HERPETOZOA 31 (3/4): 157 - 171
Wien, 28. Februar 2019

Oviposition site selection by the Asian Common Toad *Duttaphrynus melanostictus* (SCHNEIDER, 1799), in an Indian biosphere reserve
(Anura: Bufonidae)

Laichplatzwahl von *Duttaphrynus melanostictus* (SCHNEIDER, 1799)
in einem indischen Biosphärenreservat
(Anura: Bufonidae)

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KURZFASSUNG

Im Wissen um die Bedeutung der Mikrohabitat-Bedingungen bei der Fortpflanzung der Anuren beschreiben die Autoren die Wirkvariablen bei der Wahl des Eiablageortes der Schwarznarbenkröte *Duttaphrynus melanostictus* (SCHNEIDER, 1799). Die Datenerhebung erfolgte an verschiedenen Tagen an 60 Wasserkörpern (30 Laichgewässer mit 108 Laichplätzen und 30 Nicht-Laichgewässer) im Similipal Biosphärenreservat, Odisha, Indien über die Dauer von fünf aufeinanderfolgenden Laichperioden (2012–2016). Die Mikrohabitat-Variablen pH, Wassertiefe, Luft- und Wassertemperatur, relative Luftfeuchte, Deckungsgrad des Kronendaches, organisches Material im Wasser, Farbe des Wassers, Wassertrübe und submerse Vegetation wurden mit Hife multivariater statistischer Verfahren einschließlich Pearson Korrelation und Clusteranalyse untersucht. Letztere ordnete die untersuchten Feuchtlebensräume nach Übereinstimmungen in ihren Mikrohabitat-Parametern an, wobei die Assoziation der Cluster mit der Anwesenheit oder dem Fehlen von Laich an der Untersuchungsstelle deutlich war. Logistische Regressionsmodelle zum paarweisen Vergleich verschiedener Kombinationen von Mikrohabitat-Parametern wurden nach der Stärke der Assoziationen zwischen Laichplatz und Parameter mit Hife des Akaike Informationskriteriums gereiht. Nach den Untersuchungsergebnissen bevorzugt *D. melanostictus* Laichgewässer im schwach sauren Milieu, bei eher geringer Wassertiefe und -temperatur sowie mäßig entwickelter submerser Vegetation. Für das Management der Lebensräume und zum Schutz von *D. melanostictus* könnte es nützlich sein, die hydrologischen Gegebenheiten zu erhalten, welche die Habitate dieser Kröte entstehen lassen sowie stark frequentierte Laichplätze auszuweisen und zu schützen.

ABSTRACT

Bearing in mind the importance of micro-habitat conditions in anuran reproduction, the authors characterized predictors of oviposition site selection of the Asian Common Toad, *Duttaphrynus melanostictus* (SCHNEIDER, 1799). Information was acquired on different dates at 60 water bodies (30 water bodies with 108 breeding points and 30 non-breeding aquatic bodies) in the Similipal Biosphere Reserve, Odisha, India over five consecutive breeding seasons (2012–2016). The microhabitat variables: pH, water depth, air temperature, water temperature, relative air humidity, canopy cover, aquatic organic matter, water color, turbidity and submerged vegetation were analyzed using multivariate statistical methods including Pearson's correlation, and cluster analysis. The latter arranged the studied water bodies according to similarities in their microhabitat parameters and revealed clear associations between clusters characterized by presence or absence of spawn at the studied sites. Paired logistic regression models were designed and the Akaike Information Criterion was used to rank the strength of the associations between oviposition sites and microhabitat variables. The results suggest that *D. melanostictus* prefers slightly acidic spawning sites with rather low water depth and water temperature and moderately developed submerged vegetation. Management of habitats and conservation plans for *D. melanostictus* could benefit from preserving hydrologic processes that produce these specific habitats, and by identifying and protecting high-use breeding areas.

KEY WORDS

Amphibia: Anura: Bufonidae: *Duttaphrynus melanostictus*, breeding sites, oviposition site selection, breeding ecology, microhabitat, conservation, Similipal Biosphere Reserve, Republic of India

INTRODUCTION

Selection of the oviposition microhabitat is a key determinant of reproductive success for many oviparous animals since it can affect survival, development and growth rate of the offspring (MOUSSEAU & FOX 1998). INGER (1966) identified temperature, rainfall, vegetation and competition as the major factors that ultimately limit the distribution of tropical amphibians. According to Ultsch et al. (1999), anuran breeding success depends among others on abiotic factors such as desiccation risk, water temperature, dissolved oxygen concentration and pH. The number of breeding habitats and their distribution limits the occurrence of anuran species (Zimmerman & Bierregaard 1986; Rodrigues et al. 2010). Information on habitat associations can contribute to an understanding of the species' population dynamics and lead to more effective conservation and management approaches (Morris 2003). Studies by Fukuyama & Kusano (1992); Kupferberg (1996); Gillespie et al. (2004); Alfonso & Eterovick (2007) provided valuable information on anuran breeding habitat characterization as well as its potential application for conservation.

For breeding, most Indian anuran species utilize habitats such as ephemeral ponds, damp grounds, temporary puddles, permanent ponds and rivers following the south-west monsoon rain (Saidapur 1989). The physical environment plays an important role in influencing tadpole growth rates, duration of larval period, survival until and size at metamorphosis (Alford 1999). Aquatic breeding habitats vary in their structure (e.g., stream width, pond area, water depth, and canopy cover), limnological characteristics (e.g., conductivity, concentration of dissolved oxygen, temperature, flow speed lentic or lotic) and hydroperiod (e.g., ephemeral, temporary or permanent), which influence or determine the composition of their tadpole assemblages (Gascon 1991; Barreto & Moreira 1996; Peltzer & Lajmanovich 2004; Oliveira & Eterovick 2009).

Duttaphrynus melanostictus (Schneider, 1799), is a widespread species that occurs in many south Asian countries, such as India, Pakistan, Nepal, Bhutan and Myanmar (Dutta et al. 2009; Frost & The American Museum of Natural History 2018). It is a prolific breeder that utilizes different habitats ranging from lentic (e.g., ephemeral pools, temporary ponds, permanent ponds, gutters, puddles and cement cisterns in parks) to lotic systems (e.g., rivers, creeks and streams) for breeding (Saidapur & Girish 2001).

The present study was initiated to document the ecological requirements on oviposition sites of *D. melanostictus* in the Similipal Biosphere Reserve, Odisha, India. The objective of this study was to analyze habitat selection of *D. melanostictus* at two scales: (1) identification of the microhabitats which are used for egg deposition and the significant ecological variables in the microhabitats used as oviposition sites, and (2) selection of models based on features of *D. melanostictus* spawning habitats vs. paired random locations. Although the species is classified as Least Concern (LC) (van Dijk et al. 2004; Dinesh et al. 2009), like most other species, their number must be expected to decline in future due to climate change, habitat alteration and rapid urbanisation. Such studies could form the basis of conservation and help in developing management plans like habitat restoration and natural resource management in the study area and elsewhere.

MATERIALS AND METHODS

Study site.– The study area, the Similipal Biosphere Reserve (SBR, 20°17' – 22°34' N and 85°40' – 87°10' E), covers an area of 5,569 km^2 and is situated in the heart of the Mayurbhanj district of Odisha state in India. It is located in the northern end of the Eastern Ghats and classified in the Chotanagpur biotic province of the Mahanadian biogeographical region (Dutta et al. 2009). The climate of the area is subtropical with a hot summer (March to May average maximum 40–42 °C), long rainy season (June to October, actual average precipitation, 1,283.4 mm) and a chilling winter (November to February average minimum 5–7 °C). The study was conducted in the south-eastern transition zone of SBR (21°45' N, 86°20' E) where 60 water bodies (30 permanent ponds, 10 temporary ponds, 10 ephemeral pools and 10 small streams)

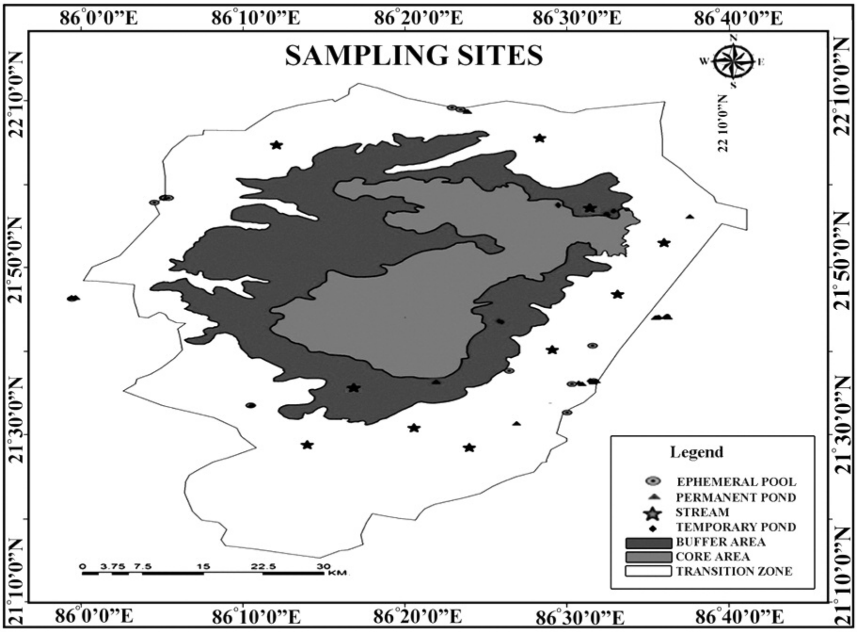

Fig. 1: Map of the sampling sites in the Similipal Biosphere Reserve, northern Odisha, India, the study area of *Duttaphrynus melanostictus* (Schneider, 1799).

Abb. 1: Karte der Untersuchungsstellen im Similipal Biosphärenreservat, nördliches Odisha, Indien, Untersuchungsgebiet von *Duttaphrynus melanostictus* (Schneider, 1799).

(Fig. 1) were surveyed randomly on different dates between egg laying and metamorphosis during five consecutive breeding seasons (May–September 2012–2016). Microhabitats were characterized both in breeding water bodies within a radius of 1 m around the egg clutches and randomly at non-breeding sites.

The study considered equal numbers ($N = 30$) of breeding and non-breeding sites. The breeding sites (15 permanent ponds, five temporary ponds, five ephemeral pools and five small streams) comprised 108 breeding points encompassing 495 egg clutches during the study period (Table 1, Fig. 2). The number of individual clutches at the 26 breeding points with multiple clutches was ascertained by visual estimation of the egg number. The specific identity of the clutches was ensured by following the amplecting *D. melanostictus* pairs in most cases and raising eight clutches of eggs in the laboratory till metamorphosis. Besides, the sympatric population of *Duttaphrynus stomaticus* (Lütken, 1864), is so low that not a single amplecting pair was observed during the study.

Data acquisition.– To locate *D. melanostictus* egg clutches aquatic habitats of the study area were searched visually (Heyer et al. 1994) during the morning hours (6:00–10:00 a. m.). The following ecological variables were recorded as close as possible to the clutch and at non-breeding water bodies twice (on different dates at each sampling point) during each breeding season (duration of the tadpole development until metamorphosis in the study area was 22–25 days; personal observation): date, air and water temperature, pH, degree of canopy cover, water depth, relative air humidity, quantity of macro-organic matter surrounding the clutches, water color, water turbidity, degree of submerged vegetation and substrate type. Geographical coordinates were obtained using a Garmin™ 76 CSX GPS. The air and water temperatures were recorded with a mercury bulb thermometer and percent relative humidity by using a thermo-hygrometer. The pH value was measured using a digital pH meter (pH Tester 10, Ecotester, Eutech Instruments). The authors used a spherical densitometer to measure canopy cover and a ruler to measure water depth. Data on rainfall of the study sites (Table 1) were obtained from the Indian Meteorology Department, Odisha. The amount of organic matter surrounding the clutches, water color and water turbidity were classified through visual inspection. Organic matter associated with the clutch was classified into (1) none, (2) little to medium, and (3) high; water color into (1) colorless, (2) light brown and (3) brown; water turbidity into (1) transparent, (2) muddy, and (3) extremely turbid; submerged vegetation into (1) present or (0) absent. A minimum distance of 1 m between two selected clutches was allowed to reduce spatial autocorrelation among the sampling sites. The substrate (soil, leaf, gravel, rocks) of the clutches was characterized in words.

Statistical analyses.– ANOVA was applied to determine differences of microhabitat parameters among study sites and t-tests to interpret the relationship between microhabitat variables. In addition to paired t-tests, the authors used multiple logistic regression models employing a logarithmic-link function to analyze the matched pairs' data and estimate habitat selection (Compton et al. 2002; Gorman & Haas 2011) for breeding purposes. Such a model allows for a more accurate assessment of the choices of *D. melanostictus* at the time of oviposition. Twenty-six models were developed by combining 10 breeding parameters that were hypothesized to be significant for egg deposition sites. The models were evaluated using Akaike's Information Criterion (AIC, Akaike 1973) with values corrected for small sample sizes (AICc, Burnham & Anderson 1998). Presence or absence of an egg clutch in a given habitat was the dependent variable and pH, water depth, air temperature, water temperature, relative humidity, canopy cover, organic matter, water color, turbidity and submerged vegetation coverage were the independent variables. To exclude collinearity between predictor variables, Pearson correlation coefficients were calculated for all the pairwise combinations of independent variables both for breeding and non-breeding sites. To reduce the bias of any extreme value, covariates were standardized so that each value was related to the mean. In addition to ranking each model using the AICc, the authors computed ΔAICc and Akaike weights to determine the strength of inference for each model (Burnham & Anderson 1998). Within the information-theoretic framework, the model with the lowest AICc was considered to have the best balance of statistical parsimony and goodness of fit, and models with $\Delta < 2$ as well as high modal weights were considered to be best supported by the data (Burnham & Anderson 2002). A generalized linear model (GLM- logit link and binomial error) was applied on the data set by using presence vs. absence of breeding (binary response) and modeled with microhabitat parameters.

Similarity and dissimilarity among the sampling sites were assessed via cluster analysis (CA) on the normalized data by means of the Ward's method, using squared Euclidean distances as a measure of similarity (Zhao et al. 2011). All analyses were carried out using the software IBM SPSS Statistics v. 20 on a Windows™ platform and *R* version 2.11.1 (R Development Core Team 2008) to identify matched pairs between the breeding and non-breeding sites.

RESULTS

Clutches were encountered only in shallow areas with stationary or very slow water movement. Breeding sites had significantly higher pH, shallower water depth and lower water temperature than the non-breeding sites (Table 2). A variety of substrates including sand, silt, gravel, rocks and organic matter such as leaves (dead and alive), and submerged vegetation were used for oviposition. The female lays a long double jelly string of eggs enclosed in a double gelatinous capsule around submerged vegetation in permanent ponds and around rocks and pebbles in ephemeral pools. The egg

Table 1: Number of rain days, rainfall, relative humidity, atmospheric temperature and number of clutches (data comprise range, mean ± standard deviation) in the months of the study of the spawning site selection of *Duttaphrynus melanostictus* (SCHNEIDER, 1799), in the Similipal Biosphere Reserve, northern Odisha, India.

Tab. 1: Anzahl von Regentagen, Regenmenge, relative Luftfeuchte, Lufttemperatur und Anzahl der Gelege (angegeben sind jeweils Spannweite, Mittelwert ± Standardabweichung) in den Monaten der Untersuchung zur Laichplatzwahl von *Duttaphrynus melanostictus* (SCHNEIDER, 1799) im Similipal Biosphärenreservat, nördliches Odisha, Indien.

Month and year Monat und Jahr	Number of rain days Anzahl Regentage	Rainfall (mm) Regenmenge (mm)	Humidity (%) Luftfeuchte (%)	Atmospheric temperature (°C) Lufttemperatur (°C)		Number of egg clutches Anzahl der Gelege (N_{tot} = 495)
				Minimum	Maximum	
May 2012 – 16	7 – 19 10.6 ± 4.58	21.0 – 228.8 120.68 ± 71.35	68.3 – 77 71.9 ± 2.91	22.3 – 28.8 25.14 ± 2.43	30.9 – 38.5 36.22 ± 2.83	1 – 6 4.0 ± 1.89
June 2012 – 16	9 – 18 14.0 ± 3.46	158.2 – 311.5 217.18 ± 51.24	70.4 – 83.8 77.96 ± 4.67	21.6 – 29.6 25.62 ± 2.72	30.8 – 37.6 34.26 ± 2.29	16 – 19 17.6 ± 1.01
July 2012 – 16	18 – 25 22.0 ± 2.96	241.4 – 509.5 365.9 ± 106.31	80.1 – 87.6 85.6 ± 2.78	21 – 28.5 24.48 ± 2.67	29.5 – 32.3 31.42 ± 1.00	24 – 45 33.8 ± 6.73
Aug 2012 – 16	20 – 25 21.8 ± 1.72	244.3 – 509.0 363.94 ± 85.87	80.5 – 89.1 85.4 ± 2.88	20.7 – 28.4 24.28 ± 2.81	29.5 – 32.6 31.4 ± 1.03	26 – 42 30.8 ± 5.74
Sept 2012 – 16	12 – 24 15.8 ± 4.48	144.5 – 370.6 249.88 ± 77.78	80.4 – 87.7 84.16 ± 2.81	20.4 – 28.0 23.86 ± 2.80	29.0 – 33.2 31.46 ± 1.37	10 – 16 12.8 ± 1.93

strings are attached to vegetation or rocks almost in a criss-cross manner through change in position of the females during egg laying. Ephemerals and temporary ponds recorded single clutches on most occasions, whereas multiple clutches were observed in permanent ponds. The highest number of egg clutches was recorded in July, 2015 (45 clutches, high rainfall, $p > 0.05$, Fig. 2).

The mean differences among various ecological variables at breeding sites (N = 108) (pH – 6.59 ± 0.44, water depth – 26.82 ± 15.54 cm, and water temperature – 31 °C ± 1.49) and at non-breeding water bodies (N = 30) (pH – 6.30 ± 0.66, depth – 64.31 ± 24.68 cm and temperature – 31 °C ± 1.49) were found to be statistically significant (pH $p < 0.05$; water depth $p < 0.001$ and water temperature $p < 0.05$, Table 2). Other factors like organic matter surrounding the clutches, water color and turbidity of water as well as submerged vegetation did not influence the oviposition site selection significantly ($p > 0.05$). The organic matter surrounding the clutches varied widely: some were almost completely enveloped with organic debris like leaves and roots whereas others were on a shallow portion of the watercourse on sand with no surrounding organic matter. Some clutches were found in turbid, brownish waters, whereas most others were in extremely clear shallow water.

Rainfall and egg laying were positively correlated ($r = 0.84$).

Paired t-tests for different variables like pH ($t = 2.015^*$, $p < 0.05$); water depth ($t = 7.024^*$, $p < 0.001$); water temperature ($t = 2.284^*$, $p < 0.05$) and relative humidity ($t = 2.844^*$, $p < 0.01$) over the entire study period comparing both types of sites yielded significant differences ($p < 0.05$, Table 2). Canopy cover, water color, turbidity and submerged vegetation were higher at non-breeding sites, but not significantly related ($p > 0.05$).

One way ANOVA revealed significant differences in pH, water depth, water temperature and relative humidity among the parameters of both types of sites ($p < 0.05$, Table 3).

Out of the 26 hypothetical models (Table 4) using paired logistic regression, the one with pH, water depth, water tem-

Table 2: Descriptive statistics of the water parameters of 60 aquatic habitats in the Similipal Biosphere Reserve, northern Odisha, India. Thirty of these contained oviposition sites of *Duttaphrynus melanostictus* (SCHNEIDER, 1799). B – breeding site ($N = 108$), N-B – non-breeding water body ($N = 30$), SD – standard deviation, SE – standard error of the mean. * significant at 5% level ($P < 0.05$), *ns* - not significant at 5 % level ($P > 0.05$) for $df = 58$. The column 'Correlation' contains the correlation coefficients resulting from correlating the environmental variables of 108 breeding points in 30 breeding water bodies and 30 non-breeding water bodies.

Tab. 2: Deskriptive Statistiken der Wasserparameter von 60 Feuchtlebensräumen im Similipal Biosphärenreservat, nördliches Odisha, Indien. An 30 dieser Gewässer fanden sich Laichplätze von *Duttaphrynus melanostictus* (SCHNEIDER, 1799). B – Laichplatz ($N = 108$), N-B – kein Laichgewässer ($N = 30$), SD – Standardabweichung, SE – Standardfehler des Mittelwertes. * signifikant auf dem 5 % Niveau ($P < 0.05$), *ns* - nicht signifikant auf dem 5 % Niveau ($P > 0.05$) für $df = 58$. Water depth – Wassertiefe, Air temperature – Lufttemperatur, Water temperature – Wassertemperatur, Relative humidity – Relative Luftfeuchte, Canopy cover – Kronendach-Bedeckung, Organic matter – organisches Material, Water turbidity – Wassertrübe, Water color – Farbe des Wassers, Submerged vegetation – submerse Vegetation. Die Spalte 'Korrelation' enthält die Korrelationskoeffizienten aus der Korrelation der Umweltvariablen von 108 Laichplätzen in 30 Laichgewässern und 30 Nicht-Laichgewässern.

Water parameters Wasserparameter	Range Spannweite		Mean ± SD Mittelwert ± SD		SE of Mean SE des Mittelwertes		Correlation Korrelation	*p*-value *p*-Wert	*t*-value *t*-Wert
	B ($N = 108$)	N-B ($N = 30$)	B	N-B	B	N-B			
pH	5.7–7.6	4.7–7.3	6.59 ± 0.44	6.30 ± 0.66	0.08101	0.12096	0.42583	0.01896	2.015*
Water depth (cm)	3.04–51.81	15.24–100.58	26.82 ± 15.54	64.31 ± 24.68	2.85811	4.54266	-0.58571	0.00067	7.024*
Air temperature (°C)	29.0–36.0	29.0–35.0	31.40 ± 1.65	32.2 ± 1.63	0.30203	0.29780	0.1951	0.30153	1.997^{ns}
Water temperature (°C)	28.0–34.2	29.0–35.0	31.00±1.49	31.89 ±1.52	0.27223	0.27917	0.44132	0.01463	2.284*
Relative air humidity (%)	67.0–89.0	53.0–87.8	79.28 ± 6.27	73.97 ± 8.06	1.14496	1.47335	0.17369	0.35867	2.844*
Canopy cover (%)	0–80	0–85	31.66 ± 26.27	41.5 ± 26.13	4.79663	4.77150	-0.22851	0.22454	1.453^{ns}
Organic matter	1–3	1–3	1.76 ± 0.72	1.56 ± 0.67	0.13290	0.12395	-0.28143	0.13192	1.101^{ns}
Water turbidity	1–3	1–3	1.73 ± 0.69	1.96 ± 0.71	0.14700	0.13116	0.050904	0.78936	1.282^{ns}
Water color	1–3	1–3	1.8 ± 0.80	1.96 ± 0.80	0.12625	0.14765	-0.010591	0.9557	0.800^{ns}
Submerged vegetation	0–1	0–1	0.43 ± 0.50	0.56 ± 0.50	0.09202	0.09202	-0.18552	0.32634	1.025^{ns}

Table 3: One way ANOVA *F*- and *p*-values of the microhabitat parameters from 108 breeding points and 30 non-breeding sites of *Duttaphrynus melanostictus* (SCHNEIDER, 1799), in the Similipal Biosphere Reserve, India.

Tab. 3: Die *F*- und *p*-Werte aus der einfachen Varianzanalyse der Lebensraumparameter von 108 Laichplätzen von *Duttaphrynus melanostictus* (SCHNEIDER, 1799) und 30 Gewässern, in denen die Art nicht laichte. Untersuchungsgebiet war das Similipal Biosphärenreservat in Indien. Erklärung der Parameter siehe Legende von Tab. 2.

Microhabitat parameter Lebensraumparameter	*F* value *F*-Wert	*p* value *p*-Wert
pH	4.06	0.048
Water depth (cm)	49.33	2.673
Air temperature (°C)	3.988	0.050
Water temperature (°C)	5.217	0.026
Rel. air humidity (%)	8.088	0.006
Canopy cover (%)	2.112	0.151
Organic matter	1.211	0.275
Water color	0.639	0.427
Water turbidity	1.643	0.205
Submerged vegetation	1.05	0.309

Table 4: Hypotheses and associated multiple logistic regression models explaining oviposition site selection of *Duttaphrynus melanostictus* (SCHNEIDER, 1799), in the Similipal Biosphere Reserve, India.

Tab. 4: Hypothesen und Variable der zugehörigen multiplen logistischen Regressionsmodelle zur Erklärung der Laichplatzwahl von *Duttaphrynus melanostictus* (SCHNEIDER, 1799) im Similipal Biosphärenreservat, Indien.

Hypotheses Hypothesen	Models and associated variables Modelle und zugehörige Variablen
Hypothesis 1: Females of *D. melanostictus* select the egg deposition microhabitat based on the structure or composition of continuous variables	● pH ● Water depth ● Air temperature ● Water temperature ● Relative humidity ● Canopy cover ● pH + Water depth ● Water depth + Water temperature ● Air temperature + Water temperature ● pH + Water depth + Water temperature ● Relative air humidity + Canopy cover
Hypothesis 2: Females of *D. melanostictus* select the egg deposition microhabitat based on the composition of categorical variables	● Organic matter ● Water color ● Water turbidity ● Submerged vegetation ● Organic matter + Water color ● Water turbidity + Submerged vegetation ● Organic matter + Water color + Water turbidity + Submerged vegetation
Hypothesis 3: Females of *D. melanostictus* select the egg deposition microhabitat based on the association of both continuous and categorical variables	● Canopy cover + Submerged vegetation ● pH + Water depth + Air temperature + Water temperature + Relative air humidity + Canopy cover ● pH + Organic matter ● pH + Water color + Water depth ● Water depth + Water color + Water turbidity ● Canopy cover + Water color + Water turbidity + Submerged vegetation ● pH + Water depth + Air temperature + Water temperature + Relative air humidity + Canopy cover + Organic matter + Water color + Water turbidity + Submerged vegetation

Table 5: Ranked modeling results from a multiple logistic regression of six explanatory variables [pH, water depth (WD), water temperature (WT), relative humidity (RH), canopy cover (CC) and submerged vegetation (SV)] against presence/absence of egg masses of *Duttaphrynus melanostictus* (Schneider, 1799), at the sampling sites in the Similipal Biosphere Reserve, northern Odisha, India. The first model is the best. AICc – Akaike's Information Criterion for small sample sizes, ΔAICc – difference in AICc to the best model, W_i – AICc weight, K – number of parameters in this model.

Tab. 5: Die gereihten Modellierungsergebnisse der logistischen Regression von sechs Einflußgrößen [pH, Wassertiefe (WD), Wassertemperatur (WT), relative Luftfeuchte (RH), Deckungsgrad des Kronendaches (CC) und submerse Vegetation (SV)] auf das Vorhandensein bzw. Fehlen von Laich von *Duttaphrynus melanostictus* (Schneider, 1799) an den Untersuchungsstellen im Similipal Biosphärenreservat, nördliches Odisha, Indien. Das erste Modell ist das beste. AICc – Akaike Informationskriterium für kleine Stichprobengrößen, ΔAICc – Unterschied im AICc zum besten Modell, W_i – AICc-Gewichtung, K – Anzahl der Parameter im Modell.

Ranking Reihung	Model Modell	AICc	ΔAICc	Log-Likelihood	W_i	K
1	pH + WD + WT + SV	50.11	0.00	1.92	0.24	4
2	pH + WD	51.39	1.28	1.83	0.23	2
3	WD	52.00	1.98	1.67	0.21	1
4	RH + CC	80.15	30.03	1.06	0.13	2
5	CC	85.04	34.93	1.02	0.12	1
6	SV	86.10	35.99	0.02	0.00	1

perature and submerged vegetation (AICc = 50.11, $W_i = 0.24$, Table 5) was the best. The second best supported model incorporated pH along with water depth (AICc = 51.39, ΔAICc = 1.28, $W_i = 0.23$); the third best supported model being only water depth (AICc = 52.00, ΔAICc = 1.98, $W_i = 0.21$). The remaining 23 models received very limited support and were > 8 ΔAICc from the top model (Table 5). Parameter estimates for this model (complementary log-log link function) indicated that the presence of egg masses increased with increasing pH (β estimate = 0.903, SE = 1.341), relative humidity (β estimate = 0.033, SE = 0.062), organic matter (β estimate = 0.396, SE = 0.714), water color (β estimate = 0.498, SE = 0.752) and decreasing water depth (β estimate = -3.786, SE = 1.33), air temperature (β estimate = -0.272, SE = 0.269), water temperature (β estimate = -0.227, SE = 0.322), canopy cover (β estimate = -0.036, SE = 0.021), water turbidity (β estimate = -0.755, SE = 0.786) and sub-

Table 6. Logistic regression model investigating parameters affecting spawning site selection (presence of egg = 1, absence of eggs = 0) of *Duttaphrynus melanostictus* (Schneider, 1799), in the Similipal Biosphere Reserve, northern Oradisha, India ($N = 60$, Wald $\chi^2 = 15.18$, $df = 8$, $P < 0.057$). The model used a complementary log-log link function. S.E. – Standard error of the mean.

Tab. 6: Logistisches Regressionsmodell zur Untersuchung der Parameter, welche die Laichplatzwahl (Vorhandensein von Gelegen = 1, Nicht-Vorhandensein = 0) bei *Duttaphrynus melanostictus* (Schneider, 1799) im Similipal Biosphärenreservat, nördliches Odisha, Indien, beeinflussen ($N = 60$, Wald $\chi^2 = 15.18$, $df = 8$, $P < 0.057$). Das Modell verwendet eine komplementäre log-log Funktion. S.E. – Standardfehler des Mittelwertes. Zur Erklärung der Parameter siehe Legende von Tab. 2.

Parameter	β	S.E.	Wald test	*df*	Significance	Expected (β)
Intercept	14.510	16.615	0.763	1	0.383	2002108.445
pH	0.903	1.341	0.453	1	0.501	2.466
Water depth	-3.786	1.337	8.019	1	0.005	0.023
Air temperature	-0.272	0.269	1.016	1	0.313	0.762
Water temperature	-0.227	0.322	0.495	1	0.482	0.797
Relative air humidity	0.033	0.062	0.294	1	0.588	1.034
Canopy cover	-0.036	0.021	2.810	1	0.094	0.965
Organic matter	0.396	0.714	0.308	1	0.579	1.486
Water color	0.498	0.752	0.440	1	0.507	1.646
Water turbidity	-0.755	0.786	0.922	1	0.337	0.470
Submerged vegetation	-1.538	1.127	1.864	1	0.172	0.215

Table 7: Generalized linear model of the microhabitat parameters in presence or absence of egg clutches as response variables [Significant values ($p < 0.05$) are indicated by stars] of *Duttaphrynus melanostictus* (SCHNEIDER, 1799), in the Similipal Biosphere Reserve, northern Oradisha, India. S.E. – Standard error of the mean. Pr – predictor for the probability value of the *Z*-value.

Tab. 7: Generalisiertes lineares Modell der Mikrohabitat-Parameter bei An- und Abwesenheit von Gelegen als Zielgröße [signifikante Werte ($p < 0.05$) sind durch Sternchen gekennzeichnet] von *Duttaphrynus melanostictus* (SCHNEIDER, 1799) im Similipal Biosphäenreservat, nördliches Oradisha, Indien. S.E. – Standardfehler des Mittelwertes. Pr – Prädiktor für den Wahrscheinlichkeitswert des *Z*-Wertes. Erklärung der Parameter siehe Legende von Tab. 2.

Parameter	Estimate Schätzwert	S.E.	*Z*-value *Z*-Wert	Pr > $\lvert Z \rvert$
pH	0.97524	1.37793	0.708	0.47909
Water depth	-4.14286	1.44803	-2.861	0.00422**
Air temperature	-0.27314	0.34553	-0.790	0.42924
Water temperature	-0.35951	0.37732	-0.953	0.34069
Relative air humidity	0.01721	0.06608	0.260	0.79457
Canopy cover	-0.03601	0.02351	-1.532	0.12563
Organic matter	1.31106	1.58495	0.827	0.40813
Water color	1.21687	1.57516	0.773	0.43980
Water turbidity	-2.00344	1.72907	-1.159	0.24659
Submerged vegetation	-1.65369	1.18117	-1.400	0.16150

merged vegetation (β estimate = -1.538, SE = 1.127) (Table 6).

The authors used a generalized linear model with response proportions skewed for breeding and non-breeding sites. Out of the 10 breeding parameters, water depth (-4.14286, $Z = -2.861$, $p < 0.001$) appeared to show maximum influence on the selection of oviposition sites followed by canopy (-0.03601, $Z = -1.532$, $p > 0.05$), turbidity (-2.00344, $Z = -1.159$, $p > 0.05$) and submerged vegetation (-1.65369, $Z = -1.400$, $p > 0.05$) (Table 7).

Cluster analysis aimed to categorize spatially similar groups based on microhabitat variables and number of egg clutches.

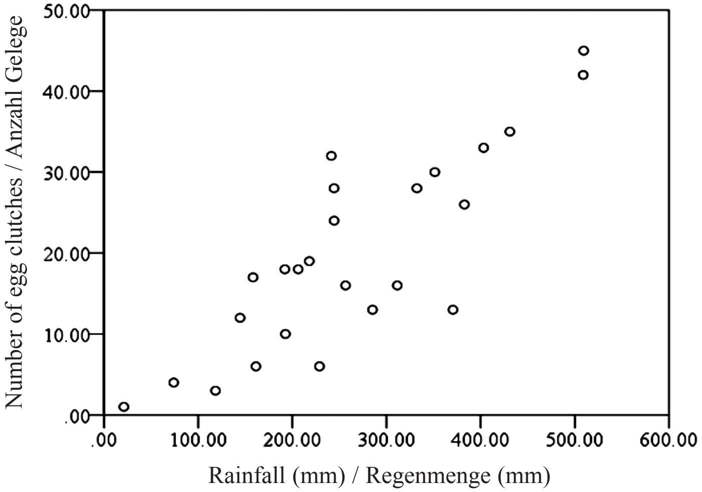

Fig. 2: Correlation between numbers of egg clutches and monthly rainfall for *Duttaphrynus melanostictus* (SCHNEIDER, 1799), in the Similipal Biosphere Reserve, northern Odisha, India.

Abb. 2: Die Beziehung zwischen der Anzahl der Gelege von *Duttaphrynus melanostictus* (SCHNEIDER, 1799) und der monatlichen Regenmenge im Similipal Biosphärenreservat, nördliches Odisha, Indien.

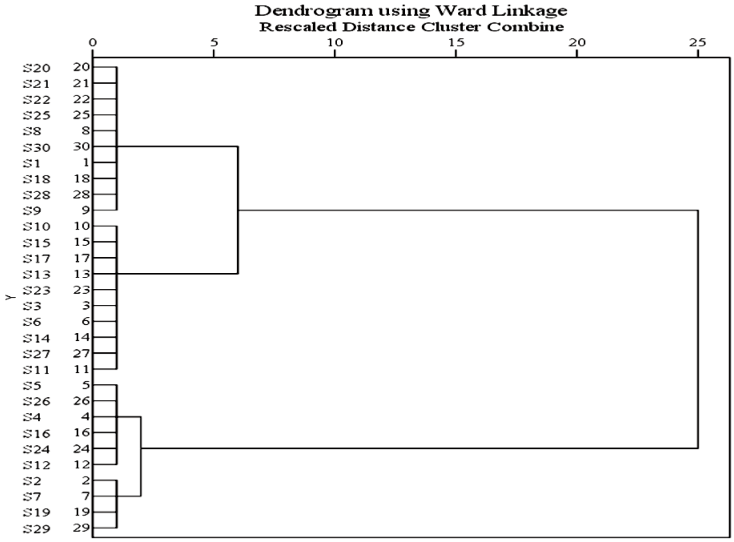

Fig. 3: Dendogram based on hierarchical clustering (Ward's method) for 30 sampling locations of breeding study sites of *Duttaphrynus melanostictus* (Schneider, 1799). In the text, the clusters are numbered 1 to 4 from top to bottom.

Abb. 3: Dendrogramm (hierarchische Clusterbildung nach der Methode von Ward) der 30 Untersuchungsstellen mit Laichplätzen von *Duttaphrynus melanostictus* (Schneider, 1799). Im Text sind die Cluster von oben nach unten mit 1 bis 4 numeriert.

Out of four clusters in the analysis of the breeding sites (Fig. 3), clusters 1 and 2 each included 10 sites, the former with more favorable hydric features and thus a higher number of clutches than the latter across the entire study period. Clusters 3 and 4 with 6 and 4 sites, respectively, comprised less clutches. The non-breeding sites (five clusters; Fig. 4) had unfavorable hydric parameters largely due to anthropogenic input (domestic use, soil leaching, surface runoff and agricultural waste dumping), the water quality being worst at cluster 1.

DISCUSSION

Anuran breeding patterns are correlated with the prevailing climatic conditions (Diaz-Paez & Ortiz 2001). Breeding activity was shown to be governed by either a single factor like temperature (Fukuyama & Kusano 1992); rainfall (Donnelly & Guyer 1994); moisture (Moreira & Barreto 1997); or a combination of factors (Lizana et al. 1994; Moreira & Barreto 1997). As amphibian embryos lack the protective outer shell cover as is present in reptile and bird eggs, their egg masses are extremely susceptible to desiccation (Snider & Janzen 2010), which is why most species lay their eggs directly into the water. *Duttaphrynus melanostictus* utilized a wide range of aquatic habitats to oviposit, including sites with perennial and ephemeral water sources, natural and constructed habitats, lentic and lotic hydrology, and the site nested within modified urban areas or surrounded by protected areas. Puddles, rain pools and temporary ponds can function as important breeding sites for anurans (Gascon 1991; Prado et al. 2005; Zina & Haddad 2005). Hence, precipitation affects the

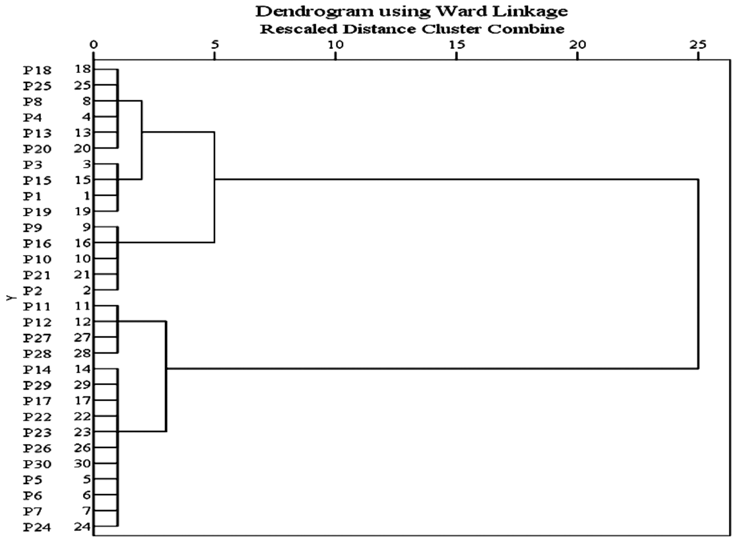

Fig. 4: Dendogram based on hierarchical clustering (Ward's method) for 30 sampling locations of non-breeding study sites of *Duttaphrynus melanostictus* (SCHNEIDER, 1799). In the text, the clusters are numbered 1 to 5 from top to bottom.

Abb. 4: Dendrogramm (hierarchische Clusterbildung nach der Methode von Ward) der 30 Untersuchungsstellen ohne Laichplätze von *Duttaphrynus melanostictus* (SCHNEIDER, 1799). Im Text sind die Cluster von oben nach unten mit 1 bis 5 numeriert.

timing of the breeding activity for most tropical and subtropical anuran species (HADDAD & SAZIMA 1992; DUELLMAN & TRUEB 1994). The synchronization of rainy season and reproductive activity of amphibians (GALLARDO 1974; CEI 1980) has been interpreted as an adaptive response to fluctuations in environmental conditions, reducing the risk of reproductive failure due to desiccation (GOLDBERG et al. 2006).

The present findings suggest that individuals of *D. melanostictus* selected oviposition sites based on microhabitat characteristics such as pH value, water depth, water temperature and density of aquatic vegetation which correlates with previous studies of this kind (FUKUYAMA & KUSANO 1992; KUPFERBERG 1996; GILLESPIE et al. 2004; RUDOLF & RÖDEL 2005; ALFONSO & ETEROVICK 2007; SRIDHAR & BICKFORD 2015).

Since amphibian ontogenesis is subjected to various abiotic factors, it is affected by almost any change in their habitat (VALLAN 2000; YOUNG et al. 2001). Ideally, amphibians oviposit in areas where abiotic and biotic factors favor the survival and growth of their eggs and larvae (KATS & SIH 1992; SPIELER & LINSENMAIR 1997; RUDOLF & RÖDEL 2005). Factors such as water depth (GOLDBERG et al. 2006; PEARL et al. 2007), water temperature (DOODY 1996; GOLDBERG et al. 2006; SNIDER & JANZEN 2010) and vegetation (NYMAN 1991; PEARL et al. 2007) were observed to influence oviposition site selection because of their differential effects on the survival of the offspring. CRUMP (1991), EVANS et al. (1996), SKELLY (2001) and GOLDBERG et al. (2006) documented the relationship of the abiotic factors: rainfall, relative humidity and water depth, which in turn can induce male anurans to produce breeding calls and select and organize breeding sites.

In the present study, a strong association was observed between specific microhabitat features and the spatial distribution of the egg masses. This association suggests parental selection of the spawning site that allows speculation about the potential importance of the particular microhabitat for the offspring. Specifically, *D. melanostictus* preferred to oviposit in sites characterized by slightly acidic pH, rather low water depth and the presence of moderate quantities of submerged vegetation that can act as a substrate for attachment of egg strings.

Amphibians use water depth or the water holding capacity of pools as a criterion for oviposition site selection (CRUMP 1991; SPIELER & LINSENMAIR 1997; RUDOLF & RÖDEL 2005; ALVAREZ et al. 2013). Generally, water depth is inversely proportional to water temperature that leads to accelerated growth and developmental rate of both embryos and tadpoles in shallow waters (SKELLY et al. 2002). Speed of growth and development correlate well with the survival rates of embryos and larvae (SEMLITSCH 2002).

The pH value of the water is an important ecological variable which influences the mortality and distribution of amphibian populations in nature (GOSNER & BLACK 1957; SABER & DUNSON 1978; FREDA & DUNSON 1986). The effects of acidification on fresh water ecosystems and amphibian habitats in particular were studied in the second half of the 20th century when acid rain became an issue (GOSNER & BLACK 1957; SABER & DUNSON 1978; LEUVEN et al. 1986; ANDRÉN et al. 1988). PIERCE (1985) reported that the species breeding in alkaline waters are highly sensitive to acidification of their breeding habitats. The present results showed that the pH of *D. melanostictus* breeding sites (5.7 – 7.6) was significantly higher than of non-breeding sites (4.7 – 7.3) which supports the views of PIERCE (1985) and FREDA & DUNSON (1986), who proposed that amphibians as a group suffer increasing mortality around pH 5 and below.

Thermal conditions of the spawning water have previously been proven as a major influence in anuran breeding site selection (SKELLY et al. 1999, 2002; FICETOLA & DE BERNARDI 2004). Comparatively low water temperature during oviposition was a significant predictor for oviposition site selection by *D. melanostictus*. Adults may prefer to oviposit in colder sections of the water bodies because of higher levels of dissolved oxygen typically found in colder water (DOUGHERTY et al. 2005).

The eggs were deposited on a wide variety of substrates like gravel bars, sand, dead or alive submerged vegetation, including leaf litter and roots, an observation similar to that of DRING (1979) and EMERSON & INGER (1992). Submerged vegetation was another significant predictor of spawning sites, which is obvious since *D. melanostictus* prefer to adhere their egg strings between submerged structures.

Given the current situation of catastrophic decline, extirpation and extinctions of species (BUTCHART et al. 2010), our understanding of habitat variables is essential. Basic information is necessary to predict the impact of the rapid environmental degradation on populations and ecosystem as a whole. The present findings have implication in conservation management as they provide the baseline for the creation of new and the preservation of existing breeding habitats of *D. melanostictus*. To an increasing degree future studies will have to revolve around microhabitat requirements of species.

ACKNOWLEDGMENTS

The authors are grateful to the Science and Engineering Research Board, Department of Science and Technology, Government of India for financial grant in the form of a research project (Ref. No. SR/S/AS-26/2012). Susmita Mahapatra is thankful to the Science and Technology Department, Government of Odisha for financial support.

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DATE OF SUBMISSION: March 9, 2018 Corresponding editor: Heinz Grillitsch

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Zeitschrift/Journal: Herpetozoa

Jahr/Year: 2019

Band/Volume: 31_3_4

Autor(en)/Author(s): Rout Jasmin, Mahapatra Susmita, Asrafuzzaman Syed, Dutta Sushil Kumar, Sahoo Gunanidhi

Artikel/Article: oviposition site selection by the asian Common Toad Duttaphrynus melanostictus (SCHNEIDER, 1799), in an Indian biosphere reserve 157-171