
**ENVIRONMENTAL PREDICTABILITY AND TIMING OF BREEDING IN THE
SAN ANDRÉS VIREO (*Vireo caribaeus*)**

Predictibilidad ambiental y temporalidad reproductiva en el Vireo de San Andrés (*Vireo caribaeus*)

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ABSTRACT

Timing of breeding is a basic trait that should be understood to determine species' requirements during a crucial stage of their life cycle, especially if conservation measures are needed. This is the case of the San Andrés Vireo (*Vireo caribaeus*), a vulnerable insectivorous bird endemic to San Andrés Island, Colombia. We explored the relative importance of biotic and abiotic cues possibly acting as factors triggering breeding in this species. We hypothesized that being a marked seasonal breeder, the San Andrés Vireo would use biotic and/or abiotic cues, both proximal and ultimate, to predict the optimum time to start breeding. We calculated environmental predictability with Colwell's model using four years of brood patch and cloacal protuberance data, and correlated nest abundance during a single breeding season with biotic (food availability) and abiotic (photoperiod, rainfall) parameters. Environmental predictability was 54% and constancy contributed twice as much as contingency to this value. Photoperiod was the most probable proximate abiotic factor triggering a hormonal state of breeding readiness given its constant, reliable and measurable change in time. The first strong rains after the dry season and insect abundance probably act as ultimate factors contributing to fine tune the timing of breeding on a year-to-year basis. However, because we did not analyze the abundance of fruits, an important component of nestling diet, we might have underestimated the correlation between breeding and food abundance. Future studies should seek to confirm our correlational observations through controlled experiments and explore the importance of fruiting phenology on the timing of breeding.

Keywords: environmental cues, Neotropics, predictability, San Andrés Vireo, timing of breeding.

RESUMEN

La temporalidad reproductiva es un rasgo importante que debe ser comprendido para inferir las necesidades de las especies durante una etapa crucial de su ciclo de vida, especialmente cuando se necesitan medidas de conservación. Este es el caso del Vireo de San Andrés (*Vireo*

caribaeus), un ave vulnerable, insectívora y endémica a la isla de San Andrés, Colombia. Exploramos la importancia relativa de parámetros bióticos y abióticos que podrían actuar como factores para desatar la reproducción en esta especie. Como el vireo es una especie de reproducción estacional, predijimos que utilizaría señales bióticas y abióticas, tanto próxima como últimamente, para predecir el tiempo óptimo para la reproducción. Calculamos la predictibilidad ambiental de acuerdo con el modelo de Colwell utilizando cuatro años de datos de parche de incubación y protuberancia cloacal, y correlacionamos la abundancia de nidos durante una estación reproductiva con parámetros bióticos (disponibilidad de alimento) y abióticos (fotoperiodo, precipitación). La predictibilidad ambiental fue de 54% y la constancia contribuyó dos veces más que la contingencia a este valor. Debido a su cambio constante, confiable y medible en el tiempo, el fotoperíodo parece ser el factor próximo que más probablemente actuaría como señal para desatar un estado hormonal de disponibilidad para la reproducción. Las primeras lluvias fuertes luego de la época seca y la abundancia de insectos actuarían como factores últimos que contribuirían a afinar el tiempo de reproducción de acuerdo a las condiciones anuales. Sin embargo, debido a que no analizamos la abundancia de frutos, un componente importante de la dieta de los pichones, pudimos haber subestimado la correlación entre la reproducción y la abundancia de alimento. Estudios futuros deberán tratar de confirmar nuestras observaciones de correlación por medio de experimentos controlados y explorar la importancia de la fenología de fructificación en la temporalidad reproductiva.

Palabras clave: señales ambientales, Neotrópico, predictibilidad, Vireo de San Andrés, tiempo de reproducción.

INTRODUCTION

Birds time their breeding seasons to coincide with environmental conditions that maximize their reproductive success (Hau et al. 2008). To do so, they have monitoring systems that track environmental changes and have adapted to breed successfully under a wide range of conditions (Perrins 1970, Wingfield et al. 1992). Such responses to the environment are triggered by proximal and ultimate factors (Mayr 1961). Proximal factors are those that indicate impending and relevant changes in the environment, such as the change in day length, whereas ultimate factors are those changes in the environment causing differential fitness during a reproductive period, such as food abundance and weather (Hahn & MacDougall-Shackleton 2008). Each species, depending on its biology and ecology, has a unique way of predicting and responding to its environment; when this can be quantified, it is termed environmental predictability (Colwell 1974).

Environmental predictability has been evaluated to discern which factors play the most important role in determining the timing of breeding of some

Neotropical bird species (Wingfield et al. 1992, Wikelski et al. 2000). Such predictability is measured using Colwell's model (1974) based on information theory (Shannon 1948), which states that environmental predictability varies according to constancy (the environment is predictable because it rarely changes) and contingency (the environment is predictable based on the degree of periodicity within a defined lapse of time; e.g. from season to season or from month to month). The relative contributions of constancy and contingency provide information on how species might integrate environmental signals to optimally time life-cycle events, like the breeding season (i.e. making sure they start breeding on the dates which will maximize fitness; Wingfield et al. 1992, Wikelski et al. 2000, Verhulst & Nilsson 2008).

A number of studies have reported on the biotic and abiotic cues used by birds of the temperate zone to time their breeding seasons. For example, breeding in the Great Tit (*Parus major*) coincides with the abundance of Winter Moth (*Operophtera brumata*) caterpillars in Europe, and, in North America, Sage and Brewer's Sparrows (*Amphispiza belli* and *Spicella breweri*) time their breeding to avoid a peak in snakes that prey upon their chicks

(Rotenberry & Wiens 1989, Van Noordwijk et al. 1995). Because all these strategies require compromises, birds regulate their energy budget to account for expensive processes like breeding and molting (Hahn & MacDougal-Shackleton 2008). Although Neotropical species have received less attention, there is a growing body of information showing that, just as temperate breeders, birds from the Neotropics adjust events in their life cycle, such as breeding, to the environmental conditions they experience (Skutch 1950, Young 1994, Hau et al. 2000, 2008, Wikelski et al. 2000, Ahumada 2001, Stutchbury & Morton 2001). Even under different constraints such as a higher incidence of predators, unpredictable resource availability, less-marked seasonal fluctuation and the unpredictability of when fluctuations occur each year, Neotropical species are still able to regulate their life cycle events (Hau et al. 1998, 2000, Wikelski et al. 2000, Beebe et al. 2005). However, it is still not clear to what extent do these constraints affect Neotropical species compared to what is known about their counterparts from temperate areas.

Because environmental conditions in tropical environments may vary greatly over short geographic distances and within short time periods, birds must have the plasticity to adapt to varying environments (Hahn & MacDougal-Shackleton 2008). An example of such plasticity is evident in Neotropical species relying on a precise evaluation of a food resource that fluctuates unpredictably, which will only breed when the abundance of such resource reaches a certain threshold (Hau et al. 1998). Other species are highly plastic in their breeding readiness and can take advantage of unpredictable environmental conditions, such as unexpected pulses of rain, breeding whenever suitable conditions exist (Wikelski et al. 2000, Ahumada 2001, Hau et al. 2004). Some Neotropical species are also highly receptive to small changes in photoperiod, allowing them to match energetically demanding aspects of breeding with the onset of optimal conditions (Wikelski et al. 2000, Hau 2001, Beebe et al. 2005). Photoperiod is thought to stimulate tropical species so that they attain a hormonal state of breeding readiness allowing them to respond to non-photoc cues to time breeding (Dawson et al. 2001, F. G. Stiles *pers. comm.*). In fact, photoperiod is believed to be

the predominant proximate abiotic factor used to time breeding in most nontropical species (King et al. 2001, Verhulst & Nilsson 2008). Avoidance of predators and of harsh climatic events predictable in time may also influence the timing of breeding of many tropical and temperate bird species (Rotenberry & Wiens 1989, Young 1994).

We studied the San Andrés Vireo (Vireonidae, *Vireo caribaeus*), an island endemic with marked breeding seasonality, to assess the relative importance of biotic and abiotic cues that could be acting as the proximate and ultimate factors triggering its breeding. We hypothesized that, being a marked seasonal breeder, the species would use biotic and/or abiotic cues, both proximal and ultimate, to predict the optimum time to start breeding. We calculated environmental predictability using data on the occurrence of brood patches and cloacal protuberances collected over four years, and correlated nest abundance during a single breeding season with biotic (food availability) and abiotic (photoperiod, rainfall) parameters. We propose how might this species perceive its environment and how it predicts the onset of optimal conditions, and we suggest how the biotic and abiotic cues might influence its timing of breeding.

METHODS AND MATERIALS

STUDY SPECIES.- The San Andrés Vireo is a small (10 g) insectivorous bird endemic to the Caribbean Island of San Andrés, Colombia (12°N, 81°W). It is common in all habitats (mangrove, dense forest, matrix of coconut plantations and pastures, gardens, etc.), but nests predominantly in the dry scrubland restricted to the south of the island (Gómez & Moreno 2008). The species' breeding season runs from January to June, peaking in April, with each pair producing a single brood (Gómez & Moreno 2008). Clutch size is 1-3 eggs; incubation takes 17 to 19 days, the nestling period 9 to 11 days, and post-fledging care is sustained for 3 to 4 weeks (Barlow & Nash 1985, Gómez & Moreno 2008). The species has a wide range of foraging strategies but is mostly an active "foliage gleaner" concentrating on vegetation from 1 to 5 m in height (Rosselli 1998, Moreno & Devenish 2003). Adults are exclusively insectivorous, but fruits as well as

arthropods form an important part of the nestlings diet (Rosselli 1998, Gómez & Moreno 2008).

ENVIRONMENTAL PREDICTABILITY.- Environmental predictability for the San Andrés Vireo was determined using information from four annual cycles (2004 to 2007) consisting of brood patch and cloacal protuberance data collected monthly with constant effort at bird banding stations in San Andrés. Brood patches and cloacal protuberance development were evaluated semiquantitatively using five-point and three-point scales, respectively, as defined by Redfen & Clark (2001). The San Andrés Vireo is not sexually dimorphic and males develop a partial brood patch, so our analyses only included birds that were sexed by presence of fully developed brood patches (codes 3 and 4 as in Redfen & Clark 2001) and cloacal protuberances (code 3). To use Colwell's (1974) model, we constructed a matrix showing the percentage of birds captured in breeding condition, the percentage in non breeding condition, and the total number of individuals captured monthly for the four-year dataset (Table 1).

Colwell's model states that the environment is maximally predictable when the same pattern is repeated in all time periods and minimally predictable if all states, i.e. breeding or non-breeding, are equally likely in any given period. Maximum predictability (Pr) can be attained as a consequence of complete constancy (C , where the state, i.e breeding, is constant in all time periods) or complete contingency (M , where there are changes of state from period to period but the whole cycle is

repeated over and over; e.g. always breeding in April, never breeding in September), or of a combination of both. Thus, $Pr = C + M$ and ranges from 0 to 1 (0 to 100%). Using Colwell's equations (see Table 1), we calculated the uncertainty of observing the yearly breeding pattern of the San Andrés Vireo (H) with respect to time/month ($H(X)$), to breeding state ($H(Y)$) and to the combination of both ($H(XY)$), and then calculated Pr , C and M . We also calculated G statistics to determine if Pr , C and M were significantly greater than zero and calculated the ratio of M/C to obtain the environmental information factor (Ie), a measure of the type of information that the species might need to evaluate the onset of optimal breeding conditions (i.e. how much do contingency and constancy contribute to predictability; Wingfield 1992, Colwell 1974).

NEST MONITORING DURING ONE BREEDING SEASON.- We systematically searched for and monitored San Andrés Vireo nests during the breeding season of 2004 in six 100-m² study plots placed within three habitat types: dry scrubland, mangrove forest, and dense forest. Nest searching effort was constant at all sites and throughout the field season. Each nest was monitored every three days on average until the fledglings left the area or the nest failed (Martin & Geupel 1993, Martin et al 1997, Gómez & Moreno 2008). A total of 19 nests were found, with a peak of findings (12/19) in April; most were nests in incubation stage (Gómez & Moreno 2008). The periodicity of these encounters is referred to hereafter as nest abundance and was correlated to changes in biotic and abiotic cues.

Table 1. Frequency matrix of breeding condition for the San Andrés Vireo (*Vireo caribaeus*) per month from 2004 to 2007. Figures are shown as percentage of birds in each state (either breeding or non breeding) calculated from captures. Values for Colwell's equations are: N_{ij} = each of the cells in the matrix or the number of cycles in which birds were in state i at time j . $X_j = \sum N_{ij}$ for every state (s), and, $Y_i = \sum N_{ij}$ for every time (t). Z is the grand total sum of the matrix. n is the total number of individuals captured in the four years.

State (s)	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Yi
% Breeding (N_{ij})	11	13	27	38.6	71	14	2.22	0	1	2.3	4.5	3.1	188
% Non Breeding	89	87	73	61.4	29	86	97.8	100	99	98	96	97	1012
X_j	100	100	100	100	100	100	100	100	100	100	100	100	1200
n	76	135	368	166	167	114	21	18	103	132	134	127	

Note: Colwell's equations used were:

$$H(X) = -\sum(X_i/Z)\log(X_i/Z); H(Y) = -\sum(Y_i/Z)\log(Y_i/Z);$$

$$H(XY) = -\sum\sum(N_{ij}/Z)\log(N_{ij}/Z); P = 1-(H(XY) - H(X))/\log s; C = (1-H(XY))/\log s;$$

$$M = (H(X)+H(Y)-H(XY))/\log s.$$

BIOTIC CUES – FOOD AVAILABILITY.- Insect abundance and availability was assessed in dry scrub, mangrove and dense forest using two methods. Potential insect prey abundance was measured through branch clipping using a 60 x 100 cm collapsible cloth bag held by a wooden pole (Johnson 2000). We bagged five randomly chosen branches 1 to 5 m above the ground, the species' preferred foraging height (Barlow & Nash 1985, Roselli 1998), in every study plot once a week for 13 weeks starting on 8 March 2004. All insects found (including larvae) were counted and potential prey density was calculated as the number of individuals per square meter of foliage (Wolda 1990, Johnson 2000). Because conducting a detailed analysis of the diet of the species was not the purpose of the study, we did not classify the arthropods in the samples. Instead, we assumed that all arthropods encountered made up the potential prey for the San Andrés Vireo on the basis that they occupied the species' preferred foraging microhabitat. To determine if the species' behavior supported this assumption, food availability was measured by quantifying prey capture attempts by five randomly chosen individuals for a fixed time period of 5 min (Hutto 1990). This was repeated once a week in every study plot on the same dates when we clipped branches to sample arthropods (13 occasions). Measurements of potential prey density from branch clipping and rate of capture attempt per minute were correlated to check the reliability of those measurements as reflections of the actual availability of food. We acknowledge that capture attempts may be influenced by multiple factors other than prey abundance, like increasing energetic demands placed by the breeding season (Nagy & Holmes 2005). To aid in clarifying if the change in food intake (measured from capture attempts) corresponded to an increase in insect abundance or to the onset of the breeding season, we used Akaike's information criterion (AIC; Burnham & Anderson 1998) to compare the fit of two general linear models (GLM) relating insect density and date (as a substitute for increasing energetic demands associated with the breeding season) to number of capture attempts.

ABIOTIC CUES – PRECIPITATION AND PHOTOPERIOD.- Annual rainfall on the island averages 1900 mm and shows a bimodal pattern, with a dry season

(February to April < 50 mm) and rainy season peaks in June (> 200 mm) and November (>350 mm) (IDEAM 2004). The rainy season often includes hurricane storms from the Caribbean, especially in November. We obtained precipitation data for the study period of 2004 as daily rainfall measured at an official weather station on the south end of the island (Hoyo Soplador; IDEAM 2004). We compared our field data with official precipitation records for the previous ten years (obtained from IDEAM data 1959-2004) to determine if our study year had been similar to the average of previous ones. Precipitation data were plotted against nest abundance and arthropod abundance.

Photoperiod data were compiled using a trial version of the PFSTools software (Mantiuk et al. 2000), with the coordinates 12° 33'N, 81°41' W and with -5 hour time zone, from January to June 2004. The resulting variation in day length was plotted against nest abundance.

Temperature (26 to 28°C) and humidity (mean 80% +/- 2%) are relatively constant year round in San Andrés (Barriga et al. 1969, CORALINA 1998, IDEAM 2004). It remains an open question if such subtle variations in temperature and humidity could also affect timing of breeding, but we did not evaluate them in this study.

RESULTS

ENVIRONMENTAL PREDICTABILITY.- Four years of brood patch and cloacal protuberance data confirmed that breeding activity in the San Andrés Vireo was largely restricted to the first half of the year, with minor monthly variation between the four years sampled (Table 1). According to Colwell's model, predictability was 0.54 ($G_{Pr} = 303.44$; $p < 0.001$; $gl_{t(s-1)} = 12$), with constancy = 0.37 ($G_C = 24.82$; $p < 0.001$; $gl_{(s-1)} = 1$) and contingency = 0.17 ($G_M = 278.82$; $p < 0.001$; $gl_{(s-1)(t-1)} = 11$). This means that the predictability of the monthly breeding state of the San Andrés Vireo is two times more dependent on constant environmental factors relative to factors changing from month to month. In fact, the environmental information factor was 0.45, owing to the higher proportional contribution of constancy to predictability.

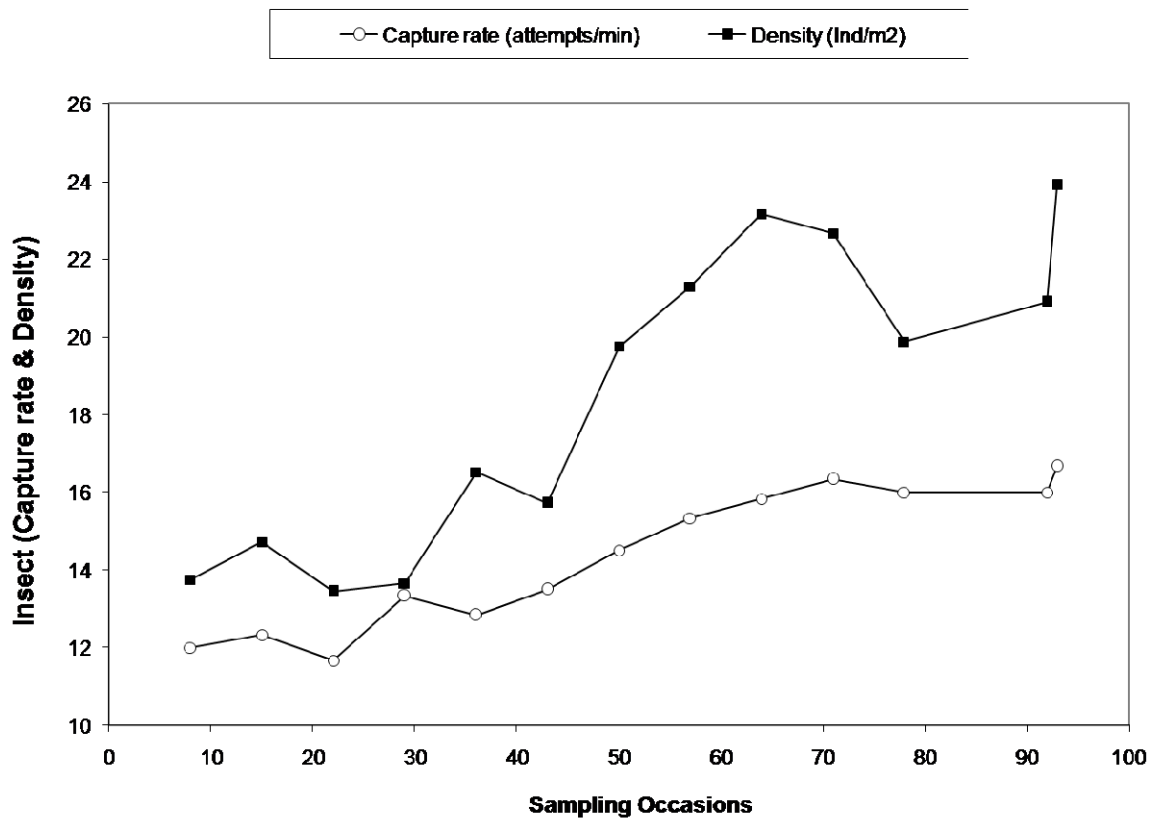


Figure 1. Potential prey density and change in capture attempts by San Andrés Vireos over time (100 days) in early 2004. Averages are presented across all habitats seen through all the sampling occasions on San Andrés Island. The first sample was taken on 8 March, the last one on 1 June.

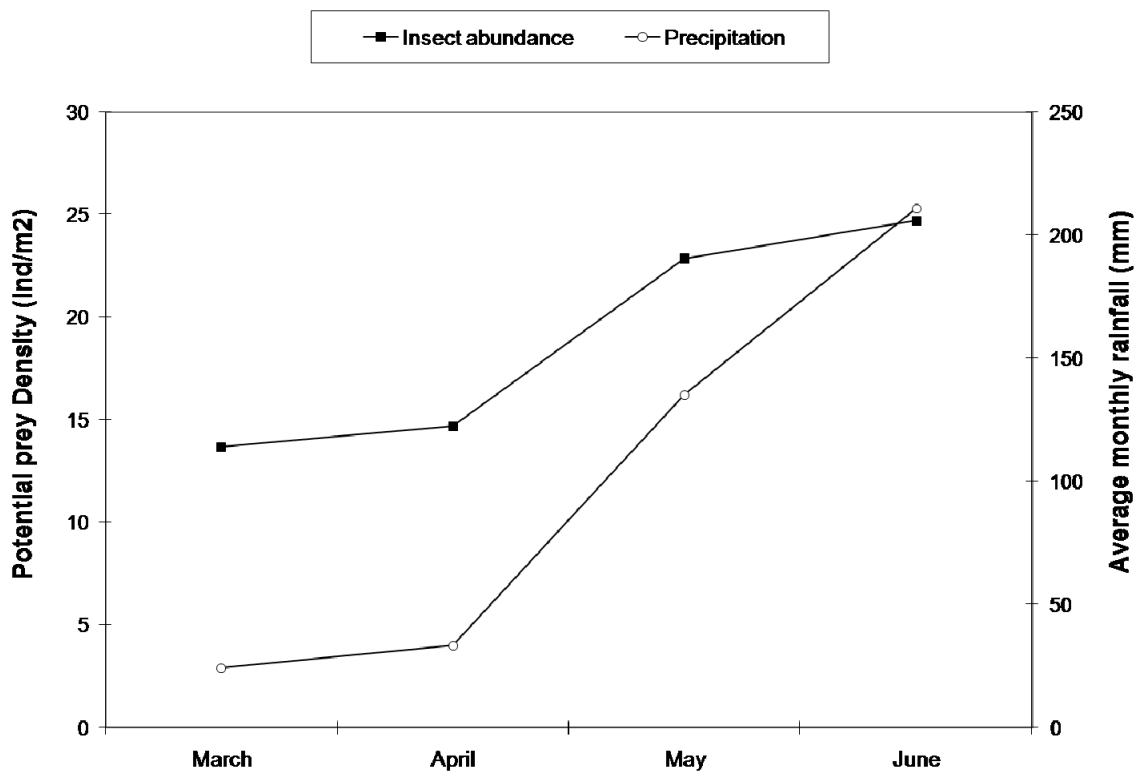


Figure 2. Potential prey density compared to average monthly rainfall in San Andrés Island from March to June 2004.

BIOTIC CUES – FOOD AVAILABILITY.- Branch clipping showed an increase in potential prey density in all habitats from March to June 2004. As expected, the pattern of increase varied slightly between habitats, with dry scrubland having the fastest increase followed closely by mangrove forest; dense forest showed a slower but steadier growth (Fig. 1). The overall change in arthropod abundance was highly correlated between habitats ($r = 0.80$, $n = 13$). Prey capture attempts also increased in every habitat and did so significantly with both insect density (GLM, $F(1, 11) = 90.47$; $p < 0.001$) and date/progression of the breeding season (GLM, $F(1, 11) = 101.61$; $p < 0.001$). However, the comparison of the two models using the AIC indicated that the variability in capture

attempts was 1.96 times better explained by date than by insect density (Table 2).

ABIOTIC CUES – PRECIPITATION AND PHOTOPERIOD.- Year 2004 was typical in terms of temperature and rainfall in San Andrés relative to the previous 10 years. The period from January to March was virtually dry, with only eight rainy days and a daily average of 0.4 mm of rain. The first strong rains fell on 26 March (40 mm in 24 h) and precipitation increased gradually after that, reaching its first peak in June.

We found a high correlation between insect abundance and average monthly precipitation ($r = 0.91$, $p < 0.05$, $n = 13$), as expected for understory-

Table 2. Akaike weights for two general linear models explaining variation in capture attempts of the San Andrés Vireo according to (1) time/date or advancement in the breeding season and (2) a change in insect density. K = number of parameters in model, RSS = Residual sum of squares, AICc = Akaike information criteria values, Δi = Difference in AICc for each model, W_i = Akaike weights for each model.

Model (i)	K	RSS	AICc	Δi	W_i
Date	3	3.788	-7.364	0	0.663
Density	3	4.203	-6.012	1.35	0.337

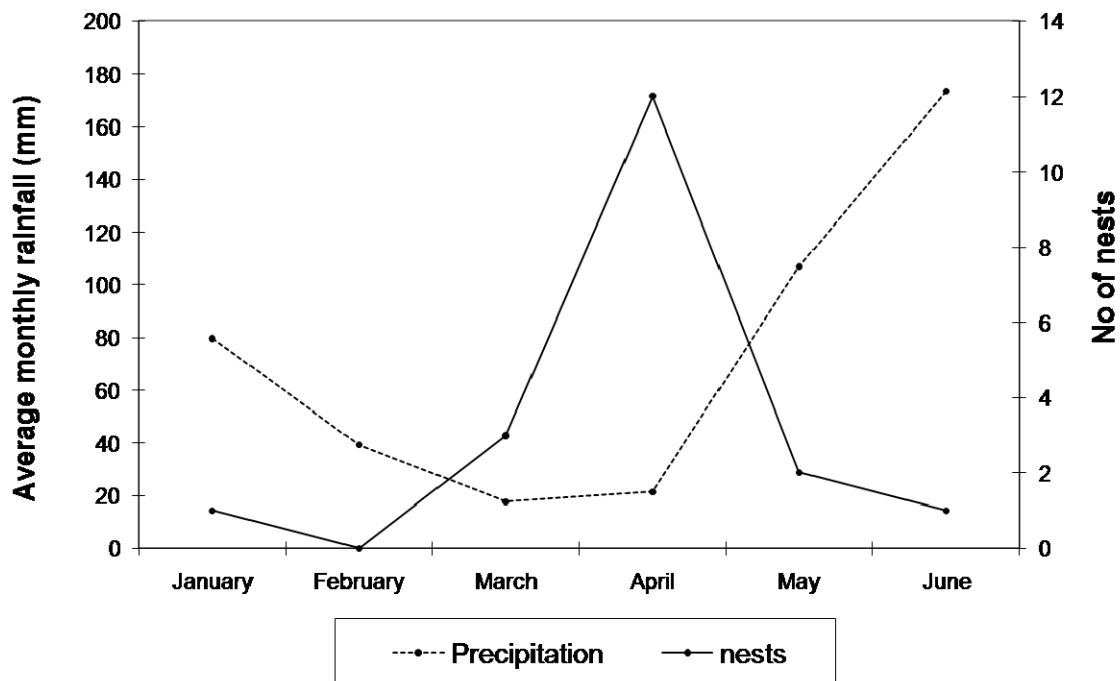


Figure 3. Abundance of nests of San Andrés Vireo in relation to precipitation from January to June 2004.

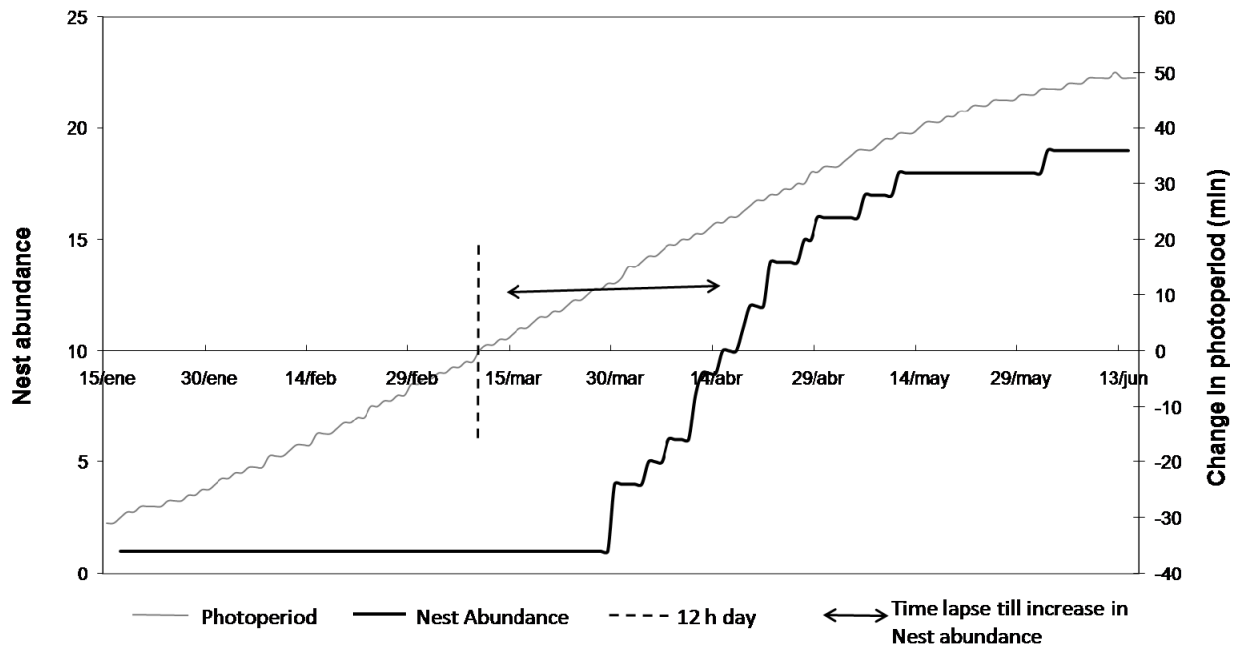


Figure 4. Change in photoperiod compared with cumulative nest abundance of the San Andrés Vireo during 2004. The arrow and vertical dashed line indicate time lapse between the start of increase in day length from 12 h and the steepest increase in nest abundance.

dwelling arthropods (Fig. 2). However, the correlation was not as strong between nest abundance and rainfall ($r = 0.21$, $p = 0.45$, $n = 13$); the peak in nest abundance preceded the peak in rainfall by about one month (Fig. 3).

Photoperiod calculated from the difference in dawn and dusk times according to geographic position revealed that day length in San Andrés varies from 11.5 light hours in January to 12.5 in June. Nest abundance was highly correlated with day length ($r = 0.92$, $p < 0.05$, $n = 19$), such that the start of the steepest increase in nest abundance during mid April (Fig. 4) occurred one month after the winter solstice (12 h photoperiod) of 10 March. In addition, males singing courting-songs were detected only after 15 March (Gómez & Moreno 2008).

DISCUSSION

Our results suggest that environmental changes are relatively predictable (54%) to the San Andrés Vireo and that this predictability is partly associated with a marked seasonality in breeding behavior. However, compared to other species for which predictability has been calculated, the value

of 54% found in this study is low. Predictability for the Spotted Antbird (*Hylophylax naevioides*) in Panama was 70% and temperate-zone species reach values of 90% (Wikelski et al 2000, Silverin et al 2008). Lower values of breeding season predictability, such as those of Darwin's finches (*Geospiza* spp.; 50%), are associated with unpredictable arid environments where precipitation, and thus food abundance, is irregular (Wikelski et al 2000). It is unclear, however, whether our results imply that the breeding season of the San Andrés Vireo is less predictable than that of other species like the Spotted Antbird or equivalent to that of Darwin's finches. Our relatively low value of predictability could be an underestimate because we determined breeding state only based on presence of brood patches and cloacal protuberances, and did not employ more precise metrics like gonadal development state and hormone level measurements (Wikelski et al 2000, Hau et al 2008). Further studies will need to verify if this is the case, and to illuminate the nature of the differences in breeding season predictability existing among Neotropical and temperate-zone species.

Our results show that constancy contributed

substantially more than contingency to the predictability value for the San Andrés Vireo. Again, this is not the case for Spotted Antbirds in Panama, which rely more on contingency to predict optimal conditions for breeding (Wikelski et al 2000). Because Panama is located at a lower latitude than San Andrés, a possible explanation for this difference may relate to geographic position; the relative contribution of constancy to predictability can decrease with latitude, with other environmental factors appearing to play a more important role as cues at lower latitudes (Silverin et al 2008).

Because photoperiod is a constant and reliable cue of measurable change in San Andrés, this comes to mind as the main factor contributing to the measure of constancy and it represents an ideal candidate variable to be the main proximal factor triggering the onset of breeding activity in the San Andrés Vireo (Silverin et al 2008, Verhulst & Nilsson 2008). Indeed, the one-month delay between the onset of a 12-h photoperiod and the increase in nest abundance corresponds to the typical time period for gonadal development in tropical birds after a hormonal signal has been triggered by photoperiod (Hau et al. 1998, 2008, Wikelski et al. 2000). Further, an increase in male song has been shown to induce gonadal growth and breeding activity in females (Hau et al. 1998, 2000), and we detected courting songs shortly after photoperiod passed the 12-h threshold.

Of the variables that we measured, precipitation and insect abundance probably contribute to the contingency component of predictability. The timing of nesting, prior to the peak in rainfall and food abundance, could represent a plastic response ensuring that resource availability is sufficient for the survival of fledglings and dependent juveniles (Young 1994, Hau et al. 2000). Potential food abundance has been shown to be a crucial characteristic sought for by species when choosing good quality nesting sites and it can limit life-history traits such as breeding success (Martin 1987, Burke & Nol 1998). Because rainfall did not increase until after the peak in nesting activity (Fig. 3), it would seem that precipitation itself is not an ultimate factor triggering breeding activity in the San Andrés Vireo. However, tropical species in a

state of breeding readiness could use the first strong rains, which typically precede the peak of the rainy season by several weeks, as the actual trigger for breeding (F. G. Stiles, pers. comm.). During our study, the first strong storm occurred on 26 March, shortly before the peak in nesting activity. Further, although rain is known to have negative effects on nestling survival (Young 1994, Jovani & Tella 2004), most San Andrés Vireo nestlings hatched during a period of heavy rains when food abundance was also higher. It thus appears that when timing their breeding, the adults face a tradeoff between the potential damage that excess rain could have on their open-cup nests and the benefits of taking advantage of increased food availability during wet periods.

Even though prey capture attempts showed a high correlation with insect abundance, it is not clear whether the measure of insect abundance reflected the resources available to the vireos. Indeed, a model including date as a surrogate for increasing energy demands with the progress of the breeding season received more support than a model including insect abundance when predicting capture attempt rates. Also, other climatic variations such as wind could increase branch swaying and have an impact on foraging rate (J. Wingfield *pers. comm.*). Because there could be complex relationships between all these variables, it is difficult to disentangle their effects on foraging rate. Nonetheless, whatever the reason for the higher foraging rate, it is likely that the timing of the breeding season is programmed to take advantage of the increase in insect abundance (Fig. 2) to fulfill both the high energy requirements of the breeding season and the demands of nestlings (Skutch 1950, Martin 1987). Because the main increase in insect abundance occurred after the peak in nesting activity (nests with eggs), insect availability is unlikely to be a proximate factor triggering the start of the breeding season. It more likely acts as an ultimate cue helping to fine tune breeding on a year-to-year basis. We also note that we did not measure fruit abundance and because fruits are an important source of food for nestlings (Gómez & Moreno 2008), future studies should investigate the relationship of fruit abundance and fruiting phenology with the start of the breeding season of

the San Andrés Vireo.

Another factor possibly contributing to the observed timing of breeding in the first half of the year is the hurricane season that generally occurs during the second half of the year in the Caribbean. Although hurricanes do not pass over or near San Andrés on an annual basis, when they do land, they carry with them a high risk of nest failure, and the general increase in rainfall associated with hurricanes is expected to be detrimental to open-cup nesters (Young 1994).

In summary, we found that photoperiod is probably the main proximal factor causing a hormonal state of breeding readiness in the San Andrés Vireo. The first strong rains after the dry season and the resulting increase in food abundance likely act as ultimate factors providing information that allows vireos to adapt the timing of breeding to conditions on a year-to-year basis. We acknowledge that most of the inferences presented in this short-term study are based on correlational analyses; accordingly, further studies should aim to test our hypotheses through experimental designs controlling conditions such as photoperiod and food availability. However, basic information like that presented here is essential to build on the knowledge of vulnerable species such as the San Andrés Vireo and to shed light on the breeding ecology of other Neotropical species.

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