

Dry-season retreat and dietary shift of the dart-poison frog *Dendrobates tinctorius* (Anura: Dendrobatidae)

Marga Born¹, Frans Bongers¹, Erik H. Poelman² and Frank J. Sterck¹

¹ Forest Ecology and Forest Management Group, Center for Ecosystem Studies, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands. E-mails: marga.born@planet.nl, frans.bongers@wur.nl, frank.sterck@wur.nl.

² Laboratory of Entomology, Wageningen University, P.O. Box 8031, 6700 EH Wageningen, The Netherlands. E-mail: erik.poelman@wur.nl.

Abstract

Dry-season retreat and dietary shift of the dart-poison frog *Dendrobates tinctorius* (Anura: Dendrobatidae). Seasonal rainfall affects tropical forest dynamics and behavior of species that are part of these ecosystems. The positive correlation between amphibian activity patterns and rainfall has been demonstrated repeatedly. Members of Dendrobatidae, a clade of Neotropical dart-poison frogs, are well known for their habitat use and behavior during the rainy season, but their behavior during the dry season has received little attention. We studied habitat use and diet of the dendrobatid frog *Dendrobates tinctorius* in French Guiana during the rainy and dry seasons. Unlike many other dendrobatid frogs, *D. tinctorius* does not maintain territories for the entire rainy season. Both sexes colonize recently formed canopy-gaps and stay in these forest patches for only a few weeks. The frogs in these patches consume a great diversity of prey, consisting of ants, beetles, wasps, insect larvae, and mites. During the dry season, frogs move to retreat sites in mature forest, such as palm bracts and tree holes. The frogs are less active and consume fewer prey items in the dry season, and they consume fewer wasps and insect larvae, but more termites. Ants are the most common prey items during both the wet and dry seasons. We discuss the effects of shifts in seasonal habitat use on the territorial behavior of dendrobatid frogs.

Keywords: Anura, Dendrobatidae, *Dendrobates tinctorius*, habitat, prey, retreat-sites, seasonality, site fidelity, tree-fall gap.

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Resumo

Abrigos durante a estação seca e mudanças na dieta do sapo-veneno-de-flecha *Dendrobates tinctorius* (Anura: Dendrobatidae). A precipitação sazonal afeta a dinâmica das florestas tropicais e o comportamento das espécies que fazem parte desse ecossistema. A relação positiva entre os padrões de atividade dos anfíbios e a precipitação já foi demonstrada repetidas vezes. Os membros da família Dendrobatidae, um clado de sapos-veneno-de-flecha neotropicais, são bem-conhecidos por seu uso de hábitat e comportamento durante a estação chuvosa, mas seu comportamento durante a estação seca tem recebido pouca atenção. Estudamos o uso de hábitat e a dieta do dendrobatídeo *Dendrobates tinctorius* na Guiana Francesa durante as estações chuvosa e seca. Ao contrário de muitos outros dendrobatídeos, *D. tinctorius* não mantém territórios ao longo de toda a estação chuvosa. Ambos os sexos colonizam clareiras recentemente abertas e permanecem apenas poucas semanas nessas manchas, onde os animais consomem uma grande variedade de presas, principalmente formigas, besouros, vespas, larvas de insetos e ácaros. Durante a estação seca, os animais movem-se para locais de abrigo na floresta madura, como brácteas de palmeiras e ocos de árvores. Nesse período, são menos ativos e consomem um menor número de itens alimentares; consomem menos vespas e larvas de insetos e mais cupins. Formigas constituem a presa mais comum durante as duas estações. Discutimos os efeitos das mudanças sazonais no uso de hábitat sobre o comportamento territorial dos dendrobatídeos.

Palavras-chave: Anura, Dendrobatidae, *Dendrobates tinctorius*, clareiras, fidelidade de hábitat, locais de abrigo, presas, sazonalidade.

Introduction

Activity patterns of Neotropical amphibians are positively correlated with rainfall (Duellman and Trueb 1986). During the wet seasons, most amphibian species are active and reproduce. Typically, male frogs establish short-term territories for reproductive purposes and forage elsewhere (Wells 1977). However, long-term territoriality has been reported for all members of the Neotropical dart-poison frogs of the family Dendrobatidae (Cope 1865) that have been studied (Pröhl 2005, Poelman and Dicke 2008, Brown *et al.* 2009, Ringler *et al.* 2009). In the wet season, males of most species of dart-poison frogs defend territories for reproductive purposes, but these territories often also provide conditions for other activities, such as sites for hiding and feeding (Pröhl 2005).

Prey consumption by the colorful members of Dendrobatidae is highly specialized. Species that forage primarily on ants accumulate toxins in their skin and are brightly colored (Santos *et al.* 2003, Darst *et al.* 2005). Beetles, millipedes, and mites also have been identified as a dietary source for skin toxins in the aposematically

colored dart-poison frogs (Dumbacher *et al.* 2004, Saporito *et al.* 2004, Takada *et al.* 2005). Some of the smallest dart-poison frogs have a specialized diet that consists of mites (Valderrama-Vernaza *et al.* 2009), which also may represent the largest source of alkaloids for some dendrobatids (Takada *et al.* 2005, Saporito *et al.* 2007). Although aposematic dart-poison frogs do specialize on particular prey items, these may vary considerably in abundance, depending on the habitat and seasonal changes (Toft 1980, Biavati *et al.* 2004). Thus, the use of the habitat by some dart-poison frogs may be in response to reproductive activity, as well as the availability of prey items that are a source for their skin alkaloids. However, habitat use and prey consumption by dart-poison frogs has received little attention with regard to seasonal shifts.

We studied the habitat use and diet of the dendrobatid frog, *Dendrobates tinctorius* (Schneider, 1799), in French Guiana during the rainy and dry seasons. *Dendrobates tinctorius* is diurnal and inhabits pristine tropical rainforest areas in northern Brazil, French Guiana, Suriname, and the southeastern part of Guyana.

Because it is brightly colored and toxic, we anticipated that the frog would be specialized to forage on prey that would provide a dietary source of alkaloids. This study specifically addresses the ways in which the habitat and diet of *D. tinctorius* vary during the wet and dry season within a rainforest. We discuss the effects of seasonal changes in habitat, diet, and reproductive behavior on the territorial behavior of this dendrobatid frog.

Materials and Methods

Study Site

Fieldwork for this study was conducted between April and November 1991 at the Nouragues Research Station (04°5' N, 52°41' W) in French Guiana (Bongers *et al.* 2001), where annual rainfall varies between 3000 and 3250 mm (Grimaldi and Riéra 2001). A short dry season (<100 mm rain/mo) lasts from February until the end of March, and a long dry season extends from September–November, but the duration and timing of these dry seasons vary. Between the dry seasons, rainy seasons occur from April–August and December–January (>100 mm rain/mo). The Nouragues area (102,000 ha) is topographically variable and includes the steep foothills of an Inselberg (the Balanfois Mountains), a hilly zone, and a creek valley. The forest is dissected by creeks, which

are part of the Approuage River Basin. Apart from these streams, there is only one isolated forest pond in the vicinity of the station (Born and Gaucher 2001). Elevations range from 25–60 m (river basin and lower hilly zone) to 411 m on the Inselberg (Charles-Dominique 2001).

We studied frog activity in a forest area of 12 ha (400 × 300 m), which was not disturbed by other researchers and which includes the structural diversity characterizing larger areas of the forest at this site (Van der Meer *et al.* 1994). We discriminated three types of habitat related to the phase of forest development. Most of the forest area was covered by a closed, 30–40-m mature forest; however, two forest patches consisted of fresh, natural tree-fall gaps and two other forest patches were older tree-fall gaps that were maturing. Each of the four forest patches covered about 350 m², based on the method of defining gap areas developed by Runkle (1981) and Van der Meer *et al.* (1994). We sampled a much larger area of mature forest, because it was easier to walk in this and frog density was lower in the mature forest than in the younger forest phases. We characterized forest types by noting dominant species, understory height or herbaceous layer, and height of canopy trees exceeding 20 m (Table 1).

The amphibian community at Nouragues consists of at least 54 species placed in 21 genera and 8 families. In Dendrobatidae, there are two dendrobatines (*Dendrobates tinctorius* and

Table 1. Summary of the forest study-plot characteristics at the Nouragues Research Station, French Guiana. Code to numbers: 1 = *Cecropia* sp.; 2 = *Melastomataceae*; 3 = *Bromeliaceae*; 4 = *Musaceae*; 5 = *Cyclanthaceae*; 6 = *Piper* sp.; 7 = *Pteridaceae*; 8 = *Zingiberaceae*; 9 = *Vouacapoua americana*; 10 = *Sapotaceae*; 11 = *Inga* sp.; 12 = *Bauhinia* sp.

Phase of forest development	Height	Height of surrounding trees	Dominant species	Dominant canopy species
Recently formed gap	<1 m	20–45 m	—	9, 10, 11, 12
Maturing gap	0.5–10 m	20–40 m	1, 2, 3, 4, 5, 6, 7, 8	9, 10
Mature forest	30–45 m	30–45 m	—	9, 10, 11

Ranitomeya ventrimaculata) and one colostethenine (*Ameerega hahneli*). Species of Aromobatidae include two allobatines (*Allobates femoralis*, and *A. granti*) and two anomaloglossines (*Anomaloglossus baeobatrachus* and *A. degranvillei*) (Born and Gaucher 2001, Grant *et al.* 2006, Kok *et al.* 2006, Frost 2010).

Study Species

Dendrobates tinctorius is mainly terrestrial, although we observed frogs climbing tree trunks to heights of 40 m (Born 1994). The frogs forage in the leaf litter and deposit their clutches of 3–14 eggs there. Males do not have advertisement vocalization, but instead, produce weak buzz calls when courting a female (Born 1994). Eggs hatch within 14–28 days and males transport the tadpoles, one or two at a time, on their backs to discrete bodies of water (e.g., palm bracts, water-filled bromeliad axils or tree holes, and other suitable places high up in trees). Metamorphosis is reported to occur within 90–120 days after oviposition (Masurat and Wolf-Rudiger 1991). We observed metamorphosis to occur in 90 days at Nouragues (Born 1994). In contrast to members of the dendrobatine sister genera *Oophaga* and *Ranitomeya*, females do not provide tadpoles with unfertilized eggs to eat; the larvae are omnivorous, feeding on detritus, insect larvae, and other frog eggs or tadpoles (Summers and McKeon 2004, Grant *et al.* 2006). *Dendrobates tinctorius* is well known for its geographic variation in aposematic color and pattern (Wollenberg *et al.* 2006, 2008, Noonan and Gaucher 2006). The Nouragues population has blue legs and flanks (sometimes bearing yellow spots), and a dorsal pattern of yellow and black. Each frog has a unique pattern (Silverstone 1975) of yellow lines on its back and flanks (Figure 1); we used these patterns to identify individuals in the field. At first capture, we recorded the yellow dorsal and flank patterns of the frog on identification cards (Summers 1989, 1992) and measured the snout–vent length (SVL) with calipers. We considered animals with a

SVL less than 25 mm as juveniles. Frogs were sexed by measuring their snout–vent lengths and the widths of their fingertips. Male *D. tinctorius* have wider fingertips ($2.7 \text{ mm} \pm 0.3$) than females ($1.8 \text{ mm} \pm 0.5$; Silverstone 1975). Females are larger than males (female SVL: $38.3 \text{ mm} \pm 2.3$, male SVL: $34.8 \text{ mm} \pm 2.4$).

Habitat Use

One of us (M.B.) visited the study area up to four times per week between 06:30 and 19:00 h and conducted visual-encounter surveys for *Dendrobates tinctorius*. This entailed walking slowly and stopping at regular intervals to make observations. A randomized walking design was followed in each patch or in the surrounding mature forest (Crump and Scott 1994). The behavior of the frog was recorded at the time it was first encountered. Similar amounts of time were spent in each phase of forest development and in each different patch. We calculated the encounter rates (observations per observation time) to correct the number of observations per phase of forest development for the time spent on the survey. Observations in each of the three forest development phases were similarly distributed throughout the day. Special attention was paid to potential hiding places, such as tree holes, caves, palm bracts, and logs during the surveys. Frogs were caught by hand so that we could record the dorsal and flank patterns, measure the SVL, and determine the sex. When the same individual was observed in the same day, we did not consider it to be a second capture in the analysis, because our aim was to estimate the densities of animals in different locations. Recaptures were recorded only when the subsequent observation was made on a different day. To investigate site fidelity, we recorded the number of days between captures, and the distance between sites of capture and recapture. Distances between capture locations were measured in a straight line with a tape measure. At each observation we recorded the (1) time of day, (2) relative humidity, and (3) temperature in



Figure 1. Examples of dorsal pattern variation in *Dendrobates tinctorius*. Three specimens recorded in the Nouragues forest and one (bottom right) in the Saul forest, French Guiana, 1991.

the frog's microhabitat. We observed the (4) activity in which the frog was engaged, distinguishing among (4a) foraging, (4b) tadpole transport, (4c) courtship, (4d) intra-specific aggression, (4e) inactivity, and (4f) climbing trees, but not foraging. At each observation we noted (5) the substrate types on which frogs were

found and distinguished the following classes: (5a) on (fallen) trees, branches, buttresses, tree bases (further referred to as "wood"); (5b) under decaying wood (= "decaying wood"); (5c) in leaves of crowns of fallen trees (= crowns); (5d) on litter surface (= litter); and (5e) in bracts of palm inflorescences (= bracts). We measured

ambient humidity and temperature with a battery-powered psychrometer (Hygrophil type 4456). We recorded daily rainfall and maximum and minimum temperatures each morning and evening, at an open spot less than 100 m from the study area.

Prey Consumption

To investigate whether there is a correlation between prey consumption by *Dendrobates tinctorius* with habitat and season, stomachs of frogs were flushed and prey items were identified (Legler 1977, W. Bosman pers. comm.). New tree-fall gaps can be difficult to access; therefore, some of the frogs observed were not flushed because attempting to capture them would cause too much habitat disturbance. Flushing was performed with a 60-ml syringe attached to a flexible tube; flushing was repeated three times to retrieve most of the stomach contents of the frog. Although flushing may not fully guarantee the collection of all prey items in a frog's stomach, we specifically chose this method because it is non-destructive. After their stomachs were flushed, individuals were released at the capture site and observed for a short time. Frogs did not seem to show any negative effects and usually started to forage again within 30 min. Prey and prey parts in stomach-flush samples were counted with the aid of a binocular stereomicroscope; items were sorted into seven groups—termites, ants, beetles, mites, larvae, wasps, flies, and unidentified prey items. Samples were fixed in 10% formalin. Most ants were identified to species level (Appendix I).

Statistical Analysis

We used Chi-square tests to analyze the effect of habitat, as characterized by the phase of forest development and substrate class on frog abundance. We also tested whether the recapture frequency differed between sexes, using Chi-square and the Yates correction for one degree of freedom (Fowler and Cohen 1990). Frog

abundance in one habitat was calculated as the number of frogs found in that habitat, divided by the total number of frogs encountered. Subsequently, we analyzed whether habitat use by *Dendrobates tinctorius* varied during the season relative to the amount of rainfall. We used a Spearman Rank correlation, corrected for ties, to test whether rainfall affected frog activity by relating the percentage of inactive frogs from the total number of frogs observed to rainfall on the observation day. A factor analysis was used to determine the influence of season, habitat, and sex on the diet of *D. tinctorius*. We transformed counts of prey items into percentages of the diet of the subject frog. Each sample was coded by the habitat in which the frog was collected and the season in which the frog was captured. We divided the samples into two seasonal groups—the rainy season (June until the end of August, with an average rainfall of more 315 mm per month) and the dry season (September and October, with an average rainfall of less than 50 mm per month). We did the analyses using SPSS.

Results

Habitat Use

Most *Dendrobates tinctorius* were active during the early morning between 08:00–09:30 h and in the late afternoon between 16:30–17:30 h. We made 520 observations (including recaptures) of *D. tinctorius* during the study period. The observations comprised 299 adults (444 observations, including recaptures)—88 females, 85 males and 126 individuals of unknown sex. In addition, 38 juveniles (43 observations, including recaptured frogs) and 33 tadpoles were observed. We recaptured only 65 of the 299 individual frogs—29 males, 24 females, 9 individuals of unknown sex, and 3 juveniles. Only 31 frogs were captured more than twice; most of these frogs were recaptured within a week at the same site, and some individuals were recorded through periods longer than 120 days (Figure 2). No

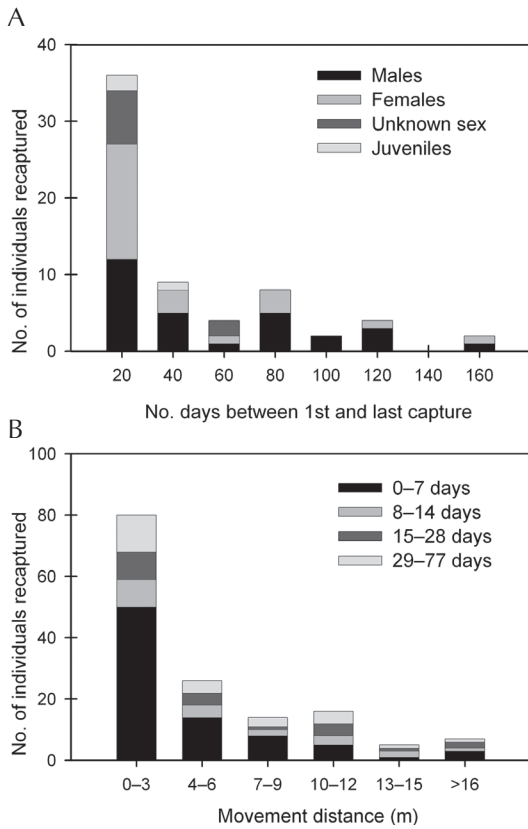


Figure 2. Recaptures of *Dendrobates tinctorius*. Total number of recaptures in relation to (A) number of days between first and last capture, and (B) movement distance between captures.

differences in recapture were found between males and females ($X^2 = 1.17$, $df = 1$, $p > 0.05$). Most recapture locations were only 0–3 m away from the previous capture sites (Figure 2). Frog densities were estimated at 3.1 frogs per 100 m² (1.5 males, 1.4 females, 0.2 juveniles/100 m²), but differed significantly between forest development patches ($X^2 = 38.91$, $df = 2$, $p < 0.005$) (Figure 3). Frogs were captured more frequently in recently formed canopy-gaps than in canopy-gaps that were maturing, or in mature forest (contribution to Chi-square of this numerator is 22.07). Most of the frogs observed (315) were foraging. Eight frogs were engaged

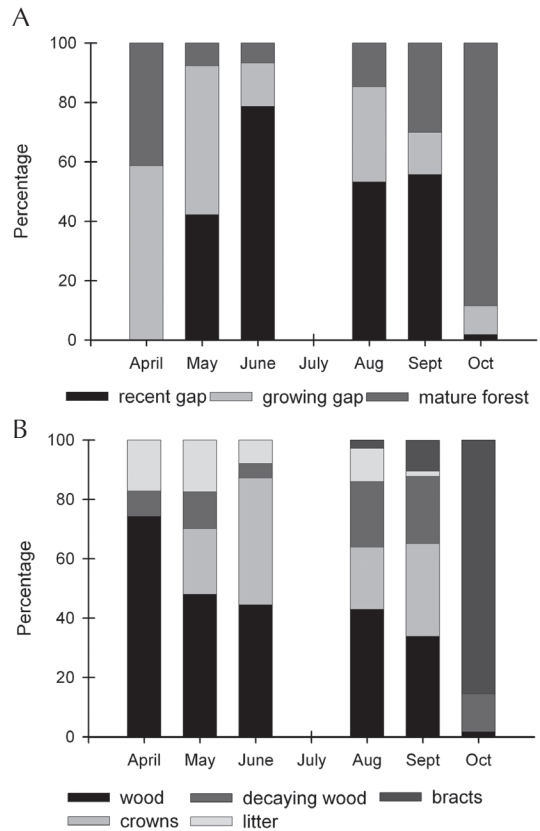


Figure 3. Occurrence of *Dendrobates tinctorius* expressed per month as (A) percentage of frogs observed per habitat type (recent tree-fall gap; maturing tree-fall gap; mature forest); (B) percentage of frogs observed per substrate category ([wood] = on [fallen] trees, branches, buttresses and tree bases; [decaying wood] = under decaying wood; [crowns] = in fallen tree crowns with leaves; [litter] = on litter surface; [bracts] = in bracts of palm inflorescences). No observations were made in July.

in courtship behavior; four exhibited intra-specific aggression. Five frogs were transporting tadpoles and seven were climbing trees but not foraging. Frogs were most likely to be encountered in recently fallen crowns of trees (37.3%) and only sporadically found in litter or under decaying wood ($X^2 = 117.10$, $df = 9$, $p < 0.005$; Figure 3).

Activity of *Dendrobates tinctorius* was positively correlated with rainfall (Spearman rank correlation, corrected for ties, $r = 0.52$, $p < 0.001$; Figure 4). Rainfall decreased to nearly nothing from the end of August to the end of October. There was increased frog activity during a few days with rainfall in the second half of September. Few active frogs were found during October (Figure 4). In the wet months (April–June), most individuals were found on wood and in recently fallen crowns of trees (Figure 3). Use of retreat sites was strikingly low (<15%) during this time of the year. In the dry months, *D. tinctorius* increasingly seek retreat sites. In the driest month (October, <4 mm precipitation), more than 95% of all frogs were captured on the ground in bracts of the inflorescences of the palms

Oenocarpus bacaba and *Jessenia bataua*. These large (up to 170 cm), canoe-shaped bracts fill with water in the wet season and provide retreat sites. In nine cases, we found two or three frogs in the same retreat site (Born 1994). Humidity in the immediate environment of the animal (RH 84.2 – 100%) was higher than ambient humidity (RH 76.6 – 91.4%) (Wilcoxon Signed Ranks test, $p < 0.001$).

Prey Consumption

Of the total of 97 stomach samples, 67 contained prey items (46 females and 21 males; Table 2). Frogs captured in recently formed tree-fall gaps tended to have more prey items in their stomachs than frogs captured in mature forest

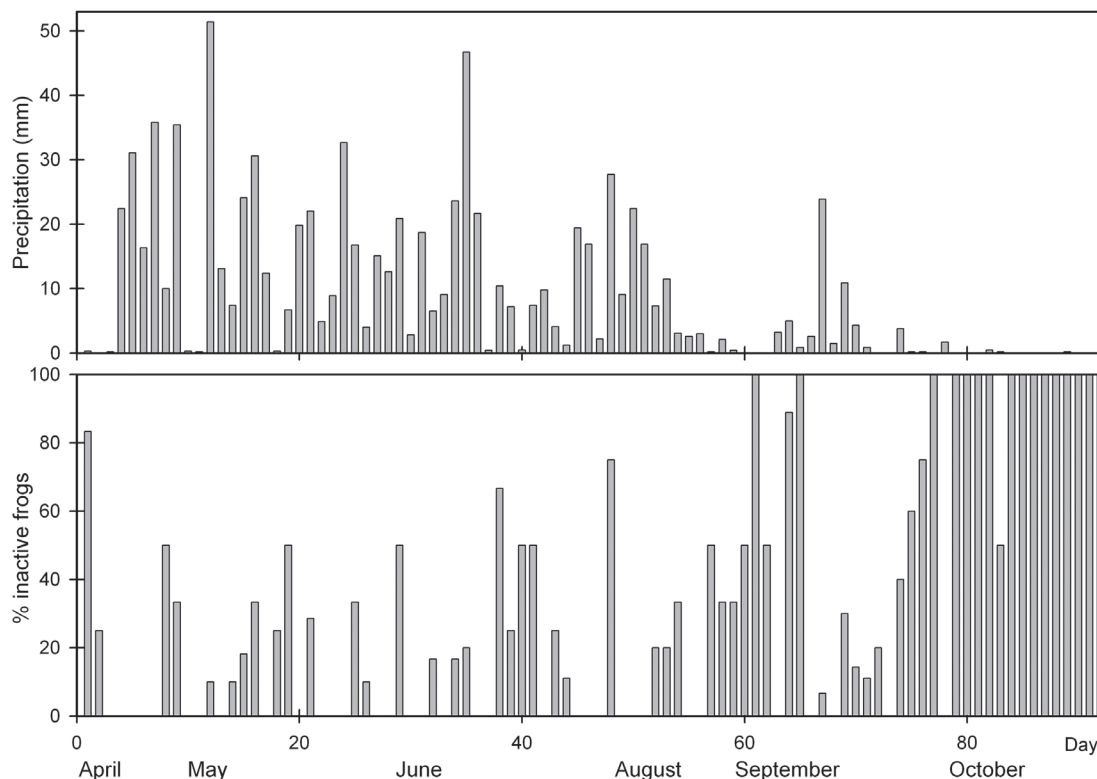


Figure 4. Histogram of daily rainfall (mm) (upper panel) during observation days and the percentage of inactive *Dendrobates tinctorius* frogs encountered in their retreat sites (lower panel).

Table 2. Total number of prey items consumed by *Dendrobates tinctorius*. Larvae include all insect larvae. Miscellaneous includes all other insect categories found in the stomachs.

Prey type	Females (n = 46)			Males (n = 21)		
	No. prey items	% Total no. items	No. stomachs	No. prey items	% Total no. items	No. stomachs
Ants	1895	78.6	45	550	80.8	20
Termites	75	3.1	14	10	1.4	3
Beetles	157	6.5	33	48	7.0	15
Mites	148	6.1	27	45	6.6	11
Larvae	91	3.8	22	15	2.2	6
Wasps / Flies	39	1.6	21	11	1.6	4
Miscellaneous	6	0.2	4	2	0.3	1
Totals	2411	100	—	681	100	—

(independent sample t-test, $p = 0.052$). Females (mean = 52.4, SD = 41.2) had more prey items than males (mean = 32.4, SD = 36.9; independent sample t-test on log-transformed data, $p = 0.015$). Ants were the most abundant prey items accounting for 78.6% and 80.8% of the diets of females and males, respectively. Nearly all stomachs contained ants, including diurnal, nocturnal, terrestrial and arboreal species (Appendix I). Of the total variation in prey items, 45.8% was explained by the first two factors of the factor analysis (28.2% and 17.6%, respectively). Habitat was significantly related to Factor 1 (gaps > mature forest, $p = 0.035$) and season to Factor 2 (rainy season > dry season, $p = 0.027$; Figure 5). Factor 1 has a strong negative correlation with ants and a positive correlation with beetles and mites (Table 3). Thus, frogs consumed ants more frequently in mature forest and most of the other prey items in gaps. Factor 2 correlated negatively with termites and positively with insect-larvae and wasps (Table 3). This correlation suggests that in the dry

season, frogs consumed more termites and fewer insect-larvae and wasps. The consumption of ants and the remaining prey items was unaffected by season.

Discussion

Activity patterns of *Dendrobates tinctorius* responded to seasonal variation in rainfall. During the rainy season, both males and females colonized recently formed tree-fall gaps and stayed in these forest patches for only a few weeks. The recently fallen, leafy tree crowns probably offered shelter while foraging, as well as a large variety of prey items that were consumed by *D. tinctorius* (e.g., beetles, mites, wasps, and insect larvae). Frogs that were caught in mature forest during the wet season had lower diversity of prey items in their stomachs and primarily consumed ants. During the dry season, frogs were found primarily in mature forest where they occupied retreat sites in palm bracts, under decaying wood, and in tree holes. These

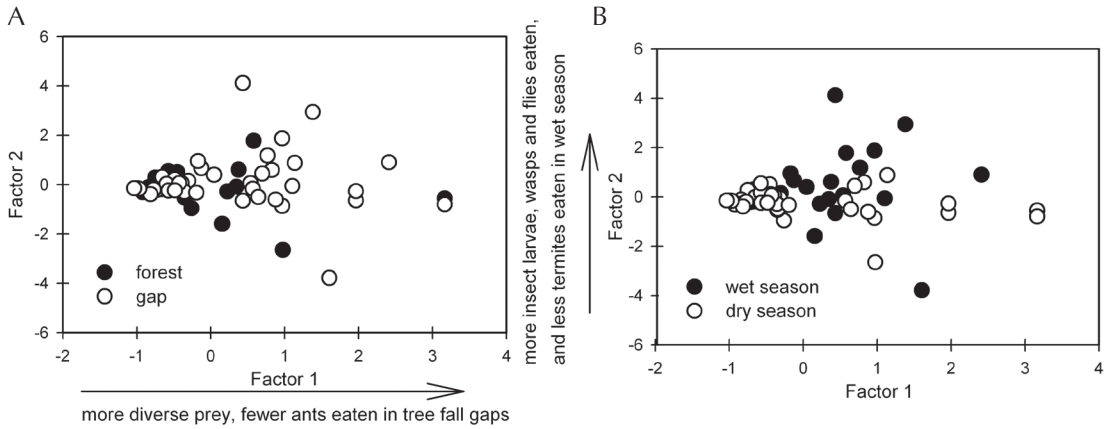


Figure 5. Factor analysis of selected prey items in *Dendrobates tinctorius*. Only cases for which stomachs contained prey items are used. Factor 1 is significantly related with habitat and Factor 2 with season. Panel (A) represents tree-fall gap versus mature forest. Panel (B) represents the rainy versus the dry season. Correlations of prey items with Factors 1 and 2 are presented in Table 3.

retreat sites were used collectively by the frogs, as also is the case in the sister species, *D. auratus* (Gray and Green 2000). Retreat sites also were used as sites for tadpole deposition. Although tadpoles are known to be cannibalistic, we found five of them together in a water-filled palm bract (Born 1994).

Not only did frogs reduce their activity when rainfall decreased, they also consumed fewer prey and a lower diversity of prey items during the dry season. During the dry season, the diet shifted towards a reduction in the consumption of wasps and insect larvae, and more commonly contained termites. Ants were the most common prey items during wet and dry season. Our results show that during the wet season, *Dendrobates tinctorius* opportunistically colonizes recently formed tree-fall gaps and individual frogs stayed there for only a few weeks.

Male *Dendrobates tinctorius* did not establish territories that lasted for the entire rainy season, in contrast to the behavior of most other species of dart-poison frogs. Typically, male dart-poison frogs have been reported to defend the same territories throughout the entire rainy season (Pröhl 2005, Poelman and Dicke

Table 3. Statistics of the factor analysis of selected prey items of *Dendrobates tinctorius*. Factors 1 and 2 are significantly related habitat and season, respectively; see Figure 5. Correlations of prey items with the two factors are presented.

Prey items	Factor 1 (~habitat)	Factor 2 (~season)
Ants	-0.97	0.15
Termites	0.23	-0.63
Beetles	0.57	-0.07
Mites	0.70	0.01
Larvae	0.38	0.66
Wasps	0.11	0.61
Miscellaneous	0.04	-0.06

2008, Ringler *et al.* 2009). Territoriality in some species of dendrobatid frogs has been attributed to defense of food, water, and hiding places, but in most species, territoriality is associated with reproductive activities (Pröhl

2005). Males that defend territories for reproductive purposes have been hypothesized to either defend perches that enhance sound transmission of their advertisement vocalizations (Roithmair 1994, Pröhl and Hödl 1999, Pröhl 2003) or for access to reproductive resources (Donnelly 1989a, b, Poelman and Dicke 2008). Among the reproductive resources essential for dart-poison frogs are distinct places where eggs or tadpoles can be deposited, such as favorable sites in leaf litter or water, contained in tree holes or leaf axils of plants. Like *Ranitomeya ventrimaculata*, *D. tinctorius* lacks an advertisement vocalization and only vocalizes when courting a female or in agonistic interactions with other males; thus, *D. tinctorius* does not defend territories to ensure vocalization perches (Poelman and Dicke 2008). Furthermore, *D. tinctorius* deposits eggs in the leaf litter, which is not a limiting reproductive resource for dart-poison frogs (Donnelly 1989b). The tadpoles of *D. tinctorius* are only rarely deposited in the leaf axils of plants. Male *D. tinctorius* deposit their tadpoles in tree holes or palm bracts that may be found scattered throughout the forest. In other species of dart-poison frogs, tadpoles are commonly transported to bodies of water outside the male's territory and reproductive resources are not defended (Donnelly 1989b, Poelman and Dicke 2007). Thus, the suite of behavioral characteristics described for *D. tinctorius* suggests that there is no long-term territorial behavior associated with reproduction.

Habitat use by *Dendrobates tinctorius* may be determined more by opportunities for foraging than by resources that are defended for reproductive purposes. The number and type of prey items consumed by *D. tinctorius* is positively correlated with rainfall. During the dry season, frogs consumed fewer prey and ate more termites, which were likely encountered near their retreat sites in palm bracts and tree holes, or under decaying wood. After leaving their retreat sites, the frogs had a more diverse diet during the wet season. Although seasonal aspects may largely

determine the variation in diets of dart-poison frogs (Valderrama-Vernaza *et al.* 2009), different habitats may offer variation in types of prey available for consumption (Toft 1980, Biavati *et al.* 2004). We found that *D. tinctorius* foraging in recent tree-fall gaps had a more diverse diet than frogs found in mature forest. Prey richness and abundance probably is high in tree-fall gaps because the insect fauna inhabiting the canopy tree crowns is available to leaf-litter frogs. Foraging in recently formed tree-fall gaps may provide *D. tinctorius* with variation in their diet or a key component of their diet, including ants that contribute to the evolution of aposematic color of dart-poison frogs (Santos *et al.* 2003, Darst *et al.* 2005, Saporito *et al.* 2009), and mites and beetles that act with ants as sources of alkaloids and skin toxins (Dumbacher *et al.* 2004, Saporito *et al.* 2004, Takada *et al.* 2005). *Dendrobates tinctorius* may be opportunistic in its colonization of recently formed tree-fall gaps to forage more efficiently on prey items from which frogs can acquire most of the alkaloids for their own defense. During the dry seasons, frogs ate more termites. Remarkably, frogs preferred termites to ants, as shown in a small-scale prey-choice experiment in the forest (Born 1994), thereby suggesting that prey items with greater nutritional value (Paoletti *et al.* 2003) were preferred to those with lower nutritional value, even when the latter is the toxin resource. Female *D. tinctorius* may require a more diverse diet to meet the energetic requirements of vitellogenesis (Donnelly 1991, Valderrama-Vernaza *et al.* 2009). In fact, females consumed more prey items than males, but the sexes did not differ in the composition of their diet.

The short-term stay of many of individual frogs found in the recently formed tree-fall gaps may indicate that both prey abundance and sheltering conditions diminished in the weeks following the tree fall. Therefore, frogs may experience a reduced benefit of continued foraging in recently formed tree-fall gaps. Alternately, *D. tinctorius* may reproduce away from canopy gaps. Both males and females

were more common in recently formed tree-fall gaps. The response of the two sexes to the abundance and richness of different prey items in canopy gaps may result in a reliable predictor of mate presence. Often within a few days after a new tree-fall gap is formed, the first frogs are observed around fallen trees. Several times at Nouragues, we observed the colonization of new canopy gaps by *D. tinctorius* within few days after gap formation (Born and Poelman, pers. observations). In one case, more than 40 individuals were encountered in a new tree-fall gap. Here males not only find females, but females can sample the quality of different males. Hypothetically, a pair of frogs then might leave the preferred foraging ground to search for a reproduction site. At the site of reproduction, the male can be recollected for several weeks. Eggs of *D. tinctorius* hatch within 14–28 days and are attended by the male. After the eggs hatch, the male transports the tadpoles to bodies of water where the tadpoles are left without further parental care. Males then may return to better foraging grounds or continue caring for another clutch of eggs that the female deposited. In this way, the habitat use by both males and females is determined by their behavioral state—reproduction or optimal foraging—and this results in a short-term or non-territorial system typical of many anurans (Wells 1977).

Foraging behavior of *Dendrobates tinctorius* determines habitat use and constrains a territorial system in this species; thus, we have identified the first case of an absence of a territorial system in the genus *Dendrobates*. Moreover, our work demonstrates that habitat use by dart-poison frogs also is constrained by dry seasons, and that habitat use and territorial systems should be studied across different seasons or years to understand the demography of dendrobatid frogs (Ringler *et al.* 2009). For future studies, we suggest including prey item availability in different habitats to distinguish between the effects of habitat and food-item preference for anuran diets.

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Appendix I. Ant taxa recovered in 23 stomach samples of *Dendrobates tinctorius* from French Guiana. “Defense” refers to the presence (+) or absence (–) of a distinctive system of defense. Under “number of samples,” parenthetical values indicate the number of stomach samples taken from frogs that were foraging and captured in tree-fall gaps. Identifications by G. Delye, Marseille.

Ant genus/species	No. samples	Diel activity	Habitat	Defense
<i>Acanthognathus</i> cf. <i>rudis</i> (Myrmicinae)	1 (1)	Day/Night	Terrestrial	?
<i>Acromyrmex</i> sp. (Myrmicinae)	4 (0)	Day/Night	Terrestrial	+
<i>Anochetus mayri</i> (Ponerinae)	1 (0)	Night	Terrestrial	–
<i>Apterostigma</i> sp. (Myrmicinae)	5 (2)	Day/Night	Terrestrial	–
<i>Azteca</i> sp. (Dolechoderinae)	2 (1)	Day/Night	Arboreal	+
<i>Camponotus</i> sp. (Formicinae)	1 (1)	Day	Terrestrial	?
<i>Crematogaster</i> cf. <i>stolli</i> (Myrmicinae)	1 (1)	Day	Terrestrial/Arboreal	–
<i>Crematogaster</i> sp. (Myrmicinae)	18 (11)	Day	Terrestrial/Arboreal	–
<i>Cyphomyrmex costatus</i> (Myrmicinae)	1 (1)	Day/Night	Terrestrial	–
<i>Cyphomyrmex faunulus</i> ¹ (Myrmicinae)	4 (2)	Day/Night	Terrestrial	–
<i>Cyphomyrmex hamulatus</i> (Myrmicinae)	1 (1)	Day/Night	Terrestrial	–
<i>Cyphomyrmex peltatus</i> (Myrmicinae)	1 (0)	Day/Night	Terrestrial	–
<i>Cyphomyrmex</i> sp. (Myrmicinae)	1 (1)	Day/Night	Terrestrial	–
<i>Eurhopalothrix bolaii</i> (Myrmicinae)	1 (1)	Day/Night	Terrestrial	?
<i>Eurhopalothrix</i> sp. (Myrmicinae)	1 (1)	Day/Night	Terrestrial	?
<i>Gnamptogenys horni</i> (Ponerinae)	2 (1)	Day/Night	Terrestrial	–
<i>Gnamptogenys minuta</i> (Ponerinae)	1 (0)	Day/Night	Terrestrial	–
<i>Gnamptogenys pleurodon</i> (Ponerinae)	1 (0)	Day/Night	Terrestrial	–
<i>Gnamptogenys</i> sp. (Ponerinae)	1 (1)	Day/Night	Terrestrial	–
<i>Hypoponera</i> sp. (Ponerinae)	4 (3)	Day/Night	Terrestrial	–
<i>Lachnomyrmex</i> sp. (Myrmicinae)	1 (0)	?	Arboreal	?
<i>Monacis bispinosa</i> (Dolechoderinae)	1 (0)	Day/Night	Arboreal	+
<i>Myrmicocrypta</i> sp. (Myrmicinae)	3 (2)	Day/Night	Terrestrial	–

¹ Uncertain identification at species level.

Appendix I. Continued.

Ant genus/species	No. samples	Diel activity	Habitat	Defense
<i>Neivamyrmex</i> sp. (Dorylinae)	2 (1)	Night	Terrestrial	+
<i>Neostruma</i> sp. (Myrmicinae)	2 (1)	Day/Night	Terrestrial	?
<i>Nesomyrmex</i> sp. (Myrmicinae)	2 (1)	?	Arboreal	?
<i>Octostruma balzani</i> (Myrmicinae)	3 (2)	Day/Night	Terrestrial	?
<i>Octostruma batesi</i> (Myrmicinae)	2 (2)	Day/Night	Terrestrial	?
<i>Oligomyrmex</i> sp. (Myrmicinae)	4 (2)	?	Terrestrial	?
<i>Pachycondyla</i> sp. (Ponerinae)	1 (0)	Day/Night	Terrestrial	–
<i>Paratrechina</i> sp. (Formicinae)	2 (0)	Day/Night	Terrestrial/Arboreal	?
<i>Pheidole</i> sp. (Myrmicinae)	21 (12)	Day	Terrestrial	–
<i>Quadristruma emmae</i> (Myrmicinae)	1 (1)	Day/Night	Terrestrial	?
<i>Sericomyrmex</i> sp. (Myrmicinae)	1 (1)	Day/Night	Terrestrial	–
<i>Smithistruma</i> sp. (Myrmicinae)	1 (0)	Day/Night	Terrestrial	?
<i>Solenopsis</i> sp. (Myrmicinae)	14 (8)	Day	Terrestrial	+
<i>Stegomyrmex</i> sp. (Myrmicinae)	1 (0)	?	?	?
<i>Strumigenys elongata</i> (Myrmicinae)	3 (3)	Day/Night	Terrestrial	–
<i>Strumigenys prospiciens</i> ¹ (Myrmicinae)	1 (1)	?	?	?
<i>Strumigenys</i> sp. (Myrmicinae)	6 (3)	Day/Night	Terrestrial	?
<i>Trachymyrmex</i> sp. (Myrmicinae).	1 (0)	Day/Night	Terrestrial	–
<i>Typhlomyrmex</i> sp. (Ponerinae)	1 (1)	Day/Night	Terrestrial	–
<i>Zacryptocerus minutus</i> (Myrmicinae)	1 (0)	?	Arboreal	?

¹ Uncertain identification at species level.