



Phenotypic divergence across populations does not affect habitat selection in an Amazonian poison frog

Martin Mayer^{a,b,*}, Lia Schlippe Justicia^c, Bibiana Rojas^{c,d}

^a Department of Forestry and Wildlife Management, University of Inland Norway, Anne Evenstads Vei 80, Koppang 2480, Norway

^b Department of Ecoscience, Aarhus University, Nordre Ringgade 1, Aarhus 8000, Denmark

^c Department of Interdisciplinary Life Sciences, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Savoyenstrasse 1, Vienna 1160, Austria

^d University of Jyväskylä, Department of Biological and Environmental Sciences, P.O. Box 35, Jyväskylä 40014, Finland

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ABSTRACT

Understanding intraspecific variation in habitat selection by polytypic species, where distinct variants occur in separate populations, can improve our knowledge of population-specific selective pressures and inform conservation measures. Here, we investigated differences in habitat selection across six populations of the dyeing poison frog (*Dendrobates tinctorius*), an aposematic species characterized by great phenotypic variation. In each population, we recorded the locations and associated habitat of frogs and systematically scored available habitat. We hypothesized that habitat selection differs (1) among populations containing different variants, predicting that larger-bodied frogs are less dependent on moisture-retaining structures; (2) between disturbed and pristine areas, predicting frogs in disturbed areas being more reliant on structural diversity and water bodies; and (3) between males and females, predicting stronger differences in habitat selection in populations with greater sexual size dimorphism. We found little variation in habitat selection among populations or between disturbed and pristine areas but detected strong general patterns across populations. Frogs selected for proximity to tree falls, dead woody material, presence of water pools, and avoided areas with extensive ground vegetation and little canopy cover. Moreover, males tended to show a stronger selection for proximity to water and females stronger selection for tree falls. Combined, our results suggest that in aposematic species, habitat selection might be relatively constant across populations, potentially because of reduced susceptibility to local predation risk. Our findings provide important baseline data regarding the habitat requirements of this emblematic species, which can be relevant for efficient conservation measures in the future.

1. Introduction

The way organisms choose or avoid certain habitats and features can have direct repercussions on their fitness, for example by selecting patches that reduce the risk of predation, with more food resources, and better thermoregulatory conditions (Huey, 1991; Brown and Kotler, 2004). Thus, understanding how species use the resources in a habitat across time and space (i.e. habitat use) and

* Corresponding author at: Department of Forestry and Wildlife Management, University of Inland Norway, Anne Evenstads Vei 80, Koppang 2480, Norway.

E-mail addresses: martin.mayer@inn.no, martin.mayer@ecos.au.dk (M. Mayer).

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the use of habitats in relation to their availability (i.e. habitat selection) is of critical importance in applied ecology and wildlife conservation. Patterns of habitat use and selection can help us assess how land use change and other environmental factors affect species (Mayer et al., 2019; Tarjuelo et al., 2020), and their capacity to adapt to new conditions (Knopff et al., 2014; Evans et al., 2024). These studies are essential to identify priority habitats and resources for species persistence, and to develop effective management plans to protect or restore them (Wang et al., 2018; Sanz-Pérez et al., 2021). This is especially important in tropical areas, where primary rainforests host some of the highest terrestrial biodiversity on our planet (Gibson et al., 2011), but at the same time experience one of the fastest deforestation rates (Myers, 2023).

Habitat selection is complex, with trade-offs between animal requirements, e.g. protection from predators versus mating opportunities, which might differ between sexes (Oliveira et al., 2018; Evans et al., 2024). For example, males and females often differ in body size and energetic demands, leading to variation in their optimal habitats and sex-specific spatial segregation (Oehlers et al., 2011; Slezak et al., 2024). Other physical, behavioral or environmental differences within and among populations can also lead to differences in habitat use and selection. Polymorphism in coloration, for instance, can lead to selection of visually different substrates by distinct phenotypes to reduce predation risk, for example via background matching (Lovell et al., 2013; Camacho et al., 2020). Likewise, individuals with different appearance within a population can select microhabitats with more or less sun exposure to suit their respective thermoregulatory needs (Karpestam et al., 2012). These differences can also manifest across populations when there is geographic variation in morphological characteristics, such as body size and coloration. However, few studies to date have quantified intraspecific differences in habitat selection across geographic ranges, especially in polytypic species where distinct variants occur in separate populations. This may have important ecological implications and can inform us about the species' habitat requirements across their distribution range. Further, consistent differences in habitat selection could also have evolutionary implications, leading, for example, to contrasting natural selection regimes affecting the survival and reproduction of the individuals (Endler and Rojas, 2009).

The dyeing poison frog (*Dendrobates tinctorius*), endemic to the Eastern Guiana Shield, is an excellent model species to investigate intraspecific differences in habitat use and selection due to their large interpopulation differences in coloration, pattern, body size and sexual size dimorphism (Wollenberg et al., 2008; Schlippe Justicia et al., 2023). In addition, *D. tinctorius* has been classified as a protected species in French Guiana in 2020 (Decree No. TREL2032100A from November 19th, 2020), which highlights the importance of improving knowledge concerning habitat selection in its various populations to establish baseline knowledge for appropriate conservation measures.

Dendrobates tinctorius are terrestrial frogs, although they frequently climb vines and trees. They are often restricted to rainforest in elevated ridges or plateaus (Noonan and Gaucher, 2006) but have been recorded from 0 to 600 m a.s.l. (Born et al., 2010). They are diurnal and characterized by bright color patterns (Wollenberg et al., 2008; Rojas and Endler, 2013) coupled with the possession of skin alkaloids (Daly et al., 1987; Lawrence and Rojas et al., unpublished) presumably sequestered through their arthropod-based diet, as shown in closely related species, *D. auratus* (Daly et al., 1994, 2000). The combination of warning coloration and alkaloid defenses (i.e. aposematism) is believed to protect them from potential predators (Noonan and Comeault, 2009; Lawrence et al., 2019). In contrast to most Dendrobatidae species, *D. tinctorius* does not seem to defend long-term territories, with both males and females found occasionally in aggregations around tree-fall gaps (Born et al., 2010; Rojas and Pašukonis, 2019). This species shows elaborate parental care behaviors, including egg attendance (Rojas and Pašukonis, 2019; Weygoldt, 1987) and tadpole transport (Born et al., 2010; Rojas, 2014). Females lay their eggs on leaf litter or under/inside hollow fallen logs, that are then cared for by the male (Rojas and Pašukonis, 2019). Males deposit newly hatched tadpoles in a wide variety of small pools formed in vegetation structures (i.e. phytotelmata), where they remain unattended until metamorphosis (Born et al., 2010; Clough and Summers, 2000; Rojas, 2014).

To date, most information regarding habitat use of this species has been based on a single population, showing that during the rainy season frogs use recently formed tree-fall canopy gaps, while they become less active during the dry season and occupy retreat sites such as palm bracts (Born et al., 2010). Further, Rojas and Pašukonis (2019) found females to be more associated with open areas of leaf litter and males more associated with woody structures. However, no information is available concerning their habitat selection.

Here, we addressed three main study aims and associated hypotheses:

- (1) Describe general habitat use and intermediate-scale habitat selection during the rainy season by active dyeing poison frogs across populations. We hypothesized that habitat selection is related to fine-scale habitat characteristics, predicting that frogs select for higher altitudes, dead woody structures, proximity to fallen logs and water bodies, and cover of leaf litter.
- (2) Investigate whether habitat selection varies among populations. We hypothesized that habitat selection might differ among populations due to differences in body size and coloration, predicting that frogs in larger-bodied populations are less dependent on structures that retain moisture, such as fallen trees and water bodies. Coloration might affect susceptibility to predators, thereby altering habitat selection, but we could not make clear predictions because we had no information regarding the main predators across populations (which might perceive the color patterns of frogs in each population differently). Additionally, we hypothesized that habitat selection differs between disturbed and pristine areas, predicting that frogs in disturbed forests show a stronger selection for fallen trees/woody structures and water bodies due to reduced availability in these areas.
- (3) We hypothesized that habitat selection partly varies between males and females, predicting that both females and males select for dead woody structures and fallen trees for egg deposition/fertilization and foraging, but that males show a comparatively stronger selection for proximity to small water bodies where they deposit their tadpoles. Additionally, we predicted that sex differences are more pronounced in populations with larger sexual size dimorphism, potentially leading to niche partitioning, e. g. in relation to foraging.

2. Material and methods

2.1. Study areas and populations

Our study areas consisted of six dyeing poison frog populations located in French Guiana: (1) Kaw Nature Reserve, (2) Cacao, (3) Mataroni, (4) Mont Fortuné, (5) Nouragues Nature Reserve, and (6) Petit Matoury (Fig. 1, Table 1). These populations harbor individuals with distinct body sizes and coloration (Fig. 1). Frogs in Mataroni are large and mostly yellow and show distinct sexual size dimorphism (SSD) with females being larger than males. Frogs in Nouragues are intermediate in size, more variable in coloration, and show less pronounced SSD. Frogs in the remaining populations are the smallest and show no SSD, with frogs in Kaw and Cacao being yellow-striped and frogs in Mont Fortuné and Petit Matoury white-striped (Rojas and Endler, 2013; Lawrence et al., 2019; Schlippe Justicia et al., 2023). All study areas experience mean annual temperatures between 25 and 27 °C and annual rainfall between 2300 and 3400 mm, which mainly falls during the long rainy season from December to July, with a slight decrease in precipitation around March. The dry season ranges from August to November. Nouragues and Kaw consist of undisturbed lowland moist tropical forest, with canopy height ranging between 35 and 45 m above ground. Mataroni also consists of lowland moist tropical forest but experiences selective logging (Piponirot et al., 2016). The moist tropical forest surrounding Cacao is interspersed with agricultural land and settlements. Petit Matoury and Mont Fortuné, located only ca. 1.5 km from each other, are (at least partly) secondary forest and completely isolated by a highway and urban areas. Moreover, the study area in Petit Matoury (but no other area) contained numerous artificial water pools that were previously brought out as tadpole deposition sites. Thus, we treated these two areas as separate populations. We categorized Petit Matoury, Mont Fortuné and Cacao as habitats of high human disturbance, and Kaw, Nouragues and Mataroni as pristine (even though there is selective logging in the general area of Mataroni, the forest was completely undisturbed at our specific study site).

2.2. Data collection

Between January and March 2023, we walked transects during daytime that were located in areas where *D. tinctorius* was known to

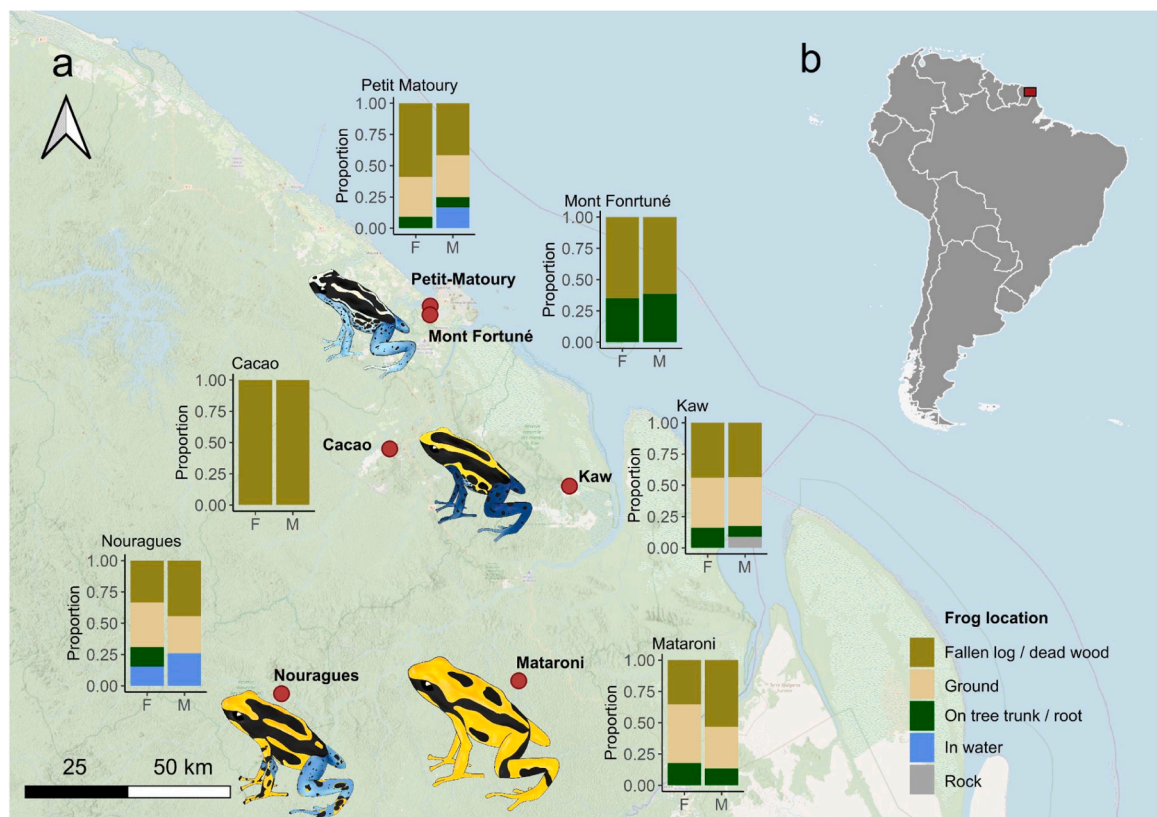


Fig. 1. Map (a) shows the locations (red dots) of the 6 study areas and illustrates the differences in body size and coloration of *Dendrobates tinctorius* among areas (frogs in Petit Matoury and Mont Fortuné as well as in Cacao and Kaw look similar). The bar plots show the proportion of the different habitat locations where frogs were observed, separately for each population and for females (F) and males (M). The small map (b) shows the location of the area within South America.

Table 1

Overview of the number of dyeing frog (*Dendrobates tinctorius*) observations, the relative population density given as number of individuals per km transect, the number of water bodies per km², the number of recent tree falls per km², the number of habitat plots, and main habitat characteristics (elevation range, ground vegetation cover, number of large trees, number of fallen trees), estimated from the habitat plots, for each study area.

Population	Frog observations (individuals)	Frog density (mean $\pm$ SD)	Water bodies per km ²	Recent tree falls per km ²	Number of habitat plots	Elevation range (m)	Ground vegetation cover (%)	Number of large trees	Number of fallen trees
Cacao	18 (15)	0.46 $\pm$ 0.42	33	77	59	121–282	25 $\pm$ 17	0.27 $\pm$ 0.45	0.24 $\pm$ 0.43
Kaw	62 (57)	1.49 $\pm$ 0.68	59	56	49	6–177	29 $\pm$ 21	0.31 $\pm$ 0.51	0.24 $\pm$ 0.52
Mataroni	58 (52)	1.75 $\pm$ 0.83	54	127	68	20–99	29 $\pm$ 24	0.25 $\pm$ 0.53	0.12 $\pm$ 0.32
Mont Fortuné	50 (43)	1.27 $\pm$ 0.8	270	135	51	45–130	15 $\pm$ 16	0.14 $\pm$ 0.35	0.24 $\pm$ 0.43
Nouragues	77 (69)	2.47 $\pm$ 1.11	132	161	53	40–179	27 $\pm$ 18	0.40 $\pm$ 0.53	0.13 $\pm$ 0.34
Petit Matoury	51 (41)	2.35 $\pm$ 0.78	65	47	32	34–94	25 $\pm$ 24	0.28 $\pm$ 0.58	0.03 $\pm$ 0.18

occur, between 7.30 h and 18 h (when frogs are active), in each study area to systematically score fine scale habitat structure and to record all frogs that we encountered (Fig. S1). Transects were partly located along small forest trails and partly went through the forest without trails. We recorded the tracklog of our footpath during the entire data collection using a handheld GPS (Garmin GPSMAP 64). We systematically scored the fine scale habitat structure every 50 m along the transects (Fig. S1), measured as straight-line distance from the last habitat plot using the handheld GPS. Each of these habitat plots (hereafter habitat locations; $n = 312$) consisted of a 2 m radius around the location where we visually quantified (1) the proportion of leaf litter on the ground, (2) the proportion of ground vegetation cover (low growing plants < 100 cm high), (3) the proportion of dead woody structures (such as fallen/rotting branches, fallen palm bracts, etc.), (4) the presence of fallen tree trunks (independent of whether they were fresh or rotting), (5) the presence of small water bodies, and (6) the number of small (< 30 cm stem diameter at 1 m height) and large (> 30 cm stem diameter) trees. The habitat scoring was consistently conducted by two observers (MM and LSJ), who independently assessed each plot and resolved any discrepancies by averaging scores. Additionally, we measured (7) ground temperature (using a laser thermometer; Bosch Universal-Temp Infrared Thermometer), and (8) canopy cover (Fig. S2). To estimate canopy cover, we took an image ca. 20 cm above ground facing the sky with an ultra-wide-angle camera. Additionally, along the entire transects walked, we recorded the GPS location of every small water body that could be used for tadpole deposition by *D. tinctorius*, such as phytotelmata, rock pools, and artificial pools (plastic bottles etc.), and the location of every recently fallen large tree, defined as fallen trees that clearly left a gap in the forest canopy and had not been grown over yet. These features were recorded independent of whether they were located on or outside the transect (but were typically located within max. 100 m from the transect line).

We recorded the GPS location of each frog encountered along the transects and scored the same habitat parameters within a 2 m radius of the frog location as described above for the habitat locations. Additionally, we recorded the position of the frog (on leaf litter, under or on top of fallen tree trunks or dead wood, etc.) and hand-captured them, changing gloves for each new individual. Frogs were photographed on millimeter paper for snout-vent length (SVL) measurement and individual identification (to avoid double counting of individuals that were previously observed), weighed, and sexed based on the shape and size of their fingertips (Rojas and Ender, 2013). All frogs were released right after at the capture site. We could not account for the detectability of frogs depending on habitat type and frog position but argue that this likely had little impact given the high visibility of active frogs (also see Section 4).

2.3. Data preparation and statistical analysis

To obtain a measure of relative population density, we estimated the number of observed individuals per km transect for each day, and then averaged daily estimates for each population. We did the estimation for separate days, because we did not walk the exact same transects each day. To estimate the density of water bodies and recent tree falls for each population (as additional measures to quantify how the study areas differed), we buffered all transects by 20 m to account for GPS location error and variation in transect distribution among study areas (Fig. S1), dissolved all buffers within the same population, and estimated the number of water bodies and recent tree falls per km². To quantify habitat differences among populations, we ran a principal component analysis (PCA) including the proportion of leaf litter, ground vegetation, dead wood, canopy cover, the number of small, large, and fallen trees, temperature, and elevation obtained from the habitat plots (only a single water body was located inside a habitat plot; thus, this variable was dropped). We used a multivariate analysis of variance (MANOVA) to quantify differences among the habitats based on the first two PC scores.

Initially, we analyzed habitat use using multinomial models of the R package ‘nnet’ (Ripley et al., 2016), including frog position as response variable. We categorized frog position as (1) on ground/leaf litter, (2) on trees or tree roots, and (3) in/on other structures, including fallen logs, dead woody structures, water bodies, and rocks (this lumping was necessary to achieve model fit). We included sex, population (excluding Cacao due to the low sample size and no variation in frog positions; Fig. 1), and their interaction as predictor variables (Table S1).

To analyze general habitat selection across all studied populations, defined as the probability of an observation being a frog (frog observation = 1 versus habitat location = 0; response variable), we used generalized linear mixed effects models (GLMM) with a binomial response distribution and a logit link. We initially attempted to include individual ID as random effect but had too few

recaptured individuals (see Section 3) to achieve model convergence. Instead, we only kept the first observation of each individual in the analysis. We included the ratio between the number of frog observations and all positions (frog and habitat) for each study area as offset in our models to account for differences among study areas. We included the proportion of leaf litter cover, ground vegetation cover, proportion of dead woody structures, the presence of tree falls (independent of how old they were), the number of small trees, the presence of large trees, ground temperature, elevation, canopy cover, and the distance to the closest water body and closest recent tree fall as fixed effects (Table S2). None of these variables were highly correlated (all Pearson correlation coefficients < 0.4). We scaled and centered all numeric fixed effects to avoid convergence issues and to be able to compare the relative effect sizes. We did decide against using scores from our PCA (see above), because the first 3 PCs only explained 56 % (cumulative variance explained) of the total variance in the data, and 6 PCs were required to explain > 80 % of the variance.

To investigate differences in habitat selection among populations, we ran the same model as above, but including the interaction of population with the other predictor variables (rather than including population as random effect; Table S2). To avoid overfitting models, we only included variables that were identified as important (effects of 95 % confidence intervals did not overlap with zero), namely ground vegetation cover, proportion of dead woody structures, the presence of tree falls, the number of small trees, the presence of large trees, elevation, and the distance to the closest water body and closest recent tree fall. Additionally, we ran the same analysis including the two-way interaction of habitat category (disturbed versus pristine; instead of population) with all fine-scale habitat variables (Table S2), to test if habitat disturbance affects frog habitat selection. Moreover, we ran separate analyses for each population to compare differences in habitat selection among populations (allowing us to conduct separate model selection for each population).

To assess sex differences in habitat selection across populations, we initially ran separate analyses for females and males (same model structure as above). However, because it is not possible to assign a sex to habitat locations, we could not directly quantify sex differences (i.e., include the interaction of sex with habitat variables). Consequently, we created 10 random locations (using the ‘create random points in polygons’ function in QGIS) for each individual frog observation (excluding juveniles and recaptured individuals). These points were located along the transect lines, buffered by 3 m on each side, which was the approximate maximum distance at which we could spot frogs. We then used GLMMs with observation type (frog observation = 1 versus random location = 0) as response variable and individual ID nested within population as random effect. As fixed effects, we included sex, the distance to the closest water body and closest recent tree fall, and the interactions of sex with the latter two variables to investigate sex differences in habitat selection (Table S3). We could not include the other habitat variables in this analysis, because they were not measured for the random locations. Additionally, we ran these analyses separately for each population (excluding Cacao because we only had six male and six female observations).

Model selection in all analyses was based on Akaike’s information criterion corrected for small sample size (AICc) (Burnham et al., 2011), using the R package ‘MuMin’ (Barton, 2020), selecting the model with the lowest AICc value, using a stepwise backward selection from the full model. Parameters that included zero within their 95 % CI were considered uninformative (Arnold, 2010). Model fit and assumptions were verified by plotting residuals versus fitted values (Zuur and Ieno, 2016) and performing dispersion and deviation tests, using the R package ‘DHARMA’ (Hartig, 2021), which detected no issues. To evaluate the robustness of the most parsimonious models, we conducted a 10-fold cross validation (Boyce et al., 2002). We first ran our models based on 90 % of the data, withholding 10 % for evaluation. We extracted the model coefficients of the fixed effects for each training set and used them to predict the model values of the corresponding validation set (withheld data). The validation set was then split into 10 equal-sized bins. For each bin, we calculated the relative frequency of used positions. The degree of correlation (measured as Spearman rank correlation r_s) between the rank of the bin and the relative frequency of used positions was used as an indicator of model fit. All statistical analyses were conducted in R version 4.4.1 (R Core Team, 2016).

3. Results

We recorded the locations of 316 frogs, consisting of 277 individuals, across the six populations (Table 1). These individuals consisted of 149 females, 96 males, and 17 juveniles. In 15 cases, we did not manage to capture frogs and thus, could not identify their sex. Thirty-five individuals (13 %) were recaptured once or twice (39 observations). The individuals that were recaptured (21 females, 12 males, and 2 juveniles) moved between 0 and 50 m (mean $\pm$ SD: 14 ± 13 m), with movement distance not being related to the number of days in between captures, ranging from one to 12 days, or sex (Table S4). Relative population density (individuals per km transect) was the lowest in Cacao, being ca. five times lower compared to Petit Matoury and Nouragues, and was intermediate in Kaw, Mataroni, and Mont Fortuné (Table 1). Although there was considerable overlap of PC scores among populations, the MANOVA results revealed a statistically significant difference in the multivariate means of the habitats (Pillai’s trace = 0.20, approximate $F = 6.80$, p -value < 0.001), indicating that the habitats were characterized by distinct sets of environmental conditions (Fig. S3).

We observed most frogs on or under fallen logs and dead woody structures (48 %), followed by observations on ground (30 %), on tree trunks or roots (15 %), in water bodies (6 %), and on large rocks (1 %; Fig. 1). Females, compared to males, were encountered more often on ground (32 % versus 27 %) and on tree trunks/roots (17 % versus 10 %), and males were observed comparatively more often on fallen logs/dead wood (50 % versus 43 %) and inside water bodies (9 % versus 4 %; Fig. 1). We did not observe any frogs on the ground/leaf litter in Cacao and Mont Fortuné (Fig. 1, Fig. S4). Based on the multinomial regression, sex was not included in the best model, and differences in frog positions among study areas were uninformative (Table S1, S5).

When analyzing habitat selection for all populations combined, frogs selected for proximity to recent tree falls and to water bodies, for areas with a higher proportion of dead woody structures, lower proportion of ground vegetation cover, fewer small trees, the presence of large trees, tree falls, and higher elevation (Fig. 2, Table 2). They tended to select for areas with higher canopy cover, but

this effect was uninformative (Fig. 2f, Table 2). Temperature and the proportion of leaf litter were not included in the best model (Table S2). When additionally including the interaction of habitat category with the other habitat measures, there was a trend for frogs in disturbed habitats (Cacao, Mont Fortuné and Petit Matoury) to show a stronger selection for proximity to recent tree falls than frogs from pristine populations (Fig. 2a). The other interactions were either uninformative or not included in the best model (Table S2, Table S6). When including the interaction of population with the other variables, only the interactions of population $\times$ presence of large trees and population $\times$ elevation were included in the best model (Table S2). The interaction of population $\times$ elevation indicated that frogs in Kaw and Petit Matoury selected for higher elevations whereas there was no selection for a certain elevation in the other populations (Fig. 3a). Moreover, frogs in Mont Fortuné showed a stronger selection for the presence of large trees compared to the other populations (Fig. 3b), in line with a lower availability of large trees in this population (Table 1). A Spearman-rank correlation for mean frequency values by bins ($r_s > 0.65$, $p < 0.001$; Table S2) indicated that the model predicted cross-validated frog locations moderately well.

The separate analyses for each population showed that habitat selection was generally similar among populations, with the sign of the coefficients always being consistent, though effect sizes differed, and different variables were retained in the best models among populations (Table 3). Frogs in all areas selected for the presence of tree falls and/or high coverage of dead woody structures (Table 3). Elevation was only retained in the best model for Kaw and Petit Matoury. The presence of large trees (selected for) and the proportion of ground vegetation cover (avoided) was included in the best models for Mataroni, Mont Fortuné, Nouragues, and Petit Matoury, but not Cacao and Kaw. Distance to the closest water body was not included in the populations with high human disturbance (Cacao, Mont Fortuné, and Petit Matoury), but was selected for in the other populations (Table 3). Conversely, frogs in Mont Fortuné and Petit

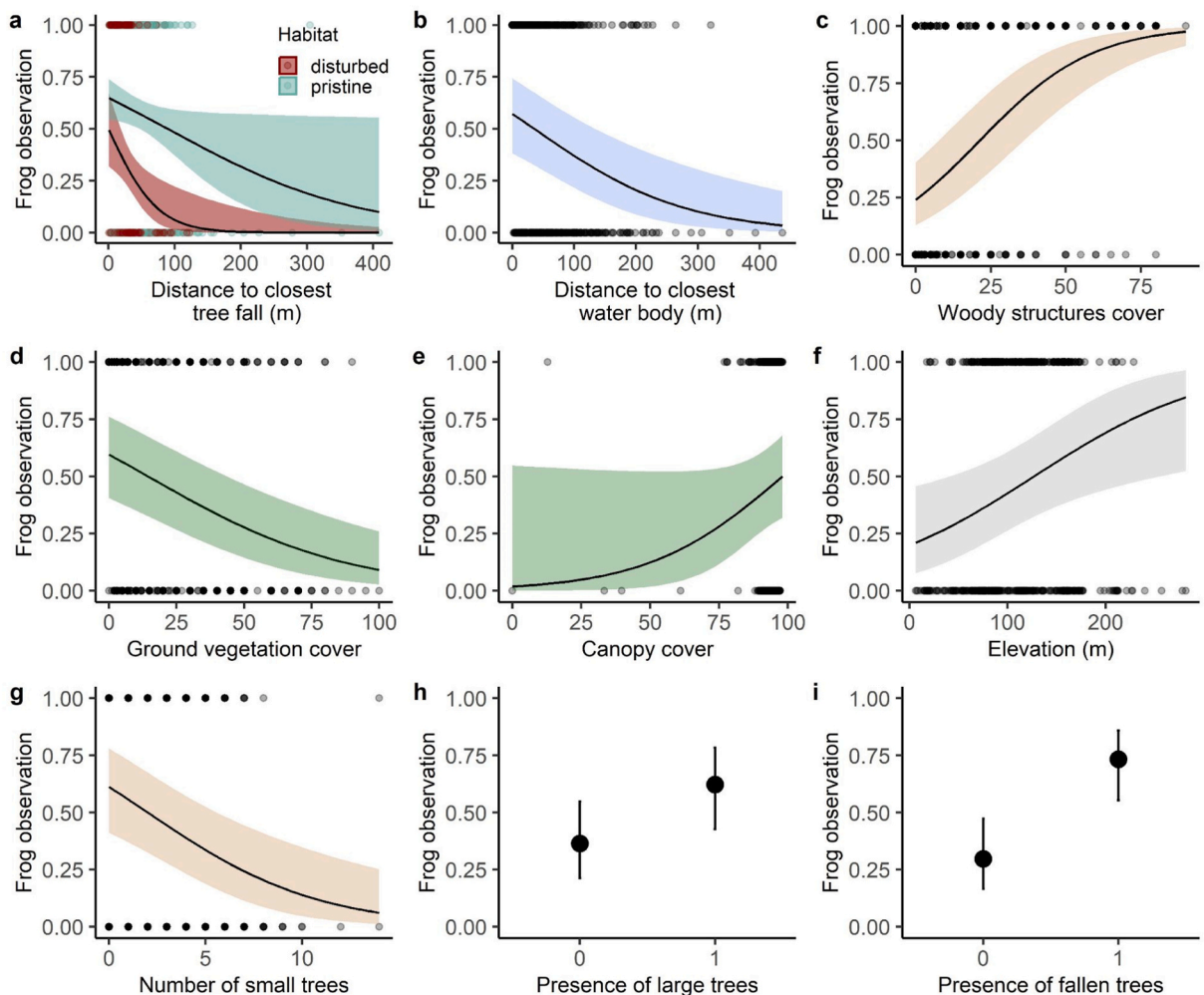


Fig. 2. The predicted probability of an observation being a frog (as opposed to being a habitat location) in relation to (a) the interaction of habitat disturbance $\times$ distance to the closest fallen tree, (b) distance to the closest known water body, (c) dead woody structures cover, (d) ground vegetation cover, (e) canopy cover, (f) elevation, (g) number of small trees, (h) presence of large trees, and (i) the presence of tree falls. This analysis was based on a linear mixed effects model including frog population as random intercept. The 95 % confidence intervals are shown as shading (a–g) or bars (h–i), and raw observations as small dots (a–g).

Table 2

Estimates, standard error (SE), lower (LCI) and upper (UCI) 95 % confidence intervals for the analyses of habitat selection by 277 dyeing poison frogs (*Dendrobates tinctorius*) from six populations. Informative parameters are presented in bold (95 % confidence intervals do not overlap with zero).

Parameter	Estimate	SE	LCI	UCI
Intercept	− 0.42	0.40	− 1.21	0.36
Elevation	0.51	0.20	0.12	0.90
Canopy cover	0.27	0.15	− 0.02	0.57
Ground vegetation cover	− 0.53	0.13	− 0.78	− 0.28
Number of small trees	− 0.47	0.14	− 0.75	− 0.20
Presence of large trees	1.06	0.25	0.56	1.55
Proportion of woody structures	1.14	0.16	0.82	1.45
Presence of fallen trees	1.87	0.27	1.35	2.39
Distance to closest water body	− 0.49	0.14	− 0.77	− 0.21
Distance to closest recent tree fall	− 0.30	0.14	− 0.58	− 0.02

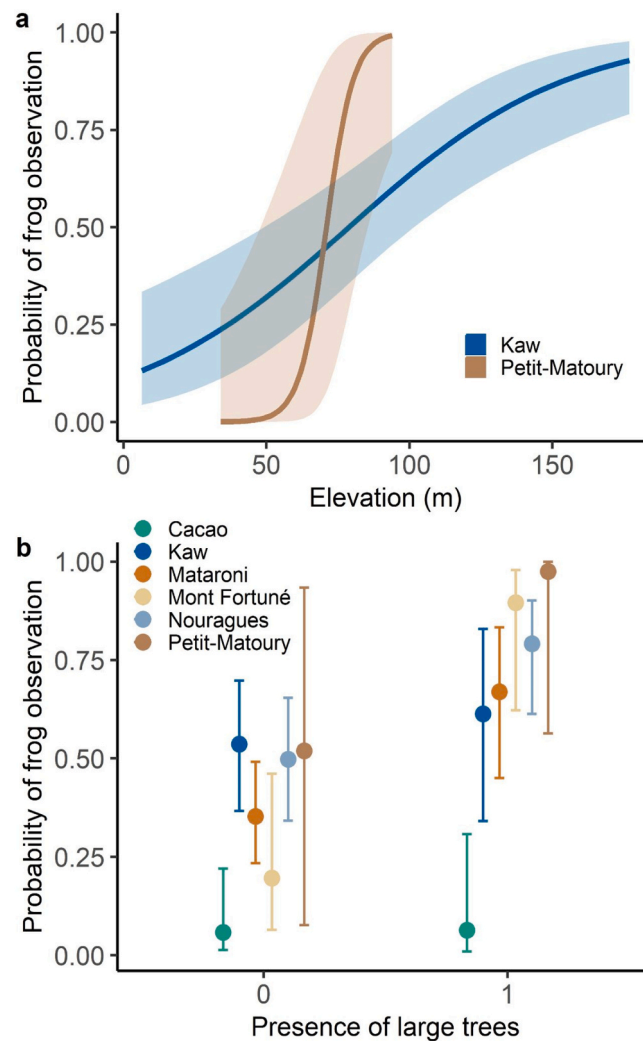


Fig. 3. The predicted probability of an observation being a frog (as opposed to being a habitat location) in relation to the interaction of (a) population $\times$ elevation and (b) population $\times$ presence of large trees. Elevation was only included in the best model for the population of Kaw and Petit Matoury (when habitat selection was analyzed separately by population). Populations where the effect of elevation was uninformative are not shown for visualization purposes. The 95 % confidence intervals are shown as shading (a) or bars (b).

Matoury selected for closer distances to tree falls, but this variable was not included in the best model in the other populations (Table 3).

When running separate models for females and males, comparing frog to habitat positions, habitat selection was generally similar

Table 3

Estimates and standard errors (SE) for the analyses of habitat selection by 277 dyeing poison frogs (*Dendrobates tinctorius*) separately for each of the six populations. Informative parameters are presented in bold (95 % confidence intervals do not overlap with zero).

Parameter	Estimate $\pm$ SE					
	Cacao	Kaw	Mataroni	Mont Fortuné	Nouragues	Petit Matoury
Intercept	-2.2 ± 1.00	0.9 ± 0.29	-0.54 ± 0.36	-1.19 ± 0.86	-0.60 ± 0.41	-2.31 ± 1.03
Elevation		1.28 ± 0.31				2.84 ± 1.11
Ground vegetation cover			-0.59 ± 0.27	-1.62 ± 0.82	-0.90 ± 0.30	-1.39 ± 0.94
Number of small trees		-0.76 ± 0.35		-1.06 ± 0.45		
Presence of large trees			1.31 ± 0.57	3.56 ± 1.08	1.34 ± 0.54	3.57 ± 1.59
Proportion of woody structures	1.30 ± 0.49	1.15 ± 0.41	1.07 ± 0.30	3.34 ± 1.05	1.00 ± 0.32	
Presence of fallen trees	3.66 ± 1.12		2.49 ± 0.57	1.35 ± 0.85	3.09 ± 0.76	9.00 ± 4.45
Distance to closest water body		-0.85 ± 0.32	-0.49 ± 0.27		-0.89 ± 0.36	
Distance to closest recent tree fall				-0.88 ± 0.55		-2.65 ± 1.22

between the sexes (Table S7). However, proximity to the closest tree fall was not included in the best model for males while females selected for proximity to recent tree falls, and males showed a stronger selection for proximity to water bodies compared to females (Fig. 4, Table S7). Based on the analysis comparing frog locations to random locations, the interactions of sex $\times$ distance to the closest recent tree fall and sex $\times$ distance to the closest water body were not retained in the best model, though the interaction of sex $\times$ distance to closest water body was retained in the second-best model (delta AIC < 1; Table S3). When running separate analyses for

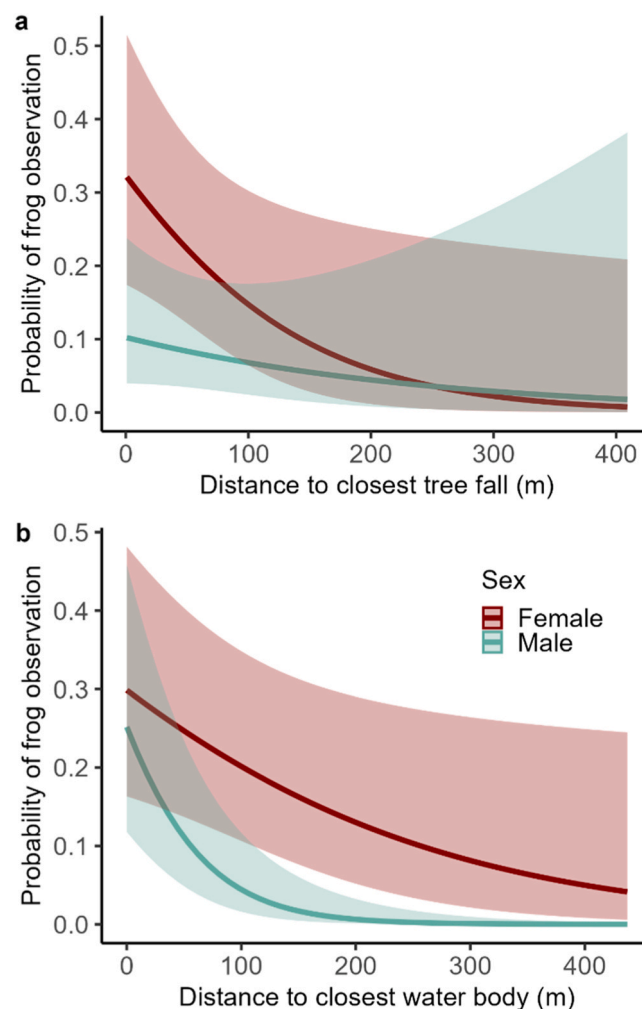


Fig. 4. The predicted probability of an observation being a frog (as opposed to a habitat location) in relation to the (a) distance to the closest recent tree fall and (b) distance to the closest water body, shown separately for females and males. The 95 % confidence intervals are shown as shading. Note that the effect of distance to the closest tree fall was uninformative for males (a; 95 % confidence interval overlapped zero).

each population, males in Petit Matoury and Kaw tended to show a stronger selection for proximity to water bodies compared to females, and females in Kaw tended to show a stronger selection for proximity to recent tree falls compared to males (Table S8). We did not detect sex differences in the other populations (Table S8).

4. Discussion

Our findings of habitat selection by dyeing poison frogs across populations in French Guiana are largely in line with previous descriptions concerning habitat use in this (Noonan and Gaucher, 2006; Rojas and Pašukonis, 2019) and other aposematic frog species (Rasoarimanana et al., 2023). Small water bodies are important for males to deposit tadpoles (Pašukonis et al., 2019; Weygoldt, 1987) and for both sexes to avoid dehydration in periods with little rainfall (Born et al., 2010). Similarly, areas with fallen logs and other dead woody structures may provide increased arthropod prey abundance, higher humidity conditions, serving as retreat and oviposition sites, as well as shelter from predators (Born et al., 2010; Rojas and Pašukonis, 2019).

4.1. Differences among populations

Despite large differences in coloration, body size, and sexual size dimorphism among populations (Wollenberg et al., 2008; Schlippe Justicia et al., 2023), we found little variation in habitat selection among populations. A priori, we would expect different phenotypes to evolve preferences for distinct microenvironments in which they experience the highest fitness. For example, unstriped red-backed salamanders (*Plethodon cinereus*), which are more sensitive to predation and thermal stress, selected refuges more often and were more fossorial compared to the striped variant, which occupied the soil surface under a broader range of conditions (Straub et al., 2024). Importantly, the above example refers to a polymorphic species, where different variants occur within the same population. In contrast, different variants of *D. tinctorius* do not co-occur in the same population and have an aposematic coloration, potentially allowing them to move freely and openly (Speed et al., 2010) without having to adjust habitat selection in response to predation risk or intraspecific competition. Moreover, our findings indicate that the different variants depend on the same ecologically relevant structures and (food) resources, reducing potential differences in habitat selection among populations.

The observed habitat selection for higher elevation in two populations but not in the other four might be related to underlying biological mechanisms. The presence and abundance of potential predators and competing species, such as other phytotelm breeding frogs with a similar feeding ecology, might vary with elevation in some populations, but not others. Thus, future studies should also investigate the role of interspecific competition and potentially predator abundance on habitat selection by *D. tinctorius*. For example, it has been shown that interspecific competition can induce habitat niche shifts in birds (Tarjuelo et al., 2017) and predation risk can affect habitat selection in mammals (Hughes et al., 1994). Moreover, frogs in Mont Fortuné showed a stronger selection for the presence of large trees compared to the other populations, consistent with the lowest availability of large trees in this human-modified area. Similarly, frogs in disturbed forests tended to show a stronger selection for proximity to recent tree falls. This suggests that in more disturbed areas, the relative importance of structural habitat diversity increases, potentially providing shelter, food, and phytotelmata for tadpole deposition.

Disturbed areas (Cacao and Mont Fortuné) had lower population densities, providing some evidence that they likely cannot support similar densities compared to pristine forests, which might be related to the specific habitat requirements, such as the abundance of small water bodies, tree falls, and large trees. However, in Petit Matoury, which also experienced high habitat disturbance, the population density was among the highest in this study. This might have been related to the availability of artificial pools there, as has been shown in another poison frog (Donnelly, 1989). Additionally, differences in population density among the different areas might be related to (partly unmeasured) differences in microhabitat composition and prey availability.

4.2. Sex differences

When analyzed separately for males and females, we found a stronger selection of water bodies by males compared to females (when comparing frog observations and habitat plots). Further, females but not males, selected for proximity to recent tree falls. This pattern seems to differ from the findings of Rojas and Pašukonis (2019), who found more males than females in treefall gaps up to 51 days after the occurrence of the treefall. However, this might have been the result of different movement patterns between males and females (Pašukonis et al., 2022), rather than differences in habitat selection. Moreover, the period during which we considered recent tree falls was well beyond Rojas & Pašukonis definition, making a true comparison difficult. When using random points instead of our habitat plots, we found little evidence for sex differences concerning habitat selection, also when analyzed for the separate populations (with the exception of Kaw and Petit Matoury). Similarly, Pašukonis et al. (2022) found no significant sex differences in home range size or movement extent based on radio tracking *D. tinctorius*. Moreover, we found no support for the prediction that sex differences in habitat selection are more pronounced in populations with larger sexual size dimorphism. Potentially, niche separation between sexes might be related to other factors, such as feeding rate, rather than habitat selection. For example, Born et al. (2010) reported females at the Nouragues population to have more prey items in their stomach compared to males.

4.3. Study limitations

One obvious shortcoming of this study is that we could not account for detectability of frogs depending on habitat structure and frog coloration/behavior. However, based on previous findings showing that frogs with the color patterns present in our studied

populations are highly discriminable from the substrate by avian predators (Rojas et al. unpublished), we deem unlikely that we missed many frogs provided that they were active. One exception might be the finding that frogs avoided areas with high ground vegetation cover, as we might have missed frogs in such areas. Moreover, our results only refer to habitat use and selection by active frogs. To resolve these issues, future studies could use radio tracking (Pašukonis et al., 2022) to get a more holistic picture of habitat selection, also by inactive frogs. In addition, our habitat scoring had some limitations. For example, we were unable to identify tree species, which could be important as the trunk and root structures of certain species (e.g. *Vouacapoua americana*) create more opportunities for the formation of phytotelmata, or if certain prey species of *D. tinctorius* are associated with certain plant species. However, despite its apparent preference for ants, *D. tinctorius* has been previously shown to forage on a wide range of arthropod prey, including also beetles, wasps, insect larvae, and mites (Born et al., 2010), making this unlikely. More importantly, we certainly underestimated the number of water bodies, as it was previously shown that these frogs can deposit their tadpoles in tree phytotelmata (whose presence might also be affected by tree species) up to 20 m above ground (Fouilloux et al., 2021). Finally, although we found few differences in habitat selection among populations, it would have been challenging to disentangle between habitat differences (that might be driven by variation in microclimatic conditions) and differences in frog morphology, because these factors were partly correlated among sites, and we did not have enough replicates both regarding habitat disturbance (3 pristine versus 3 disturbed sites) and morphology (4 different variants).

4.4. Conclusions

Our study is the first to investigate habitat selection in *D. tinctorius* across a large portion of its range, including disturbed sites. As a polytypic species, understanding whether different variants have distinct habitat requirements is critical for effective conservation planning and prioritization. Our findings reveal consistent habitat selection patterns across populations, suggesting that the space use behavior of dyeing poison frogs is relatively constant regardless of their variation in size and phenotype. Habitat selection in aposematic species might generally be less impacted by predation risk due to local adaptations to predator communities (Noonan and Comeault, 2009). Unlike other poison frog species that may adapt to human-modified landscapes (Robinson et al., 2013), *D. tinctorius* shows strong selection for fallen logs and dead woody structures, especially in disturbed areas where these resources are scarcer. This emphasizes the specific habitat requirements for forests with high structural diversity and stresses that habitat disturbances, such as deforestation, agriculture, and mining activities, likely will have negative impacts on *D. tinctorius* populations. Overall, our findings provide key baseline data for the recently identified emerging research priorities in amphibian conservation (Campbell Grant et al., 2023) and point towards the importance of conservation strategies that prioritize maintaining structural diversity to ensure the long-term survival of this species' populations.

Author Contributions

MM, LSJ, and BR conceived and designed the study. MM and LSJ developed the methodology, conducted fieldwork and data collection. MM analyzed the data. MM and LSJ wrote the manuscript. BR provided editorial advice, acquired funding and was the supervisor of LSJ.

Ethical approval

All capture and handling procedures were approved by the Direction Générale des Territoires et de la Mer Guyane (DGTm; R03-2022-12-28-00004) after an evaluation by the Regional Scientific Committee (CSRPN). Protocols employed at Nouragues Research Station were also approved by the Reserve's scientific committee. Our study met the ASAB/ABS Guidelines for the treatment of animals in research and teaching ASAB/ABS (Buchanan et al., 2012). None of the frogs was injured during capture and handling and all individuals were successfully released at the site of capture after handling. Based on recaptured individuals, we detected no negative effects of capture and handling.

Ethics Statement

If this manuscript involves research on animals or humans, it is imperative to disclose all approval details.

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Data statement

Relevant raw data is available on the public repository figshare: <https://doi.org/10.6084/m9.figshare.23607537.v1>.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e03358](https://doi.org/10.1016/j.gecco.2024.e03358).

Data availability

<https://doi.org/10.6084/m9.figshare.23607537.v1>.

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