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SPATIAL AND TEMPORAL VARIABILITY IN NEST SUCCESS OF SNAIL KITES IN FLORIDA: A META-ANALYSIS

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Abstract. Nesting success of Snail Kites (*Rostrhamus sociabilis*) in Florida is highly variable among years and locations, and hydrology is the most frequently reported explanatory factor. We conducted a meta-analysis to evaluate the extent of spatial and temporal variability in nesting success, and explicitly tested for the effects of annual minimum water levels. Data were obtained from six independent studies spanning 22 years and 11 wetlands. Our results indicated there was substantial spatial and temporal variability in nest success and that annual minimum water level, either as a categorical or continuous response, was not a significant source of this variation. Our results do not imply that low water levels do not influence nest success. Rather, they indicate that the number of nests affected by low water conditions was quite low (<1%). A wetland area experiences low water once every 5 to 10 years, and seldom does such an event encompass the entire range of Snail Kites in Florida. During a low water event, kites are capable of moving to alternative locations. Thus, relatively few birds may exhibit low nest success as a result of low water events, and management aimed at preclusion of such events may be unnecessary and detrimental to maintenance of the habitat over long time scales.

Key words: endangered species, Everglades, Florida, meta-analysis, nest success, Rostrhamus sociabilis, *Snail Kite.*

Variabilidad Espacial y Temporal en el Éxito de Anidación de *Rostrhamus sociabilis* en Florida: Un Meta-Análisis

Resumen. El éxito de anidación de *Rostrhamus sociabilis* en Florida varía ampliamente entre años y localidades. La hidrología es el factor que se ha propuesto con mayor frecuencia para explicar dicha variabilidad. Llevamos a cabo un meta-análisis para evaluar la magnitud de la variabilidad espacial y temporal en el éxito de anidación y pusimos a prueba explícitamente el efecto de los niveles mínimos anuales de agua. Los datos fueron obtenidos de seis estudios independientes comprendiendo 22 años y 11 humedales. Nuestros resultados indicaron que hubo gran variación espacial y temporal en el éxito de anidación y que el nivel mínimo anual de agua (ya sea como una respuesta categórica o continua), no fue una fuente significativa de esta variación. Nuestros resultados no implican que niveles bajos de agua no afectan el éxito de anidación. En cambio, indican que el número de nidos afectados por condiciones de aguas bajas fue bastante bajo (<1%). Un área de humedales presenta aguas bajas una vez cada cinco o diez años y es raro que uno de estos sucesos abarque todo el rango de *R. sociabilis* en Florida. Durante una época de aguas bajas, las aves están en capacidad de moverse hacia otros sitios por lo que relativamente pocas podrían tener bajo éxito reproductivo como consecuencia de la escasez de agua. El manejo dirigido a suprimir estos eventos podría ser innecesario e ir en detrimento del mantenimiento del hábitat a largo plazo.

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INTRODUCTION

The tolerance for environmental stochastic events differs among species, with some having life-history strategies that allow greater tolerance than other species. Variability in environmental factors (e.g., temperature and rainfall) can influence life-history traits, and the degree to which each species responds to environmental heterogeneity varies by orders of magnitude both temporally and spatially (Rhodes and Odum 1996). For conservation strategies and management decisions it is important to determine the critical environmental factors that influence populations and to what extent populations can adjust to environmental variation (Ricklefs 1973). For many wetland species, hydrology is a key environmental factor that influences life history strategies and thus, the population dynamics of these species (Ogden et al. 1980, Johnson et al. 1991, Cézilly et al. 1995, Sykes et al. 1995).

The Snail Kite (*Rostrhamus sociabilis*) occurs within the wetlands of central and southern Florida. Reproduction, particularly nest success, of Snail Kites in Florida has been well studied (Beissinger 1986, Sykes 1987, Bennetts et al. 1988, Snyder et al. 1989). Nest success of Snail Kites is highly variable among years and wetland areas (Snyder et al. 1989, Sykes et al. 1995). Water levels, particularly low water conditions associated with droughts, have been the factor most frequently reported to influence nest success (Beissinger 1986, Sykes 1987, Snyder et al. 1989).

Assessments of the environmental factors that influence life-history traits are commonly limited by the spatial and temporal extent of most research. Studies conducted at one or two study sites for one or two years offer little potential to assess variation expressed across broad landscapes over many years. Recent advances in the use of meta-analysis offer some relief from this limitation. Meta-analysis enables one to derive a quantitative summary of data from multiple studies and to assess variation over time and space (Arnqvist and Wooster 1995, Burnham et al. 1996). A major benefit of meta-analysis is that it has an improved control over Type II error because of larger effective sample size (Arnqvist and Wooster 1995). Meta-analysis has been used in a number of ecological studies (Gurevitch et al. 1992, Burnham et al. 1996, Kennedy 1997, Franklin et al. 1999). Only a few of these studies examined the ecology of individual species: the Northern Spotted Owl (*Strix occidentalis caurina*; Burnham et al. 1996, Franklin et al. 1999) and Northern Goshawk (*Accipiter gentilis*; Kennedy 1997). Here we conduct a meta-analysis on the nesting success of Snail Kites in central and southern Florida using data collected during studies encompassing more than 22 years. We use this analysis to test for the effect of low water conditions on nest success and to evaluate other potential sources of the spatial and temporal variability in nest success.

METHODS

Data used for the meta-analysis were obtained from studies that were conducted from 1972 through 1997, excluding 1984, 1985, 1988, and 1989, in which no data were collected. The studies covered 11 wetland areas (Table 1). These studies differed in the way they defined nest initiation. Some studies (Beissinger 1986, Snyder et al. 1989) considered structures prior to egg laying as the initiation of a nesting attempt. However, pair bonds for this species are not often established during the pre-laying stage. Failures at this stage constitute courtship failure rather than nest failure (Bennetts et al. 1994). Thus, we followed the definitions of Steenhof (1987) and considered a nesting attempt to begin with the laying of the first egg. A nest was considered successful when at least one young reached 24 days (80% of age of first flight, Steenhof and Kochert 1982). After this time, fledglings begin to leave the nest and may or may not be found in the immediate vicinity of the nest. The Mayfield method (Mayfield 1961, 1975) for estimating nest success was not used because data for each nest visit were not available for most studies. The Mayfield method takes into account the biases (i.e., overestimation of nest success) associated with not finding a nest on the first day of the nesting period (Hensler and Nichols 1981). The success rate for years and areas for which only one nest (n = 10) was reported cannot be estimated (i.e., success rate = 0 or 1) and were excluded from the analysis.

Previous literature regarding water-level effects on Snail Kites (Beissinger 1986, Sykes 1987, Snyder et al. 1989) have used the term "drought", without defining whether droughts denote low rainfall or low water levels, although the discussions imply the latter. Nor have these authors defined any criteria regarding magnitude, duration, or spatial extent of droughts (Bennetts and Kitchens 1997a, Bennetts et al. 1999). Because water levels in Florida's wetlands have become increasingly disconnected from rainfall as a result of management (Kitchens et al. 2001), we focused on water levels,

TABLE 1. Data from six sources used to conduct a meta-analysis on nesting success of Snail Kites at 11 wetland areas in Florida, and resulting estimates of nest success ($\hat{S}$) and corresponding standard errors ($\hat{SE}(\hat{S})$).

Year	Area[a]	Type	Number of nests	($\hat{S}$)[b]	$\hat{SE}(\hat{S})$[b]	Water[c]	Source
1972	Lake Okeechobee	Lake	3	0.33	0.27	–0.20	Snyder et al. (1989)
1973	Lake Okeechobee	Lake	18	0.22	0.10	–0.41	Snyder et al. (1989)
1974	Lake Okeechobee	Lake	13	0.00	—[d]	–1.18	Snyder et al. (1989)
1975	Lake Okeechobee	Lake	15	0.00	—[d]	–0.70	Snyder et al. (1989)
1976	Lake Okeechobee	Lake	18	0.00	—[d]	–0.58	Snyder et al. (1989)
1977	Lake Okeechobee	Lake	13	0.15	0.10	–0.28	Snyder et al. (1989)
1978	Lake Okeechobee	Lake	4	0.00	—[d]	1.01	Snyder et al. (1989)
1978	WCA-3A	Marsh	55	0.46	0.07	1.18	Snyder et al. (1989)
1979	Lake Okeechobee	Lake	12	0.33	0.14	0.96	Snyder et al. (1989)
1979	WCA-3A	Marsh	66	0.58	0.06	0.65	Snyder et al. (1989)
1980	Lake Okeechobee	Lake	2	0.00	—[d]	0.68	Snyder et al. (1989)
1981	WCA-3A	Marsh	5	0.00	—[d]	–1.29	Snyder et al. (1989)
1982	KTOH	Lake	12	0.08	0.08	0.32[e]	Snyder et al. (1989)
1983	OKKIS	Lake	6	0.17	0.15	1.09[e]	Snyder et al. (1989)
1983	WCA-3A	Marsh	12	0.33	0.14	0.54	Snyder et al. (1989)
1986	WCA-3A	Marsh	107	0.26	0.04	0.76	Bennetts et al. (1988)
1987	WCA-3A	Marsh	210	0.44	0.03	0.39	Bennetts et al. (1988)
1990	St. Johns Marsh	Marsh	26	0.08	0.05	0.96	Toland (1994)
1991	St. Johns Marsh	Marsh	41	0.34	0.07	0.91	Toland (1994)
1991	WPBWCA	Marsh	11	0.64	0.15	0.68	Mihalik (1994)
1992	St. Johns Marsh	Marsh	59	0.54	0.06	0.40	Toland (1994)
1992	WCA-2A	Marsh	15	0.47	0.13	–0.83	Bennetts et al., unpubl. data
1992	WCA-2B	Marsh	2	0.00	0.00	–0.88	Bennetts et al., unpubl. data
1992	WCA-3A	Marsh	5	0.20	0.18	0.06	Bennetts et al., unpubl. data
1992	WPBWCA	Marsh	14	0.79	0.11	–0.65	Mihalik (1994)
1993	St. Johns Marsh	Marsh	43	0.35	0.07	1.21	Toland (1994)
1993	WCA-2A	Marsh	24	0.33	0.10	0.16	Bennetts et al., unpubl. data
1993	WCA-2B	Marsh	6	0.50	0.20	0.75	Bennetts et al., unpubl. data
1993	WCA-3A	Marsh	41	0.42	0.08	1.14	Bennetts et al., unpubl. data
1993	WCA-3B	Marsh	2	1.00	—[d]	1.29	Bennetts et al., unpubl. data
1993	WPBWCA	Marsh	24	0.75	0.09	0.46	Mihalik (1994)
1994	Lake Kissimmee	Lake	30	0.50	0.09	1.42	Bennetts et al., unpubl. data
1994	Lake Okeechobee	Lake	5	0.60	0.22	0.52	Bennetts et al., unpubl. data
1994	St. Johns Marsh	Marsh	4	0.25	0.22	1.10	Bennetts et al., unpubl. data
1994	WCA-2B	Marsh	33	0.61	0.09	1.20	Bennetts et al., unpubl. data
1994	WCA-3A	Marsh	27	0.59	0.09	0.97	Bennetts et al., unpubl. data
1994	WPBWCA	Marsh	6	0.00	—[d]	0.55	Mihalik, unpubl. data
1995	Big Cypress National Preserve	Marsh	17	0.53	0.12	2.04	Bennetts et al., unpubl. data
1995	Lake Okeechobee	Lake	18	0.50	0.12	1.53	Bennetts et al., unpubl. data
1995	St. Johns Marsh	Marsh	19	0.21	0.09	1.03	Bennetts et al., unpubl. data
1995	West Lake Tohopekaliga	Lake	11	0.64	0.15	0.41	Bennetts et al., unpubl. data
1995	WCA-2A	Marsh	4	0.50	0.25	0.58	Bennetts et al., unpubl. data
1995	WCA-2B	Marsh	70	0.67	0.06	1.34	Bennetts et al., unpubl. data
1995	WCA-3A	Marsh	33	0.42	0.09	1.02	Bennetts et al., unpubl. data
1995	WPBWCA	Marsh	11	0.37	0.15	1.25	Mihalik, unpubl. data
1996	Big cypress National Preserve	Marsh	7	0.71	0.17	1.03	Dreitz et al., unpubl. data
1996	Everglades National Park	Marsh	4	0.75	0.22	0.62	Dreitz et al., unpubl. data
1996	Lake Okeechobee	Lake	22	0.36	0.10	0.84	Dreitz et al., unpubl. data
1996	St. Johns Marsh	Marsh	9	0.33	0.16	0.98	Dreitz et al., unpubl. data
1996	West Lake Tohopekaliga	Lake	16	0.13	0.08	1.69	Dreitz et al., unpubl. data
1996	WCA-2B	Marsh	3	0.33	0.27	1.12	Dreitz et al., unpubl. data
1996	WCA-3A	Marsh	60	0.48	0.06	0.99	Dreitz et al., unpubl. data
1996	WPBWCA	Marsh	4	0.75	0.22	0.63	Mihalik, unpubl. data

TABLE 1. Continued.

Year	Area[a]	Type	Number of nests	$(\hat{S})^b$	$S\hat{E}(\hat{S})^b$	Water[c]	Source
1997	Lake Okeechobee	Lake	3	0.00	—[d]	0.02	Dreitz et al., unpubl. data
1997	St. Johns Marsh	Marsh	22	0.18	0.08	0.54	Dreitz et al., unpubl. data
1997	West Lake Tohopekaliga	Lake	28	0.11	0.06	0.45	Dreitz et al., unpubl. data
1997	WCA-2B	Marsh	19	0.16	0.08	0.71	Dreitz et al., unpubl. data
1997	WCA-3A	Marsh	168	0.51	0.04	0.91	Dreitz et al., unpubl. data
1997	WPBWCA	Marsh	5	0.20	0.18	0.90	Mihalik, unpubl. data
			$n = 1541^f$	mean	$\hat{S} = 0.41^f$		

[a] WCA = Water Conservation Area; KTOH = Lake Kissimmee and West Lake Tohopekaliga (the number of nests was not reported separately for these areas); OKKIS = Lake Okeechobee and Lake Kissimmee (the number of nests was not reported separately for these areas); WPBWCA = West Palm Beach Water Catchment Area.
[b] Based on area × year model.
[c] Minimum annual water levels, measured as the number of standard deviations above or below the annual mean minimum water levels (standard normal).
[d] Not estimated due to error in convergence.
[e] Weighted average for the two areas.
[f] Based on "no effects" model.

rather than rainfall, as indications of low water. Our measure of water level for an area on an annual basis was the variation in mean annual minimum elevation of the water surface relative to mean sea level (Bennetts and Kitchens 1997a, Bennetts et al. 1999). The specific gauges used for each wetland area and the responsible agencies are found in Bennetts and Kitchens (1997a). We used this measure instead of water depth for the following reasons: (1) we were interested in the relative water levels of the entire wetland area among years, (2) ground elevation within areas is highly variable, (3) elevation data are lacking for most areas, and (4) nest-site-specific data were not available for many nests. The number of standard deviations above or below the mean annual minimum was used to account for the differences in elevation among areas (Bennetts and Kitchens 1997a, Bennetts et al. 1999). Consequently, we defined a low water event, equivalent to a "drought", as any period when water level was ≥1 standard deviation below the mean. This categorization corresponds quite well with the qualitative designation of drought years reported in previous studies (Snyder et al. 1989, Beissinger 1995) but is based on quantitative criteria (Bennetts and Kitchens 1997a).

Logistic regression was used to test for the effects of area, year, habitat type (lake or marsh), and water levels on annual nest success. We developed a suite of candidate models based on biological relevance to examine the influence of these effects (Burnham and Anderson 1998). Models were developed in which confounded effects could be compared between two separate models to determine which effect had a greater influence on annual nest success. For example, we did not develop a model in which area and habitat type were both included because habitat type is a component of the area. Also we did not develop a model containing interactions of area, year, and a water variable (i.e., water levels or water conditions) because the water variables are nested within the interaction of area and year.

Our model selection criterion was based primarily on Akaike's Information Criterion (AIC) (Akaike 1973, Shibata 1989, Burnham and Anderson 1998) corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989). The goal of model selection is to identify a biologically meaningful model that explains much of the observed variability by including enough parameters to avoid substantial bias, but not so many that precision is lost (Lebreton et al. 1992, Burnham and Anderson 1998). The models were ranked and compared in terms of their ability to explain variation in the empirical data using ΔAIC_c (Burnham and Anderson 1998) and AIC_c weights (Buckland et al. 1997, Burnham and Anderson 1998). The ΔAIC_c for a given model is the difference in AIC_c between the given model and the best (i.e., lowest AIC_c) approximating model (Burnham and Anderson 1998). Further, to better interpret the relative likelihood of a given model over a set of models, models are normalized (by summing to 1) to be a set of AIC_c weights (Buckland et al. 1997, Burnham and Anderson 1998). Therefore, the larger the ΔAIC_c, the smaller the AIC_c weight, and the less plausible the given model.

Specific effects of interest were tested with likelihood-ratio tests (McCullagh and Nelder 1989). Because annual minimum water levels have been the most frequently hypothesized influence on nest success and are of primary interest for management, we used a generalized coefficient of determination ($\bar{R}^2$) to estimate how much of the variation in our best approximating model was explained by annual minimum water levels. Such an analysis was first proposed by Cox and Snell (1989) and later modified by Nagelkerke (1991) to determine the proportion of variation explained by a model (e.g., water) relative to another model (e.g., area × year).

RESULTS

Based on a model without spatial and temporal variability (i.e., a "no effects" model), the overall proportion of nests (n = 1541) that were successful was 0.41 ± 0.01 (Table 1). Although this estimate is reasonable for overall success, the analysis indicated that there was considerable spatial and temporal variability in nest success. Based on AIC_c, the most parsimonious model that best explained the data was a model that included area effects, year effects, and an interaction effect among area and year (Table 2). The results also indicated that the spatial and temporal variability in nest success was far greater than can be explained by our measure of annual minimum water levels, either as a categorical response (i.e., drought vs. non-drought) or as a continuous linear response. In addition, the AIC_c weight (0.99) for this model suggested it was 99% more likely to be the best approximating model than all other models. The AIC_c weight for each of the other models was approximately 0.00. Likelihood-ratio tests between models with water levels as covariates and more general models of individual area and year effects strongly rejected the water-level models whether water levels were considered as a continuous linear (χ^2_{55} = 215.3, $P < 0.001$) or as a categorical (drought vs. non-drought) response (χ^2_{56} = 218.4, $P < 0.001$). Further, the logistic coefficient for the effect of water levels, after accounting for year and area effects (model: Year + Area + Water), was 0.04 ± 0.31 SE, indicating the effect did not differ from zero. The data further indicated that our measure of water levels explained only a very small amount of the overall variation in nest success (generalized $\bar{R}^2$ = 0.02). The analysis also indicated that the spatial and temporal variability was not well explained by habitat type (lake or marsh) (χ^2_{28} = 82.9, $P < 0.001$).

TABLE 2. Logistic regression models and their corresponding Akaike Information Criterion (AIC_c) scores for nesting success. Models are listed in ascending order of AIC_c, with ΔAIC_c indicating the difference between each model and the model with the lowest AIC_c value (i.e., the best model).

Model	Number of parameters	AIC_c	ΔAIC_c
Year Area Year × Area	57	1971.15	0.00
Year + Area	33	1989.01	17.86
Year + Area + Water[a]	34	1991.08	19.93
Year Habitat Year × Habitat	29	1994.73	23.58
Year + Habitat	23	1998.77	37.62
Year	22	2010.10	38.95
Year (Trend)[b] × Area	21	2011.32	40.17
Year + Water[a]	23	2011.94	40.79
Area + Drought[c]	13	2023.13	51.98
Area + Water[a]	14	2030.99	59.83
Year (Trend)[b] Area	14	2032.02	60.87
Area	13	2035.59	64.44
Habitat + Drought[c]	2	2043.01	71.86
Habitat + Water[a]	3	2045.09	73.94
Habitat	2	2056.38	85.23
Water[a]	2	2072.03	100.88
Drought[c]	1	2073.09	101.94
Year (Trend)[b]	2	2074.35	103.20
"No effect"	1	2092.48	121.33

[a] Standardized water levels considered as a continuous variable.
[b] Year treated as a linear trend.
[c] Water level considered as categorical variable more or less than 1 SD away from the mean.

DISCUSSION

The meta-analysis we conducted was not a reanalysis of the original data. It was, instead, a comprehensive analysis of the composite data set. Our results are consistent with previous reports (reviewed by Sykes et al. 1995) that there is substantial spatial and temporal variability in nest success. Our results indicate that the most parsimonious model describing nest success variability is one that includes separate parameter

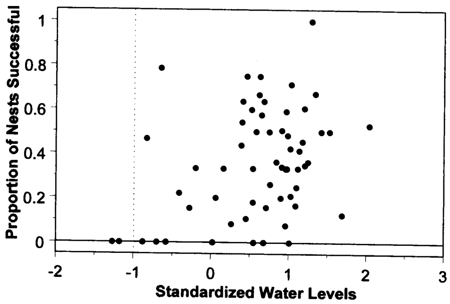

FIGURE 1. Scattergram of Snail Kite nest success and standardized water levels for 11 areas and 22 years, gathered from six previously published studies. Standardized water levels ≥1 SD below the mean (0) were considered low-water events.

estimates for area and year and their interaction. The inclusion of the area × year interaction term indicates that nest success not only differs among areas and years, but that different areas experience high or low success in different years.

Previous assessments suggest low water levels are the most important environmental factor influencing nest success of Snail Kites (Beissinger 1986, Sykes 1987, Snyder et al. 1989). Based on these previous reports, it might be easy to conclude that the interaction among areas and years represents the variation in water levels over the central and southern Florida landscape. However, our analysis suggested water levels, expressed either as a categorical or a continuous variable, are not good predictors of annual nest success. Models having only water-level effects (either categorical or continuous), in lieu of area and year effects, had among the highest AIC_c scores of all the models considered, indicating that these were the least appropriate based on the principle of parsimony. Similarly, water levels in addition to area and year were rejected based on likelihood-ratio tests. However, this does not imply that low water levels do not influence nest success. We agree with previous authors (Beissinger 1986, Sykes 1987, Snyder et al. 1989) that nest success can be substantially reduced during low water events. The data we reanalyzed are consistent with these previous assertions, as during low water events, nearly all nests failed (Fig. 1). We suggest the consequences of reduced nest success to the population as a whole during low water events are relatively minor and should not dictate long-term management strategies. First, extreme low water events in central and southern Florida occur only once every 5 to 10 years (Duever et al. 1994). Second, it is rare that such events encompass the entire range of Snail Kites in Florida (Bennetts and Kitchens 1997a, 1997b). Lastly, Snail Kites are highly nomadic, moving from one wetland area to another several times a year (Bennetts and Kitchens 2000). Thus, during most low water events birds are capable of moving to alternative wetland areas to breed (Bennetts and Kitchens 1997a, 1997b, Bennetts, Kitchens, and DeAngelis 1998). As a consequence, relatively few birds exhibit low nest success as a result of low water events. Of the data reported here, only 18 of 1541 (1%) of the nests were affected by such low water conditions.

Although the data do not support the hypothesis that low water conditions are a primary influence on nest success, they do not specifically preclude such an effect on other reproductive parameters. Beissinger (1986) suggested that a large proportion of kites did not attempt to nest during low water conditions in 1981. Although his estimate of the breeding population did not use reliable statistical methods (e.g., based on marked individuals), this is a result that one might expect during a widespread low water event (Bennetts and Kitchens 1997b). Bennetts, Golden et al. (1998) used radio-telemetry to estimate the proportion of birds attempting to breed, but their estimate was based on only one year and they too were unable to derive a valid estimate for the effect of water levels. There is insufficient data to conduct a meta-analysis on another reproductive parameter, nest productivity. However, the data suggest that there is substantial spatial and temporal variation in the number of young produced.

Studies of short duration or restricted spatial extent have limited potential to provide insights applicable to an entire population. Such insights come only from study designs spanning the temporal and spatial scales in which a population resides. We were able to extend the inference of independent studies by assessing the variation over time and space through a meta-analysis. Using only one study to measure a real effect, such as water levels, could lead to spurious results. However, combining similar studies allows for separation of real effects from random error, or "noise" (Gurevitch et al. 1992), and in this case we were able to determine that water levels had a small effect on nest success of Snail Kites when viewed over longer temporal scales and broader spatial scales.

Some of the unexplained spatial and temporal variation in nest success of Snail Kites may be attributable to several factors. For any species, it is important to recognize that the effect of a single general factor, such as water levels, on a life-history trait becomes difficult to detect when interactions are considered. Snyder et al. (1989) reported nest success was strongly influenced by nest substrate, and Bennetts et al. (1988) found that nest success exhibited strong seasonal differences. These and other factors were not considered in our analysis when summary statistics were not reported in the literature or raw data were not available. However, provided that data are available, meta-analyses provide a valuable tool that enables a comprehensive analysis of factors influencing nest success or other demographic parameters.

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