r^2 = 0.56$, $P < 0.001$: Figs. 2.6, 2.7), while territory-quality did not predict the quality of females ($F_{1, 34} = 0.4$, $r^2 = 0.01$, $P = 0.53$) and was not a significant predictor in the full model ($t_1 = -1.8$, $P = 0.09$).

DISCUSSION

As we predicted, male coastal plain swamp sparrows select habitat based on features found at both the territorial and nest-site scale, while females select habitat based on the nest-site and male quality (Figs. 2.3 and 2.7). These two strategies represent different solutions to the problem of maximizing nestling growth and nest success. Males directly select habitat features at two scales to maximize both reproductive measures, while females select habitat directly for nest success and indirectly for nestling growth through male quality. Each strategy is a result of gender-specific selection mechanisms. Males are more limited by foraging area quality than females through the added energetic constraints of territorial maintenance and paternity assurance (both sexes feed nestlings). Females benefit from the increased constraints on males through indirect selection on male quality, likely gaining other benefits of male quality in the process (e.g. good genes). As the sole constructors of nests, females exhibit small-scale preferences for nest-site microhabitat. Males' preference for this same feature likely both attracts potential mates and increases nest success. This study highlights the importance of

considering both sex and scale when designating optimal habitat or habitat preferences, even in a monogamous passerine with a relatively small territory.

Habitat Correlates of Quality

The role of salinity in determining foraging quality is likely mediated through effects on macroinvertebrate community structure both through direct physiological effects and indirect species interactions (Moon and Stiling 2004; Hart and Lovvorn 2005). In general, among soft-bottomed, tidal marshes, macroinvertebrate taxon richness is negatively associated with salinity (Levin 2000; Levin and Talley 2002). For example, within the Delaware Bay estuary, insect larvae are important components of fish prey in only the freshest areas of the bay, while annelids make up larger components further down the salinity gradient (Nemerson and Able 2004). Likewise, insect larvae make up a large proportion of both adult and juvenile CPSS diet, as determined by gastral lavage and fecal analysis, respectively (B. Olsen, unpub. data). Annelids, although present within the study site, were never found in diet samples of CPSS (B. Olsen, unpub. data). Thus, the high foraging quality of low-salinity territories may result from the larval insect community of oligohaline environments. Alternatively or additionally, issues of osmotic balance may prohibit both nestling growth and male foraging efficiency in areas of high salinity (Basham and Mewaldt 1987; Goldstein et al. 1990; Sabat et al. 2003).

Patches of *Schoenoplectus americanus* and *Spartina cynosuroides* (PC2), which predicted nest success, are common constituents of CPSS habitat. Prior analyses of the species' distribution by Beadell et al. (2003) indicated a strong positive association between sparrow presence and *Iva frutescens*, which was negatively associated with PC2. Beadell et al. (2003), however, concentrated their surveys along roads and dykes and preferentially chose survey locations with significant stands of *I. frutescens*. These methods likely biased their results towards birds along the edges of the marshes. At a population scale, *Iva* may predict swamp sparrow occupation, but our study illustrates that these areas are marginal and less contested, and it highlights the need to tie habitat associations to individual quality to construct realistic management plans.

Spartina patens, which was positively correlated with PC2, is the primary building material of all CPSS nests. Nests incorporating other plant materials into the

nest cup are rare (B. Olsen, unpub. data). Even nests that were placed in *Schoenoplectus americanus* and *Spartina cynosuroides* had significant amounts of *Spartina patens* within 5m (23.3 ± 4.5 percent cover). Thus the influence of *S. patens* presence on nest success is not uniformly negative. Rather, we suggest the negative relationship of *S. patens* with success is due to the failure of nests that were placed in nearly homogenous patches of *S. patens*. Additionally, the quadratic relationship between PC2 and territory size may reflect male preference for areas that possess both high quality vegetative cover and nest anchors (*Schoenoplectus americanus* or *Spartina cynosuroides*) and high quality nest-building material and nest cover (*Spartina patens*).

Schoenoplectus americanus and *Spartina cynosuroides* grow in dense stands that provide both aerial and ground cover. Patches of *Schoenoplectus americanus* also have the deepest, least-fluctuating water on the plot. This standing water may prevent predation by a suite of mammalian predators as it does in other wetland passerines (Greenberg 1988b; Picman et al. 1993). Furthermore, the increased water depth in these habitat patches is caused primarily by muskrat excavation and not by tidal influx, and as such these areas possess the predation-avoidance advantages of deep water without the resultant increase in flooding risk associated with vegetation patches in the lower marsh. The more complicated preference for vegetation patches rather than water depth represents a behavioral divergence from inland subspecies (Greenberg 1988b). Discrete, simple patches coupled with the unreliability of water depth in predicting nest success in tidal salt marsh may have led to this shift in preference from freshwater swamp sparrows.

Habitat Preference by Sex

Territory size represents the end result of individual competitive ability and habitat preference, where smaller territories are associated with preferred habitat and larger territories within preferred habitat are associated with individual quality. In our system we found that the smallest territories were associated with medium salinities and a compromise between taller, dense grasses and sedges and the nest material, *Spartina patens* (Figs. 2.4, 2.5). However, controlling for these habitat features, males with the largest percentage of rust in their crowns were able to procure larger territories.

Although the linear relationship between salinity and nestling growth would suggest that males gain direct benefits by establishing territories in the freshest habitats, the quadratic relationship with territory size suggests that males actually prefer an intermediate salinity. This brackish preference may be related to a tradeoff with predation. Salinity and the distance to upland habitats are confounded (Bertness et al. 2002) so that the freshest territories are found along wood and agricultural edges and may experience a higher prevalence of terrestrial predators (e.g. snakes, raccoons, and foxes). Thus, male habitat preference may be constrained on the freshwater end by nest survival and on the saline end by nestling provisioning ability. The success of nests placed in non-salt marsh vegetation along the marsh edges and in *Spartina alterniflora* at the saline maximum of the sampled area supports this tradeoff, as no nests fledged young in either extreme.

Although male swamp sparrows do not build nests (Mowbray 1997), the quality of egg deposition sites within a male's territory determines mating success in a wide variety of taxa (insects: Campanella 1974; fish: Jones 1981; amphibians: Wells 1977; Howard 1978a, b; and birds: Searcy 1979; Yasukawa 1981). In systems where female mate-choice is determined at least partially by territory quality rather than direct mate selection, males with habitat preferences similar to females' pair reliably. One therefore would expect males to prefer habitat with low values of PC2 as females do, but instead males preferred an intermediate value of the vegetation represented by PC2 near the nest. We can only speculate that males may be affected by a tradeoff involving some other, unknown feature associated with lower values of PC2.

Female preference reflects both linear, small-scale nest-site characteristics and two measures of male quality (Fig. 2.7). Interestingly, controlling for date of condition measure, females in the poorest condition occupy habitats that possess the highest nest-site quality and are the most contested among males. This implies that females in the best condition are not the most competitively successful. The little research on female territory selection suggests it may be due primarily to the time of settlement and secondarily, if at all, related to direct competition (Alatalo et al. 1981; Gronstol et al. 2003; Reid et al. 2004). If these results can be extrapolated to migratory, monogamous species, female condition may be unimportant except as an indicator of arrival date.

Although we did not collect data on female arrival date, female condition was unrelated to breeding initiation ($F_{1,30} = 0.3$, $n = 32$, $r^2 = 0.01$, $P = 0.57$).

A growing body of research suggests that species with predictable food sources use daily excesses in foraging for breeding instead of stores present at the beginning of the season (Jonsson 1997; Boyd 2000; Drent et al. 2003; Nooker et al. 2005). In these “income breeders” condition at the beginning of the breeding season is unrelated to reproductive output. The negative relationship between condition and reproductive success we report is, to our knowledge, unprecedented. Unless condition is indeed related to arrival date, we can offer no explanation of this relationship.

The Use of Individual Quality

Using individual quality to determine optimal or preferred habitat represents an improvement over more traditional used-versus-unused models, as our method avoids issues of habitat availability. An underlying assumption of this methodology is that any measure of individual quality reflects the ability of that individual to obtain habitat, which may not be true in species where plumage badges reflect parental ability and not territorial aggression. Furthermore, we assumed that the fitness endpoints used to determine habitat correlates of high quality reflected the quality of the territory directly and not the quality of the individual occupying the territory. This may not always be the case. For instance, the nestling growth curve presumably reflects the foraging ability of the parents as well as the quality of the foraging grounds, an association that may be confounded in this study. Although habitat preference may not be due to selection by the adults on foraging quality, the habitat does reliably predict nestling growth and the settlement of high quality males, if only indirectly, and is thus a good candidate for determining superior habitat for management purposes.

Regardless of the mechanisms controlling habitat preference, the use of individual quality coupled with measures of reproductive fitness resulted in a more informed description of optimal habitat for coastal plain swamp sparrows. Furthermore, it highlighted the different approaches of each sex in maximizing multiple reproductive success measures. These methods would be more powerful with an experimental approach, but even correlative studies of this sort possess inherent advantages over

historic methods of investigating habitat associations. We show that even in a socially monogamous passerine, scale and gender play an important role in predicting responses to habitat features.

FIGURES

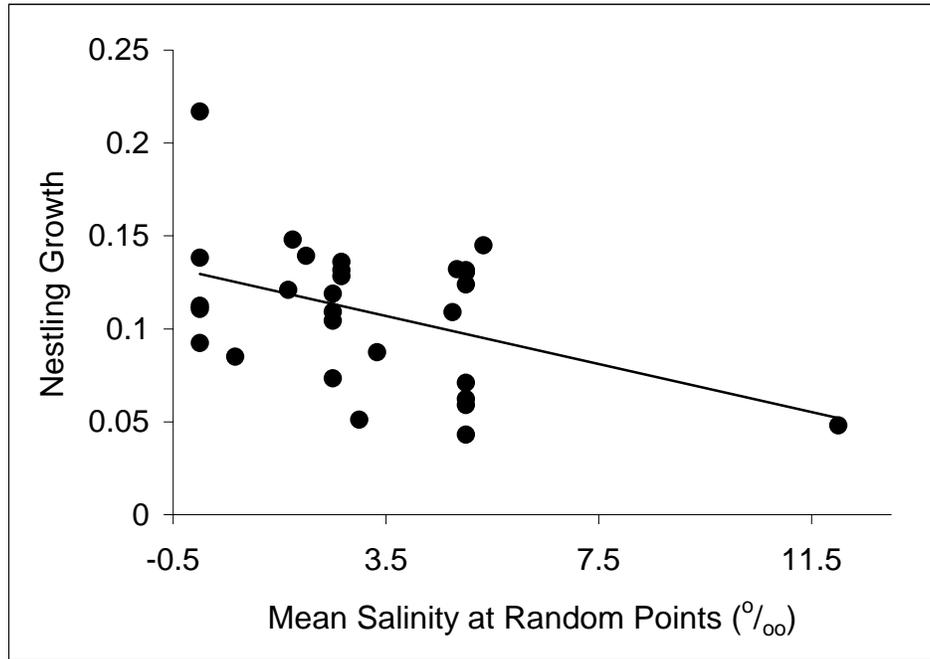


Figure 2.1. Salinity's effect on nestling growth

The relationship between nestling growth (slope of the nestling growth curve calculated as $0.25 \cdot \ln \{ \% \text{ adult weight } [1 - \% \text{ adult weight}]^{-1} \}$ per day *sensu* Ricklefs, 1967) and mean salinity of the natal territory in coastal plain swamp sparrows.

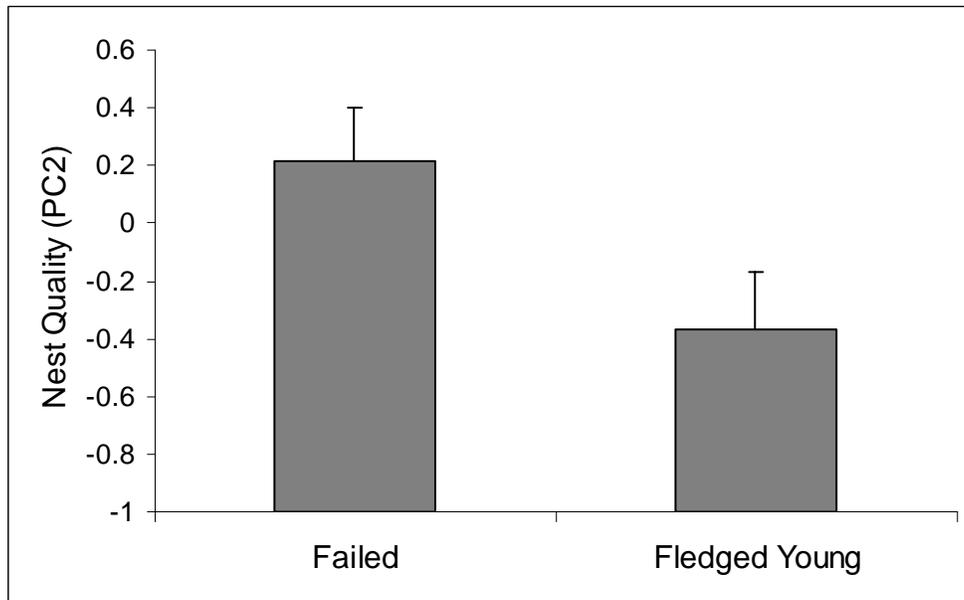


Figure 2.2. Nest site vegetation and nest success

The mean values of Principle Component #2 (with standard error bars) describing vegetative composition within 5m of initial swamp sparrow nesting attempts that fledged young and failed to do so. PC2 is positively correlated with marsh elder (*Iva frutescens*) and salt hay (*Spartina patens*) and is negatively correlated with Olney three-square (*Schoenoplectus americanus*) and cordgrass (*Spartina cynosuroides*).

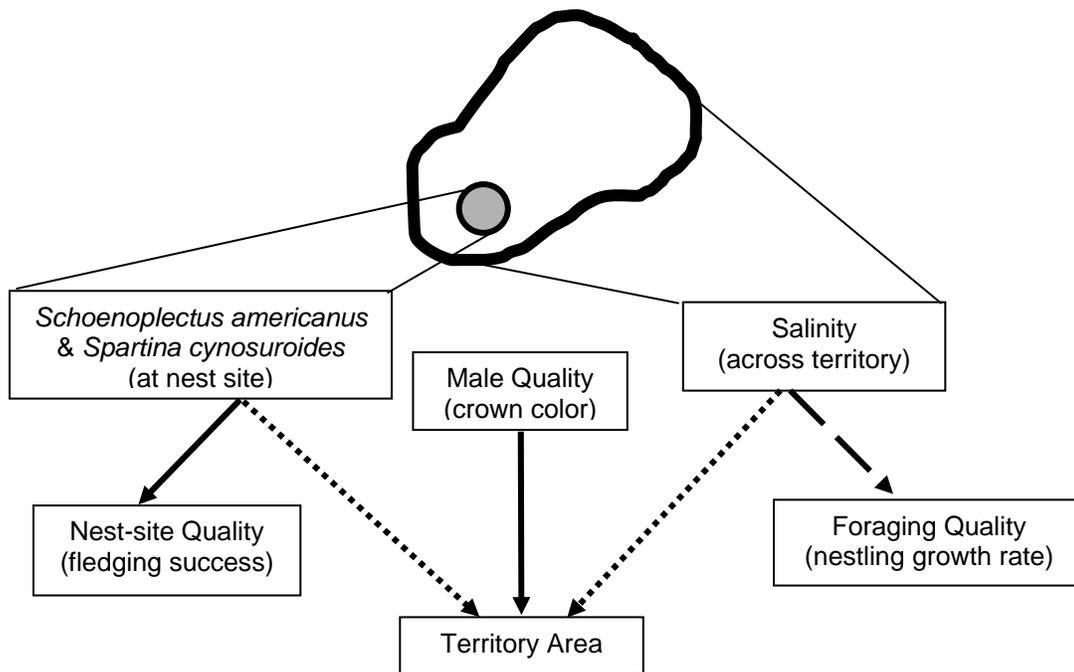


Figure 2.3. Male habitat preferences at two scales

The relationship between two fitness-correlated habitat variables (operating on different scales) and male quality on coastal plain swamp sparrow territory size. Solid lines indicate positive correlations, dashed lines represent negative correlations, and dotted lines represent positive quadratic relationships.

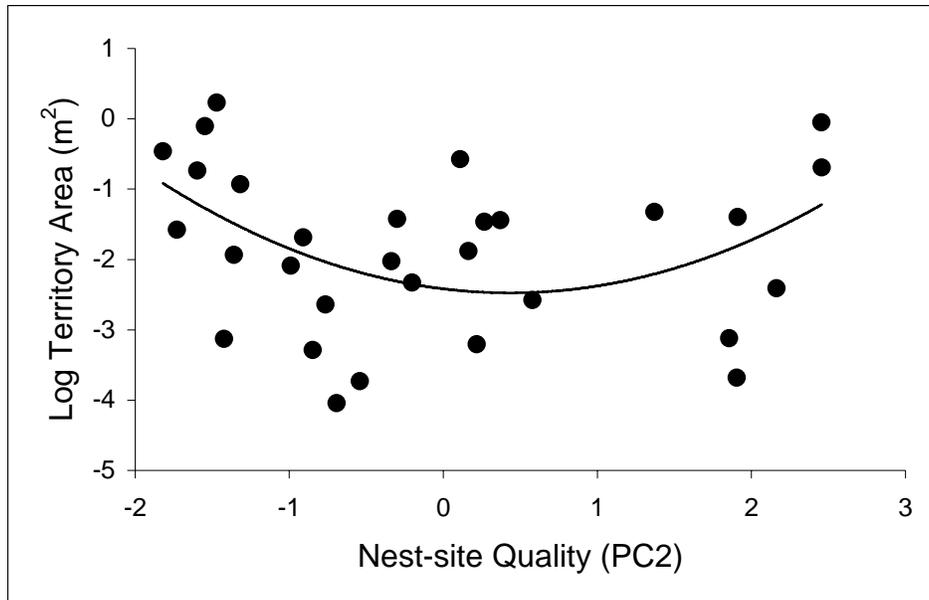


Figure 2.4. The effect of nest-site quality on territory size

Partial plot of PC2 (the principal component representing fitness-correlated vegetation near initial coastal plain swamp sparrow nesting sites) and log territory area. The complete model includes male crown size and mean territorial salinity.

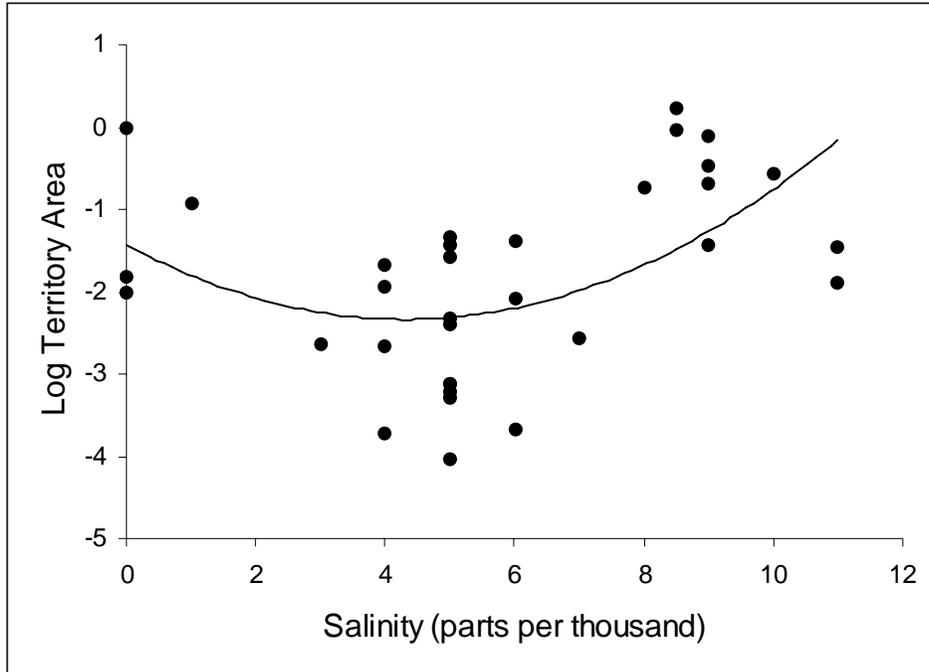


Figure 2.5. The effect of salinity on territory size

Partial plot of standing water salinity (in parts per thousand) and log territory area (m^2) of coastal plain swamp sparrow territories. The complete model includes male crown size and a principle component for nest-site quality.

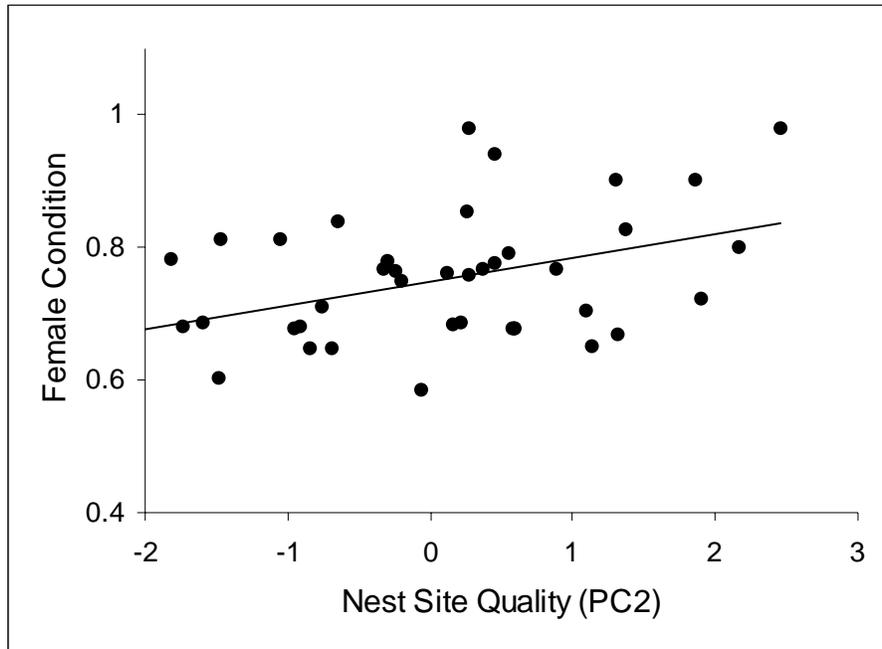


Figure 2.6. Female condition and nest-site vegetation

Correlation between female condition (weight [tarsus]⁻¹) and principal component #2, which describes a mixture of the shrub *Iva frutescens*, the grasses *Spartina patens* and *S. cynosuroides*, and the sedge *Schoenoplectus americanus*, in coastal plain swamp sparrows.

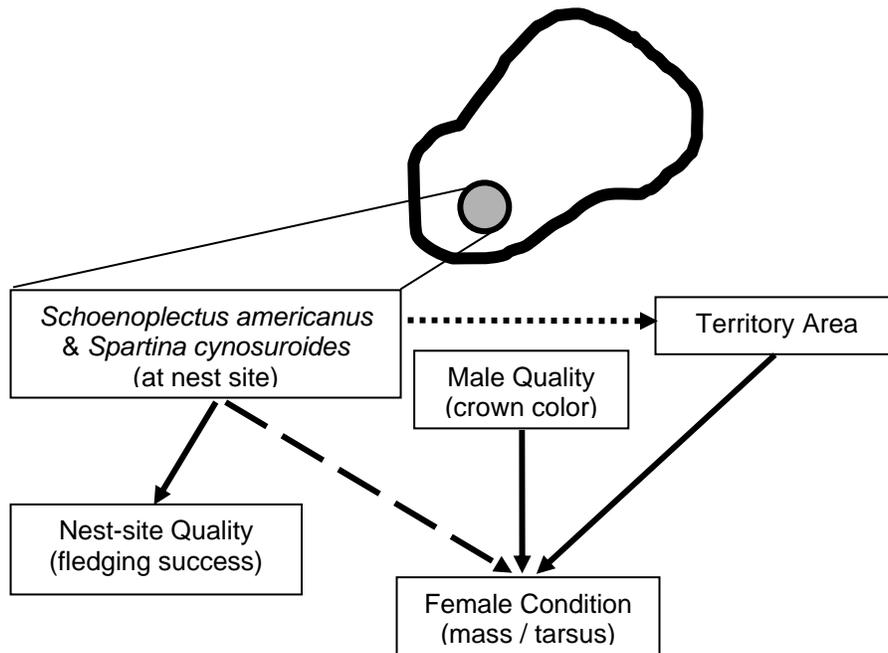


Figure 2.7. Female habitat preference at a single scale

The relationship between a small-scale, fitness-correlated habitat variable, mate quality, and female body condition. Solid lines indicate positive correlations, dashed lines indicate negative correlations, and dotted lines represent positive quadratic relationships.

TABLES

Table 2.1. Habitat Measurements

Habitat measurements of tidal salt marsh in Kent County, Delaware gathered within either one or five meters from random points within territories and within one or five meters from initial nesting sites of coastal plain swamp sparrows. The reasons each measurement was gathered are listed as ecological importance. The abbreviations listed here are used both in the text and the following tables.

Measurement	Ecological Importance	Abbreviation
% Ground Cover (within 5m)		
<i>Spartina cynosuroides</i>	Nest anchor, foraging substrate	cyn
<i>Spartina patens</i>	Nest material, foraging substrate	pat
<i>Spartina alterniflora</i>	Foraging substrate	alt
<i>Schoenoplectus americanus</i>	Nest anchor, foraging substrate	sci
<i>Iva frutescens</i>	Nest anchor, foraging substrate	iva
<i>Baccharis halimifolia</i>	Nest anchor, foraging substrate	bac
<i>Phragmites australis</i>	Invasive reed, possible aversion	phr
<i>Typha angustifolia</i>	Nest anchor, foraging substrate	cat
Water / Mud	Foraging substrate	h2o
Other	Possible aversion to upland habitat	oth
Water Measurements (within 1m)		
Deepest point at high tide	Flooding potential, predator protection	max
Shallowest point at high tide	Flooding potential, predator protection	min
Salinity in parts per thousand (‰)	Osmoregulation, foraging effects	sal
Vegetation Measurements (within 5m)		
Modal vegetation height	Predator protection, foraging substrate	mod
Highest vegetation	Predator protection	tal
Simpson's Diversity Index for Cover	Diversity of foraging, proximity of foraging to nests	sim

Table 2.2. Principle components of territory habitat

Heavily weighted variables (Pearson's correlation coefficient all with $P < 0.001$) of principal components with eigenvalues > 1.0 . These principle components were constructed from territory-scale habitat measurements gathered within coastal swamp sparrow territories in Kent County, Delaware. Abbreviations for individual measurements listed here are explained in Table 2.1.

Component	Heavily Weighted Variables	Eigenvalue	Proportion of Variation
PC1	sci (-), phr (+), cyn (+), oth (-), h2o (-), sim (-), max (+), sal (+), mod (+)	3.64	0.23
PC2	pat (+), iva (+), bac (+), max (-), min (-), tal (+)	1.90	0.12
PC3	pat (-), iva (+), sci (-), alt (+), cat (+), h2o (+), sim (+), tal (+)	1.78	0.11
PC4	pat (-), sci (+), alt (-), mod (+)	1.54	0.10
PC5	phr (-), max (+), min (+), sal (+), mod (+)	1.38	0.09
PC6	iva (-), bac (+), cat (+)	1.15	0.07
PC7	phr (+), alt (-), min (+), sal (-)	1.03	0.06

Table 2.3. Principle components of nest-site habitat

Heavily weighted variables (Pearson’s correlation coefficient all with $P < 0.001$) of principal components with eigenvalues > 1.0 . These principle components were constructed from nest-site-scale habitat measurements gathered within five meters of coastal swamp sparrow nests in Kent County, Delaware. Abbreviations for individual measurements listed here are explained in Table 2.1.

Component	Heavily Weighted Variables	Eigenvalue	Proportion of Variation
PC1	sci (-), phr (+), alt (+), cyn (+), mod (+)	1.84	0.17
PC2	pat (+), iva (+), sci (-), cyn (-)	1.59	0.15
PC3	pat (-), phr (+), oth (+), h2o (+)	1.34	0.12
PC4	pat (+), bac (+), h2o (-)	1.19	0.11
PC5	bac (+), cat (-), oth (+)	1.08	0.10
PC6	phr (+), oth (-), h2o (+)	1.02	0.09

CHAPTER III:
CAUSES OF REDUCED CLUTCH SIZE IN A TIDAL MARSH
ENDEMIC

ABSTRACT

We tested three hypotheses of clutch size variation in two subspecies of the swamp sparrow, the nominate inland subspecies (*Melospiza georgiana georgiana*), and a tidal, salt marsh endemic (*M. g. nigrescens*). Swamp sparrows follow the pattern of other estuarine endemics, where clutch size is smaller among tidal salt marsh bird populations when compared to their closest inland relatives. Predation risk and temperature were both significant predictors of clutch size, while adult survival probability was not. Both subspecies exhibited similar adult return rates and low incidences of nestling starvation. Coastal nests were fifty percent more likely to fail than inland nests, and adults visited coastal nests less often, which may decrease nest detectability. Coastal parents waited longer than inland birds to feed offspring in the presence of a model nest predator while there was no difference in the response to a predator of adults. Additionally coastal females laid more eggs than inland females over a single season, suggesting they are following a within-season bet-hedging strategy rather than a between-season tradeoff in energy expenditure. Coastal territories experienced ambient air temperatures above the physiological zero of egg development more often. Higher ambient air temperatures during laying were correlated with smaller clutches and increased egg inviability in larger clutches among coastal birds. These effects were not seen among inland nests where laying temperatures were typically below physiological zero. Both subspecies showed an increase in hatching asynchrony and a decrease in apparent incubation length under high temperatures, however coastal individuals showed less hatching asynchrony overall despite higher temperatures. This is likely an anti-predation adaptation to decrease time offspring spend in the nest. Both air temperatures during laying and predation risk

explain the decreased clutch size within coastal plain swamp sparrows, a pattern that may extend to other tidal marsh endemics.

INTRODUCTION

The study of avian clutch size variation across and within taxonomic groups, habitats, and latitudes has significantly informed life history research. Food limitation (Lack 1948), nest predation (Skutch 1949; Ricklefs 1970), adult survivorship (Moreau 1944), and climate (Ashmole 1963; Stoleson and Beissinger 1999; Cooper et al. 2005) have all explained trends in clutch variation, yet there is no consensus on a single theoretical model. Clutch size is likely determined by a number of evolutionary constraints including both phylogenetic and environmental factors (Martin 2004). The constraints may operate hierarchically (Ghalambor and Martin 2001), which would allow one to predict which factors are most important for a given population. To understand the interactions between these selective mechanisms, it is necessary to examine multiple, phylogenetically controlled, pairs of species or populations in a variety of environments. Here we present a single such contrast between two subspecies of the swamp sparrow (*Melospiza georgiana*), found at sites controlled for latitude (39.6°N vs. 39.4°N), yet varying in elevation (800m), predation risk, and climate.

Along with the classic increases in clutch size at higher latitudes and elevations, clutch size also varies predictably from coastal tidal salt marsh to inland habitats (Greenberg and Droege 1990). This convergence in decreased clutch size among tidal salt marsh birds suggests that specific aspects of this environment have selected for similar life histories among a diverse suite of species from rails to passerines. We tested three hypotheses as causes of clutch size divergence between a population of coastal plain swamp sparrows (*M.g. nigrescens*) and the nearest inland subspecies, *M. g. georgiana*, to understand the specific environmental factors underlying the tidal salt marsh trend. Specifically, we evaluated the role of nest predation risk, adult survival probability, and laying microclimate on clutch size divergence.

Predation

Increased predation may select for a smaller clutch due to decreased nest detectability (Skutch 1949; Ghalambor and Martin 2002), or a bet-hedging strategy to maximize available energy for renesting (Slagsvold 1982, 1984). The ability of predators to detect nest visits by adults may be particularly important in swamp sparrows as females utter distinct calls when departing the nest during incubation and (albeit, less frequently) nestling provisioning (McDonald and Greenberg 1991). Under this hypothesis, coastal populations should experience higher rates of nest predation and reneest more often than inland birds. Furthermore, nest attendance should be lower overall to reduce predator detection (possibly with tradeoffs to nestling growth, or increased food loads per trip), and coastal adults may show greater behavioral responses to nest predators than inland adults (Ghalambor and Martin 2002).

Survivorship

Differences in the probability of adult survival from one breeding season to the next may alter tradeoffs between current and future reproduction (Moreau 1944; Ghalambor and Martin 2001). Under this hypothesis adults with the highest survival probability should decrease clutch size to reduce energetic investment in any given reproductive cycle and maximize the chances of surviving to another breeding season. If the lower clutch size in coastal populations results from an increase in adult survivorship, return rates should be higher in coastal adults, and they should show an increased behavioral response to predators of adults relative to inland populations (Ghalambor and Martin 2001). Furthermore, coastal adults should lay fewer eggs than inland birds over the entire breeding season, not just among single nesting attempts, to reduce the total energetic investment in a given year.

Temperature

Temperatures may limit clutch size in species that experience suboptimal ambient temperatures during laying (Stoleson and Beissinger 1999; Cooper et al. 2005; Ardia et al. 2006; Cooper et al. 2006). Swamp sparrows, like many passerine cup-nesters, begin incubation upon the completion of the clutch (Mowbray 1997). Eggs that are laid before

incubation onset, therefore, are subject to variation in ambient temperatures. Physiological zero for egg development is between 24-26°C (Webb 1987), and development is suspended for eggs that experience temperatures below this. For eggs that are laid above this critical limit and below optimal incubation temperatures (36°C: Cooper et al. 2005), partial, slowed development may lead to abnormalities and inviable eggs (Deeming 1992). The first egg laid in clutches experiencing these temperatures is the most vulnerable to defects, and therefore larger clutches should be more likely to experience losses in viability (Cooper et al. 2005). Birds experiencing temperatures in this suboptimal zone during laying should decrease clutch size to limit the length of the laying period, or should increase hatching asynchrony if they begin incubation before clutch completion. If this hypothesis is correct, coastal birds should experience higher temperatures during laying, and temperatures during laying in both environments should predict clutch size. Furthermore, hatching asynchrony should be greater in coastal populations or apparent incubation length (the time from clutch completion to hatching) should be shorter in coastal birds due to the earlier onset of incubation. The hatching probability per egg should also relate negatively to clutch size in nesting attempts that experience high temperatures.

MATERIALS AND METHODS

Study Site

Investigations of coastal *M. g. nigrescens* were carried out at sea level on two ~15ha plots of *Spartina* marsh within state game lands near Woodland Beach, Delaware (75.6°W, 39.4°N) from May to August 2002-2005 (one plot was started in 2002 and the second was added in 2003). Inland *M. g. georgiana* studies were conducted at 800m elevation on two plots in cranberry fens on the Allegheny Plateau in Garrett County, Maryland (79.3°W, 39.6°N) from May to August 2004-2005. Wetlands at both sites are not shaded by trees and are thus subject to large variations in daily temperatures. During all breeding seasons adults and nestlings were captured and given unique color-band combinations for later identification.

Nestling Measurements

We located nests using female nest departure calls and rechecked them daily to ascertain hatching and fledging dates until fledging or failure. Every three days we weighed (all years) and measured the tarsi (2005 only) of nestlings in all active nests. Final measurements were taken at every nest when nestlings reached seven days of age (2005 only) and we gathered no further measurements on older nestlings to prevent premature fledging (all years). Nestling growth slopes were calculated for each territory using all nesting attempts, a measure that is much less likely to be affected by short-term weather events than one based on a single attempt. During each nest check of the 2005 breeding season when nestlings were present, we shook the vegetation lightly ~10 inches above the nest and recorded the duration of begging up to a maximum of two minutes.

Predator Model Presentations & Survival Estimates

In 2005 we observed active nests with nestlings of at least three days of age from a camouflaged location and recorded the number of feeding trips made by adults. After two hours or three trips by each parent (whichever came first), we placed one of three predator models (selected at random) in a clearly visible location 5-10m from the nest and above the modal vegetation height. Following a methodology modified from Ghalambor and Martin (2002), we then recorded the length of time until the first provisioning event by either parent. We removed the model after one hour if no visits had occurred. The models presented were an adult sparrow predator (taxidermied Cooper's Hawk, *Accipiter cooperii*), a nest predator (Flambeau® crow decoy), or a plastic milk jug to control for neophobia effects (Greenberg 1989).

The short time period of our inland study prohibited mark-recapture analysis of survival, so between year resighting rates (either by mist-net capture or visual identification of unique color combinations) are provided as an estimate. Inter-annual estimates of the return rate for coastal birds were determined for each year pair (2002-2003, 2003-2004, and 2004-2005) for comparison.

Temperature Correlates

Daily high temperatures were obtained from the Maryland/Delaware/D.C. chapter of the Atlantic Coast Observer Network (ACON 2006). Daily high temperatures for Delaware laying periods were assigned from temperatures recorded at the Bear, DE station (75.6°W, 39.6°N), and inland temperatures were assigned from the Frostburg, MD station (79.9°W, 39.6°N). Daily highs during the laying period were averaged across all days prior to and including the day of clutch completion. We tested for subspecific differences in hatching asynchrony by comparing the number of days each nest took to complete hatching.

Statistical Analysis

All data met assumptions of normality and homogeneity of variance. We tested for differences in mean clutch size and partial brood loss between the subspecies and years using two repeated-measures ANOVA measuring nesting attempts within territories. Nestling growth slopes were calculated by plotting all chick weights for each territory against a logistic growth curve via the method described by Ricklefs (1967), and we tested for subspecies, year, and brood size effects with ANOVA. We tested for differences in seven-day-old chick weights and tarsus sizes and hatching asynchrony using three repeated-measures ANOVA with subspecies, year, and clutch size within territories as our candidate predictors. We tested for differences in nestling begging and feeding rates using two, doubly-repeated-measures ANOVA for multiple measures of each nest attempt within each territory. Candidate predictors for both tests included subspecies, nestling age, Julian date, brood size, and time of day. We tested for the effects of subspecies, year, total number of eggs laid, and number of renests per season on nest success (Determined by Mayfield estimates: Mayfield 1975) with an ANOVA.

We tested for the effect of a predator-model-by-subspecies interaction, baseline provisioning rate, Julian date, brood size, time of day, and nestling age on latent feeding time using an ANOVA. Given the relatively large number of levels of the interaction and controlled independent variables, a priori power analysis (using expected effect sizes extrapolated from Ghalambor and Martin 2002) indicated an appropriate increase in α to

0.10. Latency values for each subspecies-by-treatment combination were determined post hoc using least-squares means. For all other tests α was set to 0.05.

We calculated the effect of clutch size on subspecific egg viability, the effect of temperature during the laying period on egg viability, the effect of a subspecies by clutch size interaction on laying temperature, and the mean laying temperature on apparent incubation length including Julian date, year, clutch size, and subspecies as additional candidate variable in each model. Final Model selection for all tests was based on AIC-values and the selected models had AIC-values lower than the next best model by $>2.0 \Delta AIC$. All subspecies means were determined post hoc using least-squares means. Means reported are \pm standard error, and all statistical tests were conducted using SAS 9.1.3 (SAS Institute).

RESULTS

As has been reported previously (Greenberg and Droege), we found a significantly smaller clutch size in the salt marsh population of swamp sparrows when compared to the interior population ($n = 304$, $t_{302} = -5.0$, $P < 0.001$: Fig. 3.1). Including year did not improve the final model and was dropped.

Predation and Survivorship

Nest success was significantly higher among inland birds ($n = 6$, $t_4 = -4.0$, $P = 0.02$) with a Mayfield nest success estimate of 50.5% compared to 24.2% among coastal nests for all years combined. The effect of year did not improve the model testing for differences in Mayfield estimates among our plots and was dropped. The vast majority of failures were due to predation (determined by missing or injured eggs or nestlings), with only 7% of nests (38/507) failing due to flooding (as indicated by high water marks and displaced eggs or drowned nestlings) and 3% of nests (17/507) failing due to abandonment in the coastal population (as indicated by undisturbed, unincubated eggs) and no instances of flooding and only one instance of abandonment inland. Coastal pairs laid significantly more clutches throughout the season than did those inland ($n = 164$, $t_{159} = 5.3$, $P < 0.001$), averaging 2.4 ± 0.1 (with a maximum of five per year) versus 1.6 ± 0.2 (with a

maximum of three) nests respectively. Additionally, over a single breeding season coastal females laid more eggs than inland females ($n = 164$; $t_{159} = 4.0$, $P < 0.001$), averaging 8.1 ± 0.4 eggs versus 6.0 ± 0.4 eggs respectively. Controlling for nestling age, brood size, Julian date, and time of day, coastal nestlings were provisioned less frequently by adults ($n = 52$, $t_{38} = 2.7$, $P = 0.009$), averaging 12.7 ± 1.3 minutes between visits versus 5.7 ± 1.1 minutes between visits inland.

Furthermore, controlling for baseline visitation rate, Julian date, brood size, time of day, and nestling age, inland birds waited less time to provision young in the presence of a model nest predator than in the presence of an adult predator ($n = 52$, $t_{36} = -2.0$, $P = 0.05$: Fig. 3.2). There was no parallel difference between feeding latency in the presence of the two predator types among coastal birds ($n = 52$, $t_{36} = -0.2$, $P = 0.87$: Fig. 3.2). Reduced feeding latency in the presence of the nest predator in inland birds compared to coastal pairs approached significance ($n = 52$, $t_{36} = -1.6$, $P = 0.12$: Fig. 3.2), while there was no difference between the populations in the presence of the adult predator ($n = 52$, $t_{36} = 0.2$, $P = 0.88$: Fig. 3.2). Both inland and coastal birds waited longer to feed nestlings in the presence of either predator than they did when the control was present (nest predator vs. control inland: $n = 52$, $t_{36} = 3.5$, $P = 0.001$; coastal: $t_{36} = 3.2$, $P = 0.003$; adult predator vs. control inland: $t_{36} = 5.4$, $P < 0.001$; coastal: $t_{36} = 3.3$, $P = 0.002$).

The small sample size for return rates prohibited a definitive statistical comparison, and only trends are reported. Fifty-five percent of males banded in the inland population in 2004 returned in 2005; similar values were obtained for the coastal population between 2002 and 2003 (52%), 2003 and 2004 (38%), and between 2004 and 2005 (60%). Females had slightly higher return rates in the inland population (39%) versus the coastal populations (2002-2003: 15%, 2003-2004: 16%, 2004-2005: 30%). Likewise, juvenile return was slightly higher inland (7%) than along the coast (2002-2003: 0%, 2003-2004: 0.7%, 2004-2005: 4%).

Temperature

More coastal nests (75.6%) than inland nests (40.2%) experienced temperatures above the range of physiological zero reported by Webb (1987) during laying ($n = 413$, $Wald \chi^2_1 = 44.4$, $P < 0.001$) as a result of the significantly higher mean daily high temperatures

found in Delaware ($27.8^{\circ}\text{C} \pm 0.2$) compared to those inland ($24.3^{\circ}\text{C} \pm 0.4$) during the breeding season ($n = 606$, $t_{600} = 8.0$, $P < 0.001$). Controlling for Julian date, coastal clutches experienced lower egg viability ($n = 265$, $t_{232} = -2.1$, $P = 0.04$). Furthermore, among coastal nests egg viability was predicted by clutch size ($n = 176$, $f_{3,49} = 3.0$, $P = 0.04$: Fig. 3.3), whereas the same relationship did not apply to inland nests ($n = 89$, $f_{3,21} = 0.6$, $P = 0.64$: Fig. 3.3).

Additionally, controlling for Julian date and year, there was a significant interaction between the relationship of clutch size and subspecies and the mean temperature during laying, such that the temperature was negatively related to clutch size among coastal territories but unrelated among inland ones ($n = 265$, $f_{12,403} = 27.5$, $P < 0.001$: Fig. 3.4). The mean temperatures during laying among inland nests generally fell below the range of physiological zero for egg development outlined by Webb (1987), while the mean temperatures during laying among coastal nests fell above this range in all but the largest clutches (Fig. 3.4).

Controlling for year, Julian date, and brood size, hatching asynchrony was lower among coastal territories compared to those inland ($n = 191$, $t_{193} = -3.0$, $P = 0.003$: Fig 3.5) and positively related to mean temperature during laying ($n = 191$, $F_{1,50} = 15.8$, $P < 0.001$). This relationship is best portrayed visually by calculating the mean temperature during laying for all nests that share hatching length (Fig. 3.6). Despite the decreased asynchrony among coastal broods, there was no difference in apparent incubation length between the subspecies ($n = 54$, $t_{45} = 0.2$, $P = 0.84$), and mean ambient temperature during laying was the best predictor of apparent incubation length ($n = 54$, $F_{1,45} = 15.5$, $P < 0.001$) controlling for clutch size and year (Fig. 3.7). Again, we portray this relationship by calculating mean ambient daily temperature during laying for each apparent incubation length.

DISCUSSION

The difference in clutch size between coastal (*M. g. nigrescens*) and inland (*M. g. georgiana*) swamp sparrows was consistent with two hypotheses about clutch size variation. There was no significant support for differences in survivorship as a cause for

clutch size divergence. Return rates among males were similar between the sites, and although juvenile and female return rates were lower among coastal plots, the Delaware Bay is lined with contiguous, suitable habitat for miles (Beadell et al. 2003), whereas wetlands on the Allegheny Plateau are small, disjunct pockets with miles of unsuitable habitat in between (Fenwick and Boone 1984). Under these circumstances it is probably safe to assume that dispersal is easier between coastal habitats and that the differences in the return rates of females and juveniles, which are typically less site faithful than males (Greenwood 1980; Clarke et al. 1997), can likely be explained by the dissimilarity in landscape. The behavioral responses of adult swamp sparrows agreed with this conclusion. There was no subspecies difference in the reduction of feeding rate in the presence of an adult predator, which suggests that the subspecies possess a similar tradeoff between current and future reproduction on the scale of the breeding season (Ghalambor and Martin 2001). Additionally, coastal females laid more eggs than inland females over the length of the season, which strongly supports the conclusion that coastal sparrows are not decreasing their investment in current reproductive efforts.

Predation remains a strong candidate for the cause of clutch size divergence. Coastal territories experienced a much higher predation risk, and coastal individuals exhibited behavioral adaptations to increased predation risk. They visited the nest significantly less often, as expected to limit nest detectability (Skutch 1949; Ghalambor and Martin 2000). Additionally, the increased egg production of coastal females follows a within-season, bet-hedging strategy as expected under high probability of failure (Slagsvold 1984; Eggers et al. 2006). Furthermore, coastal pairs showed an increased behavioral response to the nest predator model when compared to inland pairs. By decreasing clutch size, coastal birds would be able to decrease nestling provisioning rate even further in the presence of a nest predator with less cost in terms of nestling growth and condition upon fledging. Tidal marsh sparrows as a group (including three *Ammodramus*, two *Melospiza*, and a single *Passerculus* species) exhibit high rates of nest loss due to predation and variation in clutch size among populations of these species is strongly predicted by predation rates (Greenberg et al. 2006).

Our results also supported temperature as a cause of the clutch size difference between the subspecies. Coastal nests frequently experienced a high degree of suboptimal

temperatures during their laying periods, and showed a high degree of sensitivity to ambient temperature. Ambient air temperatures above the physiological zero of egg development resulted in smaller clutches and increased levels of egg inviability in larger clutches. These effects were not seen among inland nests where laying temperatures were typically below physiological zero. Under suboptimal thermal conditions coastal females could decrease their exposure by beginning incubation earlier which can either 1) inhibit further egg laying thereby decreasing clutch, or 2) result in a greater degree of hatching asynchrony. Both subspecies showed an increase in hatching asynchrony and a decrease in apparent incubation length under high temperature conditions, supporting the second prediction, however the reaction norm of coastal individuals was shifted to decrease asynchrony overall despite the greater temperatures they experienced. This divergence is likely a further adaptation to predation, as coastal pairs would benefit from a decrease in the time offspring spend in the nest.

Previous investigations of the effect of temperature on clutch size have been conducted on cavity-nesting birds (Cooper et al. 2005, 2006; Stoleson and Beissinger 1999). As they lack the environmental buffering effects of cavities, open cup nesters, like swamp sparrows, should be even more affected by ambient air temperatures than are cavity nesters. Ambient temperatures during laying remain an intriguing, relatively untested, hypothesis explaining clutch size variation, and the hypothesis deserves much further investigation with other non-cavity-nesting species.

A fourth hypothesis explaining clutch size variation is Lack's (1948) classic explanation invoking food limitation. We did not test this hypothesis, but we did collect some pertinent data. Both subspecies exhibited relatively equal, low levels of apparent starvation. Out of 507 nests over four seasons in the coastal population we witnessed 21 nests with dead nestlings (4.1%) that did not appear injured or did not occur during a known high water event. Six out of 149 inland nests (4.0%) found over two seasons possessed dead chicks under similar circumstances. Partial brood loss was also the same between the sites ($n = 166$, $t_{161} = -0.7$, $P = 0.47$) with 95% and 97% of hatched chicks surviving until fledging in successful coastal and inland nests respectively. Although coastal nestlings begged longer than inland nestlings during nest checks ($n = 111$, $t_{109} = 3.6$, $P < 0.001$), there was no difference in either the mass ($n = 83$, $t_{79} = 0.4$, $P = 0.70$) or

tarsus length ($n = 55$, $t_{53} = -0.5$, $P = 0.66$) of seven-day-old chicks, suggesting that pre-fledging body conditions were similar. The increased hunger response and decreased nest visitation rate, which might be interpreted as signs of food limitation, may simply be a result of decreased nest attendance to limit nest detection by potential predators. The equal pre-fledging size of young supports this idea and suggests that coastal adults may be partitioning their feeding behavior towards times that present less risk for detection by predators, as has been found in other species (Eggers et al. 2005). We can conclude that broods of neither subspecies experience food shortage very often. Experimental manipulation of clutch size would be necessary to determine whether food limitation is a cause for clutch size divergence in this system.

Clutch size is an adaptable life history trait that reflects tradeoffs by individuals in a number of areas. To understand which factors play the greatest role in specific circumstances, it is necessary to compare closely related species or populations for a variety of selection regimes. The divergence in clutch size among tidal salt marsh endemics and their nearest inland relatives is an ideal candidate for life history convergence due to environmental constraints. For one such species pair, we found that two environmental variables, predation risk and ambient temperature, explained differences in clutch size. This supports the reported correlation between predation risk and clutch size found across populations of all North American tidal sparrows (Greenberg et al. 2006b), and may represent an explanation for the convergence in clutch size within this group. Further study should address whether temperature can explain the divergence among other tidal marsh endemics or whether it is specific to the swamp sparrow system.

FIGURES

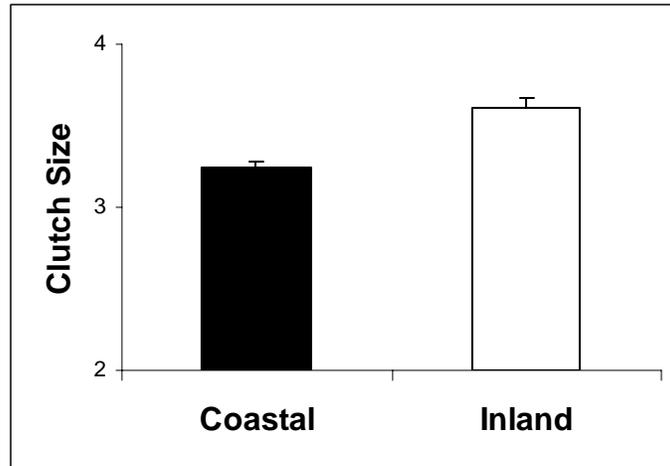


Figure 3.1. Clutch size by subspecies

Mean clutch sizes (\pm SE) of two subspecies of swamp sparrow, the coastal *Melospiza georgiana nigrescens* and the inland *M. g. georgiana*.

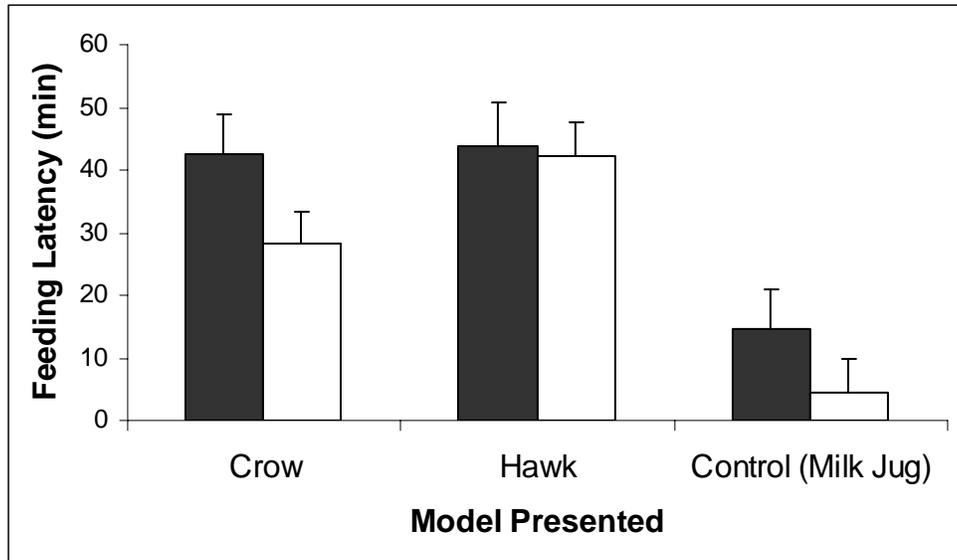


Figure 3.2. Response to predator models

Latency to feed nestlings (\pm SE) by coastal (black) and inland (white) swamp sparrows after placement of a simulated predator within 10m of the nest, controlling for baseline visitation rate, Julian date, brood size, time of day, and nestling age.

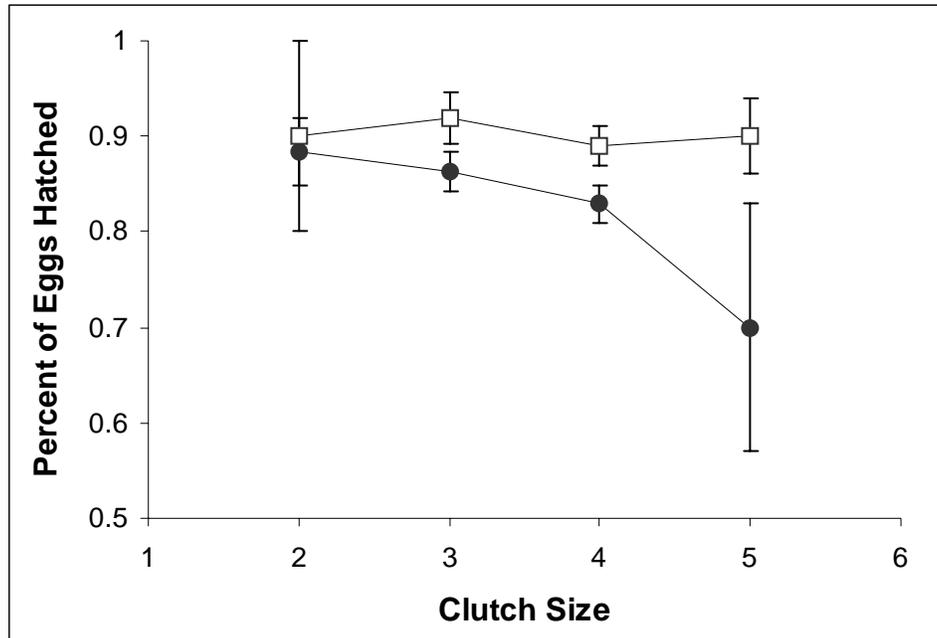


Figure 3.3. The effect of clutch size on egg viability

Egg viability (\pm SE) as a function of clutch size for coastal (black circles) and inland (white squares) swamp sparrows, controlling for Julian date.

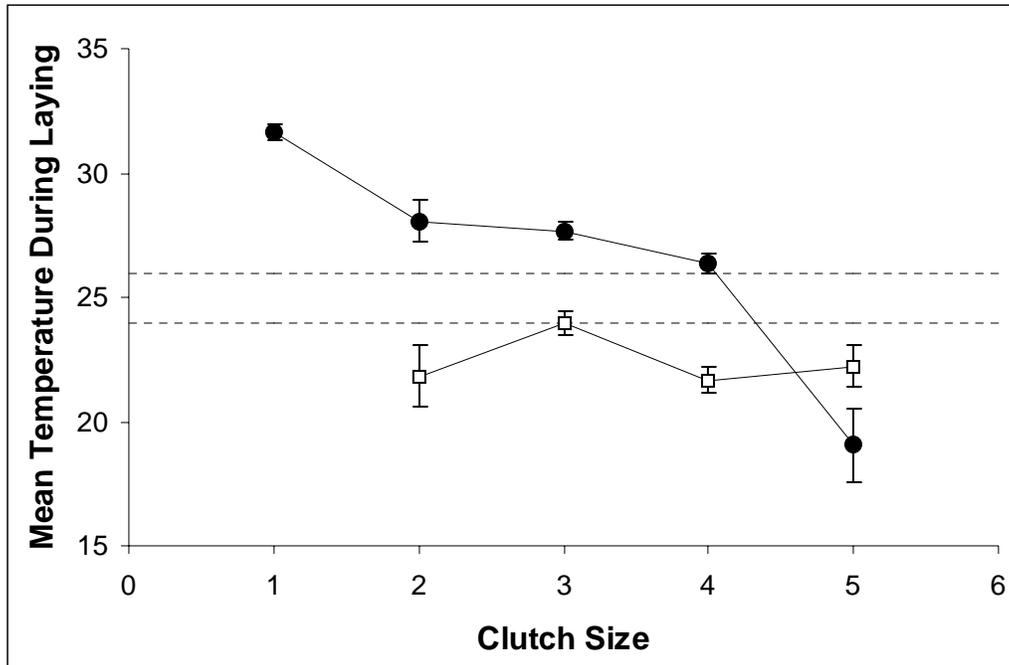


Figure 3.4. The effect of ambient temperature on clutch size

The relationship between ambient temperature (°C) during laying (\pm SE) and clutch size in coastal (black circles) and inland (white squares) swamp sparrow, controlling for Julian date and year. The dotted lines indicate the range of physiological zero for egg development outlined by Webb (1987).

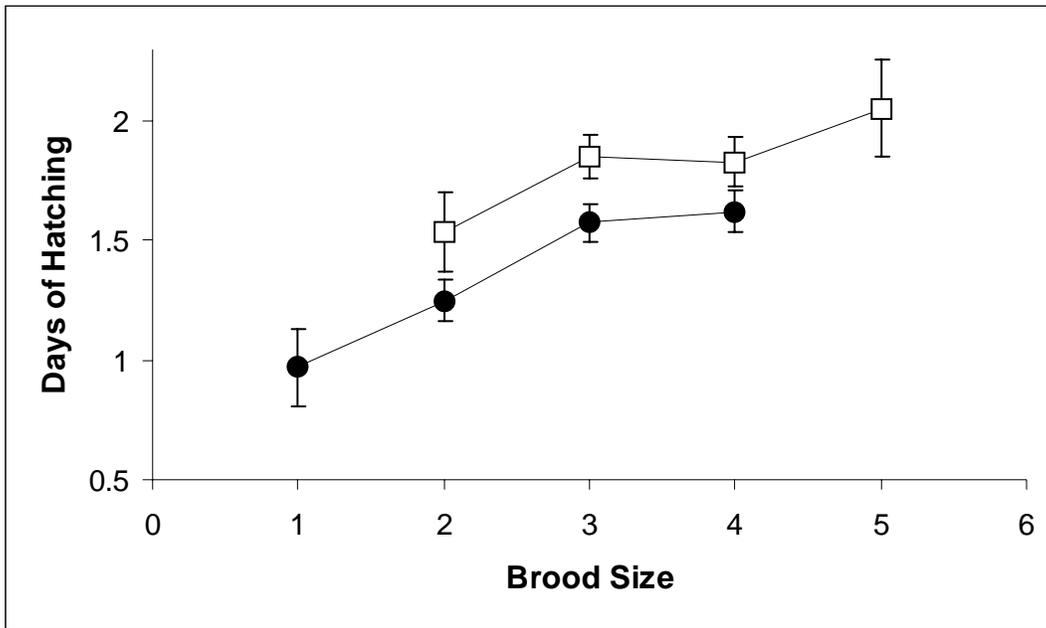


Figure 3.5. The effect of brood size on hatching synchrony

The number of days taken to hatch (\pm SE) as a function of brood size among coastal (black circles) and inland (white squares) swamp sparrows, controlling for mean laying temperature, Julian date, and year.

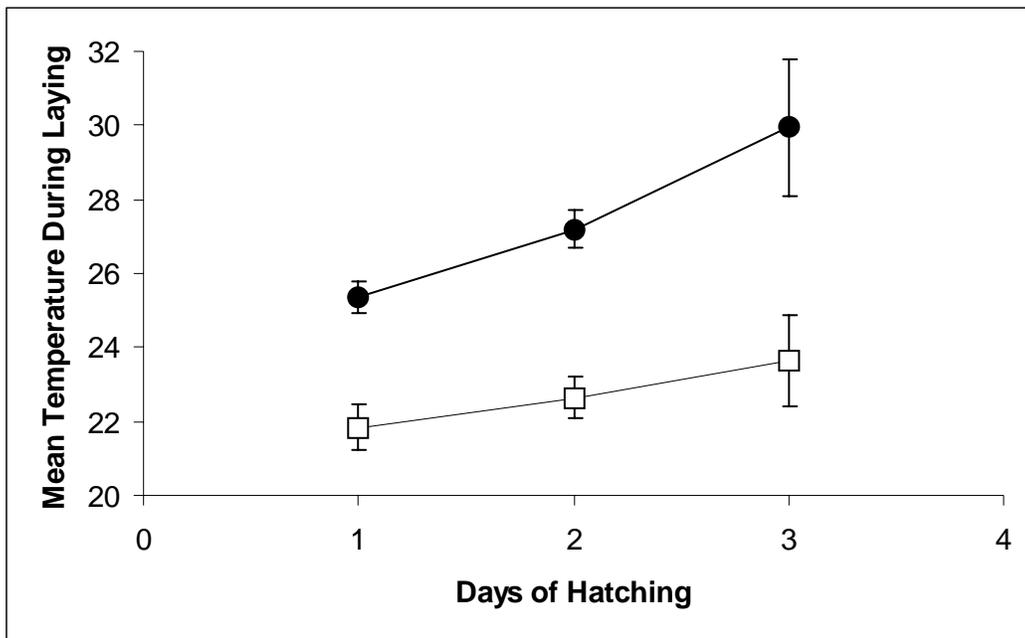


Figure 3.6. The effect of ambient temperature on hatching synchrony

The number of days taken to hatch relative to the ambient temperature (°C) during laying experienced by coastal (black circles) and inland (white squares) swamp sparrows (\pm SE), controlling for brood size, Julian date, and year.

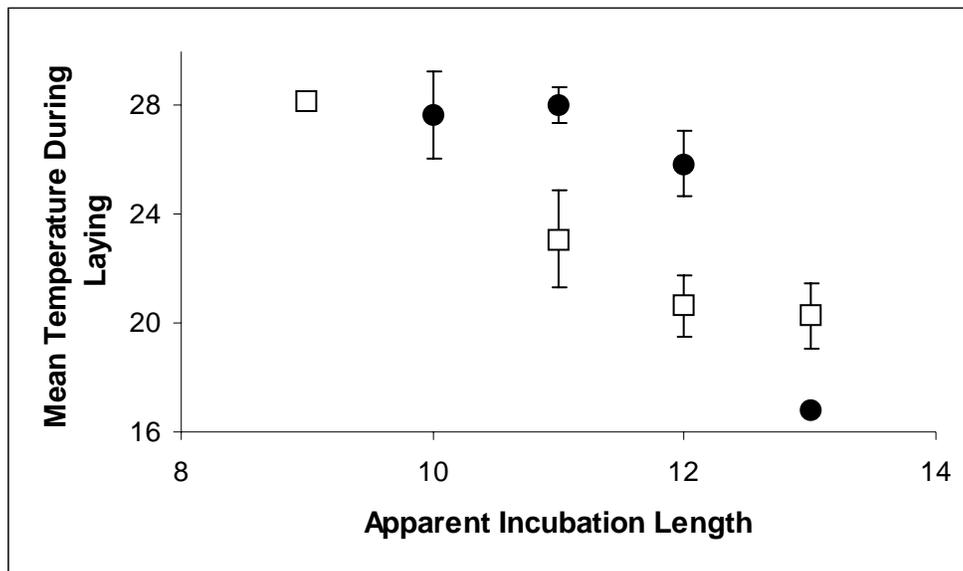


Figure 3.7. The effect of ambient temperature on apparent incubation length

The relationship between apparent incubation length (clutch completion to hatching) and air temperatures (°C) during laying (\pm SE) calculated by days of apparent incubation length for coastal (black circles) and inland (white squares) swamp sparrows.

CHAPTER IV:
EXTRAPAIR PATERNITY IN THE SWAMP SPARROW:
ACCESS OR PREFERENCE?

ABSTRACT

Over the past two decades the combination of molecular and field methods has revealed considerable variation in the level of extrapair fertilizations among socially monogamous birds. Models predicting extrapair young range in scale from a single population to multiple Orders, and there is no single, unifying theory of these alternative reproductive tactics. We investigated the proximate explanations of extrapair fertilizations in two subspecies of the swamp sparrow, *Melospiza georgiana georgiana* and *M. g. nigrescens*, across a range of social and environmental conditions. The presence of extrapair young was best predicted by two measures of a sexually dimorphic male plumage patch (male crown size and position), their interaction, mean territory size, and the mean value of the same plumage measures among neighbors. Females paired to males with a small rusty crown patch positioned farther from the bill that neighbored males with large rusty patches and narrow foreheads were most likely to possess extrapair young. Females paired to males with large, forward-positioned crowns with small, rear-positioned crowned neighbors were the least likely. Controlling for these crown measures, males with larger territories were less likely to suffer losses in paternity. There was no effect of breeding density, synchrony, their interaction, subspecies, or air temperature or precipitation during the fertile period on the presence of extrapair young. These results suggest that female preference plays a role in the proximate causes of extrapair interactions among swamp sparrows, and further study into the proximate controls of extrapair fertilizations should account for relative mate quality.

INTRODUCTION

Despite two decades of research exploring the discrepancies between genetic and social mating systems and a number of synthesizing reviews, there is no unifying explanation of extrapair parentage in avian mating systems (Griffith et al. 2002; Westneat and Stewart 2003; Neudorf 2004). Although most of the interspecific variation in extrapair fertilization (EPF) is explained by phylogeny and fundamental life history traits at the level of the Family or higher (Møller and Birkhead 1993b; Fleischer 1996; Bennett and Owens 2002; Griffith et al. 2002), the proximate mechanisms that lead to this pattern must ultimately occur among an individual, its social mate, and an extrapair parent (Westneat and Stewart 2003). There is little consensus about mechanisms at the level of the individual or population, but a number of hypotheses have been put forth, including breeding synchrony (Emlen and Oring 1977; Stutchbury and Morton 1995), mate quality (Møller 1988; Petrie and Lipsitch 1994), territorial density (Møller and Birkhead 1993a), and weather (Bouwman and Komdeur 2006). In general these hypotheses are concerned with the social or environmental conditions that affect either the ability of females to assess males during their fertile period, the ability of males to prevent extrapair copulations (EPCs) with their social mate, or the ability of males and females to pursue EPCs. Ultimately all of these explanations relate to two sex-specific tradeoffs: 1) the tradeoff in males between mate/territorial defense, foraging, and the pursuit of EPCs and 2) the tradeoff in females between the benefits of multiple matings and the costs of EPCs in terms of social mate retaliation. Whether one sex or both has control of the frequency of EPC and the resulting EPF (the two are not necessarily tightly linked: Fossoy et al. 2006) remains an unanswered question.

We tested these proximate hypotheses for EPF in two subspecies of the swamp sparrow, the tidal, salt-marsh endemic *Melospiza georgiana nigrescens*, and the inland, freshwater-breeding *M. g. georgiana*. Due to the highly variable environmental conditions within and between their breeding grounds, these two subspecies possess a wide array of breeding densities, breeding synchrony, and weather conditions. We

predicted that in male-controlled mating systems, EPFs would be predicted by factors involved in the male tradeoffs: breeding density, territory size, male quality, and breeding synchrony. EPFs in female-controlled systems would be predicted primarily by factors affecting female preference: mate quality and neighbor male quality. Although breeding synchrony has often been cited as an important determinant for female extrapair behavior (allowing females to simultaneously compare male quality: Griffith et al. 2002), females may be able to compare males outside of their fertile period. Longer-term assessment may be particularly important in multiple-brooding species such as the swamp sparrow. Breeding synchrony should thus affect EPFs only as a means of preventing males from seeking EPCs when they are preoccupied by territorial defense or mate guarding during their social mate's fertile period. If weather affects the overall time budget of individuals and determines the opportunities to seek EPFs (Bouwman and Komdeur 2006), it should affect the control of both sexes equally. With these considerations in mind, we tested for relationships between the presence of EPFs and territorial male quality, neighboring male quality, territory size, local density, breeding synchrony, and ambient air temperature and precipitation during the fertile period.

METHODS

Study Sites and Individual Measurements

We conducted all investigations on four plots, two for each subspecies, from May until August. Populations on coastal plots were studied from 2002-2005 on *Spartina* marsh within Delaware state game lands along the Smyrna River (75.6°W, 39.4°N). Inland plots were observed from 2004-2005 in minerotrophic fens on the Allegheny Plateau in Western Maryland (79.3°W, 39.6°N). All adults were mist-netted and marked with unique color-band combinations to assist in individual recognition in the field. Territories were delineated using minimum convex polygons defined by male song-posts throughout the season. We located nests throughout the breeding seasons using the female nest-departure call (McDonald and Greenberg 1991), which is a highly successful

means of finding nests in the building, laying, and incubation periods. Blood was drawn from the brachial vein on adults during capture, and nestlings were bled and banded between five and eight days of age.

For each captured adult we determined the amount of rust-colored feathers within the crown patch, which is a sexually dimorphic plumage character in this species (Greenberg 1988a). The rusty crown is acquired before the breeding season and lost soon after. Such seasonally acquired plumage characteristics are usually signals reflecting male quality (Mulder and Magrath 1994; Örnborg et al. 2002; McGraw et al. 2003). Furthermore, male crown size is correlated with behavioral variables related to territorial behavior within our population (Chapter 5). Rusty crown patches vary in both their size (length) and position. Patch position was measured as the width of the black forehead patch from the proximal end of the culmen to the anterior line of the rusty feathers. Individuals without rusty patches were given a forehead width of 10.5 mm, which is equal to the longest width among individuals with discernable patches.

We determined the area and centroid of all territorial polygons using ArcMap 8.3 (ESRI 2002). Breeding density was defined for each polygon by counting the number of territories that fell within a distance of two mean territory diameters from the centroid (assuming a circular territory of mean area across all sites, twice the mean diameter was 95.3m). Studies to date have implicated neighboring or nearby males as the primary extrapair mate rather than floater/non-territorial males or distant birds (e.g. Stutchbury et al. 1994; Langefors et al. 1998; Dickinson 2001; Tobias and Seddon 2002; Mennill et al. 2004; Woolfenden et al. 2005; but for exception see Woolfenden et al. 2005). Likewise, breeding synchrony was defined for each nesting attempt within this buffered area, counting the number of females whose fertile period overlapped that of the territorial female. Viable stored sperm has been found in the reproductive tract of female passerines from two (Birkhead et al. 1997) to five days (Briskie 1994) before the initiation of laying. Therefore, we determined the percent of neighboring females whose fertile period overlapped each territory's female for two intervals, two days before laying until the onset of incubation (clutch completion) and five days before laying until clutch

completion. We calculated the mean neighbor quality within this area by averaging the crown patch and forehead patch sizes of all males that fell within the two-diameter distance.

We obtained daily high and low temperatures and precipitation accumulation from the Maryland/Delaware/D.C. chapter of the Atlantic Coast Observer Network (ACON 2006). Temperatures and precipitation values for coastal laying periods were assigned from those recorded at the Bear, DE station (75.6°W, 39.6°N), and inland values were assigned from the Frostburg, MD station (79.9°W, 39.6°N). Two values for each weather measurement were calculated. The first averaged all temperatures or precipitation during the fertile period lasting from two days prior to the onset of laying through clutch completion, and the second averaged weather measurements beginning at five days prior to laying.

Genotyping and Parental Exclusion

All captured adults and offspring were genotyped at six polymorphic DNA microsatellite loci (Table 4.1). Five of these were developed for *M. melodia* (Mme2, Mme3, Mme7, Mme8, Mme12: (Jeffery et al. 2001) and the last was developed for *M. georgiana* (Mg2we: RC Fleischer, unpublished data). We extracted DNA using a Qiagen Dneasy Tissue Kit following the manufacturer's instruction for animal tissues. The annealing temperatures and 10 µL PCR mixtures differed by loci (Table 4.1). We ran electrophoresis on an ABI 3100 capillary electrophoresis system (Applied Biosystems, Inc.), sized genotypes with GeneScan 3.7 (Applied Biosystems, Inc.) and scored alleles using Genotyper 2.5 (Applied Biosystems, Inc.). Two base pairs were added to each allele score to account for instrumental differences from published values. Four base pairs were added to Mme8 alleles. Two loci were Z-linked (Mme3 and Mme7) and females were not included in the calculation of allele frequencies for these loci. Mme8 violated Hardy-Weinberg Equilibrium and was subsequently removed from further analysis.

Parental assignment was initially completed using Cervus 2.0 (Marshall et al. 1998). Allele frequencies, the significance of deviations from Hardy-Weinberg equilibrium, and

simulation of assignment values was conducted for each plot separately using males only. We combined data from adult males (sexed by cloacal protuberance) and juvenile males (sexed by heterozygosity at Mme7 or Mme3) to determine allele frequencies and capture the most allelic diversity. Coastal samples were 53% and 55% juvenile and inland samples were 78% and 74% juvenile for Mme3 and Mme7, respectively. Due to the inability to differentiate between juvenile male homozygotes and juvenile females, when testing for deviation from Hardy-Weinberg Equilibrium, we set alpha *a priori* to 0.15 for homozygote deficiency and 0.00 for homozygote excess. Parentage was assigned at a 95% confidence level for male offspring (sexed by Z-linked loci) with a known, genotyped mother and at an 80% confidence level for those without a genotyped mother. This resulted in successful paternal assignment in 81%, 84%, 90% and 86% of offspring in the two coastal and two inland plots respectively. Mean observed error rates in detection probability across all loci were 0.09, 0.17, 0.15, and 0.19 in the two coastal and two inland plots. We then calculated the likelihood of each adult male siring each male offspring using the natural log of the products of the likelihood ratios across all loci. The most likely or the second most likely sires were assigned to broods to minimize the number of males required to explain allelic diversity. The number of required sires agreed with the results calculated by hand based on Mendelian inheritance. We calculated the minimum extrapair sires necessary to explain each full brood including female offspring based on heteromorphic chromosomal (for Z-linked loci) and Mendelian (for other loci) inheritance. Exclusion analysis was conducted on 350 offspring in 113 broods and 97 territories. We made no attempt to assign sires to offspring, as we were not able to sample all candidate males in the populations. We calculated the minimum extrapair young for 22 broods of four or greater offspring that lacked both scored candidate parents and for nine broods of three or more offspring that lacked a scored territorial male but possessed a scored female. Broods with less than three offspring and no scored parent were excluded from analysis.

Statistical Analysis

All statistical tests were run using the Genmod procedure of SAS 9.1.3 (SAS Institute 2005). We tested for relationships between social and environmental conditions and the

presence or absence of extrapair young within each brood using a repeated-measures logistic regression for nesting attempts within territories. Candidate predictors included territory area, crown size, crown position, the interaction of crown size and position, mean neighbor crown size, position and their interaction, territorial density, breeding synchrony (at either the two or five day levels), mean daily high temperatures during the fertile period (at either the two or five day levels), mean daily low temperatures during the fertile period (at either the two or five day levels), and mean precipitation during the fertile period (at either the two or five day levels). We tested for two additional interaction effects based on previous findings: subspecies by temperature (B. Olsen, unpublished data) and breeding synchrony by territorial density (Thusius et al. 2001). Candidate blocking effects included year, subspecies, Julian date, and nesting attempt. Model selection was based on Scaled Pearson's χ^2 divided by error degrees of freedom, and models with scores closer to 1.0 were ranked higher (McCullagh and Nelder 1989).

RESULTS

For 241 coastal and 184 inland males, we found an average of 12.8 alleles for our five loci (Table 4.2), which gave us high power of exclusion for broods with one (coastal = 0.96, inland = 0.97) or two (coastal = 0.993, inland = 0.995) genotyped parents. Extrapair males sired 20.9% of offspring (31/149 coastal and 42/201 inland offspring), which included 41.6% of broods (21/54 coastal and 26/59 inland). These levels are similar to the average of other Emberizid sparrows reported in the literature (24.1% of offspring, 41.0% of broods: Griffith et al. 2002). There was no difference by subspecies ($n = 94$, $\chi^2_{1, 110} = 0.02$, $P = 0.89$). The complete dataset (where all data had been adequately gathered on all males and territories) included 198 offspring from 65 broods in 54 territories.

The highest ranked model explaining the presence of extrapair young (Scaled Pearson's $\chi^2 = 1.01$) included crown patch size ($n = 54$, $\chi^2_{1, 55} = 6.9$, $P = 0.009$), crown patch position ($n = 54$, $\chi^2_{1, 55} = 7.6$, $P = 0.006$), the interaction of size and position ($n =$

54, $\chi^2_{1,55} = 6.8$, $P = 0.009$), territorial area ($n = 54$, $\chi^2_{1,55} = 6.7$, $P = 0.01$), mean neighbor crown patch size ($n = 54$, $\chi^2_{1,55} = 4.6$, $P = 0.03$), mean neighbor crown patch position ($n = 54$, $\chi^2_{1,55} = 4.2$, $P = 0.04$), and the interaction of neighbor crown size and position ($n = 54$, $\chi^2_{1,55} = 4.3$, $P = 0.04$). Rusty crown patch length is shorter (Fig. 4.1) and positioned further back on the head (Fig. 4.2) among males with nests that include extrapair young. Additionally there is an interaction between crown size and position such that males with nests with extrapair young show a tradeoff between crown size and position (in which smaller crowns are positioned further from the bill) while males without extrapair young show no such relationship (Fig. 4.3). Controlling for crown characteristics, males with smaller territories are more likely to suffer losses in paternity than males with larger territories (Fig. 4.4). The social environment also predicted the presence of extrapair young, with males that did not suffer paternity losses possessing larger crowns and smaller foreheads than their neighbors (Fig. 4.5)

These patterns in crown characteristics were echoed in the reproductive success of all measured males. Crown patch position ($n = 161$, $\chi^2_{1,156} = 5.8$, $P = 0.02$), size ($\chi^2_{1,156} = 7.7$, $P = 0.005$), and their interaction ($\chi^2_{1,156} = 6.7$, $P = 0.01$) predicted the number of broods each male fledged in a given season. Males fledging two broods ($n = 31$) had larger crowns and smaller foreheads than did males that fledged zero or one brood (Fig. 4.6).

The next best model (Scaled Pearson's $\chi^2 = 1.02$) included territory area alone ($n = 54$, $\chi^2_{1,63} = 2.8$, $P = 0.09$). The highest ranked model was not improved by the addition of breeding density ($n = 54$, $\chi^2_{1,54} = 0.9$, $P = 0.34$), breeding synchrony at the two day ($\chi^2_{1,54} = 0.4$, $P = 0.52$) or five day levels ($\chi^2_{1,54} = 1.8$, $P = 0.18$), the interaction of breeding density and synchrony at the two-day ($\chi^2_{1,54} = 0.3$, $P = 0.62$) or five-day levels ($\chi^2_{1,54} = 1.1$, $P = 0.29$), mean daily maximum temperatures during the fertile period at the two-day ($\chi^2_{1,54} = 0.2$, $P = 0.62$) or five-day level ($\chi^2_{1,54} < 0.01$, $P = 0.98$), mean daily minimum temperatures during the fertile period at the two-day ($\chi^2_{1,54} = 0.2$, $P = 0.69$) or five-day level ($\chi^2_{1,54} = 0.09$, $P = 0.93$), or mean precipitation accumulation during the fertile period at the two-day ($\chi^2_{1,54} = 0.4$, $P = 0.51$) or five-day level ($\chi^2_{1,54} = 0.4$, $P =$

0.55). All blocking effects were not significant and did not increase model rank and so were dropped.

Furthermore, none of these other candidate predictor variables explained significant variation by themselves ($n = 54$; density: $\chi^2_{1,63} = 0.4$, $P = 0.56$; two-day synchrony: $\chi^2_{1,63} = 0.3$, $P = 0.56$; five-day synchrony: $\chi^2_{1,63} = 2.3$, $P = 0.13$; density · two-day synchrony: $\chi^2_{1,63} = 0.03$, $P = 0.86$; density · five-day synchrony: $\chi^2_{1,63} = 0.7$, $P = 0.42$; two-day high temperatures: $\chi^2_{1,63} = 0.07$, $P = 0.79$; five-day high temperatures: $\chi^2_{1,63} = 0.06$, $P = 0.80$; two-day low temperatures: $\chi^2_{1,63} = 0.1$, $P = 0.71$; five-day low temperatures: $\chi^2_{1,63} = 0.02$, $P = 0.90$; two-day precipitation: $\chi^2_{1,63} = 0.01$, $P = 0.92$; five-day precipitation: $\chi^2_{1,63} = 0.3$, $P = 0.58$).

DISCUSSION

Our results show a clear relationship between presumed measures of male quality and the presence of extrapair young. Males with smaller crown patches and patches positioned further back on the head were more likely to suffer losses in paternity (Figs. 1 and 2). Males that deviated from the tradeoff between crown size and position were more likely to avoid losses in paternity (Fig. 4.3). Furthermore, males with large caps and smaller foreheads relative to their neighbors were less likely to suffer paternity losses than were males with smaller caps and larger foreheads (Fig. 4.5).

These results match our predictions for an extrapair mating system controlled by female preference. Females paired to rusty crowned males in areas with less rusty crowned neighbors were the least likely to raise extrapair young, while females paired to males of poorer quality in areas of high quality males were the most likely. These results support the growing body of evidence suggesting a strong role for female preference in the explanation of extrapair young (Møller and Birkhead 1994; Yezerinac and Weatherhead 1997; Owens and Hartley 1998; Garamszegi and Møller 2004; Coppack et al. 2006) and for female control of EPFs (Birkhead and Møller 1993; Stutchbury et al. 1994; Gray 1996; Double and Cockburn 2000; Forstmeier 2004). Furthermore our

results support the conclusion that females follow a “trade-up” strategy (Fishman and Stone 2006), assessing the relative quality of their social mates to that of their neighbors (Langefors et al. 1998; Sheldon and Ellegren 1999; Václav et al. 2003; Olendorf et al. 2004), possibly for the benefits of superior genes (Møller 1988; Hamilton 1990; Birkhead and Møller 1992). Females may assert this control either through extra-territorial forays or through the acceptance of (or cessation of resistance to) trespassing extra-territorial males (Westneat and Stewart 2003). Additionally, differences in relative mate quality may explain the significant inter-annual variance seen in some species (Lubjuhn et al. 1999; Dietrich et al. 2004).

We cannot rule out the possibility that EPCs occur because lower quality males are unable to prevent trespassing by higher quality males. We found no correlation, however, between the presence of EPFs and factors that should affect the ability of males to attempt EPCs (territorial density, breeding synchrony, temperature, and precipitation). It appears that in swamp sparrows it is relative male quality alone that determines EPFs, either through direct selection by the female or indirect female acceptance of males that can gain territorial access. These conclusions are supported across a wide variety of environmental variables and two vastly different habitats, lending credence to the proposition that social interactions and relative male quality are the best proximate explanation for extrapair fertilizations.

We did not find a relationship between the number of birds within the two-territory width radius and the presence of extrapair young, suggesting that increased opportunities for either male-male comparisons by the female or extrapair male trespassing did not affect the relative level of EPFs. We did find a negative relationship between territory size and EPFs, and there is certainly a connection between territory size and territory density. Territory area, however, is not only tied to territory density, but is also an indication of male territoriality and quality, with higher quality males defending larger territories in densely occupied habitat (B. Olsen, unpub. data). The strength of density as an indicator of EPFs in other studies (Griffith et al. 2002) may be due merely to a correlation with neighbor or individual quality (Fretwell and Lucas 1970; Fretwell

1972). If this is the case, controlling for male quality and territory area in these systems should either reverse or eliminate the relationship between density and EPFs in these systems. Furthermore, the necessity of controlling for individual quality *relative* to neighboring males may explain the lack of a density effect among other studies at the population level (Griffith et al. 2002; Westneat and Stewart 2003).

Although most of the variation in extra-pair fertilizations among species can be explained by phylogeny, these differences must have arisen by the relative tradeoffs of more proximate mechanisms meted out in interactions among individuals. The results of this study indicate that female preference in the swamp sparrow plays a role in extrapair fertilizations at the population scale. Environmental factors are likely to shift the relative costs and advantages associated with the strength of these preferences, ultimately opening the way for social mating system divergence, selection for specific mate phenotypes, and the larger-scale differences seen among Orders and Families.

FIGURES

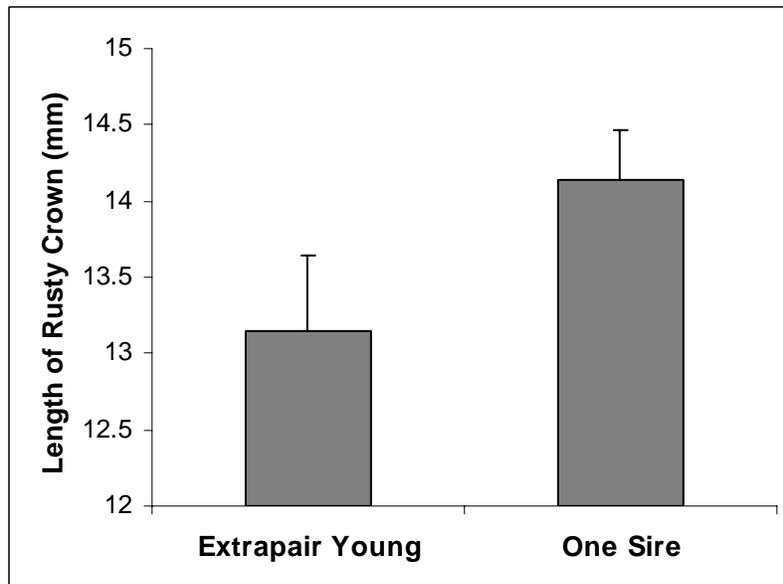


Figure 4.1. Crown and extrapair fertilizations: Rusty cap

The mean length of the rusty patch (\pm SE) on the crown of swamp sparrow males with nests that included or did not include extrapair young.

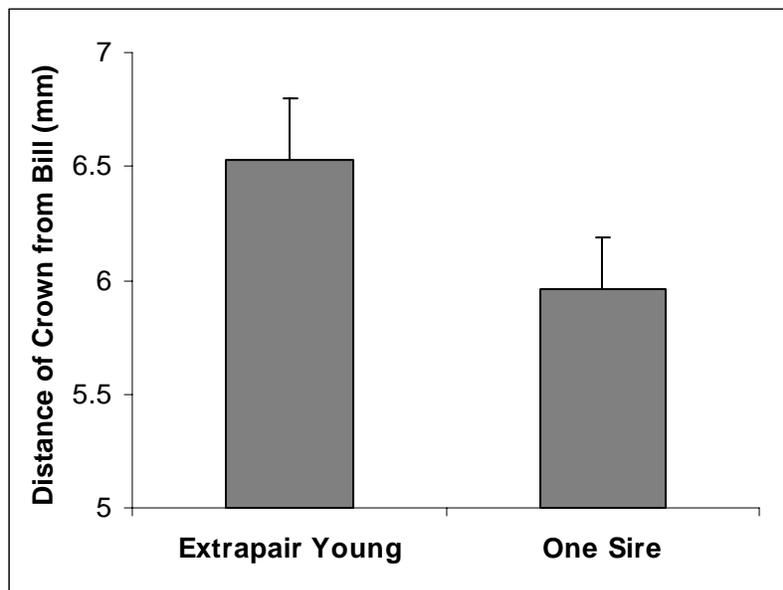


Figure 4.2. Crown and extrapair fertilizations: Black forehead

The mean length of the black forehead (\pm SE) of swamp sparrow males with nests that included or did not include extrapair young.

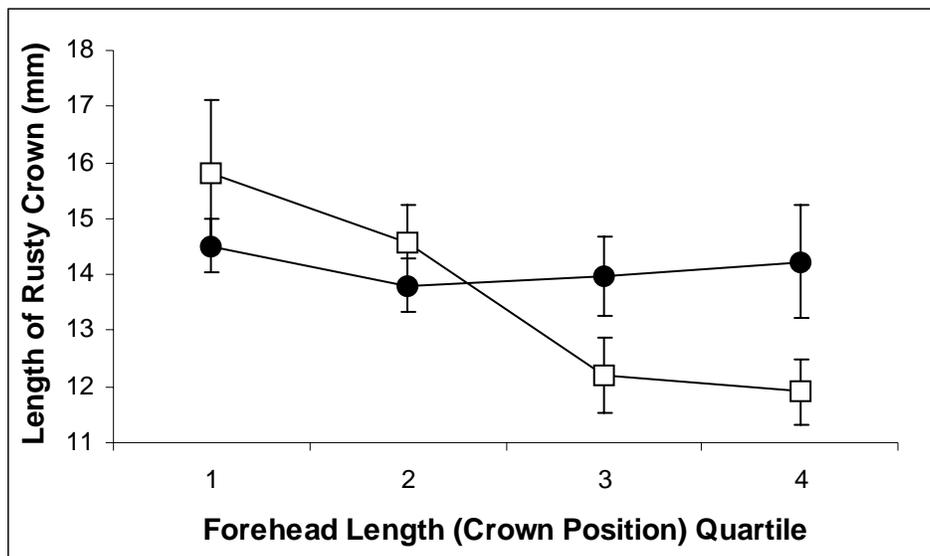


Figure 4.3. Tradeoffs between rusty crown and black forehead length

The mean length of the rusty crown patch (\pm SE) versus the relative distance of the crown patch from the bill (computed for each quartile) for swamp sparrow males with nests that included (white boxes) or did not include (black circles) extrapair young.

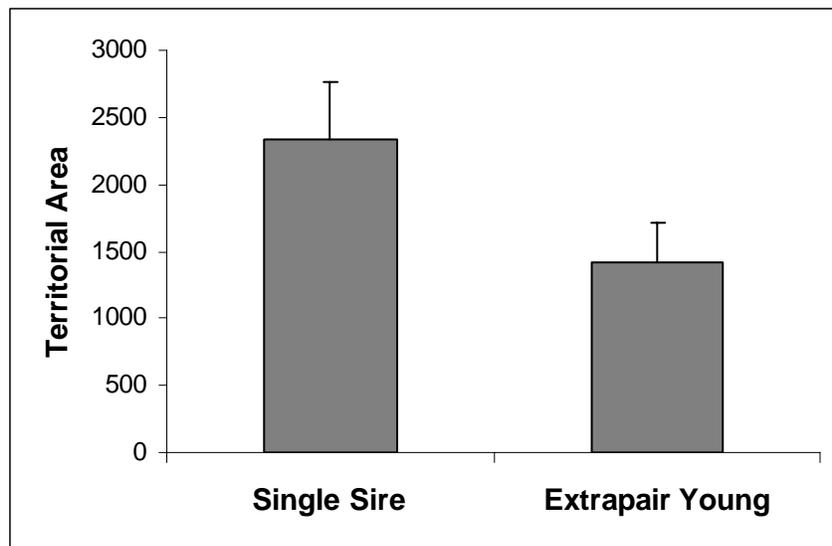


Figure 4.4. Territory area and extrapair young

The mean territory size (\pm SE) of swamp sparrow males with nests that included or did not include extrapair young.

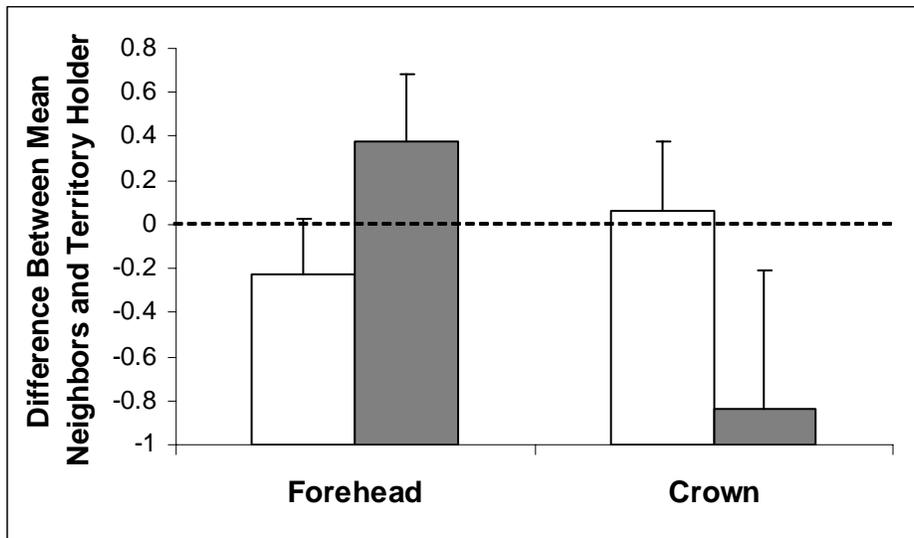


Figure 4.5. Relative neighbor plumage color and extrapair young

The mean difference in crown and forehead length (\pm SE) between the mean value of neighboring male swamp sparrows and the territory holder for males with nests that included extrapair young (white bars) and those that did not (gray bars). The dashed line shows where neighbors and territorial holders are equal, and negative values indicate that neighbors on average have smaller values than territory holders.

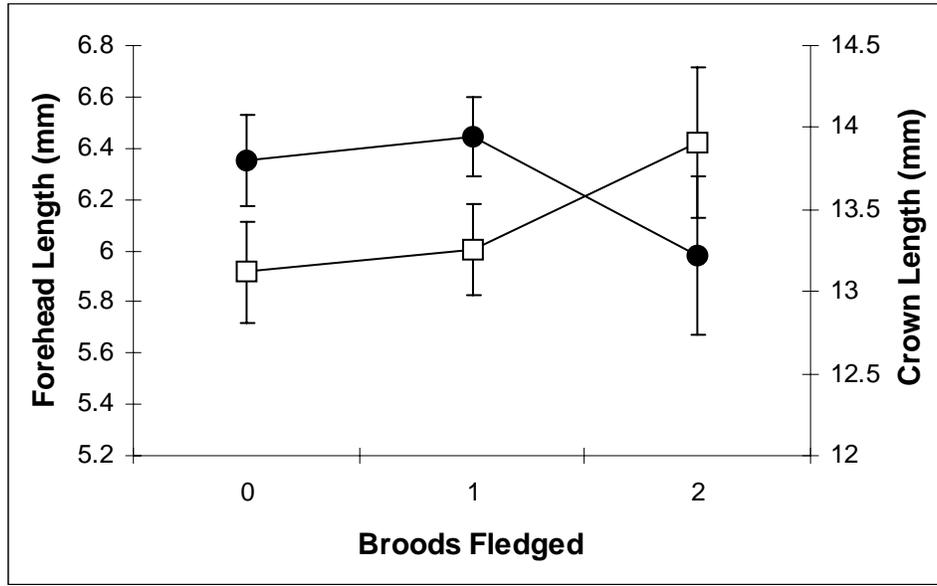


Figure 4.6. The effect of crown and forehead size on offspring production

The means (\pm SE) of rusty crown patch length (white squares) and the relative distance of the crown patch from the bill (black circles) for swamp sparrow males who provisioned zero, one, or two nests that survived to fledging.

TABLES

Table 4.1. PCR conditions and allelic diversity

PCR conditions and allelic diversity for six microsatellite DNA primers developed for either song or swamp sparrows. All volumes are in μL .

Locus	Label	Annealing Temp ($^{\circ}\text{C}$)	Amplitaq Gold DNA Polymerase	Primer	dNTP	MgCl ₂	10X PCR Buffer	DNA	BSA	Betaine	H ₂ O
Mme2	Fam	65	0.1	2.0	1.0	1.0	1.0	0.5	0.8	0	3.6
Mme3*	Hex	58	0.1	2.0	1.0	0.8	1.0	1.0	0.8	0	3.3
Mme7*	Fam	60	0.2**	0.8	0.3	0.7	1.1	0.5	0	1.6	4.9
Mme8	Tet	65	0.1	2.0	1.0	0.8	1.0	1.0	0.8	0	3.3
Mme12	Fam	65	0.1	2.0	1.0	0.8	1.0	0.5	0.8	0	3.8
Mg2we	Hex	60	0.1	1.0	1.0	0.4	1.0	0.5	0.8	1.6	3.6

*Z-linked Loci

**Amplitaq DNA Polymerase (not gold)

Table 4.2. Parental exclusion results

Results of genetic analysis for five polymorphic DNA microsatellite loci analyzed in *Cervus* on whole blood samples of two subspecies of swamp sparrow.

Locus	Alleles Detected	Males Sampled	Heterozygotes	Homozygotes	Exclusion Probability (1 Parent)	Exclusion Probability (2 Parents)	Null Allele Frequency Estimate
Among Coastal Males							
Mme7**	12	210	163	47	0.57	0.72	0.05*
Mme3**	21	218	150	68	0.63	0.78	0.13*
Mg2we	22	218	189	29	0.67	0.81	0.02
Mme2	4	223	101	122	0.11	0.19	0.01
Mme12	5	222	134	88	0.17	0.31	-0.04
Among Inland Males							
Mme3**	11	160	108	52	0.49	0.66	0.10*
Mme7**	24	182	147	35	0.73	0.84	0.07*
Mg2we	23	184	161	23	0.75	0.86	0.03
Mme2	2	184	104	80	0.13	0.19	-0.06
Mme12	4	184	87	97	0.11	0.23	-0.02

* Alpha set to 0.15 for homozygote deficiency and 0.00 for homozygote excess for Z-linked loci

** Z-linked Loci

CHAPTER V:
INTERACTIONS BETWEEN SEXUAL AND NATURAL
SELECTION IN THE PLUMAGE DIVERGENCE OF THE
COASTAL PLAIN SWAMP SPARROW

ABSTRACT

Sexually dimorphic signals are expected to differ as interactions between sexual and natural selection change across environments. Increased melanization has been noted in 24 tidal marsh vertebrates, suggesting that the differences are at least partially a result of natural selection. Tidal-marsh endemic swamp sparrows (*Melospiza georgiana nigrescens*), however, are sexually dimorphic and previous studies have linked crown characteristics to territorial behavior and mate choice. To understand the relative roles that natural and sexual selection play in plumage badge divergence, we investigated the relationship of rusty cap and black forehead patch size with territorial aggression and reproductive success in males of *M. g. nigrescens* and an inland subspecies, *M. g. georgiana*. Across both subspecies, the extent of rust in the male cap explained increases in male parental care and decreases in both the production of aggressive ‘growl’ notes and the intensity of response to territorial intrusion. The extent of black in the forehead was positively related to the response intensity. Differences between subspecific male crowns can be explained by changes in sexual selection due to male-male competition, with darker-crowned, coastal males showing more frequent production of aggressive call notes and songs. Female choice, however, appears to operate similarly in both subspecies, selecting for rusty crowns. Pairing success was explained directly in coastal males and indirectly in inland males (through territory quality) by the extent of cap rust. Although coastal birds of both sexes are more melanic than those inland, the difference in plumage coloration is more dramatic between females. Female plumage color has likely diverged as a result of natural selection, whereas male crown color has been controlled by

sexual selection, becoming slightly blacker due to increased male-male competition yet remaining largely rusty due to female choice. The lack of any observed sexual dimorphism among the melanic body contour feathers of coastal birds supports this conclusion. The increased sexual dimorphism among coastal birds provides a clear example of the interplay between sexual and natural selection in subspecies divergence.

INTRODUCTION

Sexual dimorphism can result from niche partitioning, intra-sexual competition, or female choice (Andersson 1994). The evolution of sexually dimorphic signals is also influenced by their impacts on individual fitness within specific habitats, levels of predation, foraging strategies, and sensory systems, all of which lead to interactions between natural and sexual selection (Endler 1978, 1989, 1992; Andersson 1994). We would expect then that within species, differences in sexually meaningful signals are likely to develop across environments due to varying natural selection regimes.

The socially monogamous swamp sparrow, *Melospiza georgiana*, possesses a seasonally molted, sexually dimorphic crown with cap that ranges from black with a gray median stripe in females to completely rusty in males during the breeding season and a forehead that runs from brown to black (Greenberg 1988a). These plumage characteristics are correlated with both habitat settlement (Chapter 2) and the production of young outside of the social pair bond (Chapter 4). Seasonally acquired plumage dimorphism is rare among sparrows and absent from other *Melospiza* and its closely related genera, *Junco*, *Passerella*, and *Zonotrichia* (Greenberg 1988a). Thus, swamp sparrows may harbor relatively little phylogenetic inertia in their dimorphism, and represent a good system for studying the interaction of natural and sexual selection in the evolution of plumage signals.

The plumage of freshwater-breeding swamp sparrow subspecies differs from that of the tidal salt marsh endemic, coastal plain swamp sparrow (*M. g. nigrescens*). The coastal sparrow is generally less rusty overall, with significantly more black feathers in the crown and nape (Greenberg and Droege 1990). Similar increased melanin production characterizes 24 vertebrate species endemic to the tidal salt marsh (Grinnell 1913;

Greenberg and Maldonado 2005), suggesting that natural selection may be operating similarly on color across tidal marsh ecosystems. Within the swamp sparrow, however, an increase in the black crown feathers also represents a shift from the most masculine crown type to a more feminine one (Greenberg and Droege 1990). Other tidal marsh endemics are universally monomorphic, so the larger pattern is unlikely to be the result of convergence in the strength of sexual selection. The question remains, has natural selection within the salt marsh environment altered the strength of sexual selection among coastal plain swamp sparrows or merely shifted the variation in a sexually selected signal along a previously evolved axis? The clear ecosystem pattern paired with a rare case of sexual dichromatism makes the swamp sparrow system ideal for investigating the relative roles of natural and sexual selection in species divergence.

To examine the interactions between these two selection regimes on the evolution of swamp sparrow crown color, we studied two populations, one of the coastal plain subspecies and a second of the nearest inland subspecies, *M. g. georgiana*. Within and between the populations, we tested for plumage correlates of male-male competition (territory size, reaction to intrusion, vigilance, and the production of song and aggression call notes) and reproductive success (breeding initiation date, offspring production, and male provisioning rate). We hypothesized that the described differences between inland and coastal crowns (Greenberg and Droege 1990) could evolve as a result of change in 1) the natural selection regime, 2) the sexual selection regime, or 3) a combination of changes in both regimes.

These three hypotheses lead to unique predictions. First, if the darker plumage of coastal birds has evolved purely from the natural selection regime of the salt marsh, we should find similar degrees of sexual dimorphism between the subspecies. Furthermore, under this scenario variation in coastal male crowns will occur over a more black-shifted range than found among inland males, but similar relationships will exist within each subspecies between crown characteristics and male fitness. If the crown color divergence has evolved due only to changes in sexual selection, the relationship between male crown characteristics and male fitness should be altered as well, while sexual dimorphism should remain constant as female crown color shifts equally due to genetic correlates (Price et al. 1987). Finally, if the plumage divergence is due to both natural and sexually

selective forces, we should find differences in the degree of sexual dimorphism as male color is shaped by both selection regimes (or sexual selection alone), while female color is driven primarily by natural selection.

METHODS

Study Site & Individual Measurements

We investigated the coastal subspecies at two sites in brackish *Spartina* marsh on Delaware state game lands along the mouth of the Smyrna River during the 2002-2005 breeding seasons (May-August). Inland studies were conducted on two minerotrophic sphagnum fens on the Allegheny Plateau in Garrett County, Maryland from 2004-2005. Each season we captured and banded adults and nestlings older than five days with a numbered, aluminum band and a unique combination of colored bands for later visual identification. Rust-colored feather coverage on the crown was classified into four categorical variables sensu the original description of swamp sparrow sexual dimorphism (Greenberg 1988a), ranging from a completely black (1) to a completely rusty (4) cap patch (Fig. 5.1). We also measured the length of the black forehead patch from the proximal end of the culmen to the first rusty cap feather and the length of the rusty cap patch from the end of the forehead to the last rusty feather. We photographed the crowns of all adults, digitally selected and isolated rusty cap and black forehead feathers using Adobe Photoshop 5.5 (Adobe Systems Inc. © 1999), and determined the area of these patches using Carnoy 2.0 (Schols 2001). In addition we aged adults based on banding returns (with age on the year of capture set as one or after one years of age based on plumage wear) and determined mass to the nearest tenth of a gram and tarsus length to the nearest tenth of a millimeter. Adults were initially sexed by brood patch or cloacal protuberance. The vast majority of males were captured after territory establishment, and a significant number were measured during or after the initial nesting attempt. Hence, temporally dynamic measures, such as weight, likely reflect either short-term costs of nestling provisioning, or the longer-term, additive costs to territory maintenance. Plumage and tarsus characteristics, on the other hand, are relatively stable throughout the breeding season.

Reproductive Measurements

We located nesting attempts of banded individuals from the first of May until either the end of August or the cessation of breeding using the female nest-departure call (McDonald and Greenberg 1991), which is an extremely effective way of locating nests during the building, laying, or incubation stages (Greenberg 2003). The earliest clutch completion within coastal plots was on 9 May, and the earliest inland nesting began on 10 May. Nests were monitored daily until they failed or offspring left the nest (fledged). In 2005, we observed 31 nests (15 coastal and 16 inland) with chicks of at least three days of age from a camouflaged location for two hours or six feeding trips (whichever occurred first). The sex of the provisioning parent was determined by colored band identification. For each territory we defined ‘nest initiation date’ (a measure of pairing success) as the Julian date of clutch completion during the initial nesting attempt. For initial attempts that were not found during the building or laying phase, dates were assigned based on the date of egg hatch, assuming that females incubated eggs for 11 (coastal) or 12 (inland) days until hatch (Chapter 3).

Territoriality Measurements

We delineated territories with minimum convex polygons drawn around male singing locations during the active breeding season. Territory area was calculated in ArcMap 8.3 (ESRI 2002). We defined the territorial neighbors for each male as all birds with song-posts that were less than a distance of two mean territory diameters from the center of each territory. We observed males from 45 territories (27 coastal and 18 inland) for one hour to record the baseline rates of song, aggressive ‘growl’ notes (Reinert and Golet 1979; Ellis 1980), and movement (as a measure of territory vigilance). Observation occurred between sunrise and 1100 hours on males paired to incubating females or males without an active nest (including birds prior to their initial nesting attempt and birds between attempts). We made no observations of male territoriality during the nestling period. After this hour of observation, we presented each male with a subspecies-specific, mounted, adult male with a type-4 crown, accompanied by subspecies-specific song recorded within four kilometers of our study plots (but not on our plots). The

recording consisted of four minutes of silence, followed by four-minutes of a single song type with ten seconds between each song to match natural song frequency (Ellis 1980), followed by four minutes of silence. During this 12-minute period we recorded the length of time males actively responded to the mount, including aggression and mobbing call notes, wing-flashes, rapid perch-changes within two meters, and physical contact with the mount.

For 11 additional banded males intrusion was simulated in 2005 using only song (via the methods described by Searcy et al. 1997) to control for changes in territorial response due to relative crown differences between the mount and the focal male (Garamszegi et al. 2006). To avoid problems of pseudoreplication associated with using the same song for each trial (Kroodsma 1989), we constructed 24 tapes (12 of each subspecies) from clean audio recordings made within four kilometers of each site, including six *M. g. georgiana* songs recorded by B. Ballentine from Crawford County, Pennsylvania. For each six-minute tape, two songs were taken from the repertoire of a single bird, which were broadly classified as having a slow and a fast trill rate. On each recording we alternated the two song types, playing two 1.5-minute bouts of nine songs separated by 1.5-minute bouts of the second type, randomly selecting the first song type. Tapes were randomly selected for broadcast from a camouflaged, mounted speaker (model SC-A70, Saul Mineroff Electronics Inc., Elmont, New York) placed at the territory edge. From three minutes before the broadcast to six minutes after the end of the recording, we noted the male's distance from the speaker in 15-second intervals, the time spent within 10m of the speaker, and the rate of song production.

Statistical Analysis

We carried out all statistical analysis using SAS 9.1.3 (SAS Institute 2005). We tested for differences in cap and forehead characteristics as a function of subspecies and age, using a two-way ANOVA. Once the degree of sexual dimorphism and age effects were determined using our five primary crown measures (cap patch area and length, forehead patch area and length, and crown class), we constructed two principle components describing male crowns. The first component (hereafter Cap-PC) had the highest eigenvalue of the principle components created from cap patch length, cap patch area,

and crown class. The second component (hereafter Fore-PC) was the highest ranked principle component of those composed of forehead patch length and area. Correlations between the five primary measures were conducted using Pearson correlations.

Due to differences in clutch size (Greenberg and Droege 1990; Chapter 3), climate (Chapter 3), and territory size between the subspecies (which may have diverged for reasons other than sexual selection: Chapter 3), we used multiple linear regression within each population to test for crown effects on the number of chicks fledged, the Julian date of incubation initiation for the first nesting attempt, and territory size. Candidate predictors for offspring production included Cap-PC and Fore-PC, body condition (defined as mass over tarsus length), age, territory area, and nest initiation date (to control for territory establishment and pairing success). Similar models were tested for nest initiation date and territory area (without those variables as candidates within their own model).

Similarly, we tested for differences in song rate, perch changes per minute (as a measure of territory vigilance), and mount engagement length using multiple linear regression. Candidate predictors included territory area, observation date and time of day, the number of territorial male neighbors, male condition, age, indicator variables for subspecies and nesting period, Cap-PC and Fore-PC. Tests for the effect of crown characteristics on the audio playback experiment used only forehead and cap patch lengths, as we only had photographs of four of these males with which to calculate either patch area or the two principle components.

Final models with categorical variables were analyzed *post hoc* for interaction terms with subspecies using the generalized linear model procedure in SAS. Models predicting the occurrence of growl notes were tested using multiple logistic regression and the same candidate predictors as the linear aggression models. Multiple linear regression model selection was based on Mallows' C_p , and multiple logistic regression was based on stepwise selection with entrance and exit criteria set to $\alpha = 0.15$. All residuals were tested for normality and homogeneity of variance where appropriate, and we log-transformed territory area to meet assumptions. All means given are \pm standard error.

RESULTS

Subspecies Divergence in Crown

Variation in the extent of rust in the male cap was not explained by age. Controlling for the effect of subspecies, there was no effect of age on crown class ($n = 93$, $F_{3, 89} = 0.6$, $P = 0.59$), cap patch length ($n = 93$, $F_{3, 56} = 0.3$, $P = 0.81$), cap patch area ($n = 93$, $F_{3, 45} = 0.4$, $P = 0.77$), forehead patch length ($n = 93$, $F_{3, 56} = 1.9$, $P = 0.13$), or forehead patch area ($n = 93$, $F_{3, 27} = 1.3$, $P = 0.31$).

The extent of rust in the crown did, however, vary significantly by subspecies and sex. Crown class was predicted ($n = 569$, $F_{3, 565} = 197.5$, $r^2 = 0.51$, $P < 0.0001$) by subspecies ($F_{1, 565} = 126.5$, $P < 0.0001$), sex ($F_{1, 565} = 348.6$, $P < 0.0001$), and the interaction of subspecies and sex ($F_{1, 565} = 22.01$, $P < 0.0001$), indicating that the difference in crown class between the sexes among coastal birds was greater than those inland (Fig. 5.1). Among coastal birds, males had an average crown class of 3.19 ± 0.04 while females had an average class of 1.62 ± 0.06 . Inland, males had a crown of 3.64 ± 0.08 and females a crown of 2.70 ± 0.08 (Fig. 5.1). The same was true for cap patch area ($n = 291$, $F_{3, 287} = 62.5$, $P < 0.0001$; subspecies: $F_{1, 287} = 66.7$, $P < 0.0001$; sex: $F_{1, 287} = 121.7$, $P < 0.0001$; subspecies \cdot sex: $F_{1, 287} = 3.6$, $P = 0.06$) with significant differences within and between males (coastal: $150.7 \pm 8.2 \text{ mm}^2$; inland: $214.5 \pm 10.8 \text{ mm}^2$) and females (coastal: $19.3 \pm 4.2 \text{ mm}^2$; inland: $121.6 \pm 12.2 \text{ mm}^2$) of each subspecies. There were also significant effects of sex ($F_{1, 363} = 3.82$, $P = 0.05$) and a sex by subspecies interaction ($F_{2, 363} = 6.07$, $P = 0.003$) for cap patch length ($n = 367$, $F_{3, 363} = 4.82$, $P = 0.003$), again showing divergence in plumage between and within males (coastal: $12.9 \pm 0.2 \text{ mm}$; inland: $14.1 \pm 0.3 \text{ mm}$) and females (coastal: $12.8 \pm 0.4 \text{ mm}^2$; inland: $12.7 \pm 0.4 \text{ mm}^2$) of each subspecies.

Both forehead patch length ($n = 367$, $F_{3, 367} = 10.9$, $P < 0.0001$) and area ($n = 193$, $F_{3, 189} = 19.8$, $P < 0.0001$) were best predicted by the interaction of sex and subspecies alone. Coastal males had a mean forehead patch area of $67.5 \pm 2.2 \text{ mm}^2$ while coastal females had a forehead patch area of $52.0 \pm 8.3 \text{ mm}^2$. Inland males ($44.4 \pm 2.9 \text{ mm}^2$) and females ($39.6 \pm 4.1 \text{ mm}^2$) had smaller forehead patch areas than their coastal counterparts but were not significantly different from each other ($n = 85$, $F_{1, 83} = 1.1$, $P = 0.30$: Fig.

5.2). Forehead patch length was also greater among coastal birds in both sexes and in coastal males (6.6 ± 0.1 mm) versus coastal females (6.2 ± 0.2 mm), but did not differ between the inland sexes ($n = 135$, $F_{1,133} = 0.7$, $P = 0.41$; males: 5.8 ± 0.1 mm; females: 5.6 ± 0.2 mm). Furthermore, among coastal birds cap patch length was inversely related to forehead patch length ($n = 230$, $F_{1,228} = 10.8$, $P = 0.001$: Fig. 5.3), while no such pattern existed among inland birds ($n = 135$, $F_{1,133} = 0.6$, $P = 0.44$: Fig. 5.3).

Among males crown class was significantly correlated with both cap patch length ($n = 182$, $r = 0.16$, $P = 0.03$) and area ($n = 143$, $r = 0.64$, $P < 0.0001$). The two cap patch measures were also correlated with each other ($n = 143$, $r = 0.51$, $P < 0.0001$). Likewise, forehead patch length and area were significantly related ($n = 127$, $r = 0.53$, $P < 0.0001$). Cap-PC and Fore-PC had eigenvalues of 1.9 and 1.5 and explained 63 and 76 percent of the variation in the original variables, respectively. All individual variables were positively related to their respective principle component (Table 5.1).

Reproductive Success & Parental Investment

Among inland birds the best model for the number of chicks fledged ($n = 47$, $r^2 = 0.23$, $F_{2,44} = 6.4$, $P = 0.004$) included a positive correlation with Cap-PC ($t_{1,60} = 2.1$, $P = 0.04$: see Fig 4) and a negative correlation with the date of nest initiation ($t_{1,60} = -2.8$, $P = 0.007$). For coastal sparrows the best model ($n = 58$, $r^2 = 0.23$, $F_{3,54} = 5.4$, $P = 0.003$) included a positive correlation with Fore-PC ($t_{1,54} = 2.3$, $P = 0.03$: Fig. 5.5) and negative correlations with nest initiation date ($t_{1,54} = -2.5$, $P = 0.02$), and log-transformed territory area ($t_{1,54} = -2.9$, $P = 0.005$).

For inland birds the best model predicting nest initiation date included only a positive relationship with log-transformed territory area ($n = 43$, $r^2 = 0.08$, $F_{1,41} = 4.3$, $P = 0.05$), suggesting that birds on smaller territories bred earlier. For coastal birds, however, the earliest breeding males were explained best by a low Cap-PC ($n = 72$, $r^2 = 0.07$, $F_{1,70} = 5.6$, $P = 0.02$). Among nests of both subspecies observed during the nestling period, Cap-PC alone was the best predictor of the proportion of feeding trips made by males ($n = 30$, $r^2 = 0.33$, $F_{1,28} = 13.6$, $P = 0.001$: Fig. 5.6), and subspecies had no significant explanatory power ($n = 30$, $r^2 < 0.01$, $F_{1,31} = 0.3$, $P = 0.60$: Fig. 5.6).

Territory Size & Territorial Aggression

Among coastal males, log-transformed territory area was best predicted ($n = 109$, $r^2 = 0.52$, $F_{2,106} = 57.6$, $P < 0.0001$) by plot ($t_{1,106} = 10.4$, $P < 0.0001$) and increasing male condition ($t_{1,106} = 2.8$, $P = 0.006$), such that the size of male territories in the densest coastal plot were positively related to male condition, although this was not true for any other plot (less dense coastal plot: $F_{1,29} = 0.1$, $P = 0.76$; denser inland plot: $F_{1,14} = 3.0$, $P = 0.10$; less dense inland plot: $F_{1,29} = 0.5$, $P = 0.50$). Among inland sparrows log-transformed territory was predicted by increasing Cap-PC ($t_{1,34} = 2.1$, $P = 0.05$) and decreasing Fore-CP ($t_{1,34} = -2.1$, $P = 0.04$), such that males defending the smallest territories possessed both larger forehead patches and decreased percentages of rust in the cap ($n = 37$, $r^2 = 0.19$, $F_{2,34} = 4.0$, $P = 0.03$).

Coastal males were more aggressive overall. During the hour observation periods coastal males changed perch more frequently ($n = 42$, $r^2 = 0.23$, $F_{1,40} = 11.7$, $P = 0.002$), sang more ($n = 45$, $r^2 = 0.13$, $F_{1,43} = 6.7$, $P = 0.01$), and were more likely to give aggressive ‘growl’ notes ($n = 45$, $X^2_1 = 7.3$, $P = 0.007$). Furthermore, subspecies alone was the best predictor of song rate. Movements around the territory (a likely reflection of vigilance), however, were explained best by several variables (overall model: $n = 39$, $r^2 = 0.58$, $F_{6,32} = 7.4$, $P < 0.0001$), including subspecies ($F_{1,32} = 12.0$, $P = 0.002$), nesting period ($F_{1,32} = 11.4$, $P = 0.002$), decreasing hour of observation ($F_{1,32} = 5.2$, $P = 0.03$) and increasing male age ($F_{1,33} = 3.3$, $P = 0.03$). Both subspecies were more vigilant during incubation than in periods where there was no active nest, and coastal males were more vigilant overall (Fig. 5.7).

Although ‘growl’ notes were more common among coastal birds, the effect of subspecies was not significant when crown characteristics were taken into account. The best model ($n = 32$, $X^2_2 = 13.2$, $P = 0.001$) showed that the notes were uttered more frequently earlier in the day ($X^2_1 = 6.7$, $P = 0.01$) and by birds with a smaller Cap-PC ($X^2_1 = 7.6$, $P = 0.006$; Fig. 5.8).

Intrusion Simulations

During the mount presentation, the best model ($n = 27$, $r^2 = 0.34$, $F_{2,24} = 6.3$, $P = 0.006$) indicated that birds with the lowest Cap-PC values mobbed the mount the most

aggressively ($t_{1,24} = -3.0, P = 0.007$), controlling for male condition ($t_{1,24} = 2.7, P = 0.01$). Controlling for Cap-PC and male condition, there was no effect of subspecies ($t_{1,23} = 0.2, P = 0.81$). During the audio playbacks among both populations, forehead patch length was greater in birds that stayed close to the speaker ($n = 11, r^2 = 0.56, F_{1,9} = 11.6, P = 0.008$; Fig. 5.9) and in birds that spent more time within 10m of the speaker, controlling for the trial date ($n = 11, r^2 = 0.61, F_{1,8} = 6.3, P = 0.02$). Controlling for these effects there was no influence of subspecies on the average distance to the speaker ($F_{1,8} = 0.1, P = 0.73$) or time spent within 10m of the speaker ($F_{1,7} = 0.02, P = 0.89$). The number of songs produced over the audio trials was best predicted by increasing male age ($n = 11, r^2 = 0.44, F_{1,9} = 7.1, P = 0.03$) with second year birds producing 23.0 ± 5.5 songs during the trial and older birds producing 46.0 ± 2.0 songs.

DISCUSSION

Female Release from Sexual Selection

Paralleling the general trend found among all tidally endemic sparrows (Greenberg and Droege 1990), coastal bird crowns were more melanistic overall, with lower crown classes (sensu Greenberg 1988a), smaller rusty cap patch lengths and areas, and larger black forehead patch lengths and areas. The subspecific differences existed for both females and males, although they were generally greater for females. The degree of sexual dimorphism was thus greater within coastal populations than within inland populations. As a sexually selected signal (Chapters 2, 4), changes in male crown color are meaningful to mating success, and it is likely that sexual selection has prevented as large a shift in coastal male crown color as that found in females, which are subject more exclusively to natural selection. Biologists as early as Wallace (1889) have speculated that the degree of sexual dimorphism is due to natural selection on females as much as it is due to sexual selection on males, and there has been some quantitative evidence to support this (e.g. Björklund 1991; Irwin 1994; Martin and Badyaev 1996; Bleiweiss 1997; Gotmark et al. 1997; Burns 1998; Badyaev and Hill 2003). It is even probable that strong natural selection on females must oppose sexual selection in males in order to alter a trait's inheritance by sex (Fisher 1930; Lande 1980; Lande and Arnold 1985). It may

be that in the swamp sparrow system both sexes are under strong natural selection for more melanistic plumage, but only females are released from the sexual implications of crown color.

A Dual Signal for Parental Care and Aggression

In both subspecies we found evidence that the extent of rust in the male cap is related to parental ability and the extent of black in the forehead is related to territorial aggression. Males with larger caps provisioned young more. Similar correlations between non-black melanin badges and parental ability have been reported (Owens and Hartley 1998; Siefferman and Hill 2003). Additionally, we found that cap size was negatively related to two measures of aggression (aggressive call notes and mount mobbing length) and such tradeoffs between parental care and territorial aggression have often been noted (Wingfield et al. 1987; Ketterson et al. 1992; Stoehr and Hill 2000; Duckworth 2006). We found a similar behavioral tradeoff among inland males, where birds with increasing forehead patch size and decreasing cap patch size possessed smaller territories, which are presumably more highly contested (Fretwell and Lucas 1970; Fretwell 1972; Chapter 2). Furthermore, forehead size in both subspecies was directly related to two measures of aggression (average distance from the playback speaker, and time spent close to the speaker). Black melanin patches are similarly correlated with aggression or social rank in other species (Rohwer 1975, but see review in Senar 1999) and negatively correlated with parental care (Bókony and Liker 2005).

Sexual Selective Pressures Vary by Environment

The difference in crown coloration between inland and coastal males can be explained by sexual selection alone. The crown differences within and between the subspecies are closely related to behavioral differences within and between the subspecies, and crown eumelanization correlates with three different measures of territoriality better than subspecies alone. This suggests that the increased black crown plumage among coastal males is due to selection for territorial aggression and not from natural selection on phenotypes independent of reproductive behavior. The relative importance of territorial

defense has thus diverged between the two subspecies, although the signals indicating aggression have remained similar both within and between them.

This is further supported by the plumage correlates of offspring production. Controlling for pairing success (via nest initiation date), coastal males with darker crowns produced the most offspring, while among inland males those with the highest signals of parental contribution did. This suggests that the ability to maintain high quality habitat is more important in the salt marsh while the ability to provide high levels of parental care is of more importance inland. Presumably selection for the defense of habitat is met through intrasexual selection on aggression, of which the forehead patch is a signal, while the selection for parental ability is met through female choice on the rusty cap.

Interestingly, nest initiation date, a measure of pairing success, was predicted by increasingly rusty caps in both subspecies, suggesting that female choice operates in the same direction within each ecosystem. Additionally, cap size in both subspecies (relative to neighbors) is an important predictor of extra-pair young (Chapter 4), suggesting that swamp sparrow females use the rusty cap in mate selection for both social and extra-pair bonds.

It thus appears that increased crown eumelanization among coastal plain swamp sparrow males is due to increased sexual selection for territorial aggression. Sexual dimorphism among coastal forehead patches (while it is absent inland) supports this conclusion. The divergence likely occurred through intrasexual competition using a plumage signal shared by the common ancestor of both subspecies. Furthermore, the behavioral divergence may be related to the increased importance of habitat quality for offspring production in the abiotically dynamic, tidal salt marsh. Supporting this claim, we detected increased physiological costs among the most aggressive males defending the smallest, most contested coastal territories. Territorial defense is energetically expensive in both subspecies (as indicated by the relationship between intrusion reaction and male condition), but the energetic expenditure of coastal males in the smallest territories on our densest plot is higher than elsewhere, as shown by their low mass (controlling for body size). These costs are expected if intrasexual competition is responsible for the divergence of coastal male behavior and plumage patches signaling that behavior.

Selection for increased size in the forehead patch of coastal males, however, has been limited by head size and selection for the rusty cap through female choice. Among coastal males there is a significant negative relationship between forehead and cap size, suggesting a tradeoff between the production of one signal over the other and an inability to produce large signals for both aggression and parental care simultaneously (Fig. 5.3). Tradeoffs between parental care behavior and territorial aggression have been reported in other systems where the two traits are important (Wingfield et al. 1987; Ketterson et al. 1992; Stoehr and Hill 2000; Duckworth 2006). Whether the variance in the morphological tradeoff reflects an underlying endocrinological tradeoff between these behavioral states is unknown, but one can imagine the honesty of such a signal being reinforced by these morphological limitations. No such morphological tradeoff exists among inland males, however, which may be due to the lessened intrasexual selection for territorial aggression.

Natural vs. Sexual Selection on Swamp Sparrow Plumage

The differences in crown coloration between males of the two subspecies, with rustier caps and smaller foreheads among inland sparrows, can be explained completely by differential sexual selection on aggressive versus parental behavior. This conclusion is supported by the fact that similar relationships exist between a number of behavioral measures and crown color in both subspecies. Had natural selection been responsible for increased eumelanization among coastal males, similar behavioral states in each population would be represented by different crown colors, with darker crowns in the coast and rustier crowns inland. Instead, behaviors related to both territorial aggression and male parental care are represented by similarly colored crowns in both subspecies. This suggests that environmental differences in the coastal population has altered the fitness payback associated with the behavior represented by rustier crowns, and that sexual selection for more aggressive behavior (through male-male competition) has resulted in the plumage characteristics that represent that behavior. The different top models of offspring production in each population corroborate this conclusion.

Higher proportions of offspring provisioning, lower territorial aggression, and correlations between cap size and offspring production support the conclusion that rusty

crown plumage is maintained in inland wetlands by the importance of male parental care. Among coastal males, lower levels of offspring provisioning, higher territorial aggression, ties between forehead patch size and fledging success, and tradeoffs between forehead and cap patch size all suggest that increased eumelanization is maintained by the importance of intrasexual competition for male fitness. Coastal plain swamp sparrows across both sexes, however, show greater plumage melanization overall, a pattern which converges across a wide variety of tidal salt marsh vertebrates and suggests a strong natural selection regime (Greenberg and Droege 1990; Greenberg and Maldonado 2005). Female coastal plain swamp sparrows, which are presumably under much lower levels of sexual selection but similar levels of natural selection, possess dramatically darker crowns than inland birds of both sexes. The increased sexual dimorphism in coastal crowns is caused by a large shift in eumelanin (black) production among females due to natural selection and a smaller shift in eumelanin production among males that is explained by sexual but not natural selection. Continued sexual selection for phaeomelanic (rusty) crowns from female choice has prohibited environmental conditions in the salt marsh from producing males with crowns similar to females, providing a clear example of the interplay between sexual and natural selection in subspecies divergence. The overall color of male and female body feathers are *equally* darker than the bodies of inland subspecies (B. Olsen, pers. obs), further supporting the claim that sexual selection on male crowns has prevented eumelanin production while the same has not occurred among feathers that lack this evolutionary pressure. Furthermore, increased feather wear on the rusty caps of coastal versus inland males at the end of the season (B. Olsen and R. Greenberg, pers. obs.) suggests that environmental conditions selecting for increased eumelanin production (which resists wear in environments that cause higher rates of feather abrasion: Muza et al. 2000; Burt and Ichida 2004; Goldstein et al. 2004) may increase the cost of rusty cap maintenance in coastal males, thereby augmenting the signal's honesty (Maynard-Smith and Harper 1988; Jawor and Breitwisch 2003; McGraw 2003).

FIGURES

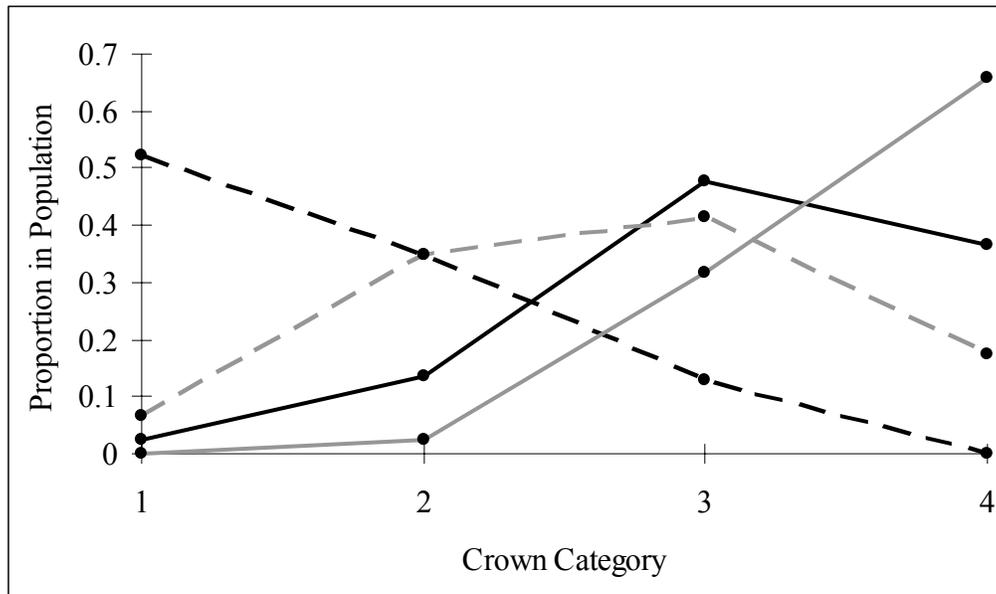


Figure 5.1. Crown color by sex and subspecies

The proportion of individuals that possessed four crown types (1 = black crown with gray or brown median stripe, 2 = cap patch included > 0 % and < 50 % rusty feathers, 3 = cap patch included > 50% and < 100% rusty feathers, and 4 = 100% rusty feathers) for males (solid lines) and females (dashed lines) from populations of coastal (black line) and inland (gray line) swamp sparrows.

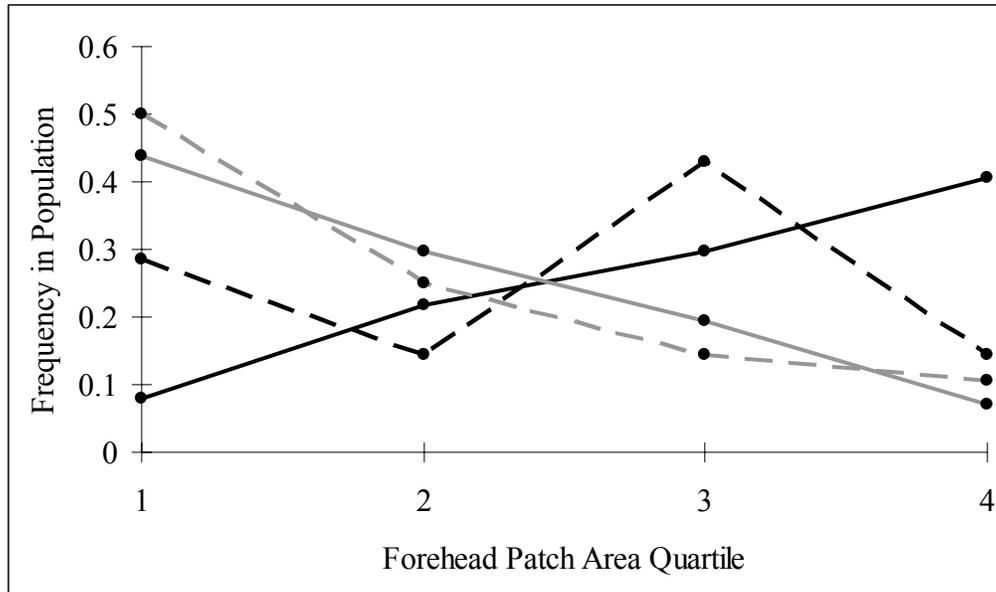


Figure 5.2. Forehead patch size by sex and subspecies

The proportion of individuals in each of the four quartiles of forehead patch area for males (solid lines) and females (dashed lines) from coastal (black line) and inland (gray line) swamp sparrows.

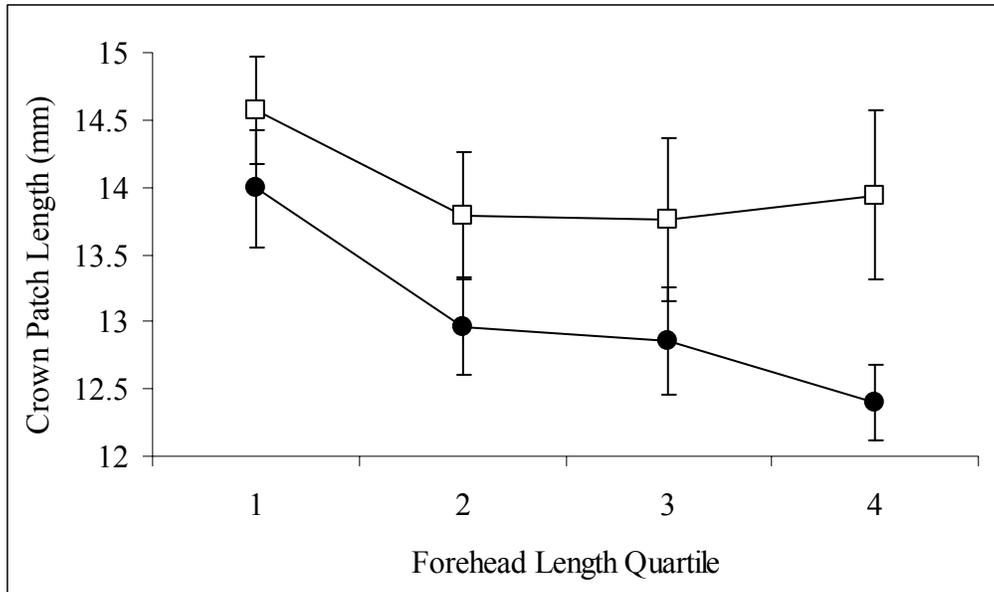


Figure 5.3. Tradeoffs between forehead and crown size

The mean cap patch length (\pm SE) for each quartile of forehead patch length for coastal (black dots) and inland (white squares) swamp sparrows.

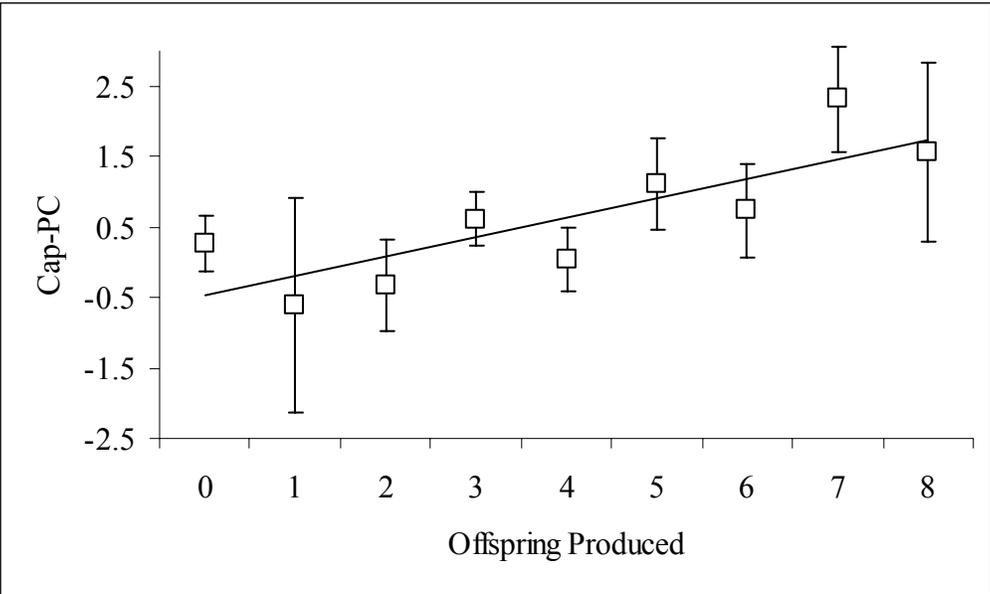


Figure 5.4. The effect of cap color on inland offspring production

The mean value (\pm SE) of the principle component describing rusty cap patch computed for inland male swamp sparrows that fledged between zero and eight offspring, controlling for initial nest completion date.

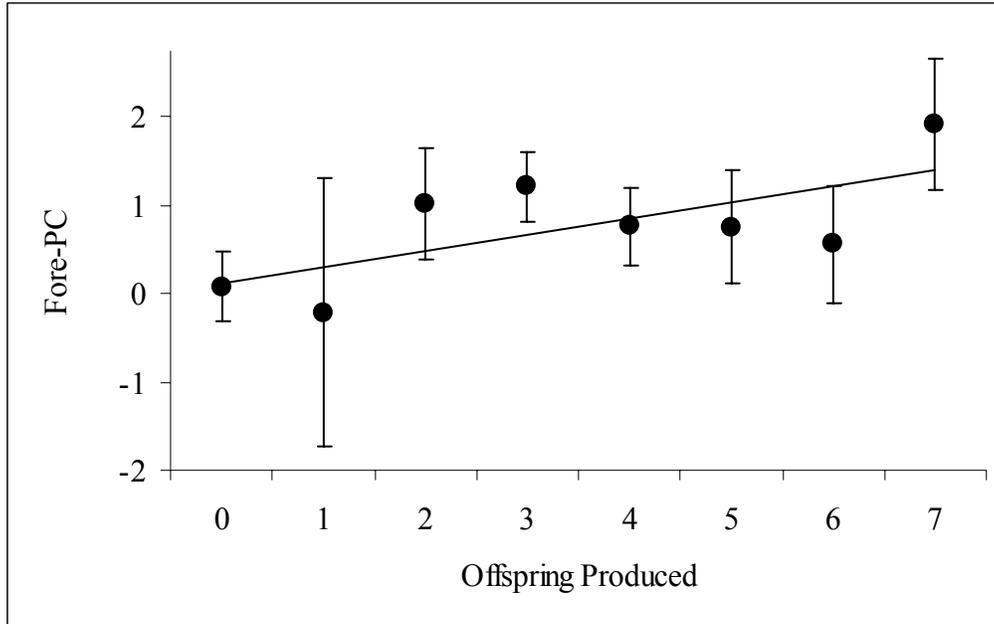


Figure 5.5. The effect of forehead color on coastal offspring production

The mean value (\pm SE) of the principle component describing black forehead patch computed for inland male swamp sparrows that fledged between zero and eight offspring controlling for initial nest completion date and log-transformed territory area.

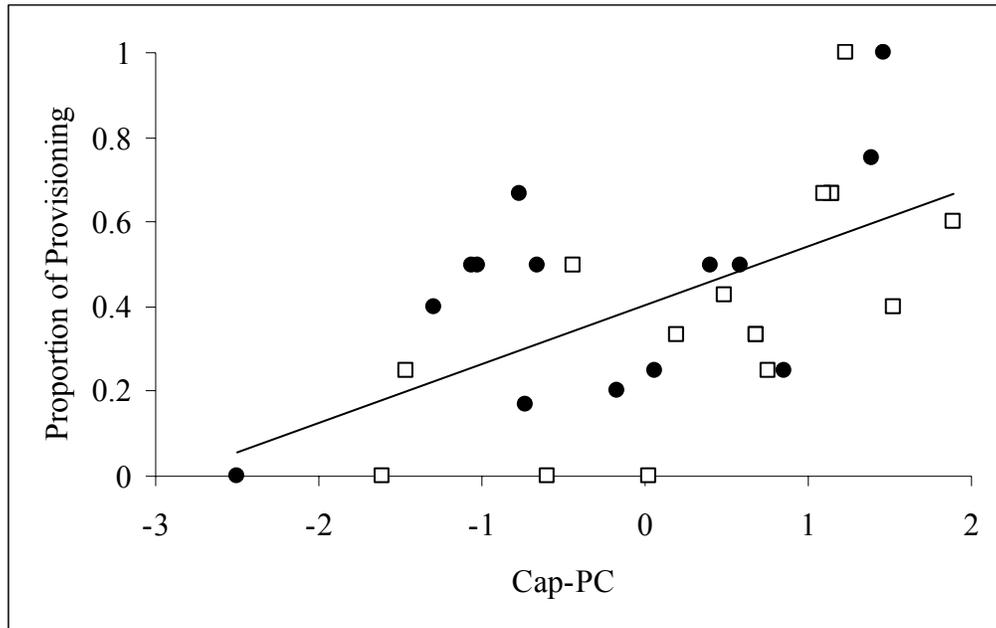


Figure 5.6. The effect of cap color on offspring provisioning

The proportion of offspring provisioning trips made by the male versus a principle component describing the extent of rust-colored feathers in the cap patch of inland (white squares) and coastal (black circles) swamp sparrows.

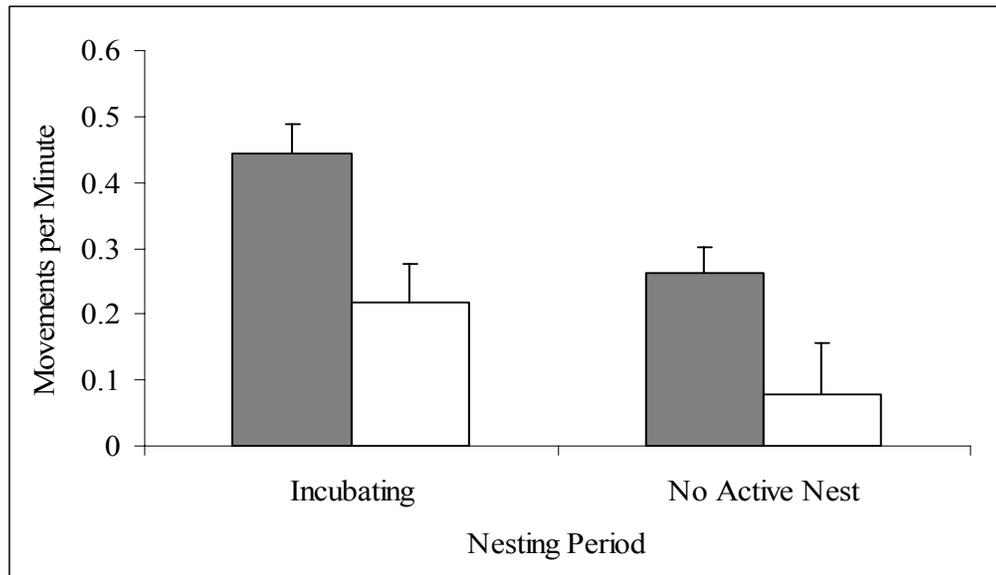


Figure 5.7. Territorial vigilance by subspecies and nesting period

The mean number of changes in perch per minute (\pm SE) for males paired to incubating females and males without active nests (which includes periods prior to the initial nesting attempt and between nesting attempts) for coastal (gray bars) and inland (white bars) swamp sparrows.

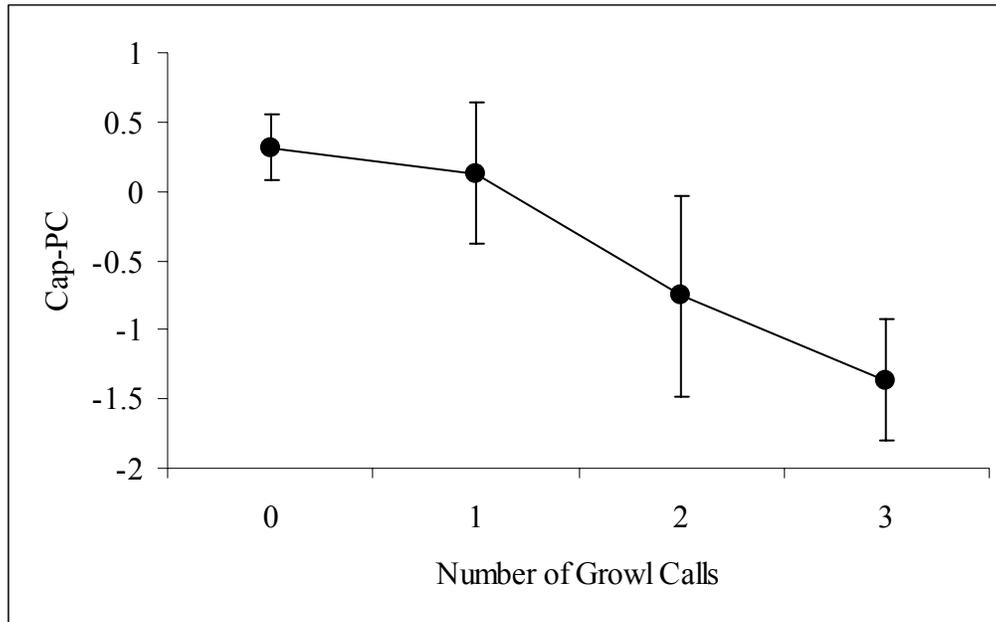


Figure 5.8. Cap color by frequency of growl call notes

The mean value (\pm SE) of a principle component describing the extent of rust-colored feathers in the cap patch for male swamp sparrows of both subspecies that uttered between zero and three aggressive ‘growl’ notes during one hour of observation.

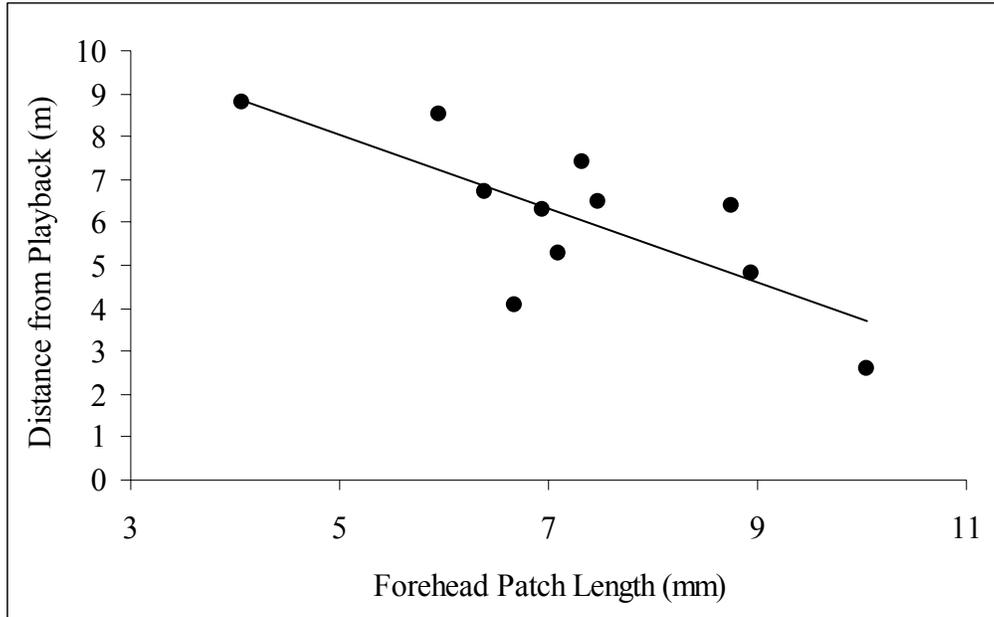


Figure 5.9. The effect of forehead patch size on approach distance

The mean distance from the playback speaker versus the length of the black forehead patch during playback of non-neighbor song among inland and coastal swamp sparrows.

TABLES

Table 5.1. Crown principle components

Descriptive statistics of two principle components describing swamp sparrow crown characteristics.

	Fore-PC		Cap-PC		
Eigenvalue	1.53		1.88		
Proportion of Variation	0.76		0.63		
Sample Size	121		130		
Variables	<i>Forehead Patch Length</i>	<i>Forehead Patch Area</i>	<i>Cap Patch Length</i>	<i>Cap Patch Area</i>	<i>Crown Class</i>
Eigenvectors	0.71	0.71	0.52	0.65	0.55

CHAPTER VI:
NEST PLACEMENT AS A TEST FOR CONSPECIFIC
ATTRACTION IN THE SWAMP SPARROW

ABSTRACT

Conspecific attraction influences settlement and thereby affects the distribution of a number of species. For territorial species, where a single sex is primarily responsible for the formation and defense of territory boundaries, the distribution of the opposite sex has generally been regarded as a function of either mate or habitat selection. Nest construction for many bird species, however, represents a secondary site selection by females and may be influenced by the presence of conspecifics independently of male preference. Multiple passerine species have been shown to preferentially place nests along territory boundaries. We hypothesize that such placement may increase opportunities for extrapair copulations, increase the benefits of group nest defense, or increase proximity to preferred habitat that is contested by multiple territorial males. We tested these three hypotheses on two subspecies of the swamp sparrow: the tidal-salt-marsh endemic, coastal plain swamp sparrow (*Melospiza georgiana nigrescens*), and the nominate inland subspecies (*M. g. georgiana*). Nests of both subspecies were placed significantly closer to territory boundaries than random points. Furthermore, nests were built significantly closer than random to both the centers of the nearest four territories and the nearest four neighboring nests that were active the previous year (a measure of habitat preference controlling for conspecific effects). Nests were randomly placed, however, in reference to the nearest four neighboring nests that were active during the same time period. The mean distance between nests and neighboring territory centers was the best predictor of the proximity of nests to their own territory boundary. Furthermore, this pattern was quadratic, making nests placed near territory boundaries closer or further than random from the nearest four neighboring males. Avoidance or proximity may change

depending on the quality of the social mate relative to nearby males. Habitat preference, although important, did not explain nest placement near territory boundaries.

INTRODUCTION

In many species conspecific attraction determines settlement and helps explain species distributions at some scales (Stamps 1988; Smith and Peacock 1990; Reed and Dobson 1993). In territorial species where territory establishment and defense is carried out primarily by a single sex, opportunities for conspecific effects on the opposite sex may be limited. Furthermore, in socially monogamous species that exhibit mixed reproductive strategies, conspecific attraction may benefit one sex at the expense of the other. Females, for example, may maximize their chances for extra-pair copulations by increasing proximity to multiple males, whereas paired males lose paternity under these circumstances (Stutchbury et al. 1994; Langefors et al. 1998; Dickinson 2001; Tobias and Seddon 2002; Mennill et al. 2004; Woolfenden et al. 2005).

Although nest-site selection has historically been regarded as a function of habitat quality (Danchin and Wagner 1997; Martin 1998), nest placement may be viewed as a secondary settlement within the territory, when females are solely responsible for nest construction. Females may then be subject to conspecific effects at this scale as much as males at a larger scale during territory establishment. In a number of songbirds, females disproportionately build nests near territory boundaries (*Limnothlypis swainsonii*: Griscom and Sprunt 1979; *Spizella pallida*: Knapton 1979; *Melospiza georgiana*: Mowbray 1997; and *Poecile atricapillus*: Ramsay et al. 1999). This pattern may be explained by the conspecific attraction of females to neighboring males in order to gain extra-pair matings (Hoi and HoiLeitner 1997; Ramsay et al. 1999; Westneat and Mays 2005). Alternatively, nests may be grouped near territory boundaries due to the partitioning of a high-quality habitat patch among multiple territorial males (Weidinger 2004; Davis 2005) or as a result of conspecific attraction to other nesting females to gain benefits of group nest defense (Post 1998; Picman et al. 2002).

We tested these three hypotheses of nest-site selection (attraction by females to males, habitat, or other females) in two subspecies of the swamp sparrow: the salt-marsh

endemic, coastal plain swamp sparrow (*Melospiza georgiana nigrescens*), and the inland, nominate subspecies (*M. g. georgiana*). Male swamp sparrows arrive before females on the breeding grounds and establish territories prior to pairing (Mowbray 1997). Previous research suggests that swamp sparrows tend to place their nests near territory boundaries (Mowbray 1997) and that all three hypotheses may play a role in female site selection. An investigation on the same populations as this study showed that 41.6% of broods (20.9% of all young) contained offspring sired by males outside the social pair (Chapter 4), suggesting that extrapair mating plays an important role in the swamp sparrow system. Proximity to neighboring males during the nest-building and egg-laying periods, while females are fertile, may affect a female's ability to obtain extrapair copulations (Westneat and Mays 2005). Additionally, female swamp sparrow quality is correlated with habitat attributes that predict nest success (Chapter 2), suggesting that females actively select nesting habitat during pair formation and presumably do so during nest-site selection as well. Finally, swamp sparrow pairs respond strongly to the distress calls of neighbors, especially when they possess active nests (Stefanski and Falls 1972), and exhibit group nest defense when active nests are near one another. Furthermore, females utter a distinctive series of call notes when departing nests (McDonald and Greenberg 1991). Grouped nests may both increase the benefits of communal nest defense and decrease the signal to noise ratio in these nest-departure calls, thereby diffusing the danger they pose as nest detection mechanisms for potential predators.

We predicted that if females select nest sites based on proximity to neighboring males, the proximity of their nests to their own territory boundary would be best explained by the distance to neighboring territories. Alternatively, under the female attraction hypothesis the proximity of nests to their own territory boundary would be best predicted by their proximity to other active nest sites. If habitat quality explains territory boundary proximity, we predicted that the distance to nests from the previous year should best explain boundary proximity, since vegetation is relative constant between years while territory boundaries are not (B. Olsen, unpub. data).

METHODS

Study Site & Territory Measurements

To study the coastal subspecies we established two ~15ha plots in *Spartina* marsh along the Smyrna River near its junction with the Delaware Bay. We monitored one plot for four complete breeding seasons (1 May – 31 Aug, 2002-2005) and the second for three seasons (2003-2005). During the last two seasons of this study (2004-2005), we examined two parallel plots 350km inland at similar latitude (inland = 39.6°N, coastal = 39.4°N) and 800m higher in elevation in cranberry fens on the Allegheny Plateau. We captured adult swamp sparrows and banded them with a numbered aluminum band and a unique combination of colored bands for later visual identification. Territories were delineated by minimum convex polygons surrounding midseason male song posts. We believe we located all nesting attempts that survived beyond a few days using the nest-departure call, which is easily detected by human observers (Greenberg 2003) and always used by females leaving the nest.

Distance Measurements

All spatial measurements were calculated using ArcGIS 8.3 (ESRI 2002). To determine whether nests were grouped along territory boundaries, we measured the distance from each nest location to both the geometric center of the territory (the centroid of the minimum convex polygon) and its nearest territory boundary. As a preliminary test of our methods, we placed 11,000 random points in 34 randomly selected territories (20 coastal, 14 inland). The mean distance from random points to the centroid was significantly greater than the mean distance from random points to the territory boundary ($n = 34$, $F_{1,32} = 166.4$, $r^2 = 0.84$, $P < 0.0001$), and the relationship was described by a simple linear relationship (distance to centroid = $2.0 + 2.2 * [\text{distance to boundary}]$). We therefore defined ‘boundary proximity’ as the distance from each nest to its territory centroid minus ($2.2 * \text{distance to territory boundary} + 2.0$).

To test for conspecific attraction to males, we compared the distance from both the geometric center of the territory and each nest attempt to the nearest four territory centroids. Preliminary analysis showed that the mean distance from random points

within territories to a point outside the territory was nearly perfectly predicted by the distance from the centroid to the same point outside the territory ($F > 50,000$, $r^2 > 0.99$, $P < 0.0001$) where $\beta_1 = 0.99$.

For conspecific attraction to females, we compared the distances from each nest to the four nearest active nests and the distance from each centroid to the same four nests. We defined 'active nests' as those that were building, incubating or brooding chicks less than three days of age (all periods of the nesting cycle during which the female gives the nest-departure call) while the focal nest was being built. For nests that were not found during the building phase, building dates were assigned as the day prior to egg laying, assuming that females laid a single egg each day until clutch completion (Mowbray 1997) and incubated eggs for 11 (coastal) or 12 (inland) days until hatch (Chapter 3).

To test for the effect of female habitat preference on boundary proximity, we compared the distance from each nest to the nearest four nests that were active (see definition above) during the same period in the previous year, thereby removing conspecific effects. Vegetation and standing water characteristics were consistent between years (B. Olsen unpub. data). To control for the limiting effect of territory boundaries on female nest-site options, we determined which territory from the previous year would have contained each nest and excluded all previous year nests from that territory. Furthermore, as marsh vegetation changes dramatically over the length of the breeding season, we only used nesting attempts that were active during the same time period (using the same definition as the within year comparison) to control for temporal shifts in habitat suitability. Nests that were farther than 200m on average from either the nearest four territory centers, active nests, or active nests from the previous year were discarded from analysis, as these females are unlikely to gain any advantage from boundary proximity based on the three hypotheses we tested.

Statistical Analysis

All statistical analyses were carried out using SAS 9.1.3 (SAS Institute 2005) and all data met assumptions of normality and homogeneity of variance. We ran paired t-tests for each distance-comparison pair (nest to centroid versus $2.0 + 2.2 \times$ nest to territory boundary, nest versus centroid to nearest territories, nest versus centroid to nearest active

nests, and nest versus centroid to nearest active nests from the previous year) subsampling nesting attempts within territories to test for random nest placement in comparison to territory boundaries, neighboring males, neighboring nesting females, and preferred habitat patches respectively. We adjusted alpha *a priori* to 0.0125 based on a Bonferroni correction (Bonferroni 1936).

To determine which orientations (towards males, females, or habitat) play the strongest role in determining boundary proximity, we used a repeated-measures analysis of covariance, covarying the nested effect of site within subspecies and subsampling nesting attempts within territories. We selected our final model(s) using AIC_C values, considering models with $\Delta AIC_C > 2.0$ as different. Candidate predictors of boundary proximity ($2.0 + 2.2 \times \text{distance from nest to territory boundary} - \text{distance from nest to territory center}$) included all distance measures that were significantly different from random. All means reported in the text are $\pm 95\%$ confidence interval.

RESULTS

We measured 189 nests (142 coastal, 47 inland) in 125 territories (76 coastal, 46 inland) over the three year-pairs (2002-2003, 2003-2004, 2004-2005). As observed in other swamp sparrow populations (Mowbray 1997), nests on our study site were non-randomly distributed within the territory ($n = 125$, $t_{1,124} = 7.0$, $P < 0.0001$) and located 43% closer to the territory boundary than random points on average ($3.6 \pm 0.6\text{m}$ vs. $6.4 \pm 0.5\text{m}$). Nests were also significantly closer than the geometric average to the nearest four neighboring male territories ($n = 125$, $t_{1,124} = -3.3$, $P = 0.001$; Fig. 6.1) and the nearest four active nests from the previous year ($n = 125$, $t_{1,124} = -8.2$, $P < 0.0001$; Fig. 6.2). Nests were not, however, built in locations that differed significantly from random relative to the locations of the nearest four active nests from the current year ($n = 125$, $t_{1,124} = -1.5$, $P = 0.14$; Fig. 6.1).

The best model predicting boundary proximity included a quadratic relationship with male proximity ($n = 120$, $F_{3,117} = 16.1$, $r^2 = 0.21$, $P < 0.0001$; Fig. 6.3) using only the square of male proximity ($n = 120$, $F_{1,68} = 47.1$, $P < 0.0001$). This model was equivalent ($\Delta AIC_C = 1.2$; Table 6.1) to the model with the linear term for male proximity

added ($n = 120$, $F_{1,67} = 0.8$, $P = 0.36$). Explanatory power was significantly reduced ($\Delta AIC_C = 3.8$: Table 6.1) by the addition of habitat proximity ($n = 120$, $F_{1,67} = 0.5$, $P = 0.49$: Fig. 6.4), and there was no effect of subspecies alone ($n = 120$, $F_{1,117} = 0.2$, $P = 0.70$).

DISCUSSION

Within the constraints of territory boundaries, female swamp sparrows built nests that were significantly closer to both neighboring males and nests from the previous year. This reflects the important roles of both conspecific attraction and habitat quality, respectively, in female behavior. Despite the nonrandom distribution of nests relative to preferred habitat, the proximity of nests to their own territory boundary was best predicted by proximity to neighboring males and was unrelated to the location of previously used habitat. Although results from this and other studies of these populations indicate that habitat preference plays an important role in nest-site selection (Chapter 2), preferred habitat patches are likely large enough or plentiful enough that suitable patches are not clumped solely along territory boundaries. Furthermore, territory boundaries are likely unstable enough between years (while habitat is relatively stable) that females cannot use territory edges as a reliable predictor of habitat quality.

The systematic preference for nest sites along territory boundaries, however, can be explained by female preference for proximity to neighboring males. This result was also found in another cup-nesting marsh species (Westneat and Mays 2005) and in two studies of black-capped chickadees (Ramsay et al. 1999; Mennill et al. 2004), which are weakly excavating cavity nesters and arguably more restricted by nest-site availability. These results suggest that female nest-site selection may reflect extrapair, conspecific attraction, hampered at least in part by restrictions due to the social male's territoriality. Occasional shifts in male territory boundaries as a result of female nest construction support this claim (Ellis 1980; B. Olsen, pers. obs) and attest to differences in male and female preference.

Nest placement in proximity to multiple males has been suggested to be a mechanism for attaining extra-pair fertilizations (Hoi and HoiLeitner 1997; Ramsay et al.

1999), a possibility supported by some studies of territorial passerines (Westneat and Mays 2005; but for exception see Mennill et al. 2004). The nest-departure call of our focal species may make nest building, egg-laying, and incubation behavior even more detectable by neighboring males than in other species, thereby increasing the probability that nest location is an important predictor of extrapair matings for swamp sparrows.

The U-shaped relationship between territory boundary and neighboring male proximity (with a minimum centered on zero) suggests that female swamp sparrows follow two strategies, building nests near territory boundaries to avoid or increase neighboring male proximity. Since we used distance to the nearest four territories, nest placement along territory edges can either increase or decrease the mean distance to neighboring males relative to central or random nest placement. This is especially true in small groups of territories or in edge territories. The advantages of extrapair fertilizations for a given female can vary with the relative quality of social mates compared to territory neighbors (Lanfords et al. 1998; Sheldon and Ellegren 1999; Václav et al. 2003; Olendorf et al. 2004; Fishman and Stone 2006; Chapter 4). Therefore if neighboring males intrude to gain extrapair copulations and their success is dependent to some degree on the distance they must intrude, we would expect females to place nests near neighbors when they are, on average, of higher quality than their social mate, and away from neighbors when the opposite is true. This behavioral strategy affects female proximity to candidate mates during the nest-building and egg-laying stages, which overlap with their fertile period and, among swamp sparrows and some other marsh-nesting passerines (McDonald and Greenberg 1991), include easily detectable behaviors.

FIGURES

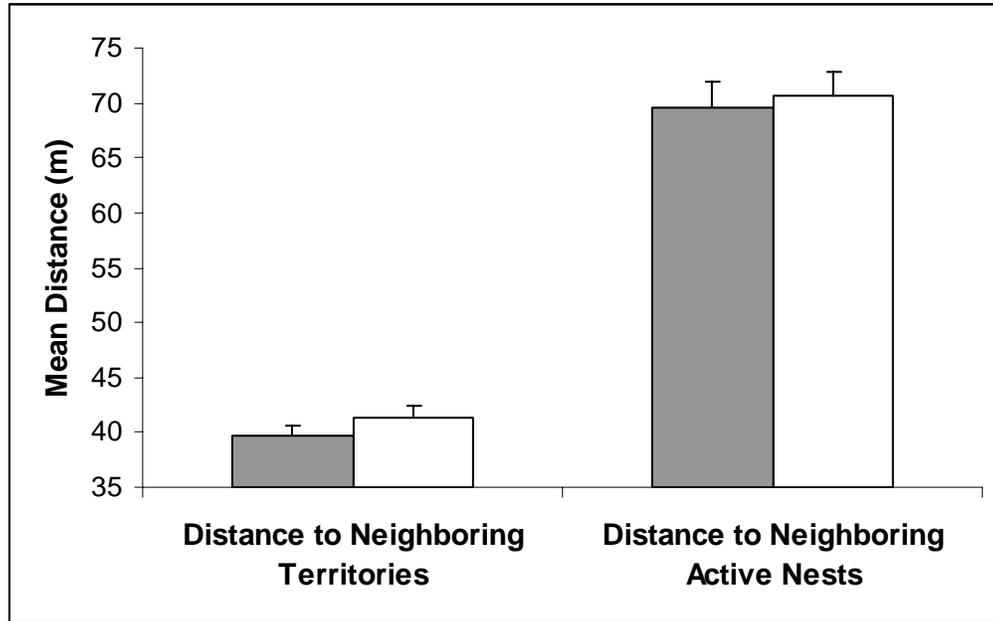


Figure 6.1. Nest position relative to neighboring territories and active nests

The mean distance (\pm SE) from nests (gray bars) and centroids of minimum convex polygon territories (white bars) to either the four nearest territorial males or the nearest four active nests.

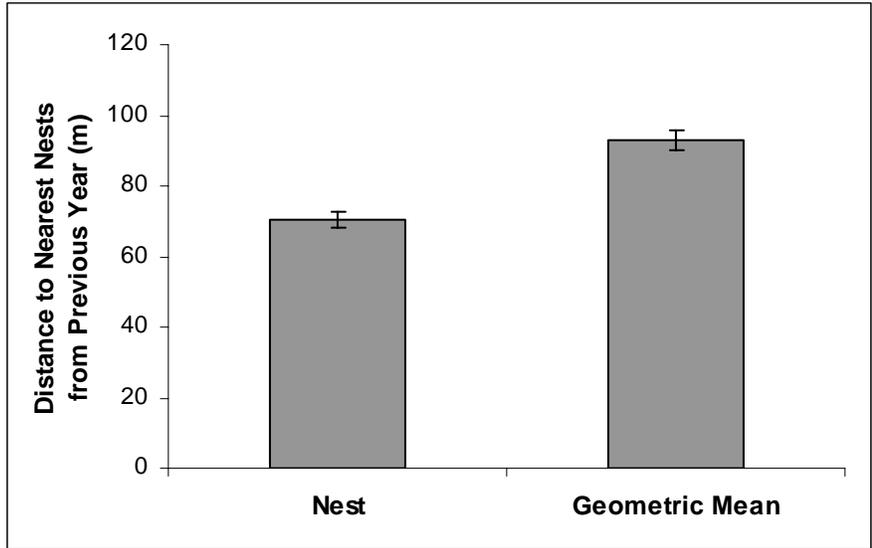


Figure 6.2. Nest distributions relative to nests from the previous year

The mean distance (\pm SE) from nests and territory centroids to the four closest nests that were active during similar calendar days in the previous year.

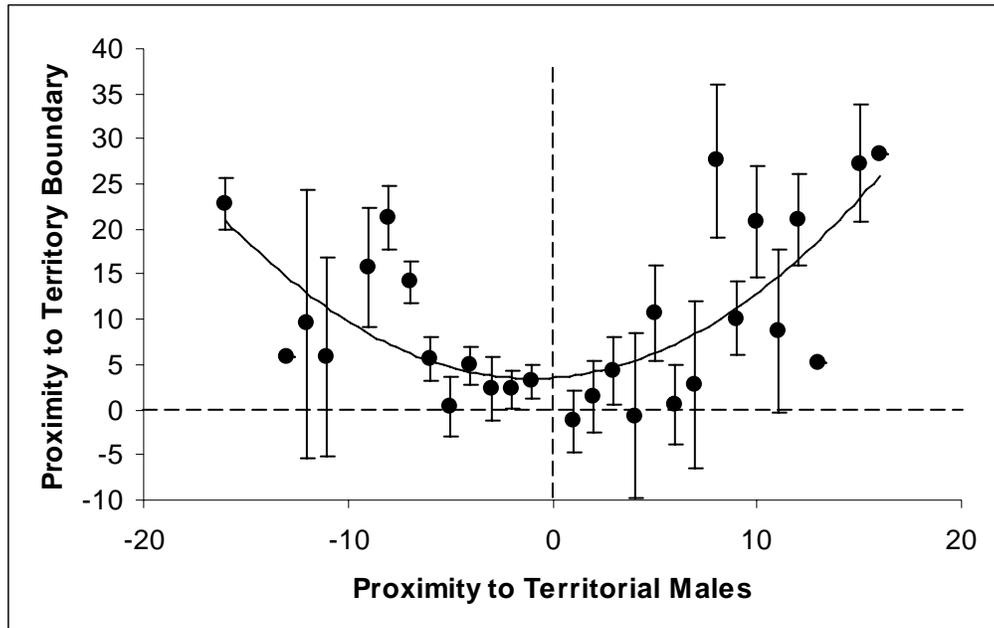


Figure 6.3. Nest proximity to territory boundaries versus neighbor males
 The mean (\pm SE) proximity of nests to territory boundaries (the distance from each nest to the territory center $- 2.2 \times$ the distance to the territory boundary $+ 2$) taken over each meter of the nest's proximity to the nearest four territorial males (the distance from the territory center to the nearest four territories $-$ the distance from each nest to the nearest four territories). Higher values of both measures indicate greater proximity to either the territory boundary or the nearest territorial males. The dashed lines indicate randomly distributed nests in relation to neighboring males (vertical) or territory boundaries (horizontal).

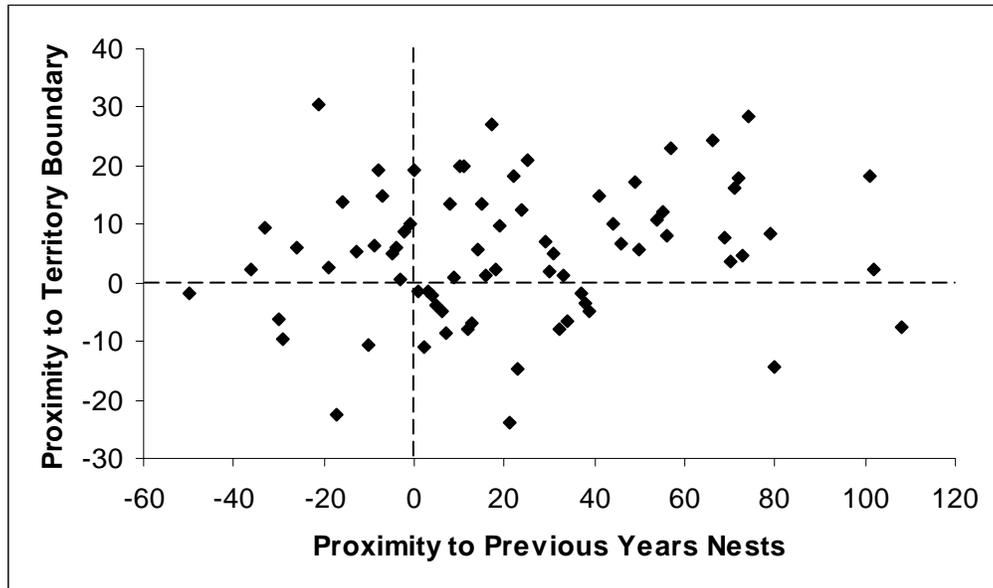


Figure 6.4. Nest proximity to territory boundary versus nests from the previous year

The mean proximity of nests to territory boundaries (the distance from each nest to the territory center $- 2.2 \times$ the distance to the territory boundary $+ 2$) taken over each meter of the nest's proximity to the nearest four nests that were active during similar calendar days the previous year (the distance from the territory center to the nearest four nests $-$ the distance from each nest to the nearest four nests). Higher values of both measures indicate greater proximity to either the territory boundary or the nearest nests. The dashed lines indicate randomly distributed nests in relation to either the territory boundary (horizontal line) or the previous year's nests (vertical line).

TABLES

Table 6.1. ΔAIC_C Values

ΔAIC_C values for all tested models. The final selected models are above the dashed line.

Model	ΔAIC_C	Cumulative ΔAIC_C
subspecies(site) + male proximity ²	0.0	0.0
subspecies(site) + male proximity + male proximity ²	1.2	1.2
subspecies(site) + male proximity ² + habitat proximity	3.8	5.0
subspecies(site) + male proximity + male proximity ² + habitat proximity	1.1	6.1
subspecies(site)	28.9	35.0
subspecies(site) + male proximity	0.9	35.9
subspecies(site) + habitat proximity	4.3	40.2
subspecies(site) + male proximity + habitat proximity	0.9	41.1

CHAPTER VII:

CONCLUSIONS

Adaptation to local environments via natural selection is a powerful mechanism for population divergence and likely one of the primary causes of speciation. To understand how specific habitats may shape local adaptation, it is helpful to study closely-related populations from widely differing ecosystems that have not had sufficient time to diverge by other means (such as genetic drift). Throughout the previous chapters I have tested for phenotypic divergence between two subspecies of the swamp sparrow due to the environmental challenges of the tidal salt marsh. It is important, however, to bear in mind that differences between the two subspecies are likely to have been shaped by three forces, namely natural selection, sexual selection, and phenotypic plasticity. Divergence in the salt marsh has occurred along three interdependent phenotypic axes (demography, behavior, and morphology) due to three separate environmental conditions: water characteristics, climate, and predation pressure (Fig. 7.1).

The phenotypic differences between coastal and inland sparrows due to coastal marsh waters are selected by the forces of salinity and tides. Salinity is negatively related to nestling growth and as such is an important cue for territorial establishment by male coastal plain swamp sparrows (Chapter 2). The wide range of salinity values found within coastal swamp sparrow habitat (0-15 parts per thousand: Beadell et al. 2003) likely increases habitat heterogeneity, which may explain both the increased size of the average coastal territory ($\mu \pm SE$; coastal: 0.21 ± 0.02 ha; inland: 0.10 ± 0.01 ha) and the increase in male territorial aggression (Chapter 5), although the rates of extrapair fertilizations (Chapter 4) give no indication that the mating system has crossed the polygyny threshold (Verner and Willson 1966; Orians 1969).

Tides likely have had similar influences. Although tides can cause nest failure there is evidence that the loss may be compensatory (Greenberg et al. 2006b), and the low prevalence of flooding among coastal swamp sparrow nests (Greenberg et al. 2006b; Etterson et al. *In Press*) is likely matched by spring storm events that flood those inland (Wetherbee 1968; Ellis 1980; Greenberg 1988b). Therefore, there are likely three main

influences of tides. First, tides periodically cover foraging substrate and eliminate potential nesting locations in low areas, thereby increasing habitat heterogeneity across the marsh and likely increasing territory size, male territorial aggression, and the plumage badges signaling that behavior (Chapter 5).

Second, tides, combined with salinity levels, eliminate the reliability of water depth as an adequate cue for habitat quality. Water level fluctuations follow daily, monthly, and seasonal cycles in addition to unpredictable storm surges that can dramatically increase water depth. Standing water, an important habitat cue for inland swamp sparrows (Reinert and Golet 1979; Greenberg 1988b, 1992), can be fresh at upland edges, brackish in lower marsh, and even hypersaline in pools that are inundated infrequently by tides. Vegetation is thus a more reliable indicator of both average water depth and salinity for a given microhabitat (Bertness et al. 2002). This pattern may explain why coastal birds are more reliant on vegetative cues for settling than on water depth (Chapter 2).

Lastly water in the upper marsh retreats during the lowest tides, leaving the majority of ground with little, if any, standing water. Standing water is an important guard against predation in many wetland birds (Picman et al. 1993) and the lack of standing water across the marsh may be partially responsible for both the increased nest predation rate and the preference among coastal males for territories with *Schoenoplectus americanus* (Chapter 2), where muskrat tunneling makes standing water more common.

Increased nest predation, whatever its cause, has been a strong selective force among coastal sparrows, favoring local divergence in the reproductive biology and demography of coastal sparrows relative to inland birds. Nesting coastal females follow a bet-hedging strategy in clutch formation (Chapter 3), laying smaller clutches in multiple nests in the face of high failure risk (yearly Mayfield success estimates as low as 18%). Furthermore, hatching occurs a day sooner on average among coastal young, and fledging events are more synchronized within clutches (Chapter 3), both adaptations that decrease a nest's exposure to predation. Coastal birds also provision young less often and show increased aversion to feeding young in the presence of a nest predator relative to inland adults (Chapter 3), which suggests that coastal adults decrease the level of activity around predation-prone nests. Additionally, coastal males show higher levels of territory

vigilance throughout the incubation period relative to inland males (Chapter 5), suggesting yet another behavioral adaptation to high predation risk. This increased territorial vigilance, although independent of crown characteristics, may have played a role in the increased territorial aggression of coastal males (Chapter 5).

The climate of the mid-Atlantic coast has also led to phenotypic changes in coastal birds relative to their inland counterparts. High ambient temperatures during clutch formation explain additional variance in the degree of fledging synchrony and both the decreased clutch size and decreased egg viability of coastal birds (Chapter 3). The longer frost-free season of the mid-Atlantic also allows for a longer breeding season (active nests from the first week of May to the first week of September). Despite this increased length and the numerous nesting attempts it contains (as many as six), however, coastal females produce 40% fewer fledglings per season than inland birds.

Multiple nesting attempts, therefore, appear to be crucial to increasing the chance of producing offspring, and coastal sparrows exhibit a number of behavioral adaptations that decrease the time between attempts. Females occasionally reuse nests from previous attempts (even those that were previously unsuccessful), and males often take over care of recently fledged young while females begin incubating the next clutch. These behavioral adaptations have also evolved in a number of high latitude (Kovshar 1981; Badyaev 1987) and high elevation (Badyaev 1997) passerines. The large effect of nest predation in the tidal salt marsh thus likely negates the advantages of a long breeding season, leading coastal birds to appear constrained by season length instead of benefiting from it.

The behavioral changes in coastal males that have occurred due to these three environmental attributes are largely the result of sexual selection through both male-male competition for the increasingly heterogeneous habitat and female choice (Chapter 5). It is clear that male crown color represents individual quality on two axes (Chapters 2, 4, 5), with the size of rusty patches indicating male parental care and the size of the black crown patches indicating territorial aggression (Chapter 5). As such, the increased advantages of territorial aggression in coastal habitats relative to inland wetlands have altered both the behavioral states of male sparrows and the plumage signals that represent those behaviors, thereby increasing the degree of crown eumelanization. Direct female

mate choice for male parental care, however, has maintained the importance of the rusty crown, leaving an interesting plumage signal that represents the relative strength of direct female choice versus male-male competition in this system and a tradeoff between rust and black-colored feathers in coastal males similar to the behavior tradeoff between aggressive and parental behavioral states found in many other bird species (Wingfield et al. 1987; Ketterson et al. 1992; Stoehr and Hill 2000; Duckworth 2006).

Natural selection on the body plumage of both sexes and the crown coloration of females, however, has increased the proportion of eumelanins and caused coastal plain swamp sparrows overall to show the same pattern of salt marsh melanization possessed by numerous other tidal marsh vertebrates (Greenberg 1990). The strong natural selection on female crowns, coupled with the strong sexual selection on rusty male caps has increased the degree of sexual dichromatism within the coastal subspecies (Chapter 5). Overall plumage color itself is thus an excellent representation of the various selective forces at work on this sparrow.

By investigating the distribution of the aforementioned phenotypes within each population, I have determined that change has occurred in two ways. First, some relationships between phenotypic distributions and their underlying environmental conditions have shifted such that similar conditions produce different results (i.e. in hatching synchrony, feeding latency, and male quality effects on offspring production). Alternatively, other such relationships between the environment (either social or abiotic) and phenotype have remained the same between the inland and coastal populations (i.e. apparent incubation length, temperature on clutch size, male quality effects on parental care and territorial aggression); although different conditions among the marshes have resulted in different population means of these characteristics. Other phenotypes (i.e. extra-pair fertilization rate) have remained the same between the populations, indicating either identical underlying social or environment conditions or simply phylogenetic inertia.

Inter-frost time, daily temperature means, predation risk, tides, and salinity have all played strong roles in the divergence of coastal plain swamp sparrows from their freshwater ancestors (Fig. 7.1). Many of these divergent mechanisms may be similar among multiple tidal marsh endemics, although some (especially those related to sexual

selection) may be specific to the swamp sparrow. In general, however, we see that the added environmental challenges of tidal ecosystems strongly alter selection regimes on a terrestrial vertebrate inhabiting this dynamic ecotone. The swamp sparrow system can therefore increase our understanding of how the interplay between environmental resources, sexual selection, and natural selection affects the local adaptations leading to evolutionary divergence.

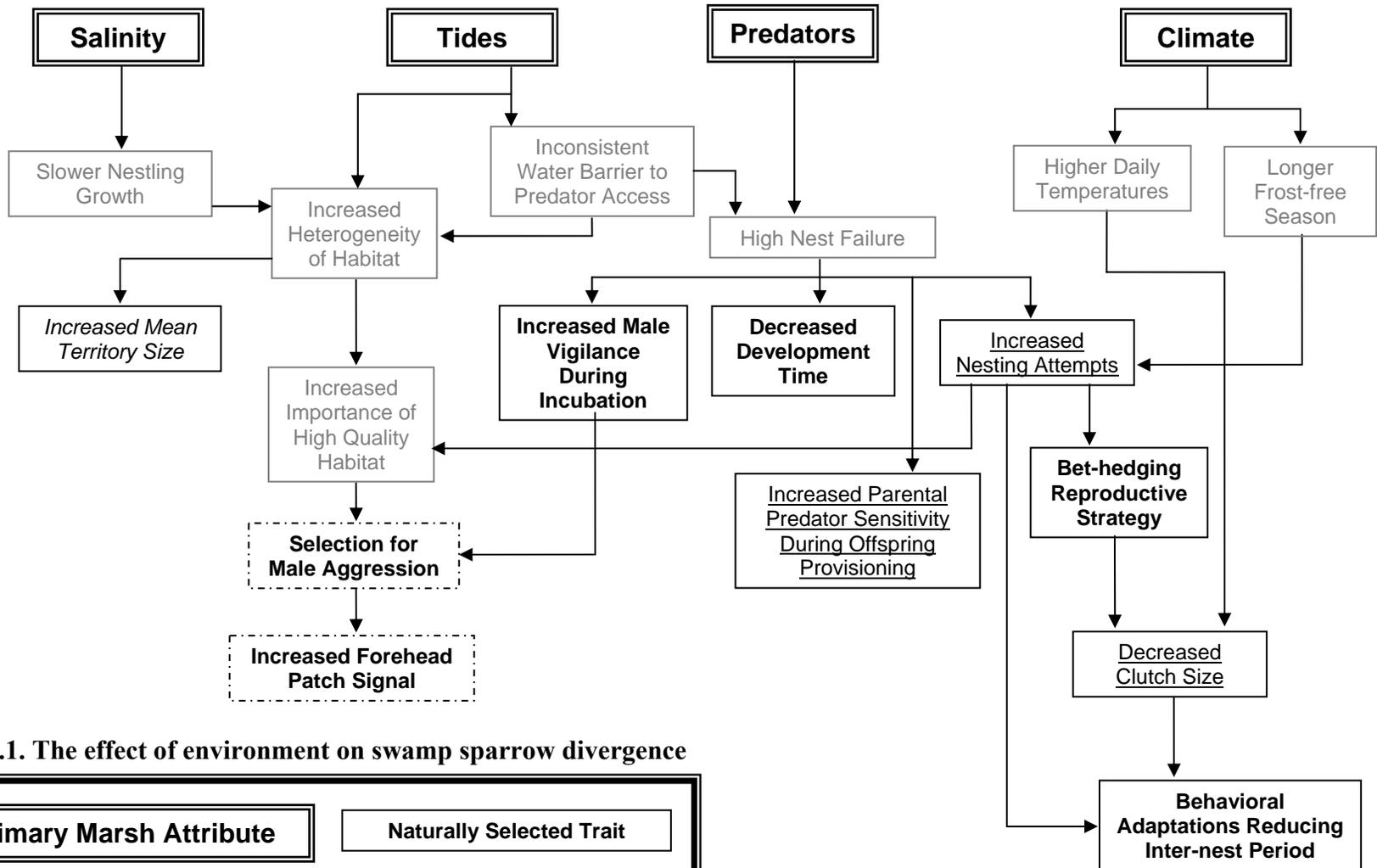
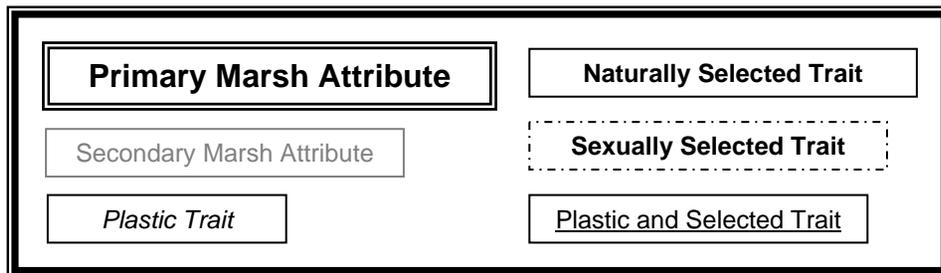


Figure 7.1. The effect of environment on swamp sparrow divergence



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