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Oviposition site selection in a complex and variable environment: the role of habitat quality and conspecific cues

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Abstract In many organisms reproductive success is strongly dependent on several breeding site characteristics, which often vary in space and time. Although we have a good understanding of how ovipositing organisms respond to single factors, we still have little information about how they respond under more complex natural conditions. We examined the oviposition behavior of a tree-hole breeding frog, *Phrynobatrachus guineensis*, with respect to abiotic and biotic oviposition site characteristics, including desiccation risk and the presence of conspecific offspring using both observation and experiments. Based on daily monitoring data, compiled from 69 natural oviposition sites during a complete reproductive season, we developed oviposition site-selection models. A model based on water presence, sediment depth and maximal possible water depth showed the best predictive performance and was transferable to the subsequent season. Field observations and experiments revealed that frogs could estimate water-holding capacity of sites and timed oviposition with respect to future water presence. Despite the negative effects on larval growth and the availability of sites without conspecifics, data suggest that ovipositing individuals are attracted to conspecific offspring because they serve as a cue for low predation risk. Our results imply that a site's potential for being used at least once for oviposition was determined by abiotic factors, whereas the relative use of breeding sites was determined by a response to conspecifics. Our study demonstrates

the importance of including multiple biotic and abiotic factors in the analysis of oviposition site-selection.

Keywords Conspecific attraction · Desiccation risk · Phytotelmata · Habitat model · Breeding behavior

Introduction

The reproductive success of organisms living in habitats of variable quality is strongly dependent on the selection of an appropriate site and the timing for oviposition. Several characteristics of an oviposition site may determine parental fitness by directly or indirectly affecting hatching success, larval development, and larval survival (Resetarits and Wilbur 1989). In many organisms, such as many insects or amphibians, the larvae are unable to leave the sites selected by their parents (i.e. a pool or host plant) if conditions become unfavorable. Hence, there should be a strong selective pressure on the ability of reproducing individuals to discriminate between high- and low-quality oviposition sites.

Oviposition site-selection can have a strong impact on the spatial distribution of a species and thereby affect population dynamics (Hassel 1987; Pearman and Wilbur 1990) and the structure of communities (review in Morris 2003). However, the mechanisms for oviposition site-selection in spatially and temporally variable environments are still poorly understood (Pearman and Wilbur 1990). To understand the selection of oviposition sites in complex natural environments, we need to know how the combinations of different factors affect this selection and what discriminatory abilities species have.

There is empirical evidence that the selection of oviposition sites is often affected by both biotic factors, like the presence of conspecifics and predators (Resetarits and Wilbur 1989; Crump 1991; Blaustein et al. 2004), and abiotic factors, like soil composition, temperature, moisture or water-holding capacity (Huk and Kuhne 1999; Reich and Downes 2003). The relative importance

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of a single factor might depend on the impact of other habitat parameters which could significantly alter its importance. The effect of one factor on oviposition site-selection would then be context dependent. However, to date most studies have focused on limited sets of parameters. Some used choice experiments in which only the presence of single biotic factors were manipulated (i.e. competitor or predator), while other habitat parameters remained equal (Resetarits and Wilbur 1989; Edgerly et al. 1998; Murphy 2003b). Others have focused on physical characters (Seal 1982; Figiel and Semlitsch 1995; Wilson 1998), while neglecting the importance of interspecific and intraspecific interactions. Breeding sites are usually characterized by combinations of several of these factors. The parameter combinations often vary considerably with time and between neighboring sites, thereby creating differences in site quality, which in turn are of major importance for the selection of sites.

Thus, while we have a good understanding about the capacity of an ovipositing organism to respond to single factors, we still know little about how this response translates into more complex situations with multiple factors. For example, a choice experiment conducted with Túngara frogs, *Physalaemus pustulosus*, indicated that ovipositing frogs avoided conspecific foam nests (Dillon and Fiano 2000), but a field study revealed that this did not apply if oviposition occurred in natural stream pools (Marsh and Borrel 2001). Thus, the key selection parameter attained from the experiment gave misleading predictions, demonstrating that it is often difficult to assess the ecological importance of experimental findings with restricted parameter sets.

We investigated the oviposition site-selection of the tree-hole breeding frog *Phrynobatrachus guineensis* Guibé and Lamotte, 1961, in a natural, spatially and temporally variable environment. We were interested in which factors determine the suitability of spawning sites. Based on data from a daily monitoring program, we developed models for selection of oviposition sites. This allowed us to investigate how oviposition behavior is affected by the presence of conspecifics when habitats differ in quality. In addition, we tested experimentally the ability of ovipositing frogs to discriminate among sites of varying desiccation risk under natural conditions.

Materials and methods

Study site and species

All investigations were done at the Station de Recherche en Ecologie Tropical (SRET, 05°50.003'N, 07°20.536'W) in the primary lowland rainforest of Taï National Park, Ivory Coast in the years 2000–2002. In the study area most precipitation falls during two distinct wet periods from March to July and from September to October. Mean annual precipitation around the SRET was

1,806 mm (± 297 mm; 1988 to 2002, data from Taï Monkey Project and own unpublished data).

We chose the West African frog *Phrynobatrachus guineensis* as our model organism. During a prolonged breeding season, typically lasting from May to November, these small frogs (mean body length ranges from 16.6 mm in males to 18.4 mm in females) reproduce in small phytotelmata and in empty snail shells (Rödel et al. 2004). These sites are well suited for quantitative assessment of characteristics affecting oviposition site quality such as desiccation risk and presence of predators or conspecific competitors, which often vary considerably among sites (Kitching 2000; Rödel et al. 2004). This makes the system an excellent model for the study of oviposition site-selection in a complex and variable environment.

Recent observations showed that male *P. guineensis* often move between breeding sites; some visit up to five different sites during a single reproductive season (Rödel et al. 2004). In most cases ($\approx 60\%$) males remained for only 1 day at a site. However, in 40% of all observations males stayed longer, some remaining up to 23 days (Rödel et al. 2004). Females always visited breeding sites for only 1 day, mostly without depositing a clutch. Females were never observed to oviposit in more than one site, and data on clutch size suggest that risk spreading by a single female depositing her eggs at different sites is unlikely (Rödel et al. 2004).

Eggs are attached to the tree bark or the snail shell above the water level. After 4–5 days, hatchlings drop into the water. The mean period from hatching to metamorphosis is 21 days. Field observation and laboratory experiments indicated that increasing conspecific density and low food-levels experienced during the larval period strongly reduce size at metamorphosis (V.H.W. Rudolf and M.-O. Rödel, unpublished data). Desiccation and predation by dragonfly larvae (*Hadrothemis camarensis*) are major factors in tadpole mortality. Study site, natural history and breeding ecology of *P. guineensis* are described in greater detail elsewhere (Rödel 1998; Rödel et al. 2004).

Monitoring program

In a daily monitoring program we investigated oviposition site-selection of *P. guineensis* during the entire reproductive season of 2001 (1 May 2001–20 November 2001) in 69 natural breeding sites. These sites comprised tree-holes, fruit capsules and *Achatina* snail shells at which *P. guineensis* males were observed calling at least once. Sites were detected in previous seasons, either by searching visually or by listening for calling males (for details see Rödel et al. 2004).

Daily monitoring data comprised measuring water level, adult presence, breeding activity, and offspring presence, including number and developmental stage of eggs and tadpoles. Adults were captured, sexed, and new adults of both sexes were marked individually by toe

clipping of the hind feet (Heyer et al. 1994). A more detailed description of the monitoring routine is given in Rödel et al. (2004) and Rödel and Ernst (2004).

Oviposition site characterization

For the oviposition site-selection model several measurements were taken at each site. Oviposition sites were categorized as: (1) holes in a living tree trunk, (2) holes in a rotten tree, (3) holes in a root, (4) fruit capsules and (5) snail shells. For every site we determined the entrance area (accuracy: $\pm 0.1 \text{ cm}^2$) and the maximal possible water surface area ($\pm 0.1 \text{ cm}^2$). Water level and sediment depth were measured with a stick and a ruler at the deepest point ($\pm 0.1 \text{ cm}$). Maximum possible water depth ($\pm 0.1 \text{ cm}$) was defined as the point where water could spill out of the site. Water volume ($\pm 1 \text{ ml}$) was measured by carefully drawing all water above the substrate into a flexible tube with a 50-ml syringe and then returning it immediately. To avoid continuous disturbances we measured water volume only once on 18 September 2001. The knowledge of daily water levels and surface area allowed for volume calculation throughout the whole study period. The pH (± 0.01) and the oxygen concentration ($\pm 0.01 \text{ mg/l}$) were measured on 24–27 August 2001 with a multi-parameter water tester (WTW Multiline 3F with a pH/oxi 340i electrode). Measurements were taken on 3 consecutive days, and mean values calculated. At 16 sites water and air temperature were recorded with small real time temperature recording devices (iButton-TMEX, version 3.12, $\pm 0.1^\circ\text{C}$). As no significant differences in air and water temperature were detected between used and unused sites for the daily mean, maximum or minimum of water or air temperature (*t*-test, $P > 0.05$, $df = 15$; $n = 16$; Rödel et al. 2004), temperature was not included in our analysis. We checked all sites for possible predators from September to November 2001. Because predatory dragonfly larvae were only found in five sites during this period (two were used for oviposition) their presence was not included in subsequent analyses of the oviposition site-selection model. For more detailed information about oviposition sites see Rödel et al. (2004).

Logistic regression model

To analyze the importance of abiotic parameters for the selection of oviposition sites we developed two separate oviposition site-selection models using multiple logistic regression. In the first model (model 1), the dependent variable was the presence/absence of eggs in tree-holes. In a second model (model 2) the dependent variable was male presence/absence in tree-holes. Multiple logistic regression allowed us to discriminate between the importance of particular parameters for oviposition site-selection (Lindenmayer et al. 1991; Peeters and Gardener 1998), and to create predictive habitat models

based on presence/absence data (Hosmer and Lemeshow 2000). The oviposition site-selection model was based on all 69 natural sites monitored and included the eight habitat parameters (see earlier). The analysis of multivariate models was run with a backwards elimination procedure using likelihood ratio statistics. We used a significance level of 0.1 for exclusion because it is considered to give models better discrimination performance than less conservative levels (Adler and Wilson 1985). To ensure independence of the predictor variables, we tested for significant correlations between variables. Except for the correlation between entrance area and water surface, all correlations were below the critical value of 0.7 (Fielding and Haworth 1995). We excluded entrance area and considered only surface area for modeling because this variable was more closely correlated with the dependent variable and is known to be a spawning site-selection criterion in other species (Marsh and Borrel 2001). It was not possible to obtain water chemistry data for all sites. Therefore, the analysis was run for the first time with a limited amount of sites ($n = 42$) with all parameters. The fact that in both models the water chemistry (pH, O_2 concentration) was dropped by the backwards exclusion indicated that it could not significantly increase the prediction rates. Thus, we ran the analysis again with all sites ($n = 69$), but without the pH and O_2 concentration.

For evaluating the goodness-of-fit of the model and its predictive performance, we used the parameter R^2_N of Nagelkerke (1991) for measuring model calibration (Backhaus et al. 2000), a 2×2 classification table, and area under a receiver operating characteristic curve (AUC) for assessing the ability of a model to discriminate between occupied and unoccupied sites (review in Pearce and Ferrier 2000). The most common value for critical P in a classification table is 0.5 (Noon 1986; Hosmer and Lemeshow 2000) and was used in this analysis. The table can be used to calculate two indices, sensitivity and specificity, which measure the proportion of the sites at which observations agree with predictions of the model. Sensitivity (true positive fraction) reflects the proportion of correct predictions for presence and specificity (true negative fraction) indicates the proportion for absence.

Relative use of oviposition sites

The number of spawning events and the relative time a site was occupied by males differed considerably between sites (Rödel et al. 2004). Therefore we examined the relationship between relative use of sites and habitat quality and volume. The equation used for the presence probability (Trexler and Travis 1993; Hosmer and Lemeshow 2000) can also be interpreted as habitat quality (Kleyer et al. 1999/2000). This allows for correlation analysis between habitat quality as predicted by the models and proportional usage. The predicted habitat qualities given by models 1 and 2 were analyzed with

the number of clutches recorded from oviposition sites. In addition, probabilities of model 2 were analyzed with the relative time a site was occupied by males (days site was occupied by males/number of observation days). Relative time of occupation was used because it was most closely related to oviposition (see Results). Receiver-nonparametric-characteristics curve, correlation and regression analysis were conducted with SPSS for Windows 10.0 (SPSS).

Resource selection model

To determine if the use of a site for spawning was random or selective with respect to conspecific presence (e.g. tadpoles, eggs), we fitted maximum likelihood models to the data of sequential spawning events from our daily monitoring. We used a modified technique introduced by Arthur et al. (1996) for analyzing habitat selection if resource availability changes and modified this technique for multiple classification variables (e.g. absence or presence of tadpoles or eggs or both) following the extension of Marsh and Borrel (2001). We defined four categories of potential oviposition sites: (1) unused, (2) containing tadpoles, (3) containing eggs, and (4) containing both tadpoles and eggs. As described in Arthur et al. (1996) the preference values were obtained for each site category by Eqs. 1 and 2 (see also Manly et al. 1993).

$$w_k = \frac{\sum_{i=1}^D o_{ik}}{\sum_{i=1}^D \frac{A_{ik}}{\sum_{j=1}^H A_{ij} b_j}} \quad (1)$$

$$b_k = \frac{w_k}{\sum_{j=1}^H w_j} \quad (2)$$

Here, k is one of the four possible particular site categories (see above) from the set $j = 1$ to H ; o_{ik} is the proportional use of a site type k by a frog i (1 for use, 0 if not used). A_{ik} is the relative availability of habitat k for frog i , D the total number of ovipositing frogs, and b_k the estimated selection index for site k . The values of b_j can be determined through iteration. For the first step, b_j is set equal to $1/H$ and used to solve Eq. 1. Then Eq. 2 is used to calculate new values for b_j , which are substituted back into Eq. 1. The process is repeated again, until $b_j = w_j$ for all j .

The obtained preference values are reported as $b_{(\text{site type})}$ and scaled from 0 to 1, summing to 1 in total. They reflect the probability that a site type would be chosen, if all types were equally available. After calculating the selection index values, the overall model was tested for significance by comparing the deviance of the model to that of a null model in which selection was random (for details see Arthur et al. 1996).

The generated overall model contains four preference values (i.e. for unused sites, sites with eggs, tadpoles, and both eggs and tadpoles), thus being a three-parameter model. These three parameters represent a parameter for tadpoles, one for eggs and one for the interaction of tadpoles and eggs (Marsh and Borrel 2001). The significance of each parameter was tested by a stepwise dropping of parameters, without changing the number of categories. If exclusion of a parameter decreased the likelihood (or increased deviance) of the model significantly, it was considered to be significant (Muller et al. 1997). For details and preference value calculation see Marsh and Borrel (2001).

For this analysis it was necessary to determine which sites were available to ovipositing females. Sites used by *P. guineensis* showed a patchy distribution within the study area and could therefore be grouped into nine patches (mean radius ≈ 15 m). Distances between neighboring patches ranged between 180 and 600 m. Each patch possessed 8–19 oviposition sites. Mark-recapture data showed no migration between patches. Mean migration distances ($x = 24$ m; Rödel et al. 2004) were much lower than distances between patches. Hence, patches were assumed to be independent from each other. Thus, likelihood was the product of the probability of getting the data for each single patch, and the data from all patches were used to generate the selection indices (the assumption being that the indices were constant across patches).

The second assumption is that the probability of usage of a particular site type increases linearly with the availability of that type of habitat at the time of spawning. If the oviposition behavior changed with availability this would not be accurate. In this study, the availability of site types was generally constant throughout the reproductive season, with used breeding sites representing $\approx 30\%$ of the available sites.

The influence of water persistence on timing of oviposition

Water persistence differed considerably between, but also within, sites during a rainy season. Therefore, we examined whether the timing of oviposition was affected by a minimum threshold of water persistence allowing for successful reproduction. We used the number of days with consecutive water presence as a measure of water persistence. The minimum number of days necessary to complete the development (including embryonic and larval, measured until emergence of at least one front limb) was 20 days (Rödel et al. 2004). Thus, a 20-day interval of water persistence was seen as the minimum threshold for successful completion of metamorphosis. Because we observed tadpoles surviving in moist sediment up to 1 day, sites were defined as dry if no water was visible above the sediment for two consecutive days. During one season, for each site used, we recorded the number of days that were followed by ≥ 19 days of

continuous water presence (i.e. days successful oviposition possible) and the number of days that were followed by < 19 days continuous water presence (i.e. days on which successful oviposition was not possible). Days within the same category of all used sites were summed, giving the total amount of days for each category. Also for each oviposition recorded, the length of the period of continuous water presence starting with the day of the spawning event was determined. Oviposition events were then divided in two categories based on the period of water persistence: (1) ≥ 20 days (above threshold) or (2) < 20 days (below threshold). The number of oviposition events in each category (above vs below threshold) was summed, giving the total amount of oviposition events for each category. Both data sets allowed for calculating the expected number of ovipositions in each threshold category if oviposition was random.

Experimental test of effects of water holding capacity on oviposition site choice

Observations of previous seasons showed that sites differed considerably in their water persistence and thereby in their desiccation risk. Therefore, it would be beneficial for the frogs to have the ability to estimate the water holding capacity of a site for the timing of oviposition. To examine this, we performed an experiment with 54 artificial oviposition sites, in which the water holding capacity was manipulated from May 2001 to September 2002. We used empty snail shells that are known to be used as oviposition sites by *P. guineensis* (Rödel et al. 2004). Six snail shells of similar size were arranged on the ground in a circle and spaced such that the nearest neighbor was ≈ 2 m apart. In each circle three shells were selected randomly in which the water amount was manipulated. The remaining three were kept at the maximal water level throughout the entire study time. Experiments started when precipitation filled the shells naturally. Then all shells of a treatment were maximally filled with rainwater by the experimenter. During the following days, water in the manipulated shells was carefully decanted daily to half of the water volume of the preceding day until no water remained or precipitation started the experiment anew. The arrangement was replicated in nine different places and monitored daily.

Results

Oviposition site-selection models

The final model for oviposition (model 1) included three parameters: maximal possible water depth, sediment depth and relative amount of days with water presence (Table 1). Sediment depth and maximal possible water depth were negatively correlated with probability of oviposition, indicating an avoidance of breeding sites

Table 1 Significant site parameters (out of eight) in the site-selection models for oviposition and male presence. A total of 69 sites were categorized as unused (0) or used (1) for oviposition ($N_{\text{used}} = 25$) or males ($N_{\text{used}} = 34$). Models were fitted by logistic regression using backwards elimination procedure ($P = 0.1$). *Water depth* Maximal water depth that could be achieved in a tree-hole; *days with water* days with water presence/days of observation; *B regression coefficient

Variables	*B	SE	df	P
Oviposition model				
Sediment depth	-0.521	0.264	1	0.049
Maximum possible water depth	-0.242	0.140	1	0.021
Days with water	0.054	0.017	1	0.002
Male model				
Days with water	0.029	0.01	1	0.004
Sediment depth	-0.340	0.145	1	0.019

with deeper water and with thick sediment layers. The relative amount of days with water corresponded positively with breeding site use (Table 1), reflecting a preference for spawning sites with a longer water presence. The final model showed a good correlation ($R^2_N = 0.451$) with the dependent variable and the high AUC value displayed a high predictive performance, indicating that the model could discriminate between used ($n = 25$) and unused sites for oviposition 85.3% of the time. The sensitivity (60.0%) and the high specificity (84.1%) of the model indicated that it predicted most of the unused and used sites correctly (78.3%).

The final model for male breeding site-selection (model 2) only included two parameters (Table 1). Again sediment depth and relative days with water presence were significant determinants for male presence. The negative correspondence of male occurrence with sediment depth and positive correspondence with water presence, indicated male preferences for sites with a thinner sediment layer and longer water persistence. Compared to model 1, the male model had a lower correlation with the dependent variable ($R^2_N = 0.234$) but still showed a good predictive performance (AUC = 75.3%, correct predictions = 71.0%, sensitivity = 76.4%, specificity = 62.9%).

To examine if the model for male presence (model 2) could also predict the use of sites for oviposition, its discrimination performance was measured by comparing the model 2 predictions to the actual observed use of sites for spawning. The proportion of correct predictions (78.3%) was similar to that of model 1. The AUC value was lower (79.2%) but still reflected good discrimination of the model (sensitivity = 76.0%, specificity = 79.6%). In general, model 2 predicted oviposition in six more sites than model 1, of which four were used, resulting in a 16% higher sensitivity than model 1.

A comparison of the predictions made by the oviposition model from 2001 with the data of the observed oviposition site use in the reproductive season of 2002 (May–September) showed that the model could also correctly predict most of the used and unused sites for the following season (correct predictions = 72.0%, sensitivity = 68.9%, specificity = 85.0%) with an excellent discrimination performance (AUC = 0.83).

Differences in relative use of oviposition sites

The numbers of clutches deposited in a site were positively, but not significantly, correlated with the predicted habitat quality of model 1 (Spearman, $r=0.359$, $P=0.091$, $n=25$) and model 2 (Spearman, $r=0.112$, $P=0.593$, $n=25$). The relative time a site was occupied by males was also not significantly correlated with the habitat quality predicted by model 2 (Spearman, $r=0.221$, $P=0.209$, $n=34$). This showed that the models could discriminate between suitable and unsuitable oviposition sites, but they could not explain the differences in their relative use.

The number of spawning events increased slightly with water volume but the correlation was not significant (Spearman, $r=0.278$, $P=0.178$, $n=25$) and could also not explain differences in clutch number between oviposition sites.

The effect of conspecific offspring presence on oviposition site-selection

In each patch 29.2% of the sites were successfully used for oviposition at least once, and the oviposition model predicted 41% of sites within a patch as suitable for spawning. However, throughout the whole reproductive season, the median of occupation of all sites within a patch (= % with tadpoles + % with eggs + % with eggs and tadpoles) was 15.8%, indicating that only half of all suitable oviposition sites were occupied at any point in time.

The resource-selection model showed that frogs did not favor (0) unused sites ($b_0=0.052$), but preferred sites containing both tadpoles (T) and eggs (E; $b_{ET}=0.456$) to habitats containing eggs ($b_E=0.265$) or tadpoles ($b_T=0.227$) only (Table 2). All three parameters were significant ($P<0.001$).

Correlation between male presence and oviposition

Male presence in sites ($n=34$) could be characterized by three main variables: relative number of days a breeding site was occupied by males (median = 8.0%; Q25/Q75 = 3.0/19.1%; range = 0.7–59.4%), median number of males in a site (median = 1.1; Q25/Q75 = 1.0/1.1; range = 1–4) and number of different males recorded from a site (median = 2; Q25/Q75 = 1/4; range = 1–9). A

nonparametric partial correlation test showed that only the relative time of occupation by males (total amount of days with male presence/observation days) was significantly correlated with the number of clutches deposited (Pearson, $r=0.615$, $P<0.001$, $n=25$). The number of spawning events increased with the days a site was occupied. The number of different males (Pearson, $r=0.348$, $P<0.05$) and the mean time individuals stayed continuously at a site (Pearson, $r=0.569$, $P<0.001$) were correlated with the total time a site was occupied, but not significantly correlated with the number of ovipositions (Pearson, $r=0.159$, $P>0.05$).

Influence of water persistence on timing of oviposition

The analysis showed that significantly ($\chi^2=33.4$, $df=1$, $n=139$, $P<0.001$) more clutches were deposited above the minimum threshold of 20 days of water persistence for survivorship of tadpoles and less below the threshold than expected by random. This indicates that oviposition was not random with respect to the threshold of water persistence in a site. Oviposition was never recorded from sites on a day when no water was present.

Effects of water holding capacity on oviposition site choice in artificial habitats

Within the 2 years' duration of this experiment we recorded 89 spawning events in snail shells with high water-holding capacity and only four clutches in snails with a low water-holding capacity. Because it was possible that spawning events were not independent of each other in a replicate (circle) we tested if the number of used snail shells within a replicate was random or affected by water-holding capacity. The analysis showed that shells with high water-holding capacity were significantly ($\chi^2=4.5$, $df=1$, $n=8$, $P=0.034$) preferred for oviposition.

Discussion

Suitability of oviposition sites

Habitat-suitability models are based on the assumption that the selected key factors are those habitat parameters that are of major importance, e.g. might affect larval

Table 2 Analysis of the oviposition site-selection model. B_0 , B_E , B_T and B_{ET} indicate the preference values for unused sites (0), sites containing eggs (E), sites containing tadpoles (T) and sites con-

taining both eggs and tadpoles (ET), respectively. The selection indices reflect the probability that a site type would be chosen, if all types were equally available (for details see Materials and methods)

Parameters	B_0	B_E	B_T	B_{ET}	Dropped term	χ^2	P-value for term
Eggs, tadpole, interaction	0.052	0.265	0.227	0.456	None ^a	26.51	< 0.001
Eggs, tadpole	0.537	0.169	0.224	0.070	Interaction	113.02	< 0.001
Eggs	0.214	0.214	0.286	0.286	Tadpoles	65.37	< 0.001
Tadpoles	0.244	0.256	0.244	0.256	Eggs	72.47	< 0.001

^a Tested against null model

development, growth, and survival. In phytotelmata, water persistence often varies considerably from site to site. This variation results in differences in food level, desiccation, and predation risk (Kitching 2000). Species reproducing in such sites face a trade-off between the risks and advantages of different sizes of sites. Small sites are more abundant, but desiccate faster and have low nutrient levels (Apsbury and Juliano 1998). Large sites have higher water holding capacity and provide more nutrients, but are less abundant and are more likely to support predators like dragonfly larvae (Fincke 1992; Rödel et al. 2004).

Our results showed that both biotic and abiotic factors played an important role in the selection and use of oviposition sites. The suitability of a spawning site was strongly dependent on the three abiotic parameters, water presence, sediment depth and maximal possible water depth. The oviposition site-selection model based on these three factors showed an excellent predictive performance and was transferable to the following year. The amount of correct predictions of the model is even likely to be an underestimate, because some of the predictions for suitable reproduction sites might have been correct and these sites were just not detected by frogs (Capen et al. 1986). This assumption is supported by the fact that some of the predicted suitable sites were used in 2001 but not in 2002 or vice versa.

It is not surprising that sites with longer water presence were preferred for oviposition. However, the negative correlation between oviposition site-selection and sediment depth and maximal possible water depth were unexpected at first. Even though sediment might be a possible food resource for tadpoles (Pfennig et al. 1991; Apsbury and Juliano 1998; Lehtinen 2004) the negative correlation could be explained if sediment depth increases with the age of sites, which in turn could be negatively correlated with water-holding capacity (Kitching 2000). However, sediment depth (Spearman, $r = 0.304$, $n = 69$, $P = 0.011$) and maximal possible water depth (Spearman, $r = 0.548$, $n = 69$, $P < 0.001$) were both positively correlated with water presence. The most likely explanation for the negative relation of oviposition site-selection and these two factors is that they are positively correlated with the probability of predator presence. Sites containing dragonfly larvae always had a thick sediment layer and a high maximal possible water depth (V.H.W. Rudolf and M.-O. Rödel, unpublished data). Dragonfly larvae were observed to retreat and hide in the substrate which made it difficult to detect them visually. Thus, the negative correlation between site use and both habitat factors could reflect a direct or indirect avoidance of predators.

Oviposition and desiccation risk

The ecological importance of water presence for oviposition site-selection is obvious. In ephemeral habitats desiccation is a major factor of tadpole mortality (Smith

1983; Wilbur 1987; Newman 1988; Murphy 2003a) and this is also the case in *P. guineensis* (Rödel et al. 2004). The positive correlation between the use of sites and length of water presence indicates that frogs preferred sites with longer water presence. These sites are more likely to provide the necessary water persistence for successfully finishing the larval period. However, the risk of desiccation varied strongly not only among sites but also within a site during the rainy seasons. Sites with a high water level or large volume after a rainfall sometimes lost water faster than smaller sites (Rödel et al. 2004). Thus, total values of water depth or volume were not reliable indicators for water persistence. If spawning events had been random within the used oviposition sites, the probability of reaching metamorphosis with a larval period of 20 days (including egg stage) would have been $< 40\%$ (V.H.W. Rudolf and M.-O. Rödel, unpublished data). Thus, there is a strong selective pressure for the ability of ovipositing frogs to correctly determine which site retains water long enough for larvae to complete metamorphosis successfully.

Our data showed that frogs could discriminate between the water-holding capacity of sites. Oviposition was timed with respect to future water persistence. For such timing, frogs must not only be able to assess the minimum water amount or level that allows successful completion of the larval stage, but also have the ability to estimate the water-holding capacity. Spieler and Linsenmair (1997) found that females of the aquatic frog, *Hoplobatrachus occipitalis*, could assess water-holding capacity by visiting familiar pools during a season repeatedly, or by using information from previous seasons. When confronted with new, and hence unfamiliar, pools, water volumes were the best predictors for egg numbers. Crump (1991) found that females of *Hyla pseudopuma* preferred experimental pools with deep water, reflecting a higher water-holding capacity. The results of our study displayed no correlation of oviposition with water volume and maximal possible water depth was even negatively correlated with oviposition site choice. Thus, the total values of these parameters were not used to estimate water-holding capacity. Recent observations show that the reproductive lifetime of *P. guineensis* is only a few months and that a high proportion of oviposition sites are used only in one season (Rödel et al. 2004). Therefore, it is unlikely that tree-holes were visited among rainy seasons repeatedly to assess water-holding capacity. Philopatry, returning to the site where an individual hatched, can also be excluded as a possible explanation as we observed breeding site turnover rates between seasons (2000–2002) ranging from 26–75% (Rödel et al. 2004). However, it is possible that *P. guineensis* visited sites repeatedly within a short time, or stayed for some days to assess water loss. The decline of water level or volume over time was highly variable among sites and reflected well the capacity of a site to hold water. Therefore, it seems probable that the decrease of volume or water level was used by *P. guineensis* for estimation. The snail shell experiments support this assumption, as all parameters were kept constant except

the water level and volume. This estimation is most likely made by males because they often stay longer at breeding sites, whereas females visit sites only shortly for oviposition (Rödel et al. 2004).

Conspecific attraction

Observed tadpole densities were remarkably high in *P. guineensis* (up to 2 tadpoles/ml water volume; Rödel et al. 2004). This resulted from multiple ovipositions, which created overlapping larval cohorts. A large body of theory holds that because conspecifics are competitors, individual fitness should decrease with increasing density (Rosenzweig 1991; Sutherland 1996). This implies that the presence of previous settlers should discourage newcomers. Hence, the use of resources should approximate an ideal free distribution (Fretwell and Lucas 1970) for optimal resource use and minimization of intraspecific competition. This theory has been supported by several studies on anurans (Resetarits and Wilbur 1989; Crump 1991; Spieler and Linsenmair 1997), which have shown that ovipositing adults avoided habitats containing conspecific eggs or larvae.

If the presence of conspecifics has negative effects on tadpole development, there should be strong selection for a female's ability to discriminate among oviposition sites based on the species present. Field observations and experiments showed that increasing conspecific density significantly decreases size at metamorphosis of *P. guineensis* down to 15% of the possible maximal size, and tadpoles from high-density environments achieved only a third of the average tadpole size found in low densities (V.H.W. Rudolf and M.-O. Rödel, unpublished data). In amphibians, size at metamorphosis is closely related to future survival probability (Berven 1990; Scott 1994; Altwegg and Reyer 2003) and reproductive output (Berven 1981; Smith 1987; Altwegg and Reyer 2003). Thus, the presence of conspecifics in an oviposition site would have strong negative effects on offspring fitness of *P. guineensis*. However, the avoidance of conspecifics might only be possible if other suitable sites are available.

The successful use of particular sites for reproduction, and the models of oviposition and male presence suggested that, on average, less than half of the suitable oviposition sites were occupied. This implies that ovipositing females had the chance to avoid high densities by using unoccupied sites. In some systems, the benefit incurred through the reduction in competitive pressure overcomes the disadvantages of lower abiotic habitat quality. Crump (1991) found that the avoidance of conspecific offspring can even lead to the use of habitats with lower quality, if high quality habitats already contain conspecifics. However, our results show that sites containing conspecifics were not avoided but might have even been preferred to unoccupied sites. Occupied and unoccupied sites were partly nearest neighbors, hence, detection probability had no effect. Thus, there

must be a benefit to compensate for the strong disadvantages arising from ovipositing in sites containing conspecific tadpoles. The fact that conspecific presence had a very strong, negative effect on size at metamorphosis suggests that this behavior may exist to avoid offspring mortality, most likely due to predation. Then, high densities would result from a trade-off between avoiding predation risk, often resulting in the complete loss of the offspring (Rödel et al. 2004), and decreased fitness through competition (Björkman et al. 1997).

Another explanation might be that high tadpole densities resulted as a by-product of similar preferences by spawning frogs for sites with specific characteristics regardless of conspecifics. A factor determining predation risk of eggs, tadpoles or adults, e.g. shape and position of a tree-hole entrance, which might affect the oviposition site choice of dragonflies (Clausnitzer 2002), may not have been detected by the analysis. If such a factor existed, high densities would be expected to be found consistently more often in certain sites. However, high densities were not always recorded from the same sites but changed.

The observed pattern is more consistent with conspecific attraction, a theory suggesting that colonizers might benefit by settling near conspecifics (review in Stamps 1988; Muller et al. 1997). A possible benefit of this behavior is that conspecifics might serve as cues for habitat quality during the process of oviposition site-selection (Stamps 1988; Muller et al. 1997; Doligez et al. 2002). In *P. guineensis*, egg and larval survival, and therefore reproductive success, are considerably affected by predation (Rödel et al. 2004). The presence of conspecific tadpoles is a reliable indicator of the absence of predators like dragonfly larvae, and might thus encourage newcomers to choose such sites for oviposition. Several studies have shown that naive colonizers prefer to settle close to conspecifics because they have no information about successful reproduction sites (Stearns 1976; Muller et al. 1997; Baltz and Clark 1999). In general, the reproductive lifetime of *P. guineensis* is not longer than one rainy season (Rödel et al. 2004). Thus, there may only be naive individuals. Observations also showed that the presence of dragonfly larvae in sites remained constant during a season but changed between seasons (V.H.W. Rudolf and M.-O. Rödel, unpublished data). Even if individuals might live longer than one season, all individuals would remain naive due to frequent changes in predator presence, given that they cannot reliably detect predators directly. In some studies amphibians avoided habitats containing predators like fish (Kats and Sih 1992; Hopey and Petranka 1994), whereas other workers could not find such evidence (Laurila and Aho 1997). Studies of Resetarits and Wilbur (1989) showed that *Hyla chrysoscelis* females could detect some predators like fish and salamander larvae, but did not avoid spawning sites with predatory dragonfly larvae. We observed five spawning events in two sites with dragonfly larvae. This suggests that *P. guineensis* might not be able to detect this predator. Therefore, *P. guineensis* could increase fitness by using

conspecific offspring as a cue for site quality in an uncertain environment. This behavior was observed by Downie et al. (2001). They found that frogs preferred pools with conspecifics for tadpole deposition even though this choice was risky due to possible cannibalism by conspecific larvae. *P. guineensis* does not have cannibalistic tadpoles, making this choice even less risky.

The interaction of males and females

Several studies with anurans have demonstrated that females and males are choosy in selecting suitable reproduction sites, thereby improving reproductive success (Crump 1991; Resetarits and Wilbur 1991; Heying 2001). In frogs breeding in phytotelmata it is common for males to select oviposition sites to which they attract females (Eterovick 1999; Jungfer 2000; Bourne et al. 2001; Heying 2001). In our study, the model of male presence at possible spawning sites included the same abiotic parameters as the model for oviposition except maximal possible water depth, suggesting that *P. guineensis* males select breeding sites with respect to abiotic habitat characteristics similar to those shown by female preferences. The male model could predict most of the used oviposition sites correctly. Thus calling site-selection of males had high predictive values for the distribution of eggs, suggesting a strong interaction between the choices made by both sexes. In some species, females reject phytotelmata selected by a male (Jungfer 2000; Heying 2001). Recent data on *P. guineensis* suggest that females inspect and evaluate males, breeding sites or both before eventually spawning (Rödel et al. 2004). The possible rejection of sites or males by females might explain why the male model was less precise in its predictions for possible oviposition sites.

In our study oviposition site use could not be explained by only analyzing single factors. The abiotic parameters determined the suitability of a breeding site, whereas the response to conspecifics' presence explained the differences in frequency of oviposition site use. This demonstrates the crucial importance of including not only habitat parameters but also intraspecific and interspecific interactions in both habitat-selection models and behavioral analyses.

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