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NEST-SITES INFLUENCE NEST PREDATION DIFFERENTLY AT NATURAL AND EXPERIMENTAL NESTS

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Resumen. – La ubicación de los nidos influye la depredación de modo diferente en los nidos naturales y los experimentales. – Las características de la ubicación de los nidos y sus influencias sobre el riesgo de depredación fueron probados tanto en los nidos naturales como en los nidos naturales-experimentales en el región central de Panamá. Los nidos naturales fueron utilizados en los sitios de anidación originales en experimentos para probar: 1) la calidad del sitio de anidación y su influencia sobre el riesgo de depredación, y 2) los supuestos de los experimentos de depredación en nidos. En 1993, para determinar el éxito reproductivo, se observó 97 nidos utilizados por *Thamnophilus atrinucha*. Después de ser utilizados por las aves, los nidos en los sitios de anidación originales fueron usados como nidos experimentales. Al menos una semana después de ser utilizados por las aves (ya sea depredados o exitosos), se colocó un huevo de codorniz en cada nido y se determinó el éxito del nido de nuevo. Se midieron las características de la vegetación de los sitios de anidación (el arbusto o árbol en el que las aves construyeron su nido) y el área de los nidos (la vegetación en un radio de 5 m, tomando como centro el nido). Se utilizó la regresión de Cox para probar la influencia de esta vegetación en el éxito de los nidos y para comparar estos efectos en los nidos activos (controles) y experimentales. El éxito de los nidos activos no tuvo relación con el de los mismos en el experimento, y la influencia de la vegetación difirió entre los nidos activos y los mismos nidos experimentales. Por ejemplo, seis de las 15 variables de los sitios de anidación fueron asociadas con el éxito en los nidos controles, mientras que una fue asociada con el éxito en los nidos experimentales. Tres de las 18 variables de las áreas de los nidos fueron asociadas con el éxito de los nidos controles, mientras que dos fueron muy importantes para los nidos experimentales. El sitio de anidación puede influenciar en el éxito del nido, pero puede ser que los nidos experimentales no proporcionen a los investigadores información acerca de los patrones de importancia en la selección de sitio de anidación y de depredación de nidos naturales.

Abstract. – Nest-site characteristics and their influences on nest predation risk were tested at natural and natural-experimental nests in central Panamá. Natural nests were used in their original sites (natural-experimental) in experiments to test: 1) nest-site quality and its influence on predation risk, 2) assumptions of

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nest predation experiments. In 1993, 97 nests used by the Slaty Antshrike (*Thamnophilus atrinucha*) were observed to determine nest fate. After being used by the birds, these nests in their original locations were used as experimental nests. At least one week after use by the birds (either preyed on or successful), one quail egg was placed in each nest and again nest fate was determined. Vegetation characteristics of nest-sites (the shrub or tree in which birds built the nest) and nest-areas (vegetation in a 5-m radius circle, centered on the nest) were measured. Cox (proportional hazards) regression was used to test the influence of this vegetation on nesting success and to compare those effects at active (control) and experimental nests. Fate of active nests was unrelated to that of the same nests during the experiment, and the influence of the vegetation differed between active nests and the same nests during the experiment. For example, six of 15 nest-site variables were associated with success in control nests, while only one was associated with success in experimental nests. Three of 18 nest-area variables were associated with success in control nests, while two were important for experimental nests. Nest-sites may influence nesting success, but experimental nests may not inform researchers about patterns of the importance of nest-site selection and nest predation at natural nests. *Accepted 21 July 2002.*

INTRODUCTION

The greatest single cause of nesting failure in passerine birds is nest predation (Nice 1957, Ricklefs 1969). Nest predation has therefore been suggested to be an important influence of life history evolution in birds (Skutch 1949, 1985; Martin 1988a, 1988b, 1996a, 1996b; Ricklefs 1989). At a proximate level, birds that reduce predation on nests will have the greatest reproductive success, all else being equal. Nest-site selection may provide a way for birds to reduce predation risk (Oniki 1979a, 1985; Best & Stauffer 1980, Murphy 1983, Blancher & Robertson 1985, Martin & Roper 1988, Marzluff 1988, Møller 1989, Holway 1991, Li & Martin 1991, Steele 1993, With 1994, Götmark *et al.* 1995). These studies suggest that nest-sites are important, but the analysis of nest sites and predation risk generates lively debate (Filliater *et al.* 1994, Wilson & Cooper 1998, 1999; Schmidt & Whelan 1999). Experimental analysis of nest-sites and predation risk are often used to bypass the difficulties associated with natural nests.

Experiments show that nest-sites, nest-areas, and nesting habitats can influence predation risk (e.g., Loiselle & Hoppes 1983, Yahner 1985, Martin 1987, 1989; Gibbs 1991, Langen *et al.* 1991, Mankin & Warner 1992, Amarasekare 1993, Laurance *et al.* 1993, Nour *et al.* 1993, Rudnicky & Hunter 1993, Burger *et al.* 1994, Leimgruber *et al.* 1994, Ritchie *et al.* 1994, see review in Major & Kendal 1996, Roper 2000). Sites may influence predation by impeding predators in some way due to vegetation structure (e.g., Bowman & Harris 1980). If so, then vegetation structure should correlate in some way with nesting success, allowing that nest-sites may include trade-offs, such as between hiding the nest from predators and providing a view for incubating birds to scan for predators (Götmark *et al.* 1995). Experiments allow testing specific site characteristics to examine these potentially conflicting predictions and allow the experimenter to choose, *a priori*, which nest site characteristics to test.

Experiments associate predation risk with habitat choice, assemblage structure, island extinctions, and the edge effect (Yahner 1985, Sieving 1992, Burkey 1993, Nour *et al.* 1993, Burger *et al.* 1994). While experimental studies may show an edge effect (Yahner 1985, Yahner & Voytko 1989, Yahner *et al.* 1989, Burkey 1993, Nour *et al.* 1993, Rudnicky & Hunter

1993, Burger *et al.* 1994), other studies have suggested that the edge effect may not be very important (Mankin & Warner 1992, Laurance *et al.* 1993, Leimgruber *et al.* 1994, Paton 1994, Haskell 1995, Heske 1995). A recent study shows that within habitats, nest predation varies on natural and experimental nests, and that rates on the former are not predicted by rates on the latter (Zanette 2002). The question remains unresolved because biases are common with the use of experimental nests or quail eggs (Willebrand & Marcström 1988, Roper 1992, 2000; DeGraaf & Maier 1996).

Nest predation rates are often much higher in Neotropical than in temperate systems (Ricklefs 1969, Skutch 1985, Roper 1992, Roper & Goldstein 1997; but see Oniki 1979b). Experimental studies in the Neotropics show that nest predation is associated with nest-sites when differences in nest-sites or nest areas are large, such as ground versus off ground, or island versus mainland (Loiselle & Hoppes 1983, Gibbs 1991, Sieving 1992). In these experiments, only Sieving (1992) attempted to examine nest-sites using characteristics of nest construction and site choice of local bird species. More subtle differences in nest-sites, such as those that are within the natural variation of nest-sites, can suggest that nest-site choice does not influence predation risk (Roper 2000), perhaps because all sites chosen have low probabilities of success.

Experiments suggest that nest predation may influence, or have influenced, many aspects of avian ecology, including assemblage composition, extinction rates, nest-site and habitat selection, and edge-effects. Yet, nest predation experiments must satisfy at least two basic assumptions if their results can be translated into conclusions about natural processes. First, nest-sites must influence predation in similar ways at natural and experimental nests. That is, if vegetation in a nest area influences predation, then nest predation risk should be similar for natural and experimental nests in the same locations. Second, nest-sites should be consistent, and repeatable, in how they influence predation. If these two assumptions are valid, then the suite of predators preying on natural nests should be the same as those preying on experimental nests, and those predators have the same behaviors at both types of nests. These assumptions remain untested because of the logistical difficulties of testing them. For example, there may be large differences in nest-site selection by humans and birds. The nearest test compared, within habitats, real nests with experimental nests, and showed no relationship between the two (Zanette 2002). Perhaps we need to make our experimental nests more natural. If nest-placement, construction, and materials are important, then bird-built nests may be inherently different than wicker nests. Here I describe a combination of natural nests and experimental nests using natural nests in natural locations as experimental trials. These natural and experimental nests were used to test that: 1) nesting success is influenced by nest-site characteristics in both natural and experimental nests; 2) nest-site characteristics that influence predation are similar for natural and experimental nests; 3) nest-success of active nests is correlated with nest-success of experiments when the same nests and sites are used.

METHODS

Study area and species. Nesting success was studied from 1 January to 12 December 1993 in tropical moist forest on Pipeline Road in the Parque Nacional Soberanía in central Panamá, near the Panamá Canal. Here, the Western Slaty Antshrike (*Thamnophilus atrinucha*, family Thamnophilidae) is a common understory passerine bird, the genus of which

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TABLE 1. Nest-site characteristics measured at all nests and used in Cox regression analysis to test the influence of nest sites on nesting success. Diameters in mm., heights and lengths in cm.

Variable codes	Variable descriptions
NH	Height of nest above ground
NTH	Height of shrub in which nest is located
LOSTEM	Height of stem nearest the ground, in the nest shrub
NSTRNK	Distance from trunk to nest
LONG & SHORT	Lengths, from nest to distal end, of nest support branches
DIALNG & DIASHT	Diameter of the two above branches
DIABS	Diameter of nest-shrub trunk, measured at ground
DIANT	Diameter of nest shrub trunk at level of nest support
DIANS	Diameter of nest support branch at nest on the side nearest the trunk.
WID1 & WID2	Two perpendicular measures of width of nest-shrub, (1) measured at the widest point
CONTACT	Number of stems of nearby vegetation touching the nest-shrub
ABOV & BELO	Number of stems at the trunk of nest-shrub, above and below the nest-support stem

is found throughout the Neotropics (Ridgely & Gwynne 1993, Stiles & Skutch 1989, Ridgely & Tudor 1994, Howell & Webb 1995). Slaty antshrikes were ideal for this study because nest predation rates are high (~ 0.08 day^{-1}, Roper 1992, 2000; Roper & Goldstein 1997), and nests are relatively easy to find in the forest understory.

Nests. Nests are usually in small shrubs or saplings and woven into the fork of a horizontal branch. Clutch size is invariably two eggs. Active nests were found by searching appropriate substrate in the understory, or by following adult birds while they carry nesting material (during nest construction) or food (while feeding nestlings) to the nest site. The fate of each active nest was determined by checking the nest every two or three days until fledging or failure. Nests were observed at the maximum distance possible given the vegetation structure at each nest (usually >3 m, often greater than 5 m because eggs can be seen through the flimsy nesting material), to minimize any observer influences on nest predation. Active nests were only closely

approached at three times in the nesting cycle: when found, when eggs hatched and to band young just prior to fledging. Most nests fail, but if successful the incubation period is 10–12 days and the nestling period is also 10–12 days (for a total of 22–24 days, rarely to 26 days). The nesting period lasted from early January to the end of September in 1993.

Experiments. At least one, but not more than four, weeks after fledging or nest failure I placed one quail egg in each nest (now "experimental nests," while active natural nests are "control nests"). Experimental nests were initiated in late January and continued through September 1993, and were checked every other day for 22 days, or until the nest failed, and so followed the same procedure of checking as active nests. Daily nest survival of active nests was already shown to be constant over the nesting cycle (Roper & Goldstein 1997), and is also constant during experiments (J. Roper, unpubl. data). Thus, the interval of exposure was approximately equal in both treatments, and both treatments had constant survival rates during that interval.

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TABLE 2. Nest-area characteristics measured at all nests (in 5-m radius circles centered on nests) to test influence on nesting success.

Variable codes	Variable descriptions
DIST1-DIST5	Distance from the nest to the nearest five trees larger than 35 cm DBH (five variables)
DIA1-DIA5	Diameter at breast height of the above five trees
SMPALM	Number of palms in any species less than 2 m height
MDPALM	Presence/absence of palms between 2-5 m height
LGPALM	Presence/absence of palms greater than 5 m height
PALMA, B, C, E, G	Presence/absence of five common genera (letter is first letter of genus name) of palms (five variables)
STM1-STM6	Number of stems less than 2 mm diameter (STM1), 2-4 mm in diameter (2), 4-6 mm diameter (3), 6-10 mm diameter (4), 10-14mm diameter (5), and greater than 14 mm in diameter (6), six variables
VINE	Number of hanging vines from canopy to nest height
VINCLMP	Number of clumps of those vines

A variety of "nest-site" (at the plant in which the nest is located) vegetation characteristics that might influence predation were counted or measured upon completion of experiments (Table 1). Similarly, vegetation within a 5-m radius circle centered on the nest ("nest-area" vegetation) was counted or measured. Also, the distance to and the diameter of the nearest five trees greater than 35 cm diameter at breast height (dbh) were measured because these trees reached the forest canopy and may have offered avenues of travel to animals in the canopy that may descend and prey on nests. Vegetation parameters chosen for measurement were selected *a priori* for their similarity to other studies of the influence of vegetation on nest-site quality (Bowman & Harris 1980, Martin & Roper 1988) or because they presented logical structures or avenues of travel that may help or hinder a predator while it is foraging (for a complete listing, see Table 2).

Statistical analysis of nest sites and areas. To test the influence of nest-site characteristics on nest predation, Cox regression (proportional hazards regression, SAS procedure PHREG, Allison 1995, SAS Institute Inc. 1995) was used. Vegetation measures (independent variables) were regressed against the number of days nests survived (dependent variable). The Cox regression procedure makes no assumptions about data distributions (Allison 1995).

An important use of regression is to predict response, and Cox regression may be similarly used (Allison 1995). The important nest-site variables were therefore examined for their potential influence on nest survival as follows. After calculating the set of important variables as described above, the important variables were incremented by two standard errors and the predicted survival curve with that increment was calculated. Thus, examining the predicted curves illustrates the predicted change in survival due to a change in the nest-site or nest-area variable of interest.

While Cox regression makes no assumptions regarding the distribution of the variables, it is sensitive to multicollinearity (strong correlations among the independent variables). Several of the original variables as measured are highly correlated. For example, nest height is correlated with the height of

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TABLE 3. Transformations of variables to remove multicollinearity. The first variable is correlated with the constrained variable, which is resolved by the transformation shown.

Variables	Constrained variables	Transformation
NH	NTH	NTH-NH = DIF
LOSTEM	NTH	NTH/LOSTEM = BOTTOM
DIANS[a]	DIABS	DIABS-DIANS = DIM1
DIANS	DIANT	DIANT-DIANS = DIM2
DIANS	DIALNG	DIANS-DIALNG = DIM3
DIANS	DIASHT	DIANS-DIASHT = DIM4
LONG	SHORT	LONG-SHORT = STEM
WID1[b]	WID2	WID1/WID2 = WIDE
DIST1[c]	DIST2	DIST2-DIST1 = DIS1
DIST2	DIST3	DIST3-DIST2 = DIS2
DIST3	DIST4	DIST4-DIST3 = DIS3
DIST4	DIST5	DIST5-DIST4 = DIS4

[a]The diameter of the nest support branch was always less than that of the shrub at nest height, or at the base. The diameter of the other stems was usually smaller than that of the nest support branch except in rare cases when the branch nodes were measured.
[b]The widest width of the nest shrub was WID1 and so WID2 was constrained.
[c]DIST1 was the nearest large tree, etc., so no distance could be less than the preceding distance.

nest shrub, and nest height can never be greater than the height of the nest-shrub. Thus, rather than use both nest height and nest-shrub height, the difference between the two provided a new variable that was uncorrelated with either original variable, and this difference was then used in the regression as an independent variable, solving the problem of multicollinearity. Other variables with similar relationships were converted in similar ways, while retaining the information of the original variable (Table 3). All variables were standardized (mean = 0, variance = 1) prior to inclusion in regressions. Standardization is suggested when variables have different measurement units, such as meters and millimeters (Johnson & Wichern 1982, Neter et al. 1985, Hair et al. 1998). Probability levels used in tests was 5%, while probabilities greater than 5% are sometimes discussed for illustrative purposes.

Testing that survival of natural nests is in some way associated with survival of experimental nests in this paired experiment was carried out in three ways. First, for comparison with published literature, daily nest survival rate in both treatments was compared using the Mayfield method (Mayfield 1961, 1975; Hensler & Nichols 1981, Johnson & Shaffer 1990). Second, survival curves were compared using Cox regression without considering the paired nature of the experiment. Third, Cox regression was used and included the paired structure of the experiment to test that nest predation in both treatments show the same trends. This analysis is unusual because it compares two, paired, survival functions, both of which are censored. Because experiments are traditionally used to understand nature, the number of days experimental nests survived was used as the independent variable, and the success of natural nests was the dependent variable. Finally, partial Correlations were used to determine the reliability of the regression models.

TABLE 4. Coefficients of nest-site characteristics in control and experimental nests (N = 87) from proportional hazards regression. Regression coefficients of standardized variables are shown under full and selected.

Variables[a]	Control		Experimental	
	Full (< 0.05)[b]	Selected (< 0.01)[b]	Full (< 0.05)	Selected (< 0.001)
NH	0.41**	0.41**		
DIF	0.56**	0.70***		
DIANS	- 0.48	- 0.24	- 0.84	- 0.92*
DIM1		0.36*		
DIM4			0.85	0.79
WID1	- 0.83**	- 0.77**	- 1.75**	- 0.95**
WIDE	0.65***	0.57***		
LONG	0.36		0.90*	
STEM			- 0.71*	- 0.58*

[a]Variables not significant in either model are not shown; confer with Table 1 for variable definitions.
[b]The full model probability is for the null hypothesis that none of the variables is significant in the model.
*** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, the others values shown $0.05 < P < 0.10$.

RESULTS

In the course of the year 105 natural nests were subsequently used as experimental nests. However, several nest sites were destroyed in a storm during which many trees fell and so not all nests were used in all analyses. The sample size used in each analysis is noted in the description of the results of each below.

Nest-sites. Nesting success was influenced by nest-site characteristics in both treatments (N = 87 nests, 16 site variables; Table 4). Using backwards selection (significance to stay at $P = 0.10$), the resultant models contained five variables for control nests and three for experimental nests. Nest sites did not influence nest predation in the same way in the two treatments since only one influential variable was shared in both treatments (width of the nest shrub WID1, Table 4).

Nest-area vegetation characteristics. Nest-area vegetation was only poorly associated with nest-ing success (N = 97, 27 area variables). The full regression model with all the site variables was not significant for control nests ($P = 0.35$), but was significant for experimental nests ($P < 0.05$, Table 5). Because all variables were potentially important, backwards selections was used to find a significant subset of the variables. Mixed (forward and backward, with significance to stay set at $P = 0.10$) selection was used also, and the resulting significant models always included the same variables within each treatments (Table 5). The model for control nests included one significant and one marginally significant variable. The model with experimental nests included six significant, and one marginally significant, variables. Note that DIS1 and DIS3 were significant but differed in directions in the two treatments (Table 5). Nest area vegetation variables that influenced nest-success for experimental nests were different from those that influenced success at natural nests.

Site and area variables may interact to influence predation. Therefore, the signifi-

TABLE 5. Coefficients[a] of nest-area characteristics in control and experimental nests (N = 97) from Proportional hazards (Cox) regression.

Variables[a]	Control		Experimental	
	Full ($P = 0.04$)	Selected (< 0.01)	Full (< 0.05)	Selected (< 0.001)
DIST1			- 1.00*	- 0.72**
DIS1	0.57*	0.31**	- 0.80*	- 0.46*
DIS3	0.34	0.19	- 0.45	- 0.27
DIA1	0.25			
DIA2	- 0.33			
PALMA			1.57*	1.52**
PALMB	- 0.35			
PALMC	- 0.77			
PALMG				1.02*
STM1	0.41*			
STM6				- 0.44*
VINE			0.39*	0.37***

[a]Variables not significant in either treatment are not included; confer with Table 2 for variable definitions. Symbols are as in Table 4.

cant variables that resulted from selection in either site or areas were used in another model to examine the possible interactions. Combining the site and area variables, selection again resulted in significant and different models in both treatments (Fig. 1). Control and experimental regression models only shared one variable (WID1). The final model for the control treatment contained only site variables (NH, DIF, WID1, and WIDE), while the final experimental model contained one site variable and eight area variables (graphically illustrated in Fig. 1). The different survival curves presented by each model illustrate that survival in experimental nests was very different than in natural nests (Fig. 2). Also, when calculating the predicted response to a change of two standard errors to the significant variable that the models had in common (WID1) the magnitude of the effect appears very different. For natural nests, the change in magnitude of WID1 resulted in a 3% increase in overall nest survival (from about 3% to 6%). In experimental nests, the change in WID1 resulted in a 12% increase in overall nest survival (from about 69% to 82%).

While nest-sites appear to influence nest predation in the Cox regression, birds apparently may not be able to choose a good nest site based on that information. The four independent variables of the regression model all have partial correlation coefficients opposite in sign with the trend expected from the regression (Table 6). For example, the regression model indicates that increases in NH, DIF and WIDE should all improve nesting success, while a decrease in WID1 should improve success. However, NH, DIF and WIDE all share negative partial correlation coefficients, while they all share a positive partial correlation coefficient with WID1. Thus, it is difficult or impossible for birds to choose nest-sites to increase NH, DIF and WIDE, while decreasing WID1 simultaneously, which would be predicted from the regression model.
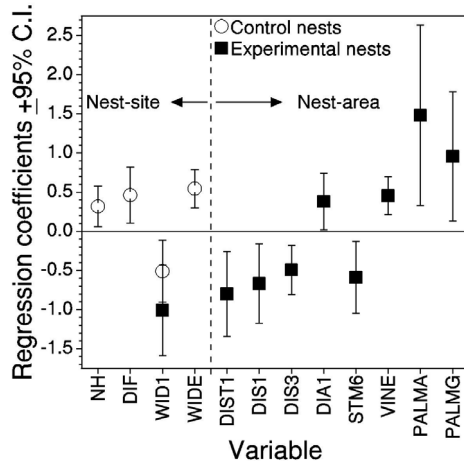
FIG. 1. Regression coefficients (± 95% Confidence intervals) are plotted from the final regression model including combined SITE and AREA variables after backwards selection. All variables at $P < 0.05$ are shown.
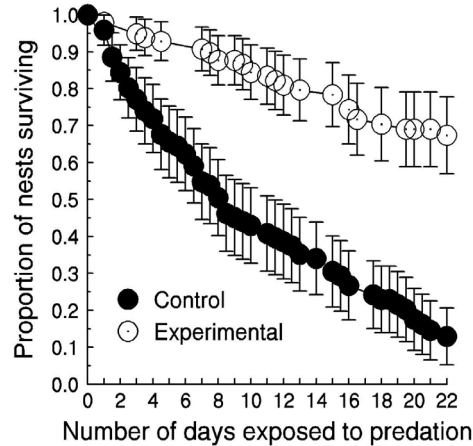

FIG. 2. Survival curve for control and experimental nests, showing the 95% confidence interval for each curve as calculated with Cox (proportional hazards) regression.

Success of control and experimental nests. Daily survival rates on natural nests were low (0.916 day^{-1}, SD = 0.009, Mayfield method) and on experimental nests were high (0.984 day^{-1}, SD = 0.003, $Z = 7.49$, $P < 0.05$, N = 105). The fate of control nests was unrelated to the fate of the same nests in experiments (Cox regression, $\chi^2 = 1.1$, df = 1, $P > 0.05$, for days, and $\chi^2 = 1.6$, df = 1, $P > 0.05$ for success, N = 98, Fig. 2).

DISCUSSION

In this Neotropical study area with high nest predation rates, nest-site analysis suggests that nest-sites may influence predation risk at both, natural and experimental nests. However, conflicting relationships among nest-site variables at natural nests may limit the ability of nest-site choice to improve nest success. Also, experimental nests do not illustrate trends that occur at natural nests in predation probability nor in the influence of nest-sites on predation risk. Why the incon-

sistencies between natural and experimental nests? While predation in both treatments may be influenced by vegetation, and the influence of that vegetation seems biologically explicable, nevertheless the reasonableness belies the fact that the influence is different in both treatments. Hence, when nest predation studies only include experimental nests, there is no way to test whether that study measures processes that occur at natural nests. This lesson is important for avian biologists interested in processes resulting from the influence of nest predation. First, I will interpret the importance of the nest-site variables, suggesting how they may influence predation. Next, I will discuss why these conclusions must be interpreted within the statistical analysis and biology of the birds.

At the nest-site scale, vegetation parameters were most important for natural (control) nests. These variables all were related to the size of the nest-shrub. Success increases in higher nests (NH) and in nests that are farther from the top of the nest-shrub (DIF,

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TABLE 6. Correlations and partial correlations among the significant variables of the regression model for active nests, and signs of each regression coefficient in the final significant regression model. A conflict occurs when the signs of the partial correlation coefficients do not agree with the signs of the regression coefficients (see text).

First	Second	Correlation coefficient[a]	Partial correlation coefficient[b]	Sign of regression coefficients (First/Second)
NH	DIF	0.179	- 0.269	+/+
NH	WID1	0.577*	0.545	+/-
NH	WIDE	- 0.176	- 0.254	+/+
DIF	WID1	0.614*	- 0.652	+/-
DIF	WIDE	- 0.284	- 0.365	+/+
WID1	WIDE	- 0.53	0.268	-/+

[a]Correlation coefficients with * $P < 0.05$.

[b]All partial correlations are significant at $P < 0.05$, N = 95.

Table 4). Nests in such locations are apparently hidden from above and below and so may be more difficult for the vegetation-searching predator to find. Narrower nest shrubs (WID1), and symmetrical shrubs (similar widths on the long and short axis, WIDE) were more successful (Table 4). How that may be important is unknown. Finally, success increased when nest-support stem diameter (DIANS) decreased and length (LONG) increased. Small diameter branches may not easily support the weight of the common predators, and so dissuade them from using them while foraging.

At experimental nests, on the other hand, neither nest height, distance from the top of the nest shrub, nor diameter of the nest-support shrub influenced predation. Experimental nest success increased directly with the longest diameter axis (WID1) of the nest shrub, but was not influenced by the shape as in control nests (Table 4). And, the length of the short nest-support branch (STEM) decreased as experimental nest success increased. The rare predators of experimental nests may somehow be influenced by these variables in unknown ways.

Nearby vegetation (nest area) was nearly unimportant for active (control) nests. Nest success increased with distance to the nearest canopy tree (DIST1, Table 5). If predators such as small mammals often travel in the canopy, or from tree to tree, then they must descend these trees to forage in lower forest levels, and nests farther from these avenues of descent may have lower chances of being found. Experimental nests were more influenced by nest area variables. Distance to the nearest tree showed the reverse trend in experimental and control nests (DIST1, DIS1, DIS3, Table 5). Perhaps being near those trees makes it difficult for monkeys or other canopy predators to see the exposed experimental nests (Roper 2000).

The results discussed above seem reasonable in that each regression model has an explanation in the biology of potential predators of each treatment. Thus, one might erroneously conclude that birds should choose nests based on patterns suggested by the regressions. However, in multiple regression equations, the influence (slope) for each variable in the model is calculated holding the other variables constant. In nature, when a

bird chooses to locate at nest in one branch it is selecting all the other aspects of a site as well. Correlations among the structures that make up a site will influence the ability of the bird to choose a good site. The partial correlation coefficients among the site variables in the model allow us to examine the consequences among the variables of nest site selection. Partial correlations are preferable to simple correlations, because they show the trends of each variable given that the other variables are included in the analysis. Upon examining the partial correlations we see that birds cannot choose nest sites as suggested by the regression models. That is, model selection may result in positive regression coefficients among the independent variables, while the same independent variables have negative partial correlations between them when considered alone. Thus, if the regression suggests that increasing two variables together would improve nesting success, and those two variables have a negative correlation between them, then the birds cannot improve the nest site by that kind of nest-site selection. Thus, Cox regression (or any regression) may often not present a realistic scenario (Allison 1995, Hair *et al.* 1998). In this study, we see that with any one variable in the model chosen in selecting a nest site, the other correlated variables should worsen rather than improve the nest sites (Table 6, Roper 2000).

If birds were able to select these variables independently, the improvement in nesting success would still not be large. If birds could choose sites such that the average values for the significant nest-site variables were increased to the limits of the 95% confidence interval for each of those variables, the change in nesting success would be between 4–15% greater than that observed, as calculated from the Cox regression. Thus, even if it were possible to choose each of the variables independently of the others, the influence of that choice on nesting success would be small.

Daily survival of control nests is much lower than experimental nests at this Neotropical site (Roper 1992, Roper & Goldstein 1997, and herein, contrasting with Zanette 2002). Also, the fates of control nests are unrelated to the fate of those same nests in experiments, probably because different suites of predators eat quail eggs than eat antshrike eggs and young (Roper & Goldstein 1997, also see DeGraaf & Maier 1996). Some evidence suggests that monkeys may prey on experimental nests (and only very rarely on natural nests) because the uncovered, light-colored egg in experiments may be seen from the canopy (Roper 2000). Regardless of the cause of lower rates of predation in experiments, the low rates suggest that predators preying on these nests are relatively unimportant as predators on natural nests in this system.

Nest predation experiments implicitly assume that the processes measured at experimental nests are similar to, and therefore can predict, those that occur at natural nests. While Martin (1987) showed that biases could exist with experimental design and nest placement, here the results suggest that not only are nest-sites biased, but they may also mislead. Nest predation experiments may not be about processes occurring at natural nests, but rather about predators that encounter experimental nests. The patterns due to those predators may not be informative, regardless of how carefully designed the experiment (Zanette 2002). When studies show higher predation rates on experimental nests (Sieving & Willson 1998, Zanette 2002), interpretation may still be difficult if different suites of predators are involved. In Alaska, predation was higher on experimental nests than on natural nests, and was related to the size of the nest and varied with forest type. These results suggested to the authors that red

squirrels (*Tamiasciurus hudsonicus*) were important predators (Sieving & Willson 1998, also see Martin 1993b). In temperate regions in North America, diurnal mammals and birds (squirrels, crows and jays) are perhaps the important predators and are able to eat both quail eggs and natural eggs. Does this suggest that in temperate regions, predation experiments may examine processes occurring at natural nests? In the tropics, predators may be small, nocturnal mammals that do not often prey on experimental nests, suggesting that nest predation experiments in the tropics are problematic. If avian ecologists wish to understand patterns of nest-site and habitat selection that may be due to nest predation (Loiselle & Hoppes 1983, Gibbs 1991, Martin 1995, 1996a, 1996b) then active nests would be most appropriately studied. Even when experiments are as realistic as possible, there is no guarantee that they measure processes that occur in natural nests or that are important from the bird's perspectives.

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