Environmental Cues that Initiate Reproduction in the Rufous Vanga (*Schetba rufa*)

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Introduction

Temperate bird species usually have breeding seasons that begin in the spring, when reproduction starts synchronously. Gonadal development is controlled by the photoperiod in many temperate bird species (e.g., Lofts & Murton 1973). For tropical birds, however, change in photoperiod has not been regarded as a proximate environmental cue for the timing of reproduction, because the change in photoperiod is small in the tropics (e.g., Voous 1950, Miller 1959). However, recent studies indicate that many tropical birds do breed seasonally, and that gonadal development responds to slight changes in photoperiod (Chandola-Saklani *et al.* 1990, Hau *et al.* 1998, Stutchbury & Morton 2001). A neotropical bird, the Spotted Antbird (*Hylophylax n. naevioides*), even responded physiologically to a photoperiod increase of only 17 minutes (Hau *et al.* 1998).

Photoperiod is probably an initial cue for physiological preparation for reproduction in many tropical birds, as it is in numerous temperate-zone birds. However, tropical birds may use supplementary cues, such as rainfall and temperature change, to fine-tune the onset of reproductive activities. For example, Baya Weavers (*Ploceus philippinus*) in India prepare physiologically for reproduction when day length increases, and they then use rainfall as a final stimulus for nest-building and egg-laying (Chandola-Saklani *et al.* 1990). Heron Island Silvereyes (*Zosterops lateralis*) engage in nest-building activity after heavy rainfall (Kikkawa & Wilson 1983), and two species of Darwin's Finch on Isla Daphne Major, *Geospiza fortis* and *G. scandens*, begin breeding shortly after the onset of rain (Boag & Grant 1984). In these species, rainfall was associated with an abundance of insects and seeds, on which the birds feed.

The Rufous Vanga (*Schetba rufa*) is endemic to Madagascar and inhabits both dry deciduous forest and rainforest (Langrand 1990). From 1994 to 2000, we conducted a field study of the Rufous Vanga at Ampijoroa Forest Station in Ankarafantsika Strict Nature Reserve (16°15'S, 46°48'E), which is characterized by dry deciduous forest and

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distinct rainy and dry seasons. Our research revealed that this tropical species has obvious breeding seasons (Eguchi *et al.* 2001). The distinct seasonality of the study site enabled us to define the start of the rainy season and made it easy to assess rainfall.

From 1996 to 2000, we collected data on temperature and precipitation. We examined whether day length, rainfall, and temperature affected the timing of breeding in the Rufous Vanga.

Material and Methods

The breeding season of the Rufous Vanga starts in late September and ends in early January (Eguchi *et al.* 2001). The Rufous Vanga is territorial and breeds monogamously, although pairs occasionally rear young cooperatively with up to four helpers (Yamagishi *et al.* 1995, Asai *et al.* 2001, Eguchi *et al.* 2002).

We located nests at the start of each breeding season and visited each nest every two to four days to monitor the progress of reproductive activities. The duration of nest building varied considerably among nests, from one week to more than a month (Eguchi *et al.* 2001). We defined the start of reproductive activity each year as the day when a pair laid its first egg; nest building was not used in the definition because its progress was unpredictable. Although the Rufous Vanga lays a single brood, replacement nests are built if the first nest fails (Eguchi *et al.* 2001, 2002). Eggs laid in replacement nests were excluded when determining the onset of reproductive activity, because they were the result of breeding that had been disturbed (e.g., by predation) rather than the result of seasonal changes.

Precipitation per day was measured from 1997 to 2000 by a rain gauge set at a station approximately 2 km from the center of the study area, where daily maximum and minimum temperatures were also measured. Data on temperature and precipitation in 1996 were collected by Drs. U. Thalmann and A. Müller (pers. comm.).

To examine whether each pair laid eggs synchronously, we applied the I_δ index (Morishita 1959) to the period from the earliest egg-laying (October 2) to the latest egg-laying (November 25) of the five study years, except for two outliers (see Results). The I_δ index is used to evaluate the degree of contagious distribution; it equals 1 if the probability of a phenomenon is constant (i.e., its frequency is randomly distributed). Because we applied the index to a period that was arbitrarily divided up, the “null” class in the frequency distribution depended on the period. Therefore, the I_δ value could not be used to evaluate the absolute degree of contagious distribution. We could, however, evaluate the relative degree of synchronicity among years.

Photoperiod data were calculated from times of sunrise and sunset posted on the Japan Coast Guard web site (<http://www.kaiho.mlit.go.jp>) using the calculator provided. Day length was calculated by subtracting the time of sunrise from the time of sunset.

In order to examine whether environmental conditions affected egg-laying strongly over the study period, we employed five physical conditions: day length, cumulative precipitation from the first rain of the rainy season, mean maximum temperature for the week, mean minimum temperature for the week, and cumulative weekly precipitation. All

five conditions were determined on the first day of egg-laying and on the day when 80% of pairs had laid eggs, to minimize the impact of pairs that had bred early. The mean temperatures were also determined for the second week before egg-laying was first observed.

Results

Most pairs laid eggs synchronously, within approximately four weeks each year (Fig. 1). We also observed egg-laying in one nest as late as December in 1996 and 2000; however, because no eggs had been laid for three weeks or more before that, we considered these two nests outliers. The annual I_δ index from 1996 to 2000 was 2.2, 2.0, 5.8, 3.0, and 3.6, respectively. Because the periods over which I_δ was calculated inevitably contained days on which egg-laying was not observed, these values are artificially larger than those of a random distribution.

The rainy season started each year in late September or October, and the pattern of rainfall fluctuated among years (Fig. 1). The first egg-laying occurred after the first rainfall in all years except 1997 (Fig. 1), when the first rain fell on the day when the egg-laying of the second pair was observed (Fig. 1). In 1998, egg-laying started after the second heavy rainfall (35.1 mm, October 24) rather than after the first rainfall (0.65 mm, October 7; see Fig. 1). The I_δ indices tended to be larger in years when there was more precipitation just before the onset of egg-laying (see Table 1a; Kendall's coefficient: $\tau = 1.00$, $P < 0.05$). The number of days from first rainfall to first egg-laying differed among years.

The mean maximum temperature differed by up to 5.6°C among years; the minimum temperature differed by up to 5.1°C (Table 1). The mean maximum and minimum temperatures for the second week before the first day of egg-laying were similar to the temperatures indicated in Table 1a (Table 2): the mean temperatures differ by only 0.3 to 1.1°C for the maximum temperature and 1.4 to 3.5°C for the minimum temperature. These differences were less than one-third the difference in daily temperature (12.5°C on average over the five years).

Day length varies from 11 hours and 10 minutes to 13 hours and 7 minutes annually in the study area. In 1994 and 1995, the day length on the first day of egg-laying (October 9) was 12 hours and 22 minutes. On the first days of egg-laying, the longest and shortest day lengths differed by 22 minutes (Table 1a); this is 19% of the annual variation in day length. On the other hand, 80% of pairs began breeding before days reached 12 hours and 50 minutes in length in each year of the study (Table 1b). Day length on the last day of egg-laying (including in replacement nests) was either 13 hours and 6 minutes or 13 hours and 7 minutes in each of the five years (Fig. 1).

Discussion

The maximum and minimum temperatures change regularly with the seasons at Ampijoroa (Mizuta 2002). Changes in these temperatures probably do not induce

Fig. 1. Maximum and minimum temperatures, precipitation, and number of nests from October to December 1996 to 2000. Upper and lower lines indicate maximum and minimum temperatures, respectively. Bars indicate the precipitation (extremely low precipitation [$< \text{approximately } 0.5 \text{ mm}$] is not shown). A solid circle indicates a nest in which egg-laying was observed. Upward arrows indicate the last day of observed egg-laying, including in replacement nests; the times accompanying the arrows are the day length. The length of the first day of egg-laying is indicated in Table 1a. Downward arrows indicate the timing of the first rainfall of each season. In 1996, the first rain fell on September 25.

Table 1. Environmental conditions (a) on the first day of egg-laying and (b) on the day when 80% of pairs had laid eggs. In some cases, mean maximum and minimum temperatures and cumulative precipitation values were calculated using data for three to six days because data were partially lacking.

(a)

Year	Date	Day length	For the week			Cumulative precipitation from first rain (mm)
			Mean max. temperature (°C)	Mean min. temperature (°C)	Cumulative precipitation (mm)	
1996	Oct. 2	12 h 16 m	32.7	17.9	0.8	0.8
1997	Oct. 7	12 h 20 m	33.0	19.2	0	0
1998	Oct. 27	12 h 38 m	38.3	18.7	35.1	35.9
1999	Oct. 27	12 h 38 m	34.6	23.0	1.2	1.2
2000	Oct. 24	12 h 36 m	36.1	20.7	33.4	33.4
Mean		12 h 29 m	35.0	19.9	14.1	14.2
SD		10.7 m	2.3	2.0	18.4	18.6

(b)

Year	Date	Day length	For the week			Cumulative precipitation from first rain (mm)
			Mean max. temperature (°C)	Mean min. temperature (°C)	Cumulative precipitation (mm)	
1996	Nov. 1	12 h 43 m	35.2	19.3	0	0.8
1997	Nov. 5	12 h 45 m	33.8	21.2	3.0	61.3
1998	Nov. 5	12 h 45 m	37.5	21.3	0.1	40.7
1999	Nov. 9	12 h 48 m	35.5	22.6	92.0	95.4
2000	Nov. 1	12 h 43 m	35.8	20.8	29.5	71.0
Mean		12 h 44 m	35.6	21.1	24.9	53.8
SD		2.0 m	1.3	1.2	39.5	35.6

Table 2. Mean maximum and minimum temperatures (°C) from the second week before the first day of egg-laying. The mean temperatures for 1996 were calculated from five days' data instead of seven. In 1997, the temperatures were not measured because egg-laying started just after field observations began.

Year	Mean max. temperature	Mean min. temperature
1996	31.6	16.5
1997	—	—
1998	37.8	16.6
1999	34.9	19.5
2000	36.4	18.0

egg-laying, however, because the seasonal changes are much smaller than the daily changes in temperature. If the Rufous Vanga were sensitive to the slight seasonal changes in temperature, daily temperature changes would perturb the species' awareness of the seasons.

Day length at the end of egg-laying was consistent among years. Furthermore, most pairs had begun breeding by the time the day was 12 hours and 50 minutes long. Day length must, therefore, be a determinant of reproductive activity. The rainy season began in September or October in the study area. Regulating its reproduction schedule by photoperiod leads to the Rufous Vanga reproducing around the start of the rainy season.

In four of the five study years, egg-laying began after the first rain. This trend suggests that the rainfall induced the laying of eggs. If the Rufous Vanga regulated its reproductive activity by slight changes in day length alone, the day length at the onset of egg-laying would be more synchronous among the five years than we observed. Variation in day length on the first day of egg-laying among the study years is probably the result of fine-tuning the egg-laying in response to the first rain. However, the number of days from the first rain to the onset of egg-laying varied considerably among years. Such variation implies that the first rain does not simply induce the onset of egg-laying. Because there was no rain in October 1996, the second and subsequent pairs to lay eggs may not have coordinated the timing of egg-laying with the occurrence of rain.

Precipitation early in the breeding season affected the synchronicity of egg-laying among pairs. Therefore, the timing of egg-laying in the Rufous Vanga is determined not only by the first rain but also by the amount of precipitation early in the breeding season. When precipitation was scarce early in the breeding season, some pairs seemed to delay egg-laying to time their reproduction with the progress of the rainy season. On the other hand, some pairs seemed to start reproducing before enough rainfall so as not to miss reproductive opportunities. Thus, we suggest that the Rufous Vanga uses photoperiod as a cue for the start of reproduction and fine-tunes its egg-laying according to the timing and abundance of the first rainfall.

Day length and rainfall are probably the proximate factors that determine the breeding season of the Rufous Vanga; the ultimate factor, however, remains unknown. Parents may determine their breeding schedule on the basis of the availability of food for the young, as Lack (1968) suggested. After the start of the rainy season, the number of aerial insects in the study area increased rapidly (Mizuta 2002). Thus, the Rufous Vanga may begin breeding around the start of the rainy season to increase the survival rate of young. Mizuta's finding is not directly applicable to the Rufous Vanga, however, because the species often feeds on the ground (Yamagishi & Eguchi 1996). Further studies are needed to identify the factors that ultimately determine the breeding season of the Rufous Vanga.

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アカオオハシモズ *Schetba rufa* において繁殖開始を促す環境要因

最近の研究成果によって、熱帯域に生息する鳥類でも温帯域の鳥類と同様に光周期によって生殖巣の発達を制御していることが分かってきた。しかし、生理学的な繁殖準備とは別に、降雨量などによって巣作りや産卵などの繁殖行動の開始時期を調整することも知られている。本研究ではマダガスカルの落葉乾燥林に生息するアカオオハシモズがどのようなタイミングで産卵を開始するか調べた。調査地は季節性がある雨季と乾季に分かれる。1996年から2000年の10月から12月について、一日の最高気温、最低気温、降雨量と、やり直し営巣を除いたクラッチの初卵日を調べた。また、海上保安庁の計算サービスを利用して調査地の日長を計算した。産卵が始まる直前の1週間の平均気温は年によってばらつき、その変動は年内の変動より大きい。一方、1997年を除いて、雨期の始まりである最初の降雨のあった日以降に全ての産卵が始まっていた。1997年の場合でも2番目のペアが初卵日を迎えた日に最初の雨が降っていた。また、初期降雨量の多い年ほど、同調して産卵が見られた。しかし、最初の降雨から各ペアの初卵日が観察される日数は一定しない。全体の80%のペアが初卵日を迎える日の日長と、再営巣を含むその繁殖期で最後の産卵日の日長は毎年非常に安定している。これらのことから、(1) 気温の変化は産卵開始の合図とするには変化が小さすぎる、(2) 日長の変化がアカオオハシモズの繁殖活動に影響を与えている、(3) 雨期の最初の降雨が産卵開始のきっかけとなっており、そのときの降雨量も産卵開始に影響することが示唆された。アカオオハシモズの繁殖行動、特にその産卵に関しては、日長に基づいたスケジュールがあり、雨期の最初の降雨とその降雨量によって産卵開始日の微調整を行っているものと考えられた。

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