AVIAN NESTING RESPONSE TO TIDAL-MARSH FLOODING: LITERATURE REVIEW AND A CASE FOR ADAPTATION IN THE RED-WINGED BLACKBIRD

STEVEN E. REINERT

Abstract. Throughout the coastal US, nests of birds breeding in saltmarshes are subject to periodic flooding by spring and storm tides. I found documentation of nest loss to tidal flooding for nine species of terrestrial saltmarsh birds and nine species of waterbirds. A review of adaptations to periodic tidal inundations in these species revealed four general categories of responses: (1) placement of nests such that they exceed the elevation of tides or float on the surface of rising flood-waters, (2) nest-repair and egg-retrieval behaviors that keep eggs in nests during and after floods, (3) rapid post-flood renesting which enables the nesting cycle to be completed just prior to the encroachment of the next flooding spring tide, and (4) timing of the breeding season to avoid periods of peak seasonal tidal amplitude. Adaptations were more advanced in species that had longer exposure to marine environments; they were most developed in colonially nesting gulls and terns for which substantive evidence indicates that environmental cues (peak high tides) are used to time and place nests such as to avoid tidal flooding. Nest repair behaviors during and following flood tides were most advanced in the Laughing Gull (*Larus atricilla*) and Clapper Rail (*Rallus longirostris*); rails generally exhibited more sophisticated post-flood responses than sparrows. To determine how a population of Red-winged Blackbirds (*Agelaius phoeniceus*) nesting in a saltmarsh in Rhode Island responded to monthly spring-tide flooding events, I studied the population during 1982–1985. Spring tides destroyed 34% of active nests, and overall nest success values were among the lowest reported for this widely studied species. Forty-four percent of successful nests were renesting attempts by females that lost early nests to tidal flooding and initiated a replacement nest within 48 hr. Females usually laid the first egg in the new nest 5 d following flooding, thus enabling young to fledge just prior to the encroachment of the next lunar flood tide 27–29 d later. My data demonstrate that salt-marsh nesting Red-winged Blackbirds employ responses to flooding similar to those exhibited by obligate *Ammodramus* sparrows, and suggest that the study population is representative of a larger population of saltmarsh inhabiting Red-winged Blackbirds that is ecologically isolated from regional populations nesting in non-tidal habitats.

Key Words: adaptations, *Agelaius phoeniceus*, *Ammodramus*, *Larus*, *Melospiza melodia*, nest survival, *Rallus longirostris*, reproductive success, saltmarsh, *Sterna*, tidal flooding.

RESPUESTAS DE ANIDACIÓN DE AVES A LA INUNDACIÓN DE MARISMAS DE MAREA: REVISIÓN BIBLIOGRÁFICA Y UN CASO PARA ADAPTACIÓN DEL MIRLO DE ALAS ROJAS

Resumen. Por toda la costa de los EU nidos de aves reproductoras en marismas saladas están sujetas a inundaciones periódicas por manantiales y mareas de tormenta. Encontré documentación de pérdida de nidos por inundaciones de marea para nueve especies de aves terrestres de marisma salada y nueve especies de aves acuáticas. Una revisión de las adaptaciones a las inundaciones periódicas de marea en estas especies, revelaron cuatro categorías generales de respuestas: (1) la colocación de nidos en la cual ellos rebasaron la elevación de las mareas o flotaron en la superficie de torrentes de agua emergiendo, (2) reparación de nido y comportamientos de recuperación de huevos que mantienen los huevos en los nidos durante y después de las inundaciones, (3) veloz reanidación de postinundación, la cual permite que el ciclo de anidación sea completado justo antes de la ocupación de la siguiente inundación por la marea, y (4) el tiempo en el que transcurre la época de reproducción para evitar periodos de estación de mareas de amplitud más alta. Las adaptaciones fueron más avanzadas en las especies que estaban mas expuestas a ambientes marinos; ellas eran mas desarrolladas en anidaciones coloniales de gaviotas y charranes, para las cuales evidencia sustancial indica que señales del medio ambiente (el punto mas alto de mareas altas) son utilizadas en tiempo para colocar nidos, como para evitar inundaciones de marea. Comportamientos de reparación de nido durante y seguido de las inundaciones de marea, fueron mas avanzadas en la Gaviota Reidora (*Larus atricilla*) y el Rascón (*Rallus longirostris*); los rascones generalmente mostraron respuestas pos-inundación más sofisticadas que los gorriones. Para determinar como una población de Mirlos de Alas Rojas (*Agelaius phoeniceus*) anidando en un marisma salada en la Isla de Rhode respondió a eventos mensuales de inundaciones de marea, estudié la población durante 1982–1985. Las mareas de muelle destruyeron el 34% de los nidos activos, y sobre todos los valores de nidos exitosos se encontró el más bajo reportado por esta especie ampliamente estudiada. Cuarenta y cuatro por ciento de nidos exitosos fueron intentos de reanidación por hembras que perdieron nidos antes de las inundaciones por marea e iniciaron un reemplazo de nido dentro de 48 horas. Las hembras usualmente ponen su primer huevo en el

nuevo nido 5 d en seguida de la inundación, permitiendo así que los juveniles emplumen justo antes de la invasión de la siguiente inundación de marea lunar 27–29 d después. Mis datos demuestran que los Mirlos de Alas Rojas de marisma salada en anidación, emplean respuestas similares a las inundaciones a aquellas exhibidas por *Ammodramus* gorriones, y sugieren que la población de estudio es representativa de una población mayor de habitantes Mirlos de Alas Rojas de marisma salada, la cual esta ecológicamente aislada de poblaciones regionales anidando en habitats de no marea.

Despite their intrinsic productivity and proximity to productive estuarine marine systems, tidal marshes provide nesting habitat for relatively few species of birds (Greenberg and Maldonado, *this volume*). Flooding, both lunar-driven tidal inundations (spring tides), and less predictable storm-driven events, may constitute a primary reason for the lack of diversity of tidal marsh breeders. Flooding events regularly inundate and destroy nests of all breeding species on a given saltmarsh (Kale 1965, Burger 1979, DeRagon 1988, Marshall and Reinert 1990, Shriver 2002). Nest loss to tidal flooding has been documented for at least nine species of terrestrial saltmarsh birds and nine species of shorebirds, waterfowl, and colonial waterbirds (Table 1). The constant threat of inundation combined with pressures from nest-robbing aerial predators such as crows (*Corvus* spp.) and grackles (*Quiscalus* spp.) presents a paradox for terrestrial breeding species—how to place their nests as high as possible to minimize flooding risks, while providing adequate vegetative cover over nests in herbaceous plant communities that are short (<1 m) in stature (Johnston 1956a, Post et al. 1983). Further, the risks of flooding for all coastal nesting birds may be heightened in future decades due to increasing rates of surface flooding from rising sea levels (Shriver 2002; Erwin et al., *this volume*).

For the few terrestrial vertebrate species that have evolved as saltmarsh specialists, and that therefore must regularly negotiate flooded habitats, the payoff is an environment featuring minimal interspecific competition (Post et al. 1983, Powell and Collier 1998) and an abundance of animal and plant food resources. Indeed, Post and Greenlaw (1982) determined that a single female Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*), raising her young with no assistance from males, matched the reproductive output of a pair of Seaside Sparrows (*Ammodramus maritimus*) with no apparent cost to her survivorship. Post and Greenlaw (1982) concluded that food was not limiting for either species, and, that in saltmarshes, events such as floods could be the principal factors in checking population levels. Post et al. (1983) also concluded, based on abundance of seeds and invertebrate animals, and lack of competition from other terrestrial bird species, that food was not limiting to Seaside Sparrows

on their breeding marshes on Long Island, New York, and in a Florida Gulf Coast site.

A further advantage of nesting on the saltmarsh may be a relatively low incidence of nest parasitism by cowbirds (*Molothrus* spp.). Parasitism of nests was rare for a saltmarsh nesting race of Song Sparrow (*Melospiza melodia samueli*) in San Francisco Bay, and Johnston (1956a) suggested that this could relate to cowbirds being unfamiliar with saltmarsh habitats. Nesting studies of Seaside Sparrows (Marshall and Reinert 1990), Saltmarsh Sharp-tailed Sparrows (DeRagon 1988), and Red-winged Blackbirds (*Agelaius phoeniceus*; this paper) in New England all found no incidents of cowbird parasitism (Greenberg et al., *this volume*).

Bird species that nest in the saltmarsh display an array of adaptive responses to tidal inundations that enable them to survive in the tidal environment and thus partake of the high food availability and potentially low nest parasitism rates. The responses fall into four categories: (1) placement of nests such that they exceed the elevation of tides or float on the surface of rising flood-waters, (2) nest-repair and egg-retrieval behaviors that keep eggs in nests during and after floods, combined with resumed incubation of eggs post immersion, (3) rapid post-flood renesting which enables the nesting cycle to be completed just prior to the encroachment of the next flooding spring tide, and (4) timing of the breeding season to avoid periods of peak seasonal tidal amplitude.

The first section of this paper reviews these responses in both terrestrial bird species, for which the marsh habitats constitute both the nesting and principle foraging grounds, and in colonial waterbirds which nest on the marshes but regularly forage in adjacent habitats. I then explore how adaptations to local tidal conditions can evolve in tidal-marsh populations of a nonspecialized species, the Red-winged Blackbird.

The Red-winged Blackbird is an abundant species nesting in freshwater wetland and upland habitats throughout North America (American Ornithologists' Union 1998). In the northeastern US, the Red-winged Blackbird commonly nests in the high-marsh zone of the saltmarsh in habitats dominated by smooth cordgrass (*Spartina alterniflora*). In conjunction with studies of Seaside and Saltmarsh Sharp-tailed sparrows (DeRagon 1988), I conducted a

TABLE 1. SALT MARSH BREEDING BIRDS THAT HAVE LOST NESTS TO TIDAL FLOODING.

Species	State(s)	Nesting habitat flooded	References
White Ibis (*Eudocimus albus*)	SC	Black needlerush (*Juncus roemarianus*)	Frederick 1987.
Mallard (*Anas platyrhynchos*)	NJ, RI	Smooth cordgrass (*Spartina alterniflora*), salt meadow cordgrass (*S. patens*)	Burger 1979, observation of author.
American Black Duck (*Anas rubripes*)	MA, RI	Smooth cordgrass	Observation of author.
Clapper Rail (*Rallus longirostris*)	CA, GA, MS, NJ, VG	Hairy gumweed (*Grindelia humilis*), smooth cordgrass, California cordgrass (*S. foliosa*), high marsh habitats	Kozicky and Schmidt 1949, Stewart 1951, Zucca 1954, Mangold 1974, Jackson 1983, Massey et al. 1984, Schwarzbach et al. 2006.
Virginia Rail (*Rallus limicola*)	NY	Smooth cordgrass	Post and Enders 1970.
Willet (*Catoptrophorus semipalmatus*)	not avail.	High-marsh habitats	Lowther et al. 2001.
Laughing Gull (*Larus atricilla*)	NJ	Smooth cordgrass, salt meadow cordgrass, often on mats rf debris	Bongiorno 1970; Montevecchi 1975, 1978; Burger 1979, Burger and Shisler 1980.
Herring Gull (*Larus argentatus*)	NJ	Smooth cordgrass, high-marsh habitats; some on mats of debris	Burger 1977, 1979.
Common Tern (*Sterna hirundo*)	NJ	Smooth cordgrass, high-marsh habitats, often on mats of debris	Burger and Lesser 1978, Storey 1978, Burger 1979, Buckley and Buckley 1982.
Forster's Tern (*Sterna forsteri*)	MD, VA	High-marsh habitats, often on mats of debris	Storey 1978.
Black Skimmer (*Rynchops niger*)	NJ	*Spartina* spp., often on mats of debris	Burger 1982.
Marsh Wren (*Cistotorus palustris*)	GA, RI	Smooth cordgrass	Kale 1965, observation of author.
Savannah Sparrow (*Passerculus sandwichensis*)	CA	Virginia glasswort (*Salicornia virginica*), bushy pickleweed (*S. subterminalis*)	A. Powell, pers. comm.
Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*)	ME	High-marsh habitats	Shriver 2002.
Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*)	ME, NJ, RI	High-marsh habitats	Woolfenden 1956, DeRagon 1988, DiQuinzio et al. 2002, Shriver 2002.
Seaside Sparrow (*Ammodramus maritimus*)	FL, MA, NJ, NY, RI,	Smooth cordgrass, high-marsh habitats	Woolfenden 1956, Greenlaw 1983, Post 1974, Post et al. 1983, Marshall and Reinert 1990.
Song Sparrow (*Melospiza melodia*)	CA	Woody saltwort (*Salicornia ambigua*)	Marshall 1948a, Johnston 1956a.
Red-winged Blackbird (*Agelaius phoeniceus*)	RI	Smooth cordgrass	Tilton 1987, this study.

4-yr study of the nesting ecology of Red-winged Blackbirds occupying a smooth cordgrass saltmarsh in Rhode Island to determine how this facultative nesting species responded to monthly spring tide flooding events. This work revealed life-history characteristics similar to those used by obligate Seaside and Saltmarsh Sharp-tailed sparrows in responding to monthly tidal inundations. Those traits and others relating to a compressed nesting cycle represent substantial deviations from Red-winged Blackbird behaviors in non-tidal habitats throughout the mid-latitudes of North America. The second section of this paper presents findings from my field research wherein I compare Red-winged Blackbird responses to flooding to those of other saltmarsh species, and suggest that Red-winged Blackbirds in coastal New England comprise an ecologically isolated population adapted to the saltmarsh environment.

ADAPTIVE RESPONSES TO TIDAL FLOODING IN SALTMARSH NESTING BIRDS

ADAPTATIONS TO TIDAL FLOODING IN COLONIAL WATERBIRDS

As aquatic specialists that have resided in coastal habitats since pre-Pleistocene times, colonially nesting larids of the Atlantic Coast would be expected to exhibit relatively sophisticated adaptations to the environmental extremes characteristic of marine habitats (Burger 1979, Frederick 1987). These ground-nesting species are extremely vulnerable to mammalian predation, and thus coastal saltmarsh islands, devoid of such predators, form their principal nesting habitat. The cost of this reduced predation risk is the frequent occurrence of wind- and storm-driven tidal-flooding events that have catastrophic effects on all nesting species. A single washout event can destroy all or most nests of all nesting species, including White Ibis (*Eudocimus albus*), Laughing Gull (*Larus atricilla*), Herring Gull (*Larus argentatus*), Common Tern (*Sterna hirundo*), Forster's Tern (*Sterna forsteri*), and Black Skimmer (*Rynchops niger*) (Storey 1978; Burger 1979, 1982; Frederick 1987).

A high degree of plasticity in reacting to the unstable environmental conditions of marine environments is the overriding factor relating to nest success (Bongiorno 1970, Storey 1978, Buckley and Buckley 1982). Observations of Laughing Gulls (Bongiorno 1970; Montevecchi 1975, 1978; Burger and Shisler 1980) and Common Terns (Storey 1978) indicate that those species assess peak tidal heights during the pre-laying period and use those cues to place nests at high elevations. Evidence presented by Bongiorno (1970) and Burger and Shisler (1980) suggest that Laughing Gulls use proximate cues of marsh-grass height and structure in selecting relatively high areas of islands for nest placement. Larids also achieve high-elevation nest sites by building tall nest structures, and by placing nests on elevated mats of marsh debris, usually wind-rows of dead eel grass (*Zostera*) and smooth cordgrass left on the marsh surface by winter storms. Placement on mats not only elevates the nests of gulls and terns, but when exceptionally high tides exceed their elevation, the mats float on the flood-waters leaving nests intact and dry. If the mat is not washed off the island, the nests atop them remain safe (Bongiorno 1970; Montevecchi 1975, 1978; Burger and Lesser 1978, Burger 1979, Storey 1978, Buckley and Buckley 1982). Common Tern nests built individually on relatively large platforms of dead vegetative material also floated safely, and adults remained in attendance regardless of their altered, post-flood location (Buckley and Buckley 1982). Montevecchi (1975) suggested that the ability to assess the timing of peak tides allows Laughing Gulls to synchronize their nesting with the onset of the lunar cycle.

Despite the array of flood avoidance strategies employed by colonial-nesting larids, storm and/or wind driven waters are often high and turbulent enough to damage nest structures, wash out eggs, float nest-supporting mats off island, and drown pipping eggs and recently hatched young. Eggs are especially vulnerable to floating off during washouts in later developmental stages, as their buoyancy increases during the course of incubation (Nol and Blokpoel 1983). The eggs of many species of saltmarsh birds—White Ibis, Clapper Rail (*Rallus longirostris*), Laughing and Herring gulls, Common Tern, Song Sparrow, and Red-winged Blackbird—can tolerate immersions of limited duration in salt water (Johnston 1956b, Burger 1979, Ward and Burger 1980, Frederick 1987). In controlled experiments, >60% of Laughing and Herring gull embryos, at varying stages of development survived to pipping after immersions of up to 120 min in salt water (Burger 1979, Ward and Burger 1980). Thus, post-inundation, larids employ several tactics to enable the continued development of remaining eggs: (1) repair of nests during and after floods to keep eggs above water and in the nest, (2) construction of nests around washed-out eggs, (3) incubation of eggs outside of the nest, and (4) retrieval of eggs back to the nest (Burger 1977, 1979; Burger and Lesser 1978, Buckley and Buckley 1982).

Renesting after nest loss is common among colonially nesting larids, and is sometimes

accompanied by colony relocation (Burger and Lesser 1978, Montevecchi 1978, Storer 1978, Buckley and Buckley 1982). Storey (1978) determined that the renesting response was especially well developed in Forster's Tern which (1) initiated nesting early enabling more seasonal nesting attempts, (2) initiated new clutches more quickly than Common Terns, thereby reducing risks from future flood events, and (3) produced relatively large second clutches. Storey considered those responses adaptations to the tidal environment.

REPRODUCTIVE SUCCESS AND FLOODING RESPONSES OF TERRESTRIAL SALTMARSH BIRDS

AMMODRAMUS SPARROWS OF THE EASTERN UNITED STATES

The Seaside Sparrow and Saltmarsh Sharp-tailed Sparrow are the only passerine species in the eastern US for which nesting activities are largely restricted to saltmarshes. Nests of Seaside Sparrows are typically placed in smooth cordgrass habitats (Woolfenden 1956, Greenlaw 1983, Post et al. 1983, Marshall and Reinert 1990), whereas Saltmarsh Sharp-tailed Sparrows (hereafter, saltmarsh sparrow) commonly place nests in stands or mixed communties of smooth cordgrass, saltmeadow cordgrass (*Spartina patens*), salt grass (*Distichlis spicata*), black needlerush (*Juncus gerardi*), and marsh elder (*Iva frutescens*) (Woolfenden 1956, DeRagon 1988, DiQuinzio et al. 2002, Shriver 2002). In Rhode Island, DeRagon (1988) demonstrated that saltmarsh sparrow nests elevated in the stems of smooth cordgrass plants achieved the same elevation as nests that were placed in higher areas of the marsh. Nests of saltmarsh sparrows in Rhode Island were most often covered above by tufts of saltmeadow cordgrass, salt grass, or black needlerush, while Seaside Sparrows wove canopies of smooth cordgrass leaves over their nests.

Flooding was a significant cause of nest mortality in all populations of these species studied in the northeast (Table 2). In a smooth cordgrass dominated saltmarsh on the Gulf Coast of Florida, some Seaside Sparrow nests were destroyed by flooding associated with storms, but most unsuccessful nests there were victims of rice rat (*Oryzomys palustris*) predation (Post et al. 1983). Flooding events that destroy sparrow nests in the marshes of southern Long Island occur when high tides are associated with storms or onshore winds; spring tides alone did not typically reach the elevation of nests (Post 1974, Post et al. 1983, Post and Greenlaw 1994).

TABLE 2. REPRODUCTIVE SUCCESS AND NEST MORTALITY FACTORS FOR SEASIDE AND SALTMARSH SHARP-TAILED SPARROWS IN THE NORTHEASTERN UNITED STATES.

Site	State	Years	N	Nest success[a]	Fledging probability[b]	Percent nest mortality			Reference
						Flood	Predation	Other	
Seaside Sparrow (*Ammodramus maritimus*)									
Long Island unaltered marshes	NY	1970–1971	>100	47[c]		36	10		Post 1974.
Long Island ditched marshes	NY	1970–1971	>15	66[c]		26	7		Post 1974.
Long Island	NY	1977–1978	144		0.35				Post et al. 1983.
Gulf hammock	FL	1979–1980	77		0.03	<50	>50		Post et al. 1983.
Allens Pond	MA	1984–1985	60	38	0.32	86	11	3	Marshall and Reinert 1990.
Saltmarsh Sharp-tailed Sparrow (*Ammodramus caudacutus*)									
100 Acre Cove	RI	1981–1982	172	59		63	11	7	DeRagon 1988.
Long Island	NY	1977–1978	238	47	0.12–0.37	28, 44[d]	38	16	Post and Greenlaw 1982.
Prudence Island	RI	1998	23	22		78	11		DiQuinzio 1999.

[a] Percent of nests fledging at least one young.
[b] Probability that an egg will produce a fledgling; calculated using method of Mayfield (1975).
[c] Percent of eggs that produced fledglings (nest success not reported).
[d] Percent failed nests lost to flooding for years 1977 and 1978, respectively.

In Rhode Island, spring-tide flooding accounted for less than half of saltmarsh sparrow nest mortality events in marshes with restricted tidal flow (DiQunizio et al. 2002). Nest success was relatively low for Seaside and saltmarsh sparrows in marshes with unrestricted, or relatively unrestricted tidal flows in southern New England where new-moon spring tides regularly exceeded the elevation of sparrow nests (Seaside Sparrow at Allens Pond, Marshall and Reinert 1990; saltmarsh sparrows at HAC, DeRagon 1988; saltmarsh sparrows at Prudence Island and Galilee, post-restoration, DiQuinzio 1999; Table 2). The proportion of failed nests attributable to spring-tide flooding events at those sites was 86%, 63%, 78%, and 91%, respectively.

In Rhode Island and Maine, respectively, DeRagon (1988) and Shriver (2002) found that flooding during new moon spring tides destroyed the majority of early saltmarsh sparrow nests. Females responded to nest destruction by immediately initiating a replacement nest. These events served to synchronize nesting activities, and most female saltmarsh sparrows were successful in completing their nesting cycle prior to the encroachment of flooding tides associated with the following new-moon period.

While saltmarsh sparrows in Rhode Island did not situate replacement nests at higher elevations following nest loss to flooding, they did place nests in the highest elevations of the high-marsh community. DeRagon (1988) and Shriver (2002) both found that the mean substrate elevation at nest sites was significantly higher (5 cm in Rhode Island) than at random points in the same plant communities. DeRagon determined that females avoided the lower 40% of that community's vertical range when selecting nest sites, and while such fine-scale selection would rarely impact nest survival during the flooding tides of new moons, such small differences in nest elevation could enable a nest to avoid flooding by lesser amplitude full-moon spring tides. The data of DiQunizio et al. (2002) suggested that in response to increased tidal flow resulting from marsh restoration efforts in a Rhode Island marsh (Galilee pre-, post-restoration; Table 2), sparrows modified their nest placement by nesting in taller vegetation and building nests higher above the substrate.

In a Massachusetts saltmarsh (Allens Pond; Table 2) Marshall and Reinert (1990) documented a nesting-cycle response to spring-tide flooding events by Seaside Sparrows that is very similar to that described above for saltmarsh sparrows. The simultaneous loss of many early season nests due to new-moon spring tide inundations acted to synchronize the subsequent nesting attempts of the unsuccessful pairs. Seaside Sparrows

had first eggs in replacement nests in a mean of 6.25 ± 1.7 d from the date of nest destruction, and the young of renesting pairs fledged, nearly simultaneously, just prior to or at the time of the next spring tide. Seaside Sparrow nest cycles extended as little as 1 d due to large clutches, or protracted incubation or nestling periods, were subject to destruction if replacement nests were not high enough to avoid the tides. Marshall and Reinert (1990) witnessed nestling Seaside Sparrows climb from their nests to avoid being drowned by spring-tide inundations, and in one nest they observed a nestling drown two siblings while elevating its own body above the flood waters. At Allens Pond, Seaside Sparrow replacement nests were higher than earlier nests as a result of the seasonal growth of the smooth cordgrass plants that supported them, and the probability of nests fledging young was greatest for such late season nests that were synchronized to the tidal cycle.

The renesting response of *Ammodramus* sparrows is not necessarily an adaptive reaction to life in the tidal marsh. Some passerines nesting in upland habitats have similarly short renesting periods (Song Sparrow, 5 d, Nice 1937; Gray Catbird [*Dumetella carolinensis*], 5.05 d, Northern Cardinal [*Cardinalis cardinalis*], 5.5 d, Scott et al. 1987) suggesting that for many passerines a minimized renesting interval may maximize reproductive output regardless of habitat type. However, Shriver (2002) found that because saltmarsh sparrow females in a Maine saltmarsh renested <3 d after a nest destroying new-moon tide, they had a nest-success rate that was 41% greater than Nelson's Sharp-tailed Sparrow (*Ammodramus nelsoni*), which initiated nesting >10 d after nest loss in the same study area. Because throughout its range Nelson's Sharp-tailed Sparrow nests primarily in freshwater habitats, Shriver concluded that saltmarsh sparrows were better adapted to the tidal environment.

SALTMARSH SONG SPARROWS OF SAN FRANCISCO BAY

Two races of the Song Sparrow (*Melospiza melodia pusillula* and *M. m. samuelis*; Marshall 1948a) are endemic to saltmarsh habitats of the San Francisco Bay area of California. The *samuelis* race occupies emergent saltmarsh habitats dominated by California cordgrass (*Spartina foliosa*), woody saltwort (*Salicornia ambigua*),California gum plant (*Grindelia cuneifolia*), and salt grass. Its nests are placed in all those plant types, but most commonly in saltwort and gum plant, both <1 m in height (Johnston 1956a). Nests are placed as high as possible in the vegetation (25–30 cm) such

as to still provide cover above, and Johnston (1956a) noted that this strategy enabled some nests to avoid inundation. Flooding spring tides occurred throughout the breeding season (March–July) and often destroyed nests—tidal inundations accounted for the destruction of 12% of eggs laid in the average year, and egg mortality was as high as 24% in some years (Johnston 1956b). N. Nur (pers. comm.) documented a renesting response in San Francisco Bay Song Sparrows that mirrors that of their East Coast *Ammodramus* counterparts—destructive flooding tides synchronized the nesting activities of females which promptly renested. This response enabled completion of the nest cycle prior to the onset of the nest flooding spring tide which followed 27–29 d later.

Johnston (1956a) determined that the salt-marsh Song Sparrow races in San Francisco Bay bred earlier by 15 d than did their upland nesting counterparts at identical latitudes. Because tidal amplitude increases over the course of the breeding season in San Francisco Bay, Johnston concluded that the early nesting represented an adaptation in the bay area birds to avoid the season's highest tides. In one year >60% of the eggs laid by a *samuelis* population in the whole season had fledged young prior to the first serious tidal event. Thus, for San Francisco Bay Song Sparrows, early nesting to avoid the season's highest tides was a critical factor in determining the reproductive success of *samuelis* (Johnston 1956a). As witnessed for the *Ammodramus* sparrows, nestling Song Sparrows were seen climbing from nests to avoid being drowned by rising tide waters, and vegetative growth throughout the breeding season enabled placement of late season renests higher over the substrate. This latter factor enabled nest elevations to keep pace with the progressively higher tides of the breeding season. Johnston (1956b) noted that some eggs in nests that were inundated for limited periods of time survived to hatching.

THE CLAPPER RAIL

The Clapper Rail nests in low- (California and smooth cordgrass), and high-marsh habitats of the saltmarsh throughout the coastal US (Eddleman and Conway 1998), and because of its propensity to nest at low elevations flooding is the most significant nest mortality factor (Stewart 1951, Burger 1979, Andrews 1980, Massey et al. 1984, Eddleman and Conway 1998). The platform nests of the Clapper Rail are bound to their cordgrass support stems, and thus do not typically float on rising tide waters as do those of saltmarsh nesting larids (Mangold 1974, Burger 1979, Andrews 1980). In southern California, however, Massey et al. (1984:71) reported that for the Light-footed Clapper Rail (*Rallus longirostris levipes*), the tall stems of California cordgrass "not only provided cover but allowed the nest to float upwards in place during a high tide." Clapper Rails compensate for their nest placement in low-elevation habitats by building high nest structures (Burger 1979). Andrews (1980) determined that rails in New Jersey placed their nests in relatively tall vegetation that allowed them to maximize nest elevation. He described rail nests as tall columns of nest material that elevated eggs 15–64 cm above the ground, and concluded that such construction was an adaptation to the demands of the saltmarsh habitat. Kozicky and Schmidt (1949) noted that a difference in nest height of only 5–8 cm could be critical to rail nesting success, and especially during the hatching period. Further, rails were observed hurriedly building their nests higher in the midst of flood-tide events (Andrews 1980, Jackson 1983). In field experiments, Burger (1979) demonstrated that Clapper Rails were able to perceive damage to their nests and immediately and rapidly rebuild them, and that their ability to do so was more advanced than in most larid and waterfowl species. These nest-building responses are important to reproductive success, since if a flood tide does inundate a rail nest, and eggs are not washed out, females will continue to incubate them and at least some eggs will survive to hatching (Kozicky and Schmidt 1949, Mangold 1974). Further, Clapper Rails are known to retrieve eggs that are washed out to some distance from the nest (Burger 1979).

Following nest loss to flooding or predation, Clapper Rails persistently renest (Stewart 1951, Mangold 1974, Andrews 1980). Rails may nest five, or even more times in one season, and in one population in San Francisco Bay, one-half of the nesting population renested at least once during the breeding season (Eddleman and Conway 1998). Eddleman and Conway (1998) speculated that their ability to repeatedly renest allowed rail populations in good habitat to recover rapidly after catastrophic flooding events. Andrews (1980) further suggested that, as for marsh nesting sparrows, late season nests are placed higher due to the seasonal growth of the supporting vegetation, thus reducing flooding risks.

AGE OF SALTMARSH TAXA AND ADAPTATION TO TIDAL FLOODING

Only colonially nesting larids exhibit substantive evidence that environmental cues (peak high tides) are used to time and place nests to

avoid tidal flooding. The nesting activities of terrestrial species, including *Ammodramus* sparrows, Song Sparrow, and Clapper Rail, also become synchronized to the spring-tide cycle, but only after initial nests are destroyed by an early season flooding event. Among larids, the ability to repair nests after damage inflicted by flooding tides, and of eggs to survive immersions in salt water, was most highly developed in the Laughing Gull, a saltmarsh specialist, and Ward and Burger (1980) attributed this to a longer evolutionary history of nesting in the saltmarsh environment. Similarly, the Saltmarsh Sharptailed Sparrow has a much longer evolutionary history as a saltmarsh specialist than does the Nelson's Sharp-tailed Sparrow (Rising and Avise 1993), which probably explains the more rapid nesting response of the former after flooding tides (Shriver 2002). This explanation may apply also to the highly developed responses to flooding—including nest building and repair, and egg retrieval—seen in the Clapper Rail relative to saltmarsh passerines. However, the history of Clapper Rails in saltmarsh habitats remains unclear (Chan et al., *this volume*).

NESTING ADAPTATIONS OF RED-WINGED BLACKBIRDS TO TIDAL-MARSH HABITAT: A CASE STUDY

In the northeastern US coastal nesting populations of the Red-winged Blackbird are sometimes found breeding in saltmarshes alongside Seaside and Saltmarsh Sharp-tailed sparrows (Reinert et al. 1981, Post et al. 1983, Reinert and Mello 1995). Yet, despite the voluminous literature on the species, little is known about the breeding ecology of saltmarsh inhabiting Red-winged Blackbirds, and in particular how they are able to nest successfully despite spring tides which inundate marshes in New England every 27–29 d. Saltmarsh Red-winged Blackbirds are not known to be morphologically distinct, and Red-winged Blackbirds show little geographic structure in neutral genetic markers, such as MtDNA (Ball et al. 1998). However, research on various taxa (Chan et al., *this volume*) shows that adaptations can occur in tidal-marsh populations that have recently differentiated or face ongoing gene flow from upland populations.

Because of the high predictability of tidal flooding events in New England saltmarshes, an evolutionary response is feasible, and selection for a contracted nesting cycle period should be strong considering the drastic consequences of a delayed response. I tested the hypothesis that such local adaptations exist using data collected from my 4-yr field study

of Red-winged Blackbird reproductive success in a Rhode Island saltmarsh. My nesting data were supplemented with parental food-provisioning data collected on the same marsh by Tilton (1987). I predicted that female Red-winged Blackbirds nesting in saltmarshes in New England have adapted to tidal cycles with a reduced renesting interval, and nestling maturation is accelerated by higher parental feeding rates, including the male's more frequent participation in provisioning.

METHODS

STUDY SITE

The study site abuts Hundred Acre Cove (HAC), a 40-ha embayment of the Barrington River estuary in Barrington, Rhode Island. The 32-ha marsh is bordered by the open water of the estuary to the south, and by deciduous forest and/or stands of common reed (*Phragmites australis*) to the north, east, and west. The Red-winged Blackbird study population inhabits a 30–60 m wide zone of smooth cordgrass bordering a 2.7 ha permanent pool centered within the study marsh. Smooth cordgrass stands, 40–80 cm in height, are poorly drained throughout, and standing water was present at the base of most stands. Small patches of salt-meadow habitat were interspersed among the smooth cordgrass habitat, and north and west of the 2.7 ha central pool, networks of smaller (<100 m^2) pools were interspersed among the smooth cordgrass stands forming additional open water-smooth cordgrass ecotones. A more detailed description of the study site is available in DeRagon (1988).

FIELD METHODS

Beginning with annual onset of nest building in early May, the study site was visited on an almost daily basis during the breeding seasons of 1982–1985. Nests were checked regularly the last 3 yr of the study, at intervals of every other day between spring-tide periods, and then daily for the several days before and after maximum spring-tide inundations. Nest contents and productivity were scored during these visits; a nest was considered successful if at least one young fledged from it.

The following nest measurements were taken most years (although not every measurement was taken for every nest every year): nest height above substrate, surrounding vegetation height, distance to nearest open water, nest-bowl depth, and nest-rim elevation relative to mean sea level. The latter was determined in

two ways: in 1982 and 1983: by rod and transit conducted shortly after the breeding season; and in 1985 by my chalked stake technique. In the latter, I determined nest elevation by (1) placing a chalked stake at each nest and at a reference marker of known elevation, (2) measuring the distance from each nest's rim and the marker to the chalk line left after a flooding spring tide, and (3) using the measurements from the reference marker to calculate the distance from the marker elevation to the rim elevation of each nest, thereby establishing the rim elevation relative to mean sea level (MSL).

In 1984, seven adult female Red-winged Blackbirds were captured in mist nets and marked with USDI Fish and Wildlife Service aluminum bands on one leg and two colored, celluloid bands on the opposite leg. In 1983, I banded 11 nestlings (nine of which fledged) from four nests, and in 1984, I banded 29 nestlings (25 of which fledged) from 10 nests.

Despite not having banded every female, the small size of my study population combined with conservative deductions allowed me to assign nearly all of the nests to specific females and thereby ascertain nesting chronology. The basis for my deduced assignment was that if an egg was laid in a newly constructed nest within 7 d of the loss of the nest of an unmarked female in the same territory, I assumed that the owner of the lost nest and the new nest was the same. While this supposition did not guarantee correct identity, my determinations were facilitated by low female/male ratios (Table 3), and were corroborated by data on marked females.

Hypothesizing that water inundation does not necessarily result in immediate embryo death, I wished to determine the number of days after laying that an egg would remain nonbuoyant, and thus resistant to flooding mortality. For this determination, I used three nests found during the nest-building period in 1985 and marked each egg with its laying sequence. I then checked the nests daily (beginning 2 d after the last egg was deposited), and at each visit placed eggs individually in a beaker of water collected at the nest site and scored their floatability. The daily check was continued until all eggs in the clutch floated to the surface.

I established the elevation of marsh-flooding tides relative to mean sea level by placing a chalked oak stake, covered with a perforated PVC pipe, in the interior of a large pool. I then subtracted the distance from the chalk mark left by the peak elevation of flood water to the top of the stake, from the known elevation of the top of the stake to establish the tidal height relative to MSL. This method yielded the peak elevation of flood tides for 33 d during the 4-yr study. To estimate the elevation of tides for nights when the tide was of insufficient height to leave a chalk mark, or when the gauge was not checked, I developed a regression model of my 33 measurements on a single predictor variable: the measured tidal elevation at a NOAA sampling station located in the Providence River of the same Narragansett Bay estuarine system, and approximately 7 km from the study site. The resulting regression equation ($r^2 = 0.90$, $P < 0.0001$) predicted tidal elevation at my study site.

TABLE 3. POPULATION DEMOGRAPHICS AND NEST-SUCCESS DATA FOR RED-WINGED BLACKBIRDS OVER FOUR YEARS.

Variable	1982	1983	1984	1985	4-yr mean
N males	14	11	9	9	10.8
N females	16	13	13	14	14.0
N 2-, 3-, and 0- female males (totals)	4, 0, 1	2, 0, 0	2, 1, 0	3 ,1 ,0	11 ,2, 1
Mean females/male	1.1	1.3	1.5	1.6	1.3
Mean nests/female (range)	2.0 (1–5)	2.5 (1–5)	1.7 (1–3)	2.0 (1–4)	2.0
Mean nests/territory	2.3	2.9	2.4	3.1	2.7
Total active nests [a]	32	32	22	28	28.5
Date first egg	5/17	5/19	5/16	5/12	-
Date first young	6/9	6/6	6/1	5/25	-
Date first fledgling	7/13	6/25	6/17	6/26	-
N (%) successful nests	7 (21.9)	6 (18.8)	12 (54.5)	7 (25.0)	8 (28.1)
N nests depredated (%, c, m, u) [b]	13 (40.1, 0, 6, 7)	8 (25.0, 0, 1, 7)	8 (36.4, 0, 4, 4)	8 (28.6, 1, 1, 6)	9 (32.4, 1, 12, 24)
N (%) nests lost to flooding	10 (31.2)	15 (46.9)	2 (9.1)	12 (42.8)	10 (34.2)
N (%) nests abandoned	1 (3.1)	2 (6.2)	0 (0)	1 (3.6)	1 (3.5)
N (%) nests lost to unknown cause	1 (3.1)	1 (3.1)	0 (0)	0 (0)	0.5 (1.8)
Total fledglings	18	12	33	11	18.5
Mean fledglings/nest (range)	0.56 (0–3)	0.38 (0–3)	1.50 (0–4)	0.39 (0–3)	0.65
Mean fledglings/female (range)	1.12 (0–3)	0.92 (0–3)	2.54 (0–4)	0.79 (0–3)	1.32
Mean fledglings/male (range)	1.29 (0–5)	1.09 (0–3)	3.67 (1–8)	1.22 (0–6)	1.71
N renests	18	19	9	14	15

[a] N nests reaching at least egg-laying stage.
[b] In parentheses: % nests lost to predation, number lost to crows (c), mammalian predators (m), unknown predators (u).

FOOD DELIVERIES TO NESTLINGS

To compare rates of food deliveries to nestlings by parent Red-winged Blackbirds on my study site in Rhode Island to non-tidal populations, I used data collected for birds at my study site by Tilton in 1984 and 1985 (see Tilton 1987 for methodology). Data from my study site were then compared, using the paired t-test (pairing on nestling day), to data on nestling provisioning from freshwater-wetland/upland populations in Indiana and Wisconsin—in Indiana (Patterson 1991; 1974 and 1975) and Wisconsin (Yasukawa et al. 1990; 1984–1987). Each of those authors presented mean food-delivery rates, by nestling day. For the t-tests, I used the mean of the 1984 and 1985 data from Rhode Island (Tilton 1987) as the food-delivery rates were not significantly different between years. Rates were different between the 2 yr at the Indiana site (Patterson 1991), and thus I made separate comparisons between the combined data for Rhode Island and each of the 2 yr for Indiana. I used data from male-assisted females only for the Indiana site because those values were not significantly different than, and very similar to, those for unassisted females at any nestling age in either year (Patterson 1991:3–4). The data from Wisconsin (Yasukawa et al. 1990) were presented cumulatively for 1984–1987. I also computed, by nestling day, the percent of total food deliveries made by males, and likewise compared those values between my saltmarsh study site and the Indiana and Wisconsin populations.

To compare the percent of successful nests at my study area to the cumulative values reported for marsh and upland habitats by Beletsky (1996), I used the two-sample test of proportions. Mean values are presented with standard deviations throughout. All statistics were performed with Stata v. 7 (Stata Corp., College Station, TX).

RESULTS

The breeding population of Red-winged Blackbirds varied from nine to 14 males and 13–16 females annually over the 4-yr period. The maximum number of polygynous males in any year was four. No male paired with more than three females, and males paired with an average of 1.3 females overall. One unpaired male defended a territory in 1982. Over the 4-yr study, the first egg, hatching, and fledgling dates were 12 May, 25 May, and 17 June, respectively (Table 3).

Four of seven females banded in 1984 returned to the study area to breed in the following year. Of the 34 banded nestlings that

fledged in 1983 and 1984, only one, a first-year male, was subsequently encountered. This male did not establish a territory, however, and was not sighted again.

Red-winged Blackbirds nested exclusively within the cover of irregularly flooded smooth cordgrass stands. Early season nests were placed among brown, persistent stems from the prior year's growing season; later nests were placed in new-growth smooth cordgrass plants. Fifty-one (81%) of 63 nests measured were placed within 1.5 m of the open water edge of a pool, over standing water, where the tallest stands of smooth cordgrass occurred. The mean height above the substrate of 74 nests measured was 39.6 cm (± 19.2); the mean height of the vegetation surrounding 50 nests measured was 58.3 cm (± 15.8).

Red-winged Blackbird females built nests in 2–4 d. They laid one egg per day, and two (3.3%), three (38.0%), or four eggs (58.7%) per clutch ($\overline{x}$ = 3.60 ± 0.49 for 92 nests for which I suspected that no eggs were lost to flooding or predation). The incubation period, measured as the interval from the laying of the penultimate egg to the hatching of the last young, was 13 d for 20 (77%) of 26 nests with complete data ($\overline{x}$ = 12.9 ± 0.7). The mean incubation period of five nests inundated during the egg laying and early incubation period (12.8 d) was not significantly different than for the 21 nests which were not flooded (12.9 d; t = 0.17, P = 0.87). The nestling period, measured as the interval from the hatching of the first young to the fledging of the last young, was 11 d for 12 (48%) of 25 nests with complete data ($\overline{x}$ = 10.8 ± 0.9, range = 9–12). The hatching period, calculated as the number of days from the first to last egg hatched, ranged from <1 d (for clutches of two–four eggs) to 3 d (for two clutches of four eggs) ($\overline{x}$ = 1.6 ± 0.7). The modal nesting cycle period (days from first egg laid to last young fledged) calculated for 17 nests with complete data was 23 d ($\overline{x}$ = 24.1 ± 1.4, range = 22–27).

For 65 nestlings in 28 successful nests with adequate chronological data, I determined the number of days in the nest under the assumption that the first-hatched young were the first to fledge. One young (1.5%) fledged after 8 d in the nest, 13 (20.0%) after 9 d, 29 (44.6%) after 10 d, 17 (26.2%) after 11 d, and 5 (7.7%) after 12 d. The mean number of days in the nest for the 65 nestlings was 10.2 (± 0.9). Of the 28 nests, 8-d-old young fledged from one (3.6%), 9-d-old from 11 (39.3%), 10-d-old from 17 (60.7%), 11-d-old from 13 (46.5%), and 12-d-old from five nests (17.9%).

The mean depth of the nest bowl (rim to bowl bottom) for 66 nests measured was 60 mm (± 6). The mean elevation of the rims of 80 nests

measured was 105 cm above MSL (± 5); the mean elevation of the bowl bottom of 63 nests for which both nest elevation and bowl depth were measured was 99.6 cm (± 4.2).

Three eggs, the last deposited in each of the three experimental nests, were immersed 2 d after their lay date, after 2 d of incubation (incubation began with the laying of the penultimate egg) and all three sank. When immersed 1 d later, one sank, one sank slowly, and one floated. All three eggs floated on day three, after 4 d of incubation.

Three eggs, the penultimate of each clutch, were immersed 3 d after their lay date, after 3 d of incubation all three sank. When they were immersed 1 d later, all three eggs floated. Three eggs, the second laid of two four-egg clutches, and the first laid of one three-egg clutch, were immersed 4 d after their lay date, and after 3 d of incubation all three floated. Two eggs, the first laid of the two, four-egg clutches, were immersed 5 d after their lay date, and after 3 d of incubation both floated. Thus, Red-winged Blackbird eggs with developing embryos became buoyant during the fourth or fifth day of incubation, with earlier laid eggs floating prior to the penultimate and ultimate eggs of the clutch.

Of the 114 active Red-winged Blackbird nests found during this 4-yr study, 59 (52%) were renesting attempts; three (5%) represented the fifth nesting attempt of individual females during a single breeding season, five (8%) represented the fourth nesting attempt, 14 (24%) represented the third nesting attempt, and 37 (63%) the second nesting attempt. Female Red-winged Blackbirds deposited at least one egg in a mean of 1.81 (± 0.99) nests per year.

Of the 37 nests for which I determined a renest interval during the 1983–1985 breeding seasons, the first egg in 23 nests (62%) was laid on the fifth day after nest loss, in five nests (14%) on the sixth day, in two nests (5%) on the seventh day, and in seven nests (19%) on the eighth or later day after nest loss. Of eight renestings among seven color-banded females in 1984 and 1985, the new nest of each was built in the same territory as the previous.

Female Red-winged Blackbirds delivered food to nestlings (Tilton 1987) at a significantly greater rate than did females at an Indiana freshwater wetland site (Patterson 1991) in both 1974 and 1975, and a Wisconsin freshwater wetland-upland site (Yasukawa et al. 1990) for the cumulative years 1984–1987 (Table 4; Fig. 1). Male Red-winged Blackbirds delivered food to nestlings at a significantly greater rate than at the Indiana site in 1974, but not in 1975, and at a significantly greater rate than in the Wisconsin population (Table 4; Fig. 1). The mean percent of food trips made by males was significantly greater at the Indiana (Patterson 1991) site than at the Rhode Island saltmarsh site (Tilton 1987) in 1975 (mean in Rhode Island = 25.4 ± 14.4; mean Indiana = 47.1 ± 21.4; t = -5.13, df = 9, P < 0.001), but not in 1974 (mean in Rhode Island = 23.1 ± 15.7; mean in Indiana = 25.1 ± 18.7; t = -0.47, df = 10, P = 0.65). The mean percent of food trips made by males was significantly greater at the Rhode Island site than the Wisconsin site (Yasukawa et al. 1990) (mean in Rhode Island = 23.1 ± 15.7; mean in Wisconsin = 15.4 ± 12.07; t = 2.63, df = 10, P = 0.03).

REPRODUCTIVE SUCCESS AND MORTALITY FACTORS

Female Red-winged Blackbirds laid at least one egg in 114 nests over the 4-yr study period.

TABLE 4. RATES OF FOOD DELIVERIES TO NESTLINGS BY PARENT RED-WINGED BLACKBIRDS.

Statistical comparisons[a]	Study area	Time period	Mean trips/ nestling/hour
Females			
1	Rhode Island[b]	1984–1985	5.3 ± 2.9
2	Indiana[c]	1974	2.1 ± 0.8
3	Indiana[c]	1975	2.9 ± 0.5
4	Wisconsin[d]	1984–1987	2.7 ± 0.9
Males			
5	Rhode Island[b]	1984–1985	1.5 ± 1.2
6	Indiana[c]	1974	0.6 ± 0.4
7	Indiana[c]	1975	1.4 ± 0.7
8	Wisconsin[d]	1984–1987	0.5 ± 0.4

[a] Paired t-test results, 1:2, t = 4.67, df = 10, P < 0.001; 1:3, t = 3.32, df = 9, P < 0.01; 1:4, t = 3.82, df = 10, P < 0.01; 5:6, t = 3.15, df = 10, P = 0.01; 5:7, t = 0.77, df = 9, P = 0.46; 5:8, t = 3.56, df = 10, P < 0.01.
[b] Tilton (1987).
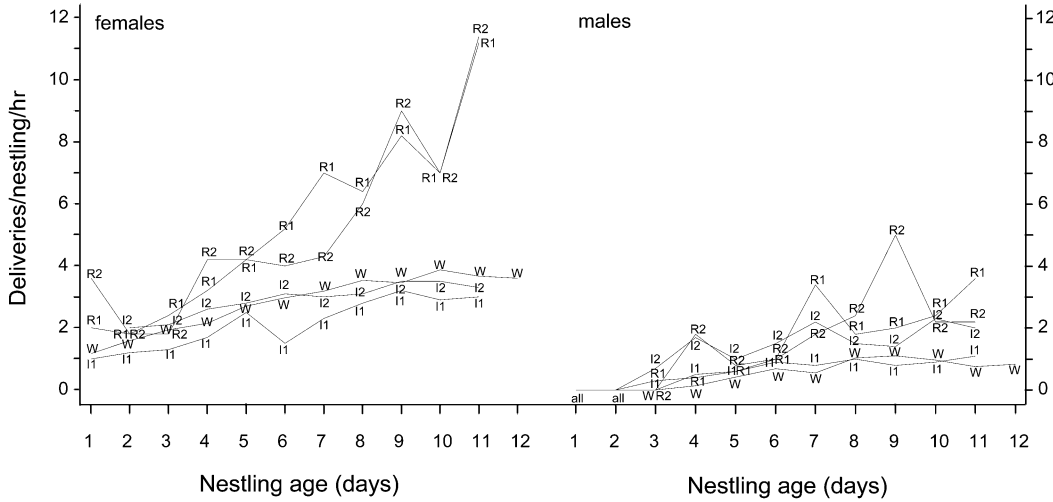[c] Patterson (1991).
[d] Yasukawa et al. (1990).

FIGURE 1. Food-delivery rates to nestlings by male and female Red-winged Blackbirds at Hundred Acre Cove salt marsh (Tilton 1987) in 1984 (R1) and 1985 (R2), at a freshwater wetland population in Indiana (Patterson 1991) in 1974 (I1) and 1975 (I2), and at a freshwater wetland-upland population in Wisconsin (Yasukawa et al. 1990) for the combined period 1984–1987 (W).

Seventy-four young fledged from 32 successful nests (1–4 fledglings/nest). The mean numbers of young fledged per nest, per female, and per male were 0.6, 1.3, and 1.7, respectively. Eighty-two nests were not successful due to tidal flooding (39 nests, 48%), predation (37 nests, 45%), nest abandonment (excluding post-flood abandonment, four nests, 5%), and unknown causes (two nests, 2%; Table 3).

Nest loss to flooding occurred during marsh inundations accompanying spring tides, which occur at new moon phases every 27–29 d in coastal New England. Such tides destroy nests by drowning nestlings, and by dispersing eggs that float from nests when the water level rises over the rim. Of the ten spring tides that occurred during the four breeding seasons of the study period, eight exceeded the mean elevation of Red-winged Blackbird nest rims (105 ± 5 cm), and all exceeded the mean elevation of nest bowl bottoms (100 ± 4 cm). The mean elevation of the ten spring tides (112 ± 8 cm) exceeded the elevation of 73 (91%) of the 80 Red-winged Blackbird nest rims for which elevation data were available, and the highest spring tides were well above the elevation of the highest Red-winged Blackbird nests (Fig. 2). At least 56 (49%) of the 114 active nests monitored in this study were completely submerged beneath spring tide waters while they were active.

Spring tides occurring during June, the peak of the breeding season, destroyed 69% (nine of 13) of active nests in 1982 (peak-tide elevation = 114 cm), 67% (8 of 12) of active nests in 1983 (peak-tide elevation = 109 cm), 20% (two of 10) of active nests in 1984 (peak-tide elevation = 106 cm), and 85% (11 of 13) of active nests in 1985 (peak-tide elevation = 114 cm; Table 3). Of the 39 nests lost to flooding, one was at the egg laying stage, 15 were at the incubation stage, five were at the incubation-nestling (hatching) stage, and 18 were at the nestling stage. Sixty-two eggs and 60 nestlings were lost to flooding tides.

Nest predation was witnessed twice when American Crows (*Corvus brachyrhynchos*) were seen removing 4–5 d old and 8–9 d old nestlings from nests (one nestling survived). We assumed that 12 nests torn from their support stems were the victims of mammalian predation, probably northern raccoon (*Procyon lotor*). Twenty-five additional depredated nests found intact and empty were likely the victims of American Crows, Common Grackles (*Quiscalus quiscula*), and mink (*Mustela vison*). A breakdown of predator types by year is presented in Table 3. Six nests were depredated at the egg laying stage, 27 at the incubation stage, and three at the nestling stage; 102 eggs and 12 nestlings were lost to predation. I rarely saw Brown-headed Cowbirds (*Molothrus ater*) on the marsh, and no cowbird eggs were found in Red-winged Blackbird nests.

CHARACTERISTICS OF SUCCESSFUL NESTS

Successful nests were not depredated, and were: (1) started during or immediately after

a spring tide such that young fledged prior to the high waters of the spring tide to follow 1 mo later, (2) inundated by spring tide waters during the egg laying or early in the incubation period, and thus the eggs did not float out of the nests, or (3) higher than the peak level of a spring tide (Table 5). Fourteen (44%) of the 32 successful nests resulted from female Red-winged Blackbirds immediately renesting after losing a nest to a May or June spring tide flooding event (Table 5). For each of those 14 nests, the first egg was laid in the new nest on the fifth day after nest loss. This uniform renesting response served to synchronize the nesting activities of all Red-winged Blackbirds (as well as Seaside and Saltmarsh Sharp-tailed sparrows) which lost nests to a spring tide. By initiating the new clutch on the fifth day after nest loss, the young of the subsequent clutch

(if the nest was not depredated) were able to fledge (or at least climb onto stems above the nest) just prior to the onset of the floodwaters associated with the next spring tide which occurs 27–29 d after the last (Fig. 3). Indeed, for many of those successful nests renesting intervals of only 1 or 2 d longer than the modal 5-d period would have resulted in the drowning of some or all of the nestlings that fledged. Five other successful nests were started during or right after a spring tide: three were first nesting attempts and two were post predation attempts (Table 5).

Of 56 active nests that were inundated for 1–3 successive days by a spring tide, 17 (30%)—11 of 13 in the egg-laying stage, three of eight in the incubation stage, and three of 17 in the nestling stage—survived the flood event(s). Eggs of nests in the egg-laying stage
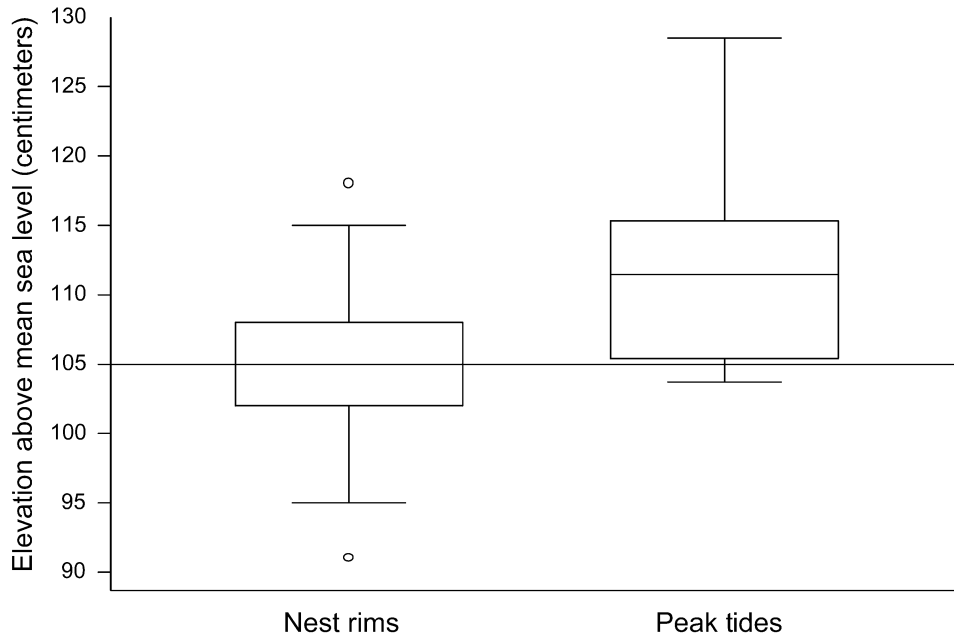

FIGURE 2. Box plots of elevations of Red-winged Blackbird nests (N = 80) and new-moon spring tides (N = 10) at Hundred Acre Cove saltmarsh. The horizontal line marks the median (and mean) elevation of nests.

TABLE 5. CATEGORIES OF CONDITIONS RESULTING IN SUCCESSFUL NESTS.

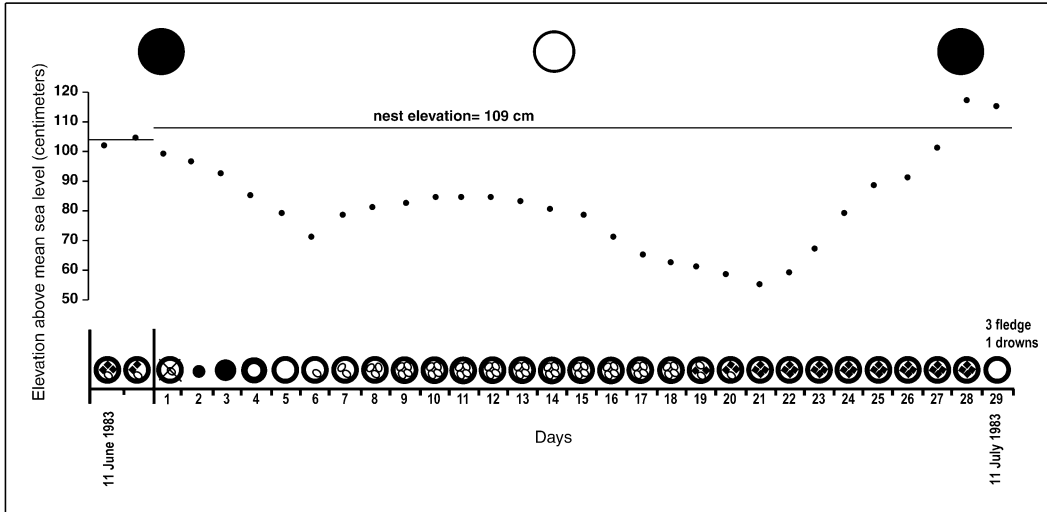|	Nest attempt				Total
	1	2	3	5	nests (%)
Post-flood renesting		10	3	1	14 (44)
Flooded, eggs did not float	4	2	1		7 (22)
Timing: nest built at spring tide	1	2			3 (9)
Timing: predation at spring tide			2		2 (6)
Spring tide too low to flood nests	4	2			6 (19)
Total nests (%)	9 (28)	16 (50)	6 (19)	1 (3)	32 (100)

FIGURE 3. Synchronization of the lunar-tidal cycle and Red-winged Blackbird nesting cycle at Hundred Acre Cove salt marsh. Plots to the right of the scale show the elevation of peak daily tides relative to nest elevations. Below the plots are the contents, by day, of two successive nests (diamonds represent nestlings) of one female and how they were impacted by flooding tides. The flood waters associated with an early June new-moon spring tide—which held three young and one infertile egg prior to flood encroachment—destroyed this female's first nest, and those of most other breeding songbirds on the marsh. Subsequent nesting activities of affected females of all species were synchronized to the tidal cycle. Although this female (1) started building a replacement nest within 1 d of destruction, (2) deposited a first egg in the replacement nest only 5 d after losing the first, and (3) completed her nest cycle (first egg to last young fledged) in the modal (for this study site) 23-d period, only three of her four nestlings avoided drowning when the next new-moon flood tide encroached 28 d after the first.

did not float and had the greatest probability (90%) of surviving an inundation, whereas eggs and young in inundated nests in the hatching period did not survive. Of 10 nests inundated during the egg-laying stage, but that did not lose all or any eggs, only one nest (containing two eggs) was abandoned. Of five nests with two–four eggs inundated early in the incubation stage, but that did not lose all or any eggs, two (with two and three eggs, respectively) were abandoned. Three nests that reached the nestling phase were inundated leaving one infertile egg in the nest; all of those nests were abandoned. Overall, seven (22%) of the 32 successful nests survived after having their eggs immersed for one–three successive nights. Thus, the propensity of female Red-winged Blackbirds to continue to incubate eggs after an inundation event was a key factor in nest survival at the study site.

Six nests survived a spring tide because their rim elevation exceeded that of the peak floodwaters. Overall, among nests for which a rim elevation was measured, the mean elevation of 17 that survived a flooding tide (107 ± 4 cm) was significantly higher than of 33 that did not survive an inundation event (104 ± 4 cm; $t = -2.45$, $P = 0.02$).

DISCUSSION

REPRODUCTIVE SUCCESS OF SALTMARSH-NESTING RED-WINGED BLACKBIRDS

Though few references in the peer-reviewed literature describe Red-winged Blackbirds nesting in emergent-saltmarsh habitats, this is a common occurrence in the coastal Northeast, and especially in stands of smooth cordgrass (Reinert et al. 1981, Post et al. 1983, Reinert and Mello 1995). Avian nests occupying emergent-saltmarsh habitats are subject to flooding by high waters associated with coastal storms, or new-moon spring tides, which occur every 27–29 d in the Northeast. Because the majority of new-moon tides exceed the height of passerine nests, most active nests during flood periods are destroyed when eggs float from nests or young drown. In my study population, tidal-flooding was the principal cause of nest loss overall, and in 3 of 4 yr (Table 3). Predation was the second most important mortality factor, overall, and the principle cause of nest failure in 1984 when only one spring tide reached the elevation of Red-winged Blackbird nests. Additionally, a few nests were lost to abandonment/starvation and unknown causes (Table 3).

During this study, nest success in 3 of 4 yr (21.9%, 18.8%, and 25.0%, respectively for the years 1982, 1983, and 1985; Table 3) was lower than any such value reported in a review of 27 Red-winged Blackbird studies (Beletsky 1996). The 4-yr mean nest success at HAC (28.1%) is among the lowest of reported values and was significantly lower than the overall mean of 40.2% for marsh habitats (z = 2.63, P < 0.01), and 46.4% for upland habitats (z = 3.73, P < 0.001) reported by Beletsky (1996).

The mean number of young fledged per nest at HAC was also relatively low. The 4-yr mean of 0.65 ranks close to the lowest reported in the reviews of Searcy and Yasukawa (1995) and Beletsky (1996), and was substantially lower than the overall means calculated for marsh (1.23) and upland (1.15) habitats in a meta-analysis by Beletsky (1996; Table 9.1). The mean number of fledglings per nest of 0.38 and 0.39 at HAC for the years 1983 and 1985, respectively, were lower than the values reported in any of the 18 studies reviewed by Searcy and Yasukawa (1995; Table 4.4), or 27 studies reviewed by Beletsky (1996).

The exceptionally low reproductive success I documented at HAC is not surprising considering the combined effects of predation and tidal flooding in this population. Beletsky (1996) summarized the causes of nest failure for 15 Red-winged Blackbird studies conducted in marsh habitats, and three studies conducted in upland habitats. Predation was the principal cause of nest failure for all of the marsh populations, and for two of the three upland populations. Starvation was the principal cause of failure in the third upland population. In only one population (Blakley 1976) did factors relating to natural catastrophes, in this case a wind storm, account for >9% of nest losses (Blakley 1976). As in other populations, Red-winged Blackbirds at HAC experienced substantial nest losses to predation; from 25–40% of nests were lost annually to predators over the 4-yr study, with an overall mean of 32.5% (Table 3). The percent of nests lost to predators averaged over the three upland populations summarized by Beletsky (1996, Table 9.2) was 32.6%, and over the 14 marsh populations, 45.2%. At HAC, however, Red-winged Blackbirds were further subjected to monthly tidal inundations resulting in the exceptionally low reproductive success exhibited.

ADAPTATIONS AND RESPONSES TO TIDAL FLOODING

Nest placement

Although the nesting cycle response to flooding of Red-winged Blackbirds at HAC was similar to that documented for Seaside and saltmarsh sparrows, the overall nesting success of Red-winged Blackbirds was substantially lower than that of saltmarsh sparrows nesting at HAC (DeRagon 1988) and of Seaside Sparrows nesting in a nearby Massachusetts saltmarsh (Marshall and Reinert 1990) (Red-winged Blackbirds 28%, Seaside Sparrow 38%, saltmarsh sparrow 59%; Table 2). This is attributable to the low rates of nest predation for Seaside Sparrows (11% of failed nests) and saltmarsh (11%) sparrows at those respective marshes compared to Red-winged Blackbirds (45%). Nests of Seaside Sparrows and saltmarsh sparrows are nearly always built beneath a tuft or canopy of marsh-grass vegetation, and thus are not visible to avian predators flying over. In contrast, Red-winged Blackbird nests are open above and thus were easily detected by avian predators. At HAC, Red-winged Blackbirds and Seaside Sparrows nested in close proximity to one another in shared stands of smooth cord-grass. Nests of Red-winged Blackbirds were on average 4 cm higher (t = -3.3, P = 0.001) than those of Seaside Sparrows (DeRagon 1988, this study), probably because sparrows had to situate their nests lower in the vegetation to enable the weaving of a canopy above. Thus, although Red-winged Blackbirds may reduce flooding risks by nesting higher in the plants, this did not offset the increased vulnerability of their nests to predation resulting from a lack of cover above. The survival advantage exhibited by the *Ammodramus* sparrows may exist because, having persisted for longer periods in saltmarsh habitats, they have adapted superior predator avoidance mechanisms.

Post-immersion egg survival

My experiment with three clutches revealed that during an inundation event at HAC Red-winged Blackbird eggs will not float from nests until the third or fourth day of incubation. Female Red-winged Blackbirds in the egg laying or early incubation period did not abandon nests after an inundation event if two or more eggs remained in the nest. Eggs remained viable after being inundated, and indeed the chance timing of early season nests such that egg laying-early/incubation periods and flooding new moon tides coincided, resulted in 22% of the total successful nests over the 4-yr study (Table 5). The viability of eggs after salt-water inundations has been demonstrated for several other species of birds nesting in saltmarshes, including White Ibis (Frederick 1987), Clapper Rail (Kozicky and Schmidt 1949, Mangold 1974), Herring Gull (Ward and Burger 1980),

Laughing Gull (Burger 1979), Common Tern (Burger 1979), and *samuelis* Song Sparrows of the San Francisco Bay area (Johnston 1956b). Burger (1979) and Ward and Burger (1980) conducted salt-water immersion experiments with eggs of Laughing and Herring gulls and determined that in general, egg survival of Laughing Gulls, which have long nested in tidal-marsh habitats, was greater than that of Herring Gulls which have only recently colonized saltmarsh islands. Those experiments indicate that Laughing Gull eggs are better adapted to marine environments, and suggest similar controlled comparisons among populations of Red-winged Blackbirds and Song Sparrows occupying saltmarsh, freshwater wetland, and upland habitats, and between obligate saltmarsh-nesting species such as Seaside Sparrow and Clapper Rail, and closely related species that do not use, or rarely use, saltmarsh habitats, such as Le Conte's Sparrow (*Ammodramus leconteii*) and King Rail (*Rallus elegans*).

Contracted nesting cycle

I predicted, based on the potentially disastrous results of an extended nesting period, that relative to other habitats, selection in saltmarsh populations would favor attributes consistent with a shortened nesting cycle and renesting interval. In the following paragraphs I apply data collected at HAC by Tilton (1987) and me to test my predictions.

At HAC, Red-winged Blackbirds completed their nest cycle (first egg laid to last young fledged) in a mean of 24.1 d (± 1.4 d, N = 17). I compared the nest cycle period of the HAC population with similarly derived periods for a freshwater wetland-upland population in Wisconsin provided by K. Yasukawa (pers. comm.). Though periods from three-egg clutches were slightly shorter in Wisconsin (23.6 ± 1.4, N = 31, Wisconsin; 24.1 ± 1.6, N = 9, HAC; P = 0.37), the nest-cycle period from four-egg clutches was nearly 1 d shorter at HAC vs. Wisconsin, and this difference approached statistical significance (24.9 ± 1.3, N = 49, Wisconsin; 24.0 ± 1.3, N = 8, HAC; P = 0.08) Thus, although these results are not conclusive, they do suggest, consistent with my prediction, a shorter nest cycle period for nests of the modal clutch size.

To further explore the hypothesis that the nesting cycle of the saltmarsh population is compressed relative to populations in other habitats, I employed a period-by-period approach. I excluded the nest-building period in this analysis because it is highly variable within and among populations (1–8 d), and

nests can be built in 1 d when necessary and thus egg production, and not nest construction, will limit contraction of the nesting cycle (Case and Hewitt 1963, Yasukawa and Searcy 1995, Beletsky 1996).

Red-winged Blackbirds could shorten their nesting cycle by laying fewer eggs, which would potentially contract the laying, incubation, and nestling periods. Indeed, saltmarsh populations of Song Sparrows (Johnston 1956a) and Swamp Sparrows (*Melospiza georgiana*; Greenberg and Droege 1990) have significantly smaller clutch sizes than populations occupying non-tidal habitats. At HAC, Red-winged Blackbirds laid one egg per day and clutches ranged from two–four eggs with a mean of 3.55. In a meta-analysis of 20 studies conducted by Dyer et al. (1977), mean clutch sizes ranged from 2.43–3.70 with an overall mean of 3.28. The meta-analysis of Martin (1995) yielded a mean clutch size of 3.49. Thus, though this analysis does not control for latitudinal variation in clutch size, the evidence available is not consistent with my hypothesis that clutch sizes at the saltmarsh site were smaller than the norm for the species.

The mean incubation period for 26 nests with complete data at HAC was 12.85 d; one half of females completed incubation in 13 d. Martin's (1995) meta-analysis yielded a mean from the literature of 12.6 d. In his review, Beletsky (1996; Table 6.2) reports incubation periods from four studies conducted in upland and freshwater wetland habitats: 10–12 d (New York), 11–14 d (California), 11–13 d (Washington), and 10–12 d (Illinois). Nero (1984) reported an incubation period of 11–12 d for his freshwater marsh population in Wisconsin. Thus, my data are not consistent with a contracted incubation period.

Martin (1995) demonstrated that among parulids and emberizids, nestling periods were shorter in species that nested in habitats with the greatest predation pressure. It follows that habitat-specific nest mortality factors could shape variability in nestling periods. A review of the available data (Table 6) reveals that Red-winged Blackbird nestlings at my site, on average, leave the nest earlier than at non-tidal sites. Other studies have demonstrated that Red-winged Blackbird nestlings will leave the nest as early as the ninth day of their lives only when disturbed (Allen 1914, Beer and Tibbitts 1950, Case and Hewitt 1963; Table 6). At HAC, >20% of nestlings distributed among 43% of successful nests fledged at 8 or 9 d of age. At approximately 20% of successful nests, premature fledging of one or more young resulted from rising tidal waters which forced young to climb into vegetation surrounding the nest to avoid drowning. Predators forced one young

TABLE 6. REPORTED NESTLING PERIODS OF RED-WINGED BLACKBIRDS.

Duration in days	Region; habitat	Notes	Reference
9–11	New York; freshwater wetland	"On the ninth [day]…The young can fly short distances, however, and can not be kept in the nest if once frightened or removed. If the nest has become polluted, as frequently occurs when it has become greatly compressed by the growing vegetation, they may leave of their own accord on this day. On the tenth the stronger of the young leave and climb to near-by supports… If the nest is approached, all leave, but otherwise the weaker remain until the eleventh day…when all scatter to the vegetation in the immediate vicinity."	Allen (1914: 100–101).
9–13	Wisconsin; freshwater marsh	"On the 9th and subsequent days a disturbance is apt to cause them to leave the nest. Normally the young leave on the 11th or 12th day but in case of cold weather may remain in the nest until the 13th day."	Beer and Tibbitts (1950:73).
9–14	New York; cattail (freshwater) marshes and upland habitats	"If disturbed, nestlings left the nest on the 9th day after hatching. If undisturbed, the stronger nestlings left the nest on the 10th day, and weaker and smaller nestlings left on the 11th or 12th day. In inclement weather, many nestlings remained in the nest up to 14 days."	Case and Hewitt (1963:14).
9.2 females 9.7 males	Michigan; freshwater marsh and upland habitats	"The mean duration of nestling life is shorter for females than males (9.2 vs. 9.7 days)." Note, the nestlings measured were handled on every day in the nest, thus their fledging dates were probably premature.	Holcomb and Twiest (1970:301).
11	Michigan; freshwater marsh/bog	"…for the 11 d of nestling life…"	Fiala and Congdon (1983:644).
11	Illinois; freshwater marsh and bog	"Birds fledge approximately eleven days after hatching."	Strehl and White (1986:179).
11	Ontario; cattail (freshwater) marsh	"…to fledging (usually day 11)…"	Muldal et al. (1986: 108).
11–12	Washington; freshwater marshes	"Fledging occurred usually at 11 to 12 days of age."	Beletsky and Orians (1990:607).
10.8	Wisconsin; freshwater-wetland/upland habitats	Nestling period period (days from first young hatched to last young fledged) for 31 3-egg clutches = 10.6 d (± 1.0); for 49 4-egg clutches = 10.8 (± 1.0).	K. Yasukawa (pers. comm.)
8–12	Rhode Island; saltmarsh	Mean nestling period (days from first young hatched to last young fledged) = 10.8 d (± 0.9, range = 9–12 d, mode = 11 [48% of 25 nests]). Mean days in nest per nestling = 10.2 (± 0.9, range = 8–12 d, mode = 10 d [45% of 65 nestlings]); see Results section).	This study.

each from two other nests to fledge prematurely. However, the remainder of nests from which young fledged at 8 or 9 d showed no evidence of disturbance.

Whittingham and Robertson (1994) found that when Red-winged Blackbird nestlings received food at a heightened rate due to male participation in provisioning, the mass of the young at 8 d of age was significantly greater than that of nestlings fed by the female alone. Such a head start could equate to the difference between life and death for nestling songbirds in saltmarshes. Tilton's (1987) data on parental food provisioning at HAC suggests that selection for early development of young has favored male participation in the feeding of

nestlings, and accelerated food delivery rates to young by both male and female parents.

At HAC, Tilton (1987) found that 11 out of 12 males fed young, which greatly exceeds the highest reported proportion from inland populations (Whittingham and Robertson 1994, Searcy and Yasukawa 1995, Beletsky 1996). Further, because the mean harem size at HAC (1.3) is among the lowest reported (Searcy and Yasukawa 1995, Beletsky 1996), and most males that provision young restrict their feeding to one nest only, or no more than one nest simultaneously (Beletsky and Orians 1990, Yasukawa et al. 1990, 1993; Patterson 1991), the percent of total nests provisioned by males at HAC is also relatively high.

At HAC, not only did most males assist females in feeding young, but the rates of food deliveries by females were significantly faster than females occupying upland and freshwater wetland habitats in Indiana (Patterson 1991) and Wisconsin (Yasukawa et al. 1990) (Table 4; Fig. 1). This finding is consistent with several Red-winged Blackbird studies that demonstrated that females at male-assisted nests do not reduce their provisioning rates as a result of receiving assistance from the male (Muldal et al. 1986, Whittingham 1989, Beletsky and Orians 1990, Yasukawa et al. 1990, Patterson 1991, Whittingham and Robertson 1994). Additionally, male provisioning rates at HAC were significantly greater than at the Indiana site in 1 of 2 yr (no difference in the other year), and significantly greater than at the Wisconsin site (Table 4; Fig. 1). While the suggestion is that the survival value of accelerated nestling development has selected for an accelerated provisioning rate, the high availability of food in saltmarsh habitats (Post and Greenlaw 1982, Post et al. 1983) may also play a role. Indeed, at HAC 70% of food trips were completed in the smooth cordgrass dominated habitats within territory boundaries (Tilton 1987). More likely, the two factors (selection and food abundance) are intertwined.

Thus, nestling provisioning behaviors at HAC (Tilton 1987) are consistent with the hypothesis that saltmarsh populations of the Red-winged Blackbird are adapted to produce young capable of fledging early—often by climbing up smooth cordgrass stems surrounding the nest—and that this ability is achieved by an enhanced nutritional status of nestlings. This is enabled by a high percentage of nests at which males assist females in the feeding of the nestlings, and a relatively high rate of food deliveries by both male and female parents. That more frequent feeding results in better conditioned young is clear, as several studies have shown that the starvation rate is lower, and the fledging success higher, for pair-fed Red-winged Blackbird nestlings vs. young fed by their mothers alone (Beletsky and Orians 1990, Yasukawa et al. 1990, Patterson 1991, Whittingham and Robertson 1994).

Renesting interval

In 62% (23 of 37) of documented cases, female Red-winged Blackbirds at HAC deposited the first egg in a new nest on the fifth day following the loss of an earlier active nest, and in 81% of cases the first egg of the replacement nest was deposited within 7 d of the earlier nest destruction event. Renest intervals of Red-winged Blackbirds as short as 4 d have been documented by Dolbeer (1976) and Beletsky and Orians (1996). Because Red-winged Blackbirds in my study area, and others (Picman 1981, Beletsky and Orians 1991), commonly produced four or five clutches within a breeding season, the energetic demands of renesting do not appear to be limiting.

Despite the ability to rapidly renest, and its apparent low cost, the available data on renest intervals reveals that not all female Red-winged Blackbirds respond to nest destruction by immediately initiating a new nest. In an Ohio old field, Dolbeer (1976) determined a mean renest interval of 9.7 d (range = 4–30 d) for 17 renests by a minimum of 16 females in 1973, and a mean of 12.1 d (range = 4–29 d) for 10 renests by a minimum of nine females in 1974. Yasukawa (pers. comm.) determined a mean renest interval of 6.1 d for 55 females renesting on the same territory, and 5.9 d for nine females that moved between territories following a nest loss. Of 877 intervals (following unsuccessful first nests only) documented in Washington by Beletsky and Orians (1996), 16% were of 5 d or fewer, 41% were of 6–10 d, and the remainder were >11 d. Thus, while timely renest responses are the norm for the populations for which data are available, females from most populations studied do not immediately initiate the replacement nest. Clearly, selection for near minimum nest intervals at HAC would be strong, as nests of females that delay initiating a new nest—even for only 1–3 d—after the loss of a nest to tidal flooding will likely be destroyed by the next spring tide should it survive to that stage. Indeed, most females at HAC initiated replacement nests immediately after suffering the loss of a nest. This contrast in renesting periods between saltmarsh and non-tidal populations of Red-winged Blackbirds parallels similar comparisons made in a Maine saltmarsh by Shriver (2002) between the Saltmarsh and Nelson's Sharp-tailed sparrows.

Renest intervals of the saltmarsh sparrow, an obligate saltmarsh species, were significantly shorter than those of Nelson's, a species for which freshwater marshes comprise the dominant breeding habitat. Shriver (2002) concluded that saltmarsh sparrows had likely evolved for a longer time with the predictable flooding effects of tides and the lunar cycle, and thus had developed, as demonstrated here for the Red-winged Blackbird, a relatively rapid post-flood renesting response.

CONCLUSIONS

Flooding is an important selective factor for shaping both the behavior and life history of birds that breed in tidal marshes. Taxa with long evolutionary histories in tidal-marsh systems show a variety of adaptations from nest construction and placement to the timing of breeding and the ability to rapidly renest. Even more interesting is the incipient behavioral adaptations of birds in tidal-marsh-breeding populations that otherwise show no local morphological adaptations to tidal marshes and are not known to be genetically distinct. The Red-winged Blackbirds of New England marshes clearly show an ability to nest rapidly in response to flooding events, which is facilitated by changes in nestling care and feeding. Such local adaptation to tidal-marsh conditions in an otherwise undifferentiated population is not surprising given the amount of differentiation that has been documented in a variety of taxa in the absence of underlying genetic divergence (Chan et al., *this volume*). Future research should focus on the degree to which the behavioral responses to flooding in tidal marsh passerines are facultative or genetically based.

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