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Source: The Condor, 104(1) : 208-215

Published By: American Ornithological Society

URL: https://doi.org/10.1650/0010-5422(2002)104[0208:WLANSO]2.0.CO;2

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COMMENTARY

The Condor 104:208–215
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WATER LEVELS AFFECT NEST SUCCESS OF THE SNAIL KITE IN FLORIDA: AIC AND THE OMISSION OF RELEVANT CANDIDATE MODELS

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Abstract. Dreitz et al. (2001) analyzed the factors affecting nest success of the Snail Kite (*Rostrhamus sociabilis*) in Florida. They concluded that success was unrelated to water levels because Akaike's Information Criterion rated models with water-level terms as poor compared to other models. Their suite of candidate models, however, did not include models with area-specific differences in the way that water levels affect nest success. We believe that such differences should have been included among the *a priori* models examined, and that their best model is neither ecologically informative nor useful for management. Using the same statistical methods, we reanalyze Dreitz et al.'s data on nesting success from the five areas with sufficient years and nests for analysis (comprising 89% of their 1542 nests) and show that, when spatial effects of water levels are included, water levels have an important influence on nest success over the entire range of water levels, not just during low water conditions. Furthermore, Dreitz et al.'s definition of nesting attempts excluded nests found during the 10–21 day prelaying period, when many nests fail. Thus, they overestimated nest success and underestimated the amount of nesting activity under low water conditions. Low water conditions occur relatively frequently throughout much of the kite's range, and under these conditions few kites nest and even fewer fledge young. The effects of low water extend well beyond nest success, causing many kites to forgo nesting altogether, shortening the breeding season, and decreasing the opportunity for multiple brooding.

Key words: Akaike's Information Criterion, AIC, Florida Everglades, model selection, nest success, Rostrhamus sociabilis, *Snail Kite.*

Manuscript received 25 June 2001; accepted 2 November 2001.

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Los Niveles de Agua Afectan el Éxito de Nidos de *Rostrhamus sociabilis* en Florida: Criterio de Información de Akaike y la Omisión de Modelos Potenciales Relevantes

Resumen. Dreitz et al. (2001) analizaron los factores que afectan el éxito de anidación de *Rostrhamus sociabilis* en Florida. Ellos concluyeron que el éxito no está relacionado con los niveles de agua porque según el Criterio de Información de Akaike, los modelos que incluían términos relacionados con el nivel de agua eran de poco valor en comparación con otros modelos. Sin embargo, entre los modelos evaluados no incluyeron aquellos con diferencias específicas de área en la manera en que los niveles de agua afectan el éxito de los nidos. Nosotros creemos que dichas diferencias han debido ser incluidas en los modelos evaluados *a priori* y que su mejor modelo no es ecológicamente informativo ni útil en términos de manejo. Utilizando los mismos métodos estadísticos, reanalizamos los datos de éxito de anidación de Dreitz et al. de las cinco áreas que tenían suficientes años y nidos para analizar (comprendiendo el 89% de sus 1542 nidos). Demostramos que cuando se incluyen los efectos espaciales de los niveles de agua, éstos tienen una influencia importante en el éxito de los nidos en todo el rango de niveles de agua (no sólo en condiciones de aguas bajas). Más aún, la definición de intentos de anidación empleada por Dreitz et al. excluyó a aquellos nidos encontrados durante el período de 10 a 21 días pre-postura, cuando muchos nidos fracasan. Por lo tanto, ellos sobreestimaron el éxito de los nidos y subestimaron la cantidad de actividad de anidación en condiciones de aguas bajas. Las condiciones de aguas bajas se presentan con relativa frecuencia en gran parte del rango de distribución de *R. sociabilis*. Bajo esas condiciones, pocos individuos anidan y aún menos crían polluelos exitosamente. Los efectos de aguas bajas se extienden más allá del éxito de los nidos, causando que muchos individuos totalmente renuncien a anidar, acortando la época reproductiva y reduciendo las oportunidades de tener múltiples nidadas.

Dreitz et al. (2001) analyzed the factors affecting nest success of the Snail Kite (*Rostrhamus sociabilis*) in the Florida Everglades and concluded that (1) nest success is unrelated to water levels; (2) few nests are affected by low water levels; and (3) low water events are rare. They reached these conclusions by analyzing the success of 1542 nests studied by many researchers over 22 years in 11 wetland areas, using logistic regression and Akaike's Information Criterion corrected for small sample size (AICc) to discriminate among a variety of models. AICc is a relatively recent and useful innovation for model selection in ecology (Hilborn

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and Mangel 1997, Burnham and Anderson 1998) that does not test statistical hypotheses, but instead evaluates how well each model in a set of candidate models fits a particular set of data (measured by the log-likelihood estimate) and penalizes models as they become more complex (measured by their number of parameters).

The results of Dreitz et al. contrast with studies of 666 kite nests conducted over 14 years in 4 areas that showed success was strongly and positively related to water levels (Beissinger 1986, 1995, Snyder et al. 1989). The nest success data of Snyder et al. (1989) contributed 254 nests and more than half the years of study to the Dreitz et al. sample, so it seems surprising that these studies should arrive at such different conclusions. Resolving these conflicting results is important because the Florida Snail Kite is a federal and state-listed endangered species that inhabits a highly modified Everglades ecosystem where water management decisions can become high profile conflicts (Walters et al. 2000).

Here we reanalyze the data of Dreitz et al. using AICc and other techniques to show that water levels do influence nest success in the major wetlands used by kites for nesting. The set of candidate models examined by Dreitz et al. did not include important spatial differences in the way that water levels affect nest success, which we would have included among the *a priori* models to be evaluated, and water levels make important contributions to explaining nest success when models include these spatial effects. Moreover, the best model of Dreitz et al. describes the data, but is not ecologically meaningful and provides little insight to guide management for population recovery.

Water levels have the potential to affect nest success of Snail Kites via three main mechanisms: predation, food supply, and choice of nest substrate. Kites nest in shrubs, trees, or herbaceous plants, and always choose sites over water in flooded marshes or lakes (Beissinger 1986, 1988, Bennetts et al. 1994). If water levels recede sufficiently, nest sites may become accessible to predators that normally avoid deeply inundated areas (e.g., raccoons [*Procyon lotor*]), and such nests usually fail (Beissinger 1986, Snyder et al. 1989, Dreitz et al. 2001). When wetlands dry out, the main food of the Snail Kite in Florida, aquatic *Pomacea paludosa* snails (Beissinger 1990a), becomes unavailable and kites may abandon nests of all stages (Beissinger 1986, Snyder et al. 1989). On the other hand, if water levels become too deep and there is little emergent vegetation for snails to reach the water surface, they may become inaccessible to kites, and this could cause nest success to decline with increasing water levels. Finally, Snail Kites choose nesting locations and substrates in response to water levels, and the choice of nesting substrate greatly affects nest success. Nests placed in shrubs or trees are much more successful than nests placed in herbaceous vegetation, which usually fail due to structural collapse and other causes (Snyder et al. 1989, Rodgers 1998). During low water conditions, however, herbaceous vegetation often provides the only potential nest sites available over water. Certainly, predation, food stress, and structural collapse can affect nest success independent of water levels. However, these primary causes of failure are likely to be influenced strongly by water levels, and the relatively low nesting success of the species is due in large part to these factors (Beissinger 1986, Snyder et al. 1989).

The rate of change of nest success with changes in water level may differ among wetland areas because of differences in the factors that affect predation, food supply, and choice of nest substrate, such as water depth, slope, hydrological response after rainfall, availability and distribution of nest substrates, and bottom substrate. The effects of water levels on predation, for example by raccoons, may vary from region to region, dependent on the relative amount and distribution of shoreline and densities of raccoons. How snail numbers change with water levels depends on the average depth that wetlands are kept flooded and the ability of snails to recover from drought in different wetlands, dependent in part on the duration of flooding, the extent that flooded refugia exist, and differences in bottom substrate, which affect the ability of snails to burrow, aestivate, and survive during drying events. Water-level changes affect the availability of potential nest substrates differently among wetlands. In lakes, kites usually nest in stable sites in shrubs or trees found along the lake margins when water levels are high, but low water conditions can force kites to choose unstable sites in cattails (*Typha* sp.) in deeper, more central portions of the lakes (Sykes 1984, Snyder et al. 1989, J. A. Rodgers Jr., unpubl. data). Although shifts in nest location and substrate with water-level changes also occur in Everglades marshes, water-level changes rarely result in kites adopting unstable sites in herbaceous vegetation, probably because patches of woody vegetation are widely distributed in these marshes. Instead, the birds sometimes move from relatively stable sites in shrubs to stable sites in trees when Everglade marshes flood deeply (Bennetts and Kitchens 1997a, 1997b). Thus, analyses of how water levels affect nest success of Snail Kites should include models with separate parameters for the relationship between water levels and nest success for each wetland unit (i.e., an area $\times$ water-level term) that can be fitted against nest success data collected in each area over many years and under a variety of water conditions. Drietz et al. did not include such models among the suite of candidate models they evaluated.

In the following sections, we examine Dreitz et al.'s analysis of Snail Kite nest success, reanalyze their data to determine if there are area-specific effects of water levels on nest success, and then revisit their three major conclusions. We conclude by discussing the role of water levels in the population dynamics of the Snail Kite in Florida.

STRUCTURAL AND BIOLOGICAL PROBLEMS WITH THE LOGISTIC REGRESSION MODELS OF DREITZ ET AL.

Annual and spatial variation in nest success overwhelmed the effects of water level in the logistic regression analysis of Dreitz et al. (2001). In their Table 2, Year, Area and the Year $\times$ Area interaction constituted by far the best model as measured by the lowest AICc. Water level, either in the form of an index or

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discrete categories, had a much greater AICc, even when included with other parameters. By expanding the number of years and areas studied, the analysis of Dreitz et al. confirms earlier studies that found nest success of Snail Kites differed greatly among areas and years (Beissinger 1986, Snyder et al. 1989). Parameters for area and year make biological and statistical sense in a ''best'' model. What is important to know, however, is not that nest success varies by area and year but *why* it varies by area and year, an understanding that does not emerge from their best model.

There are several problems in the structure of the ''best'' model created by including Year × Area. The interaction of Year and Area precludes any other factor from entering into the model, as Dreitz et al. noted, because such factors would have to be nested within the Year × Area term. More importantly, the Year × Area interaction term creates a unique parameter for every combination of Year and Area, 27 in total, which act like error terms to capture much of the variation that is not explained by other variables either in or out of the model, and create a saturated model. Dreitz et al. (2001:507) suggest the interaction term indicates ''different areas experience high or low success in different years,'' but this explanation provides no ecological insights into what causes the differences in nest success, which is what management for population recovery requires. Thus, the additional 27 parameters created by the interaction term are not readily interpretable. In summary, the best model fits the data, but the explanation of the model is neither biologically informative nor particularly useful for assisting management decisions. Burnham and Anderson (1998:224) present a similar example where the best model was uninterpretable and less useful than a model with a higher AICc value.

There is no possibility of attaining a lower log-likelihood than the value produced by the Area, Year, Year × Area model, because it is saturated and contains the maximum possible number of parameters that can be estimated for this data set. Incorporating the interaction of Area and Year produced a lower AICc partly because there was a very large sample size of 1542 nests that offset the penalty imposed on models for adding the extra, uninterpretable parameters. In Table 2 of Dreitz et al., the AICc values are almost perfectly inversely related to the number of parameters modeled.

We have no problem with the candidate models evaluated by Drietz et al. in their Table 2 except that these models were limited in the way they allowed water levels to affect nesting success. Their models assumed nest success was affected by changes in water levels in the same manner and at the same rate for all areas. Spatial variation in the manner that water levels affect nest success, a very appropriate *a priori* hypothesis, was not included in the suite of candidate models advanced. If there were substantial heterogeneity among areas in the manner that nest success changed with water levels, the models would have been unable to detect it, because only one parameter for the relationship between nest success and water level was fit to data from all areas combined. Instead, the relationship between water level and nest success should be fit for each wetland separately by including the interaction between Area and Water in candidate models.

IS NEST SUCCESS UNRELATED TO WATER LEVELS? REANALYSIS USING WETLAND-SPECIFIC RESPONSES

We re-examined the data of Dreitz et al. to determine if spatial heterogeneity in relationships between nest success and water levels was obscured when nests from all areas were pooled in Figure 1 of Dreitz et al. The vast majority (89%) of kite nests occurred in 5 of the 11 areas (Lake Okeechobee, Water Conservation Area 3A [WCA-3A], Water Conservation Area 2B [WCA-2B], St. Johns Marsh, and the West Palm Beach Water Catchment Area [WPBWCA]). One or more of these 5 areas was studied every year and each area had 6–13 years of nest success data. The other six areas (Big Cypress Preserve, Everglades National Park, Lake Kissimmee, Lake Tohopekaliga, Water Conservation Area 2A, Water Conservation Area 3B, and West Lake Tohopekaliga) accounted for few nests and each received only 1–3 years of study. Including these six poorly studied areas in our analysis of spatial variation in the impact of water level on nest success would weaken the potential for evaluating water-level effects, because fits of regressions between nest success and water variables would be based on only 1–3 data points per area.

Heterogeneity among areas in the relationship between nest success and water level is evident when viewing data in Table 1 of Dreitz et al. for the 5 areas with sufficient years and nests for analysis (Fig. 1). ANCOVA indicated significant differences in the slopes of the regression lines among the five sites ($F = 3.4$, df = 4, $P < 0.02$) and significant differences in average nest success (i.e., intercept) among sites ($F = 4.8$, df = 4, $P < 0.01$).

The three Everglades wetlands used most frequently by kites for nesting in Florida (WCA-2B, WCA-3A, and Lake Okeechobee) from the 1960s to present (Sykes 1984, Snyder et al. 1989, Dreitz et al. 2001) exhibited significant or nearly significant positive correlations between water level and nest success (Fig. 1). ANCOVA indicated no significant differences among the slopes of the regression lines ($F = 0.8$, df = 2, $P = 0.4$) or among the intercepts ($F = 0.8$, df = 2, $P = 0.4$). Nest success was positively related to water levels ($F = 23.5$, df = 1, $P < 0.001$) in these three areas, and water levels alone accounted for 50% of the variation in nest success in a separate linear regression for the combined sample ($P < 0.001$).

Nest success was unrelated to water levels in the other two areas (WPBWCA and St. Johns Marsh; Fig. 1), which have supported relatively few nesting kites compared to WCA-2B, WCA-3A, and Lake Okeechobee. The slopes suggested the possibility of a negative relationship between nest success and water level that may become clearer with additional years of study. These wetlands, however, rarely experienced low water when kite nests were monitored, and the addition of such years might shift the direction of the slope. We have had limited experience studying kites at these sites and we do not know the biological mechanisms that might account for the potential negative relation-

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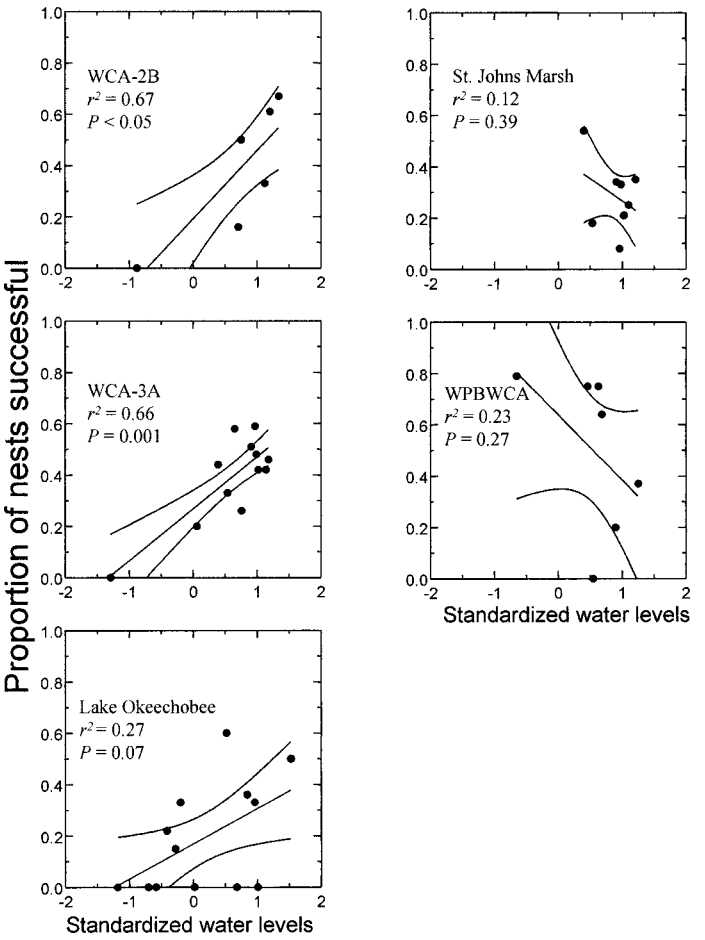


FIGURE 1. The relationship between Snail Kite nesting success and standardized minimum water levels for five areas in Florida with sufficient years for analysis, plotted directly from the data in Table 1 of Dreitz et al. (2001). The r^2, significance (P) and 95% confidence limits of the regression lines are displayed.

ships. However, WPBWCA is managed primarily as a reservoir for drinking water, and high water levels could have resulted in wetlands that were flooded too deeply for kites to forage effectively. The standardized water-level variable used in these analyses only indicates changes relative to average water levels and, since different wetlands are flooded to different depths, it does not allow comparison of water depths between areas.

Having detected significant heterogeneity among wetlands in the relationship between nest success and water levels, we reanalyzed the data of Dreitz et al. (2001) using their same statistical techniques and the 1366 nests from the 5 areas identified above. We determined the number of successful and failed nests from Table 1 of Dreitz et al. and simplified our analysis by using only their water-index metric based on the standardized minimum water levels. Logistic regression models were constructed and ranked using AICc, ΔAICc (the difference in AICc between a model and the model with the lowest AICc value, or best model), and AIC weights (the relative likelihood of a model given a set of models, normalized to sum to 1), following the methods of Burnham and Anderson (1998) as did Dreitz et al. (2001). The count of model parameters included parameters whose estimates were zero because all nests in a particular area and year had failed (Cooch and White 2001, E. Cooch, pers. comm.). Such parameters were unconstrained, and their estimates reflected true values. If sample sizes had been larger, some nests probably would have fledged and these parameters would have had nonzero estimates. To compare the relative difference in the fit of the two best models, we calculated a multiple coefficient of determination, R^2, that measures the percentage of information about parameter variation contained by the best model that is incorporated in the second-best model (Burnham and Anderson 1998: 225).

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TABLE 1. Logistic regression models for nest success of Snail Kites in Florida, with corresponding log-likelihood, number of parameters (*k*), and Akaike's Information Criterion (AICc) score. Data, from Table 1 of Dreitz et al. (2001), include all 1366 Snail Kite nests from the five areas with sufficient years sampled to detect area-specific effects of water level (WCA-3A, WCA-2B, Lake Okeechobee, St. Johns Marsh, and WPBWCA). Models are ranked by ΔAICc, which indicates the difference between each model and the best model (lowest AICc; rank 1). The second best but most informative model is bolded.

Rank	Model	Log-likelihood	*k*	AICc	ΔAICc
1	Area, Year, Year × Area	−831.73	46	1758.74	0.00
2	**Area, Year, Water index, Area × Water index**	**−849.39**	**30**	**1760.17**	**1.43**
3	Area, Water index, Area × Water index	−874.07	10	1768.24	9.50
4	Area, Year, Water index	−859.00	26	1771.05	12.31
5	Area, Year	−861.00	25	1772.97	14.23
6	Year, Habitat, Year × Habitat	−867.65	25	1786.27	27.53
7	Year	−873.00	21	1788.69	29.95
8	Area, Water index	−896.85	6	1805.76	47.02
9	Habitat, Water index, Habitat × Water index	−902.00	4	1812.03	53.29
10	Area	−902.17	5	1814.38	55.64
11	Habitat, Water index	−908.89	3	1823.80	65.06
12	Habitat	−913.97	2	1831.95	73.21
13	Water index	−916.90	2	1837.81	79.07

We tested for wetland-specific relationships between water level and nest success by including the interaction of Area and Water in the logistic regression models. Area × Water creates a unique parameter for the relationship between nest success and water levels for each area. We mainly present results from models with both main effects and interaction terms for ease of interpreting results (Hosmer and Lemeshow 2000) and to avoid data dredging (Burnham and Anderson 1998). However, we explored models with all possible combinations of interactions with and without main effects, and none changed the general pattern of model ranks. For the sake of comparison, we also modeled the data with Area, Year, and Year × Area (the best model of Dreitz et al.) even though this model offers little insight into the ecological factors affecting nest success.

Our reanalysis clearly demonstrates that water level explains important variation in nest success when considered in a wetland-specific context (Table 1). Of the 13 models tested, two of the three best models included an area-specific term for water, a result that differed greatly from the results of Dreitz et al.'s modeling effort without such a term. On the other hand, three of the five worst models had a main effects term for water but no area-specific parameter (i.e., interaction), which was consistent with Dreitz et al.'s results. Model 2 (Area, Year, Water, and Area × Water) described the data almost as well (ΔAICc = 1.43) as the much less meaningful Model 1 (Area, Year and Year × Area), and the fit was almost identical (ΔAICc = 0.36) if we excluded the main effects term Water from Model 2. Burnham and Anderson (1998) suggest models with a ΔAICc < 1–2 are equally plausible given the data. Although AIC weights favored Model 1 over Model 2 (0.66 versus 0.33), R^2 for Model 2 was 0.82, indicating that Model 2 (Area, Year, Water, and Area × Water) encompassed 82% of the total structural information contained in the less useful Model 1 (Area, Year and Year × Area). Adding 50% more parameters, none of which are easily interpretable, by moving from the second to the best model increased the ability to describe the data by only 18%. In fact, when we fit Model 2 (Area, Year, Water, and Area × Water) to the original data set of Drietz et al., it ranked second best, although still well behind the best model because of inadequate data to characterize the relationship between water level and nest success for 6 of the 11 areas.

Further support of the influence of water levels on nest success of Snail Kites emerged from likelihood-ratio (*G*) tests of nested models. Testing the model Area, Year, Water, Area × Water against the model Area, Year yielded a highly significant difference ($\chi^2_5 = 22.5$, $P < 0.001$), which indicates the models could not be collapsed without loss of explanatory power.

In conclusion, water levels do explain important variation in the nest success of Snail Kites, even under non-drought conditions. The relationship between nest success and water levels is strongest in the three main nesting areas of the kite, WCA2B, WCA3A, and Lake Okeechobee, where water management is most controversial (Fig. 1). While the approach to model selection employed by Dreitz et al. was reasonable, they did not include one model that fit the data better than all candidate models except the largely uninterpretable saturated model. The fit of our Model 2 rivals their best model in explanatory power in our analysis. Inclusion of spatial variation in the relationship between water levels and nest success in models is warranted on theoretical grounds, and is not an attempt to dredge patterns from the data from *a posteriori* analyses.

A challenge in applying AIC approaches is the selection of an appropriate set of candidate models. Burnham and Anderson (1998) discuss this issue at some length and advise that one runs the risk of overfitting data by employing AIC approaches on all possible subsets of model variables. By the same token, even experienced investigators run the risk of missing important relationships through the omission of potential candidate models. Some overfitting may be less dangerous than excluding potentially good models that

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may completely change the outcome and inference of a model selection exercise, as we demonstrate here. Sets of candidate models deserve intense scrutiny for their completeness and systematic approach to examining potentially important ecological interactions. Not only should all models with reasonable biological justification be included in the candidate set, but critical thinking about important interactions among parameters must also be demonstrated. Hosmer and Lemeshow (2000) provide useful methods for detecting interactions when applying logistic regression.

ARE FEW NESTS AFFECTED BY LOW WATER LEVELS?

In addition to finding little effect of water levels on nest success, the analysis of Dreitz et al. differed in another important way from our previously published studies. Dreitz et al. analyzed only nests found after egg laying and excluded nests found prior to laying, when kite nests often fail (Snyder et al. 1989). Although the omission of nests that fail prior to egg laying is a common approach to estimating nest success, and may entail acceptable levels of error for species whose nests rarely fail during building, this approach becomes problematic for species whose nests frequently fail during nest-building. As only 14% of Snail Kite nests found by Snyder et al. (1989) during nest-building fledged young compared to 32% of nests found during incubation, failures during the long (10–21 day) nest-building stage are frequent for Snail Kites and should not be neglected when evaluating nest success. The omission of nests failing during nest-building overestimates nest success, underestimates the number of nests affected during low water conditions, and therefore underestimates the importance of factors causing early failure, among them water-level effects.

As justification for excluding nest failures occurring before egg-laying, Dreitz et al. (2001:503) repeated the assertions of Bennetts et al. (1994) that ''pair bonds for this species are not often established during the prelaying stage'' and that ''failures at this stage constitute courtship failure rather than nest failure.'' Our data do not support these claims. At nearly all of the scores of nests we have directly observed and analyzed during nest building, both in Florida and in Venezuela (Beissinger 1990b), pair bonds clearly existed long before egg laying. This was indicated by nest building by both sexes (although such activity is often initiated by males) and by socially monogamous associations (including copulations).

Excluding nest attempts that fail before eggs appear greatly underestimates the amount of nesting activity in a kite population, and attributing early failures to courtship failure provides no insight into the ecological mechanisms causing early nest failure. In our observations, failure during the nest-building period was not attributable to disturbance by researchers, but was sometimes related to low provisioning rates of females by males (Snyder et al. 1989). This sometimes apparently resulted from food scarcity caused by low water conditions or bad weather such as cold fronts that caused snails to become nearly immobile (Beissinger 1987). As many failures occur during nest building, it is essential that this stage be studied closely in evaluating whether water levels affect nest success.

The limited definition of nesting attempts used by Dreitz et al. contributed to their conclusion that few nests are affected by low water conditions. In particular, by including only 254 of the 666 nests studied by Snyder et al. (1989), these authors excluded nearly half the nests found during low water conditions in the 1970s and early 1980s. Had these nests been included in our analyses in Figure 1 and Table 1, the correlation between water level and nest success for Lake Okeechobee would become significant ($r^2 = 0.27$, $n = 15$, $P < 0.05$) and the difference in AICc between the two best models (Models 1 and 2 in Table 1) would reduce further, to 1.29. Greater improvement might result if nests failing before laying during the years studied by Dreitz et al. could be analyzed.

While it is true that there are fewer nesting attempts under low water conditions than under high water conditions, every pair that fails to initiate a nest has the same lack of reproductive success as pairs that nest and fail. Thus, low water conditions can substantially reduce the productivity of the whole population, not just the productivity of pairs that nest.

ARE LOW WATER EVENTS RARE AND ARE THEIR IMPACTS ON NESTING MINIMAL?

Drietz et al. concluded that water levels only impact success of kite nests during extremely low water events, and that nests would rarely be affected because droughts rarely occur in Florida and kites can disperse to avoid them. Our analyses clearly show, however, that water levels can influence nest success over the entire range of water levels in the main nesting areas of kites in Florida (Lake Okeechobee, WCA-2B, and WCA-3A; Fig. 1). For example, as the standardized minimum water level declines from one unit above average (+1) to average values (0), nest success in these areas would be reduced from 41% to 21% based on the regression equation for all three areas combined. Nevertheless, success is typically the lowest under low water conditions.

Periodic droughts and floods are common, not rare, throughout the range of the Snail Kite in southern and central Florida, with a strong 5–7 year cycle (Blake 1980, Beissinger 1986). El Niño–La Niña (ENSO) rainfall cycles (Philander 1983, Fei-Fei et al. 1994) influence drought-flood cycles in Florida (Hanson and Maul 1991, Sun and Furbish 1997). The Pacific Decadal Oscillation (PDO), a long-lived ENSO-like climate pattern, modifies these effects (Mantua et al. 1997) as well as Atlantic Multidecadal Oscillation (Enfield et al. 2001). A shift from dry to wet PDO cycle took place in the early 1980s (Mantua et al. 1997), which may partly explain why water levels were typically higher throughout southern Florida during the period when Dreitz and her colleagues conducted their studies than when we did our work in the 1970s and early 1980s. Seven of eight years with negative water index values in Table 1 of Dreitz et al. occurred prior to 1986. Furthermore, water index is highly correlated with Year ($r = 0.48$, $n = 59$, $P < 0.001$) in the Dreitz et al. data set. This suggests variation in nest success was related to Year ($r = 0.40$, $n = 59$, $P < 0.005$)

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when Year was incorporated in Dreitz et al.'s models as a continuous variable in Table 2 of their analysis, because it acted partly as a proxy for water index.

Dreitz et al. (2001) and others (Bennetts and Kitchens 1997b, Bennetts et al. 1998) also suggested that low water levels have only minor effects on kites, because such events are mostly local and kites are capable of dispersing and breeding elsewhere during low water conditions. However, they presented no comprehensive data on the frequency and success of such breeding occurrences or on the frequency of local versus widespread low water events. Water levels in the major wetlands used by kites do not fluctuate independently, so there is considerable potential for widespread low water conditions (Duever et al. 1994). Bennetts and Kitchens (1997a) found high correlations ($0.53 < r < 0.86$) among minimum annual water levels in WCA-3A, WCA-2B, Lake Okeechobee, and other wetlands primarily used by kites for nesting in southern Florida. And although minimum water levels for wetlands in central Florida are more independent of each other and from water levels in southern Florida, relatively few kites have nested in these areas, even during droughts farther south. While kites move readily across the Florida landscape in search of flooded wetlands during low water (Beissinger and Takekawa 1983, Takekawa and Beissinger 1989) or other conditions (Bennetts and Kitchens 1997a), these movements often fail to place many birds in habitat adequate for breeding. In our experience, few kites have nested after dispersal under low water conditions, and their nest success has typically been poor (Beissinger 1986, Snyder et al. 1989, Takekawa and Beissinger 1989). Thus, such movements may allow many kites to escape starvation, but enable few to nest and even fewer to fledge young.

EFFECT OF WATER LEVELS ON SNAIL KITE FECUNDITY AND POPULATION DYNAMICS

Our analyses reveal problems with all three of the main conclusions of Dreitz et al. (2001). Nest success of Snail Kites is related to water levels on Lake Okeechobee and in the Everglades wetlands where the majority of kites have nested, and this relationship varies among areas (Fig. 1, Table 1). Under low water conditions large numbers of kites forgo nesting, and those that do nest are rarely successful. Finally, low water conditions occur relatively frequently throughout much of the kite's range in Florida, and under these conditions kites often find few opportunities to breed despite their mobility.

In summarizing their conclusions, Drietz et al. (2001:507) stated "the consequences of reduced nest success to the [kite] population as a whole during low water events are relatively minor and should not dictate long-term management strategies." We believe this statement gives a misleading impression of the effects of water levels on kite reproduction and could easily be misinterpreted by managers to suggest that the effects of low water levels on kites are trivial, which would be counterproductive to the conservation of this species. Our analyses show clearly that water levels have major impacts on nest success. Furthermore, when nonbreeders comprise the great majority of birds in a population, standard nest success calculations become almost irrelevant to determining productivity compared to the effect of the proportion of birds attempting to nest. Our experience in the drought year of 1981, for example, was that few birds bred anywhere in the range of the species, and while the few that did breed showed relatively low nest success, this effect was dwarfed in importance by the overall cessation in breeding. The low water levels of 1981 were devastating to productivity of the population and this would have been true even if nest success had remained unchanged.

In summary, Dreitz et al.'s major conclusions are unconvincing because they rest on an analysis composed of an incomplete set of candidate models, and they neglect important components of fecundity besides nest success that can be greatly affected by water levels. Annual fecundity, or the number of offspring produced per pair per year, is often calculated from the product of the proportion of females that nest, the average number of nesting attempts per year, the proportion of successful nests (i.e., nest success), and the average number of young produced per successful nest. The length of the nesting season (and presumably the number of nesting attempts per female per year) is highly positively correlated with Everglades water levels and rates of kite population growth (Beissinger 1995). Extensive and intensive field studies have presented ample evidence that a low proportion of females nest during drought conditions compared to high water conditions and that they nest less often and with diminished nest success (Sykes 1979, Beissinger and Takekawa 1983, Beissinger 1986, 1995, Snyder et al. 1989). The length of the breeding season, opportunity for multiple nesting, and proportion of females that nest are the most important components of fecundity affecting kite population dynamics (Snyder et al. 1989, Beissinger 1995). An approach that examines only nest success, and only nest success after egg laying, cannot evaluate overall productivity of the population or the full impacts of water levels on population dynamics in a comprehensive way.

We greatly appreciate the invitation of the editor, David Dobkin, to submit this commentary and we thank David R. Anderson, Evan Cooch, Alan Hubbard and Jim Nichols for helpful suggestions, and Victoria Dreitz for supplying unpublished water index values.

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