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Author(s) :Rebecca L. Boulton, Ben Baiser, Michelle J. Davis, Thomas Virzi and Julie L. Lockwood

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VARIATION IN LAYING DATE AND CLUTCH SIZE: THE EVERGLADES ENVIRONMENT AND THE ENDANGERED CAPE SABLE SEASIDE SPARROW (*AMMODRAMUS MARITIMUS MIRABILIS*)

Rebecca L. Boulton,[1] Ben Baiser,[2] Michelle J. Davis, Thomas Virzi, and Julie L. Lockwood

Department of Ecology, Evolution and Natural Resources, Rutgers University, New Brunswick, New Jersey 08901, USA

Abstract.—When to commence breeding is a fundamental decision made by individuals that inhabit seasonal environments. Although photoperiod determines the timing of breeding in most temperate zones, other abiotic conditions can also play a significant role by influencing food availability and, consequently, reproductive performance throughout a breeding cycle. This study used the multibrooded endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*) to test whether water conditions (rainfall and groundwater levels) influenced breeding variables in a subtropical environment, the Florida Everglades. Timing of breeding was related to rainfall preceding the breeding season, with females initiating nesting up to 1 month earlier in years with greater rainfall. Clutch size averaged 3.4 eggs, and females showed an increase in clutch size as the breeding season progressed and in response to higher groundwater levels during the laying period. This effect was more apparent for first nesting attempts, with drier conditions limiting clutch size. Although wetter conditions favored earlier breeding and larger clutch sizes, annual nest survival (range: 12–36%) was negatively associated with high average rainfall late in the breeding season. Clutch-size variation and high nest survival in Cape Sable Seaside Sparrows' first nesting attempts suggests that food-mediated processes affect their reproductive decisions early in the breeding season, whereas predator-mediated processes drove overall reproductive output, possibly through increased activity of major nest predators during wetter conditions. *Received 23 August 2010, accepted 22 February 2011.*

Key words: *Ammodramus*, clutch size, Florida Everglades, rainfall, subtropical environment, timing of breeding.

Variación en la Fecha de Puesta y Tamaño de la Nidada: El Ambiente de los Everglades el Ave en Peligro *Ammodramus maritimus mirabilis*

Resumen.—La fecha de inicio de la reproducción es una decisión fundamental que toman los individuos que habitan los ambientes estacionales. Aunque el fotoperíodo determina la fecha de reproducción en la mayoría de las zonas templadas, otras condiciones abióticas pueden también jugar un papel importante al influenciar la disponibilidad de alimentos y, consecuentemente, el desempeño reproductivo a lo largo del ciclo de cría. Este estudio usó al ave en peligro con crías múltiples *Ammodramus maritimus mirabilis* para evaluar si las condiciones del agua (lluvia y niveles freáticos) influenciaron las variables reproductivas en un ambiente subtropical, los Everglades de Florida. La fecha de cría estuvo relacionada con la lluvia que precedió la estación reproductiva: las hembras iniciaron la anidación hasta un mes antes en los años con mayores lluvias. El tamaño de la nidada promedió 3.4 huevos y las hembras mostraron un incremento en el tamaño de la nidada a medida que la estación reproductiva avanzó y en respuesta a niveles freáticos más altos durante el período de puesta. Este efecto fue más marcado durante los primeros intentos de anidación, cuando las condiciones más secas limitaban el tamaño de la nidada. Aunque condiciones más húmedas favorecieron la anidación más temprana y tamaños de nidada mayores, la supervivencia anual de los nidos (rango: 12–36%) se asoció negativamente con un promedio elevado de lluvias a fines de la estación reproductiva. La variación en el tamaño de la nidada y la alta supervivencia de los nidos del primer intento de anidación de *A. m. mirabilis* sugieren que los procesos mediados por los alimentos afectan las decisiones reproductivas a inicios de la estación reproductiva. Mientras tanto, los procesos mediados por depredadores condujeron el resultado reproductivo general, posiblemente a través de un incremento en la actividad de los depredadores de nidos más grandes bajo condiciones más húmedas.

[1]Present address: Centre for Ornithology, School of Biosciences, Birmingham University, Edgbaston, B15 2TT, United Kingdom.
E-mail: rlboulton@gmail.com
[2]Present address: Harvard Forest, Harvard University, Petersham, Massachusetts 01366, USA.

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In seasonal environments, deciding when to breed is a fundamental aspect of a species' annual cycle. Shifting photoperiod lengths generally stimulate physiological changes in reproductive hormones and organs in species that breed in temperate and high-altitude environments (Farner and Lewis 1971, Dawson et al. 2001). These physiological changes are usually correlated with seasonal fluctuation in temperature and, importantly, food availability (Hau 2001). To date, most studies of avian phenology have focused on these temperate-zone species, but some studies have shown reproductive seasonality and response to photoperiod length in tropical and subtropical bird species (Tewary and Dixit 1986, Wikelski et al. 2003), despite less-pronounced photoperiod variability.

It is also apparent that other abiotic factors, such as rainfall, can influence important components of a species' reproductive performance besides the timing of breeding, through food-mediated and predator-mediated processes (Morrison and Bolger 2002). Food-mediated processes are particularly apparent in arid-zone species, in which rain events and warm conditions are associated with increased food availability and, consequently, increased breeding activity, clutch size, and reproductive success (Lloyd 1999, Morrison and Bolger 2002, Illera and Díaz 2006, Barrientos et al. 2007). Similar food-mediated climatic effects are also evident for species breeding in subtropical environments (Morrison et al. 2007, 2009; Monadjem and Bamford 2009).

The subtropical climate of the Florida Everglades is dominated by an annual wet and dry season that varies locally with the timing and magnitude of rainfall. Reliance on these rains is evident in the large breeding colonies of wading birds, in which water levels govern both food density and availability, and, ultimately, the birds' overall breeding success (Frederick and Ogden 2001, Gawlik 2002, Lorenz et al. 2009). However, the Everglades now suffer major hydrological alterations resulting from the construction of levees, canals, and pumping stations that modify the natural water flow (Light and Dineen 1994). Such anthropogenic alterations can dramatically influence avian phenology and other aspects of breeding. For example, if colonial wading birds mistime their breeding attempts because of the loss of short-hydroperiod wetlands, summer rains can disperse prey across the aquatic landscape of the Everglades, resulting in chicks starving in large numbers (Frederick et al. 2009).

Here, we investigate the effect of rainfall and groundwater levels on the phenology and other aspects of the breeding biology of a small, multibrooded passerine that inhabits the Everglades marl prairies. Unlike the extremely mobile wading birds that are capable of long-distance flights to new foraging or nesting areas, the endangered Cape Sable Seaside Sparrow (*Ammodramus maritimus mirabilis*; hereafter "sparrow") is relatively sedentary and remains within the marl prairie year-round (Pimm et al. 2002, Van Houtan et al. 2010). Accordingly, we might expect them to time their onset of breeding in accordance with favorable water conditions. We might also expect that water conditions will dictate clutch size and overall breeding success in a species, such as the sparrow, that relies on aquatic food resources.

We used 8 years of sparrow breeding-biology data to test whether (1) timing of breeding was associated with water conditions (both rainfall and groundwater levels) during the preceding months; (2) clutch size varied with nesting attempt or water conditions during the laying period; and (3) variation in water conditions during or late in the breeding season were related to annual nest survival. We predicted that sparrows would show some patterns similar to resident multibrooded species—that is, commence breeding when they had acquired enough resources to form a clutch (Crick et al. 1993). With much of the literature originating from temperate species, it was unclear whether sparrows would show a marked midseason peak or a seasonal decline in clutch size (Klomp 1970, Perrins 1970, Crick et al. 1993, Davis 2003), because we would expect enduring resource abundance throughout a subtropical breeding season, compared with temperate environments. However, the risk of nest predation may also affect seasonal clutch-size variation (Slagsvold 1982). We already knew that nest survival of sparrows substantially declined across the breeding season (Baiser et al. 2008); therefore, we predicted that females would lay smaller clutches as the breeding season progressed.

Methods

Study species and area.—The study species is restricted to the freshwater ecosystem of the Florida Everglades. This subspecies is closely allied to the Atlantic matrilineal clade of seaside sparrows (Nelson et al. 2000), and thus has sister taxa that span both temperate and more northerly subtropical climates (e.g., the now extinct Dusky Seaside Sparrow [*A. m. nigrescens*]). The Cape Sable Seaside Sparrow is nonmigratory and remains relatively faithful to breeding locations (Van Houtan et al. 2010). Although pairs generally remain together and defend a breeding territory (~2 ha; Pimm et al. 2002) throughout the breeding season, pair bonds are not always maintained to the next year. Within the marl prairies, the sparrow constructs a small, cup-shaped nest of dead grass and sedge ~16 cm above the ground. Females re-nest after both successful and failed nesting attempts, with up to 3 or 4 attempts per breeding season (March–July), laying an average of 2–4 eggs per attempt (Lockwood et al. 1997). Although some nests fail because they are flooded (Lockwood et al. 1997), this is relatively uncommon, and most sparrow nests fail because of predation (97% of failures; Baiser et al. 2008).

We studied the sparrow during eight breeding seasons (March–July, 2002–2009) in eastern Everglades National Park, Florida (25°30′N, 80°40′W). We established a single study plot (2 km^2) at this site (referred to as "subpopulation E" in Baiser et al. 2008) in 1998, but intensive monitoring did not occur until 2002. Vegetation on the plot is dominated by Gulfhairawn Muhly (*Muhlenbergia filipes*), Jamaica Swamp Sawgrass (*Cladium mariscus jamaicense*), beaksedges (*Rhynchospora* spp.), and Florida Little Bluestem (*Schizachyrium rhizomatum*).

Field methods.—During the start of each breeding season (late March), we searched weekly for sparrow nests on breeding territories by observing the behavior of both male and female sparrows. Generally, either the male or the female was individually color-banded for identification. All nest sites were marked with a surveyor flag situated 2 m on either side of the nest and checked every 2–3 days until they successfully fledged or failed. We defined nest survival as the probability that a nest survived from the first egg laid to fledging at least one young (a 25-day period for this species; Lockwood et al. 1997).

The 2008–2009 dry season ranked as the second driest on record for most of south Florida according to the National Oceanic and Atmospheric Administration, with the eastern half of south Florida receiving rainfall totals 25–40% below average. These severe drought conditions gave way to an early and very abrupt start to the wet season. Unfortunately, because of these extreme thunderstorms late in May 2009 (>30 cm of rain in a week), we suspended field work early, which resulted in only first nesting attempts being monitored (Virzi et al. 2009). For this reason, we include only 2009 data in the timing of breeding analysis because of strong seasonal changes in nest survival (Lockwood et al. 1997, Baiser et al. 2008) and changes in clutch size between nesting attempts (see results below).

Typically, we discovered nests during the incubation or nestling period and extrapolated laying dates from known hatch dates (Lockwood et al. 1997). When nests failed during incubation, we extrapolated laying date by subtracting the incubation midpoint (5 days) and number of eggs (assuming 1 egg laid each day) from when the nest was first located. When determining timing of breeding we only used the first nesting attempt from each pair, excluding pairs whose earliest nests we discovered after the years' first renesting pair. This is a conservative measure to avoid including renesting attempts in our sample, because we likely underrepresented late first-time breeders. We calculated for each year the first egg-laying date (earliest nest found during each breeding season) and the median first egg-laying date. Clutch size was calculated from nesting attempts found during the incubation or laying periods only (after the female initiated incubation) because partial predation or mortality of nestlings can occur in this species. We calculated hatching success (the proportion of original eggs in the clutch that successfully hatched) from clutches of known clutch size only.

Water variables.—Within the Everglades, rain falls mainly during the hot, humid wet season (June–September) as intense thunderstorms and severe tropical storms. By contrast, weather during the mild dry season (October–May) is generally dry, with low humidity. At the beginning of the sparrows' breeding season, toward the end of the dry season, groundwater levels tend to be low, with very little or no permanent water in solution holes across the marl prairie. Solution holes are eroded depressions within the limestone and, unlike sinkholes, they do not meet the water table but fill via rainwater. It is around these solution holes that sparrows primarily forage during dry conditions, because the holes serve as important refuges for aquatic invertebrates (Loftus et al. 1992). We evaluated the effect of both daily rainfall and groundwater levels on timing of breeding, annual nest survival, clutch size, and hatching success. Unlike recent studies of sparrows that incorporate only groundwater levels in their analyses (Baiser et al. 2008, Cade and Dong 2008, Elderd and Nott 2008, Boulton et al. 2009), we used rainfall as well. We hypothesized that rainfall sustaining solution-hole moisture may better predict some demographic variables, such as clutch size, during periods of little groundwater variation (i.e., beginning of the breeding season).

Daily rainfall data (cm) based on Next Generation Radar (NEXRAD; coverage from 2002 to present) were obtained for the National Park Service–operated water station CR3, situated ~1.5 km south of the study site (25°29′N, 80°39′W). The precision for the gauge-adjusted radar is considered the same as standard rain-gauge precision, which is typically reported to the nearest 0.25 mm. Rainfall data from 16 to 31 December 2001 were obtained directly from the weather station NP-RPL, 15 km south of the study site (25°23′N, 80°35′W). We extracted daily groundwater depths (m) from the Everglades Depth Estimation Network (EDEN; Palaseanu and Pearlstine 2008), a hydrological module using ground-elevation measurements and continuous water-level data from 253 real-time gauge stations across the greater Everglades. Validation of the EDEN model shows that the data presented on a 400-m^2 grid is a reliable estimation (±5 cm) of field-observed water levels (Liu et al. 2009). Using the EDEN xyLocator Tool, version 1.4, we extracted water depths across the study plot, resulting in 23 EDEN cells (400 × 400 m cells). We averaged the water depth across these cells to obtain daily average groundwater levels.

In our analysis of timing of breeding, we created four water variables: average rainfall ($_R$) and groundwater levels ($_{WL}$) 3 months prior to breeding (mid-December to mid-March; $3month_R$ and $3month_{WL}$) and 2 months prior to breeding (mid-January to mid-March; $2month_R$ and $2month_{WL}$). We regard these variables as potentially important periods throughout the sparrows' annual cycle because they represent abiotic conditions experienced by sparrows before and during pair formation. We used four additional water variables in our analysis of annual nest survival: rainfall and groundwater levels during the complete breeding season (mid-March to mid-July; $Breeding_R$ and $Breeding_{WL}$) and during the late breeding season (mid-May to mid-July; $Late_R$ and $Late_{WL}$). For the clutch-size analysis, we calculated water variables for each clutch as the average daily rainfall and groundwater level for a 7-day period, running 5 days before and 1 day after laying of the first egg ($7day_R$ and $7day_{WL}$). We regard this 7-day window as the average egg-formation period, given that follicle growth in small passerines lasts 3–5 days before oviposition (King 1973, Ojanen 1983). Thus, these water variables represent the environmental conditions that females experience during egg formation, a period when food availability is critical for egg production (Ardia et al. 2006). For the hatching-success analysis, we calculated water variables for each clutch as the average daily rainfall and groundwater level for a 20-day period running from 5 days before laying until hatch day ($20day_R$ and $20day_{WL}$).

Analyses.—We used the nest-survival module in Program MARK, version 5.1, to produce annual nest-survival estimates (White and Burnham 1999, Dinsmore et al. 2002). Although MARK is a powerful program capable of assessing the influence of a wide range of independent variables on daily survival probabilities, we use only a single yearly estimate here, because Baiser et al. (2008) previously analyzed daily survival rates and their relationship to groundwater levels at this plot. Although Baiser et al. (2008) used groundwater levels from the nearby water-monitoring station, comparison with simulated EDEN data shows a difference of <0.01 m between our plot averages and their data. For nests with known clutch size, we used MARK to calculate average nest survival for first, second, and third nesting attempts.

We tested the relationship between timing of breeding (first and median egg laying dates) and annual nest survival against our water variables using generalized linear models with a normal link function, PROC GLM, in SAS, version 9.2 (SAS Institute, Cary, North Carolina). Before carrying out these analyses, we assessed the level of collinearity among the water variables by calculating variance inflation factors (VIF) for each variable (PROC REG).

Large VIF scores indicated potential collinearity, and although dropping the variable with the highest VIF value reduced VIFs to 2–3, collinearity can still be a problem with weak ecological signals (Zuur et al. 2010). Adopting the more conservative approach, we constructed models with only one of a pair of collinear water variables at a time. Models were ranked using Akaike's information criterion corrected for small sample size (AIC_c), and models with ΔAIC_c values ≤2 were considered equivalent (Burnham and Anderson 2002). We present effect sizes as linear model estimates ± SE for the top models.

We analyzed the response variable "clutch size" using generalized linear mixed models with a normal link function fitted with the SAS GLIMMIX macro (Littell et al. 1996). To control for the non-independence of multiple nests per individual female, within and between breeding seasons, we included female identity as a random effect. We also included year as a random effect to control for annual variation in clutch size due to unexplained seasonal differences. We examined the relationship between the response variable and the following predictor variables: nesting attempt (consecutive female nesting attempt per breeding season; first, second, third), date (laying date for each clutch; Julian day index standardized from 20 March), dateQ (quadratic date effect), and $7day_R$ and $7day_{WL}$. We constructed candidate models using all subsets of the global model, including the second-order interaction terms between our single categorical variable (nesting attempt) and the water variables ($7day_R$ and $7day_{WL}$). There was evidence of collinearity between the variables nesting attempt and date (VIF > 3); therefore, they were not considered in models simultaneously. Models were ranked using AIC_c. Because of the extremely small number of fourth nesting attempts ($n = 5$), we combined third and fourth nesting attempts in the analysis. We analyzed the proportional response variable "hatching success" fitted with a binomial link function.

RESULTS

Timing of breeding.—The earliest date on which an egg was observed in a sparrow nest varied from 20 March (2004 and 2007) to 21 April (2009). The earliest median first egg-laying date was 25 March (2004) and the latest was 30 April (2009). The best model indicated that there was a significant negative relationship between median first egg-laying date and average rainfall 2 months prior to breeding (Table 1A and Fig. 1), which indicated that sparrows initiated breeding earlier in years of higher rainfall. Although the best model explaining first egg-laying date indicated a negative relationship with rainfall 3 months prior to breeding (Table 1B), the standard error around this estimate was very large (i.e., the 95% confidence interval includes zero) and thus provided no confidence in the effect size.

Annual nest survival.—We monitored 315 sparrow nests from 2002 to 2008, with daily nest-survival probabilities ranging from 0.919 to 0.960. When extrapolated to a 25-day nesting period, these daily nest-survival probabilities gave an annual nest survival range of 12–36% across the study period. Only one model received substantial support (Table 1C), with sparrows experiencing reduced nest survival in years of high average rainfall late in the breeding season. Nest survival was not related to changes in groundwater levels (Table 1C).

TABLE 1. The best generalized linear models explaining variation in (A) median first egg date, (B) first egg date, and (C) nest survival in relation to water conditions for Cape Sable Seaside Sparrows in the Everglades National Park, Florida, 2002–2009. All models within five AIC_c units of the top model are included. The variables are average rainfall 2 months ($2month_R$) and 3 months ($3month_R$) prior to breeding, throughout the breeding season ($Breeding_R$) and late in the breeding season ($Late_R$).

Model	k[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	Estimate ± SE
(A) Median first egg date					
$2month_R$	2	35.0	0.0	0.93	–146.28 ± 21.55
(B) First egg date					
$3month_R$	2	42.8	0.0	0.71	–54.48 ± 76.09
$2month_R$	2	44.9	2.1	0.25	–39.52 ± 43.26
(C) Nest survival[e]					
$Late_R$	2	29.7	0.0	0.86	–33.467 ± 4.86
$Breeding_R$	2	33.7	4.0	0.12	–60.198 ± 16.76

[a]Number of parameters in model.
[b]Akaike's information criterion corrected for small sample sizes.
[c]Difference in AIC value from that of the best model.
[d]Akaike weights, indicating the relative support for the models.
[e]Nest survival data do not include the year 2009.

Clutch size.—Over the 2002–2008 study period, females laid an average (± SE) of 3.4 ± 0.05 eggs nest^{-1} (range: 2–5, $n = 175$). The largest clutch size was recorded in 2007, when females laid no 2-egg clutches and the overall average clutch size was 3.7 ± 0.11 eggs (range: 3–5, $n = 26$). In 2004, we recorded the smallest average clutch size (3.1 ± 0.16 eggs; range: 2–4, $n = 16$). Only one model in our candidate set received substantial support (Table 2A), including the variable nesting attempt and its interaction with groundwater levels during egg formation and laying. Clutch size differed among nesting attempts (Fig. 2A), with first nesting attempts

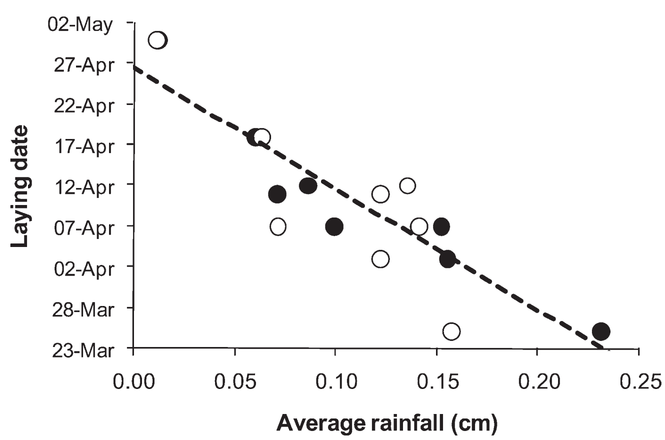

FIG. 1. Scatter plot of median first egg-laying dates of Cape Sable Seaside Sparrows (2002–2009) and average rainfall levels 2 months (filled circles; mid-January to March, $2month_R$) and 3 months prior to breeding (open circles; mid-December to mid-March, $3month_R$) in the Everglades National Park, Florida. Dashed line represents the model $2month_R$ explaining median first egg-laying-date variation with rainfall conditions 2 months prior to breeding.

Table 2. Summary of the generalized linear mixed models explaining variation in (A) clutch size and (B) hatching success of Cape Sable Seaside Sparrows in the Everglades National Park, Florida, 2002–2008. Models are ranked in ascending AIC_c and all models within five AIC_c units of the top model are shown. The variables are nesting attempt (consecutive female nesting attempt per breeding season; first, second, third), $7day_R$ (average rainfall around first egg laying), $7day_{WL}$ (average groundwater level around first egg laying), and $20day_R$ (average rainfall 20 days preceding hatching).

Model[a]	*k*	AIC_c	ΔAIC_c	w_i
(A) Clutch size				
Nesting attempt + $7day_{WL}$ + nesting attempt*$7day_{WL}$	4	318.9	0.0	0.61
Nesting attempt	2	321.4	2.5	0.17
Nesting attempt + $7day_{WL}$	3	322.9	4.0	0.08
Nesting attempt + $7day_R$	3	323.6	4.7	0.06
(B) Hatching success				
$20day_R$	2	513.4	0.0	0.64
Constant	1	515.8	2.4	0.19
Nesting attempt	2	518.2	4.8	0.06

[a]Controlling for individual female and year as random effects.

having significantly smaller clutches than both second and third attempts. As shown in Figure 2B, clutch size declined as groundwater levels dropped only in the females' first nesting attempts.

Daily nest-survival probabilities for these first nesting attempts was 0.964 (overall success 40%; 95% confidence interval [CI]: 28–52%), which is considerably higher than for both second (0.935; overall success 19%; 95% CI: 10–28%) and third nesting attempts (0.905; overall success 8%; 95% CI: 2–19%).

Only one candidate model substantially supported the 2002–2008 hatching-success data for sparrows (Table 2B), and it showed that hatching success declined when rainfall was high prior to hatching. However, the standard error around this estimate was very large ($20day_R$ linear estimate ± SE = 0.196 ± 0.604), and the interval included zero, thus providing no confidence in the effect size for our final model.

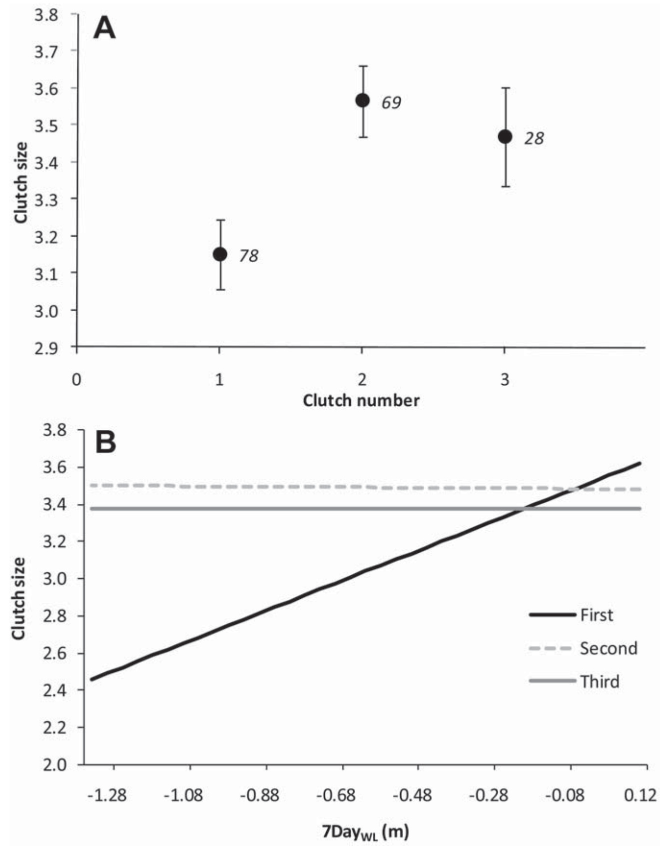

Fig. 2. (A) Clutch size for first, second, and third nesting attempts (least square means ± SE) of Cape Sable Seaside Sparrows from the Florida Everglades during the 2002–2008 breeding season. Italicized numbers represent sample sizes. (B) Clutch-size estimates for first, second, and third nesting attempts across different groundwater levels experienced during the study period, derived from the best model (nesting attempt + $7day_{WL}$ + nesting attempt*$7day_{WL}$; Table 2) explaining clutch-size variation. Estimates shown were controlled for individual female and yearly variation as random effects.

Discussion

We found that water, as either rainfall or groundwater, helped explain both within-nest and within-season variation in reproductive measurements for the Cape Sable Seaside Sparrow. Whereas wetter conditions were associated with earlier breeding and larger clutch sizes for first nesting attempts, wetter conditions were also linked to reduced annual nest survival. We hypothesize that this variation may indicate both food-mediated and predator-mediated processes influencing sparrows' reproductive decisions during different stages of the breeding cycle.

Rainfall levels appeared to influence the timing of breeding in the sparrow prior to the onset of breeding, with females initiating laying earlier with increased rain during the 2 months before breeding. Although rain late in the dry season is not as episodic or widespread as wet-season rainfalls, its absence appears to delay breeding by up to a month (most evident in 2009). This relationship may be driven by the response of sparrows to their dominant prey items; we would expect a multibrooded species to commence breeding as soon as sufficient resources become available to form a clutch (Crick et al. 1993). The mechanism behind the seasonal patterns in tropical insect abundance is poorly understood and may or may not be related to rainfall (Wolda 1978b, 1989), although environments with pronounced dry seasons often experience lower insect abundance during this period (Wolda 1978a, 1988). In the Everglades, before the sparrow's breeding season, water levels are often below ground level throughout the marl prairie, with no freely available water. The significance of rainfall, not groundwater levels, during this period may suggest rapid invertebrate response to localized rainfall or that sparrows are capable of using rainfall as a cue for future food availability (Zann et al. 1995). Although we did not measure arthropod abundance in the present study, we know from previous work that during the breeding season sparrows feed largely on the insect orders Orthoptera, Lepidoptera, and Odonata and are capable of shifting their diets in response to the changing availability of these insects (Lockwood et al. 1997).

Drier conditions during first nesting attempts were associated with smaller clutches, providing support for the view that food resources are limited at the start of the breeding season. With predation pressure in this system being lowest at the beginning of the breeding season (Baiser et al. 2008), we would expect females to lay larger first clutches, because clutch size is strongly related to predation rates in the closely related tidal-marsh sparrows (Greenberg et al. 2006). It appears that Cape Sable Seaside Sparrows lay their first clutch in suboptimal conditions (Crick et al. 1993), perhaps to allow additional time for raising multiple broods throughout the season or to avoid increasingly higher nest-predation rates later in the season.

In our study, the clutch sizes of sparrows increased midseason during the onset of the wet season, when groundwater levels began to rise and solution holes started to contain standing water. Although this increase in clutch size is in accord with a multibrooded-species model (Crick et al. 1993), it is somewhat surprising given the increase in nest predation (Greenberg et al. 2006, Olsen et al. 2008). However, females experience relatively high nest success during their first nesting attempt, and with increasingly favorable conditions lay larger second clutches. After experiencing higher predation rates, females have the opportunity to assess future offspring value and reduce their reproductive investment (Doligez and Clobert 2003, Eggers et al. 2006). Unfortunately, because of extremely high nest predation, our sample of third nesting attempts was small and we observed only a slight decline in clutch size. With a larger sample, it is possible that we would have observed a significant decline in clutch size toward the end of the breeding season.

Despite finding that lower annual nest survival in breeding seasons is clearly associated with high average rainfall, we recognize that the overall relationship between rainfall and nest survival is undoubtedly more complex. Directly linking these variables has proved difficult in this system because of the strong seasonal decline in nest survival, which is synchronized with wetter conditions late in the breeding season (Lockwood et al. 1997, Baiser et al. 2008). Although actual flooding of nests is rare, predation levels steadily increase as the breeding season advances and conditions get progressively wetter, which implies that predator-mediated processes affect breeding success (Rotenberry and Wiens 1991, Morrison and Bolger 2002, Baiser et al. 2008). We propose that late-season rainfall interacts with the sparrow's major nest predators, possibly through increased search efficiency. Two known sparrow predators are the Marsh Rice Rat (*Oryzomys palustris*) and Water Moccasin (*Agkistrodon piscivorus*) (Dean and Morrison 1998). How water levels influence their behavior is currently unknown. However, we assume that their activity in the marl prairie is limited during the dry season, when sparrows experience higher nest survival, given that both species are semiaquatic predators that rely on wet refugia (Smith and Vrieze 1979, Bernardino and Dalrymple 1992).

Evidence concerning the importance of water levels for food resources, predators, and subsequent breeding success in south Florida birds varies (Frederick and Ogden 2001; Beissinger and Snyder 2002; Morrison et al. 2007, 2009; Lorenz et al. 2009). Contrasting results among raptors, wading birds, and small passerines likely reflect the different foraging substrates and prey items consumed by each species and differing predation pressure. Clearly, the relationships we have reported here between water and breeding by sparrows is complex. We have demonstrated that wetter conditions early in the breeding season may favor reproduction through food-mediated processes, while wetter conditions late in the breeding season may have negative effects on nest survival via predator-mediated processes. We know that successful second and third nesting attempts are critical for positive population growth in this species (Lockwood et al. 2001). Therefore, wetter conditions early in the season could benefit the species, in that females could nest earlier, lay slightly larger clutches, and initiate second attempts before water level and predation rates dramatically increase. Water management for this endangered species has been and will continue to be controversial (Walters et al. 2000). Our results help highlight the potential consequences that water-management decisions can have on the sparrow's breeding biology within this subtropical environment.

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