SALAMANDRA	44	4	225-234	Rheinbach, 20 November 2008	ISSN 0036-3375

Variation in *Oophaga pumilio* (Amphibia: Anura: Dendrobatidae) in western Panama

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Abstract. We studied variation in colour pattern and morphology in ten populations of *Oophaga pumilio* from the Province of Bocas del Toro, western Panama. Our field work documented several distinct phenotypes of colouration and pattern that are highly correlated geographically. On the contrary, variation in the morphometric characters studied is small among these populations. There are examples of distinct populations in close proximity without any obvious physiographic barriers that show no evidence of hybridization. We interpret these abrupt transitions as evidence of lack of or minimal gene flow.

Key words. Anura, Dendrobatidae, *Oophaga pumilio*, colouration, distribution, morphology, variation, Panama.

Resumen. Estudiamos la variación y morfología de varias poblaciones de *Oophaga pumilio* en la Provincia de Bocas del Toro, oeste de Panamá. Nuestro trabajo de campo documenta varios fenotipos distintivos de coloración y patrones que están altamente correlacionados geográficamente. Por el contrario, la variación morfométrica de caracteres estudiados es pequeña entre estas poblaciones. Hay ejemplos de distintivas poblaciones cercanas sin aparentes barreras fisiográficas que no muestran evidencias de hibridación. Interpretamos estas transiciones abruptas como una evidencia de ausencia o de reducido flujo genético.

Introduction

The description of *Dendrobates pumilio* O. Schmidt, 1857 (strawberry poison frog) was based on material from the trail between Bocas del Toro and Volcan Chiriquí (5000-7000 Polish feet = 1150-1160 masl), Province of Bocas del Toro, Panama, collected by Josef v. Warszewicz. Schmidt (1858) provided a brief colour description and an illustration of the dorsal view of this species, now in the genus *Oophaga* (Grant et al. 2006). Two more names were proposed for this species, differing in colouration and currently referred to as synonyms of *O. pumilio*: *Dendrobates typographus* Keferstein, 1867 (type locality: Costa Rica) and *D. ignitus* Cope, 1874 (type locality: Machuca, Nicaragua). Taylor (1952) examined material from Costa Rica and was uncertain regarding the identity of O. Schmidt's *pumilio* and argued that the illustration in O. Schmidt (1858) (Tafel II, Fig. 13) "could scarcely be regarded as belonging to the species here described as *typographicus*. Until a comparison of the types of *pumilio* and *typographicus* by a competent observer proves them to be identical, I propose to use the Keferstein name" for Costa Rican specimens. Unfortunately, the type of *D. pumilio*, originally in the Krakow Museum, is lost (Savage 1968) so that direct comparisons of type material can not be done. An additional nominal species, *D. galindoi* Trapido, 1953 was described from the Province of Bocas del Toro, Panama, a name placed in the synonymy of *O. pumilio* by subsequent authors (Savage 1968, Silverstone 1975).

In accordance with most previous authors, Daly & Myers (1967) treated all populations of strawberry poison frog from Nicaragua to northwestern Panama as a single species, *O. pumilio*, suggesting that it is a polymorphic species. These authors and Summers et al. (1997, 2003) provided notes on the colour variation in *O. pumilio*. We go along with the taxonomic opinion by Daly & Myers (1967)

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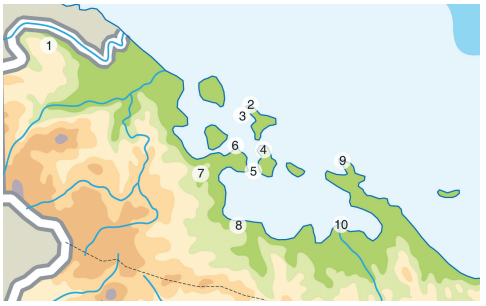

Fig. 1. Map showing the collecting sites of *Oophaga pumilio* in this study. Localities are: (1) Cerro Tebata; (2) Bastimentos Island; (3) Solarte Island; (4) Popa Island; (5) Loma Partida Island; (6) Cerro Brujo; (7) Río Uyama; (8) Quebrada La Gloria; (9) Kusapin; (10) Río Krikamola.

and Summers et al. (1997, 2003). However, we claim the lack of a detailed study of the geographic variation of phenotypic patterns and morphometrics in *O. pumilio*. Here we report upon the results of our study on the variation in colouration and morphometrics in *O. pumilio* in western Panama.

Materials and methods

Descriptions of populations are based on specimens examined by the authors. Measurements and colouration data were taken on 87 specimens of *Oophaga pumilio* from 10 localities (see Fig. 1). Abbreviations for museum collections follow those of Leviton et al. (1985), except MHCH (Museo Herpetologico de Chiriquí, Davíd, Panama).

All measurements were taken on adult specimens (males and females not distinguished) using digital calipers and were rounded to the nearest 0.01 mm. The following measurements were taken (with abbreviations indicated): length from snout to vent (SVL); head length (HL) was measured diagonally from angle of jaw to tip of snout; head width (HW) between angles of jaws; eye length (EL) from anterior to posterior edge; eye to naris distance (END) from anterior edge of eye to posterior corner of naris; internaris distance (IND) between centers of naris; snout length (SL) from anterior edge of eye to tip of snout; forearm length (FAL) from proximal edge of palmar tubercle to outer edge of flexed elbow; hand length (HAL) from proximal edge of palmar tubercle to tip of third finger; shank length (SHL) from outer edges of flexed knee to heel; foot length (FL) from proximal edge of outer metatarsal tubercle to tip of fourth toe; width of third finger (3FW) at penultimate phalanx just anterior to disc; width of disc of third finger (3FD) at greatest width; width of third toe (3TW) at penultimate phalanx just anterior to disc; width of disc of third toe (3TD) at greatest width; width of fourth toe (4TW) at penultimate phalanx just anterior to disc; width of disc of fourth toe (4TD) at greatest width; body width (BW) at greatest width of body; tympanum diameter (TD) horizontal tympanum diameter, based on a estimated circular tympanum.

Colour descriptions refer to live specimens if not stated otherwise. The capitalized colours and colour codes (the latter in parentheses), as applied here, are those of Smithe (1975-1981). In descriptions of colouration in preservative we used the terminology proposed by Grant et al. (2006) and compared our material to the illustrations therein (their Figs. 35, 46, 47, 48, 49).

Results

Description of the populations examined

Cerro Tebata (Locality 1 in Fig. 1)

Colouration in life: Dorsal ground colour varies from Spectrum Orange (17), Scarlet (14) to Yellowish Olive Green (50); dorsum usually uniform, rarely with black spots; flank coloured as dorsum; dorsal surfaces of hind limbs Dusky Brown (19), Jet Black (89), rarely same colour of dorsum; venter Orange Yellow (18), Scarlet (14) or same colour of dorsum (Fig. 2).

Colour after five months in preservative: Dorsal surfaces of head, body dark greyish, with black flecks; venter pale grey; limbs black.

Fig. 2. *Oophaga pumilio* from Cerro Tebata (Locality 1 in Fig. 1), Bocas del Toro, Panama.

Fig. 3. *Oophaga pumilio* from Isla Bastimentos (Locality 2 in Fig. 1), Bocas del Toro, Panama.

Remarks: Individuals from Costa Rica and Nicaragua mostly agree well with this description. However, it has been reported that in rare instances individuals from La Selva can be uniform dark blue with black spots (Guyer & Donnelly 2005). Based on our material, individuals from northern populations (e.g., from Nicaragua) are smaller than those from southern Costa Rica and western Panama.
Specimens examined: PANAMA: Bocas del Toro: Cerro Tebata, 9°33'37.3"N, 82°51' 18.8"W, 480 m: MHCH 578, SMF 86595-605.

Fig. 4. *Oophaga pumilio* from Isla Solarte (Locality 3 in Fig. 1), Bocas del Toro, Panama.

Isla Bastimentos (Locality 2 in Fig. 1)
Colouration in life: Dorsal ground colour varies from Opaline Green (162D), Pale Horn Colour (92), Flesh Ocher (132D) and Flame Scarlet (15) to Spectrum Red (11), usually with Dusky Brown (19) blotches (some individuals immaculate); venter immaculate dirty white with a suggestion of Pale Horn Colour (92) or of Opaline Green (162D), or Pearl Gray (81) (Fig. 3).
Colour after ten months in preservative: Dorsal surfaces of head, body and legs white to pale grey with brown blotches; venter almost white.
Remarks: We collected our series on Bastimentos Island in the area of the cemetery in the late afternoon during light rain. The frogs were active on the ground and on tree trunks up to 1.5 m above the ground. Individuals from Red Frog and Wizard Beach have a uniform red dorsum or with dark spots, venter same colour as dorsum or dirty white. Individuals from Bahia Honda are orange uniform.
Specimens examined: PANAMA: Bocas del Toro: Bastimentos Island: 09°21'41.1"N, 82°11' 26.5"W, 10 m: SMF 85359-36, 86631-34, 86636.

Isla Solarte (Locality 3 in Fig. 1)
Colouration in life: Dorsum Flame Scarlet (15) or Spectrum Orange (17), immaculate; rarely with small Dusky Brown (19) spots; venter same as dorsum, without dark spots (Fig. 4).
Specimens examined: PANAMA: Bocas del Toro: Solarte Island, Hospital Point, 10 m: SMF 85349-58.

Tab. 1. Size and proportions of adult *Oophaga pumilio* from localities 1-10 as shown in Figure 1. Each range is followed by the mean and standard deviation in parentheses; for abbreviations see text.

Character	Cerro Tebata	Bastimentos Island	Solarte Island	Popa Island	Loma Partida
SVL	21.06 -23.89 mm (22.09 ± 0.901)	18.03-22.45 mm (20.306 ± 1.15)	17.33-19.56 mm (18.8 ± 0.66)	14-17 mm (15.7 ± 0.84)	15.98-19.84 mm (18.16 ± 1.342)
HW/SVL	0.281-0.334 (0.301 ± 0.018)	0.261-0.318 (0.283 ± 0.015)	0.271-0.294 (0.28 ± 0.007)	0.270-0.306 (0.286 ± 0.011)	0.26-0.301 (0.28 ± 0.015)
HL/SVL	0.272-0.324 (0.3 ± 0.014)	0.265-0.314 (0.283 ± 0.014)	0.282-0.314 (0.3 ± 0.012)	0.269-0.300 (0.286 ± 0.008)	0.28-0.312 (0.3 ± 0.014)
SHL/SVL	0.420-0.500 (0.461 ± 0.021)	0.418-0.5 (0.45 ± 0.021)	0.413-0.5 (0.455 ± 0.02)	0.408-0.463 (0.431 ± 0.020)	0.43-0.481 (0.451 ± 0.017)
FL/SVL	0.375-0.452 (0.407 ± 0.021)	0.273-0.44 (0.371 ± 0.036)	0.332-0.404 (0.37 ± 0.022)	0.319-0.386 (0.354 ± 0.017)	0.373-0.427 (0.4 ± 0.021)
TD/SVL	0.040-0.067 (0.047 ± 0.008)	0.04-0.06 (0.05 ± 0.01)	0.035-0.061 (0.05 ± 0.01)	0.045-0.063 (0.053 ± 0.006)	0.043-0.058 (0.05 ± 0.006)
EL/SVL	0.113-0.140 (0.124 ± 0.007)	0.11-0.14 (0.122 ± 0.01)	0.104-0.122 (0.115 ± 0.005)	0.123-0.151 (0.134 ± 0.010)	0.1-0.123 (0.114 ± 0.01)
SL/SVL	0.087-0.100 (0.090 ± 0.003)	0.077-0.101 (0.086 ± 0.007)	0.081-0.1 (0.087 ± 0.005)	0.082-0.104 (0.091 ± 0.006)	0.085-0.105 (0.093 ± 0.006)
IND/SVL	0.107-0.123 (0.116 ± 0.005)	0.1-0.13 (0.115 ± 0.01)	0.102-0.117 (0.11 ± 0.005)	0.095-0.126 (0.112 ± 0.008)	0.104-0.126 (0.116 ± 0.008)
FAL/SVL	0.243-0.285 (0.258 ± 0.014)	0.233-0.313 (0.262 ± 0.022)	0.25-0.27 (0.256 ± 0.005)	0.244-0.281 (0.261 ± 0.012)	0.258-0.282 (0.27 ± 0.01)
HAL/SVL	0.232-0.275 (0.250 ± 0.014)	0.25-0.3 (0.271 ± 0.014)	0.23-0.27 (0.25 ± 0.012)	0.184-0.247 (0.222 ± 0.018)	0.244-0.27 (0.258 ± 0.007)
3FD/3FW	1.44-2.40 (1.83 ± 0.273)	1.6-2.34 (2.07 ± 0.185)	1.61-2.452 (2.076 ± 0.264)	1.486-2.000 (1.740 ± 0.182)	1.33-2.05 (1.74 ± 0.246)
3TD/3TW	1.22-1.8 (1.45 ± 0.182)	1.21-1.69 (1.4 ± 0.130)	1.18-1.69 (1.47 ± 0.145)	1.000-1.310 (1.046 ± 0.092)	1.06-1.42 (1.26 ± 0.116)
4TD/4TW	1.35-1.86 (1.55 ± 0.14)	1.3-1.84 (1.5 ± 0.181)	1.264-1.947 (1.604 ± 0.2)	1.031-1.862 (1.364 ± 0.243)	1.074-1.562 (1.36 ± 0.2)
BW/SVL	0.400-0.478 (0.437 ± 0.025)	0.41-0.52 (0.46 ± 0.04)	0.405-0.511 (0.451 ± 0.035)	0.346-0.461 (0.395 ± 0.035)	0.37-0.5 (0.458 ± 0.041)

Isla Popa (Locality 4 in Fig. 1)

Colouration in life: Dorsal ground colour Greenish Olive (49); legs Ultra Marine Blue (170A); posterior thigh Yellowish Olive Green (50); venter immaculate Sky Blue (168C) (Fig. 5).

Remarks: Our series was collected in a mature secondary forest on Popa Island, all individuals found on the forest floor during a rainy afternoon.

Specimens examined: PANAMA: Bocas del Toro: Popa Island, 9°13'14"N, 82°08'28"W, 15 m: SMF 85338-48.

Isla Loma Partida (Locality 5 in Fig. 1)

Colouration in life: Dorsal surfaces of head, body and limbs Olive Green (48), Brownish Olive (129), Indigo (73) or Turquoise Green (64), uniform or with Jet Black (89) flecks or spots; lateral surfaces of head and body Light Sky Blue (168D); upper surfaces of limbs same colour as dorsum or darker with Jet Black (89) spots; lips coloured as ventral surfaces; tympanum Jet Black (89) or same colour as dorsum; ventral surfaces of head, body and limbs uniform Light Sky Blue

Cerro Brujo	Río Uyama	Quebrada la Gloria	Kusapin	Rio Krikamola
17.2-18.88 mm (17.78 ± 0.516)	16.86-19.78 mm (17.96 ± 1.02)	16.6-18.84 mm (17.66 ± 0.93)	14.62-16.42 mm (15.4 ± 0.55)	16.22-18.84 mm (17.26 ± 0.76)
0.275-0.3 (0.285 ± 0.01)	0.271-0.313 (0.286 ± 0.014)	0.265-0.32 (0.291 ± 0.02)	0.264-0.306 (0.288 ± 0.014)	0.26-0.31 (0.284 ± 0.015)
0.277-0.312 (0.284 ± 0.011)	0.274-0.319 (0.295 ± 0.013)	0.283-0.314 (0.3 ± 0.014)	0.268-0.337 (0.304 ± 0.018)	0.283-0.33 (0.306 ± 0.017)
0.416-0.466 (0.44 ± 0.016)	0.424-0.475 (0.45 ± 0.018)	0.44-0.481 (0.461 ± 0.017)	0.425-0.466 (0.45 ± 0.013)	0.413-0.466 (0.442 ± 0.018)
0.35-0.416 (0.37 ± 0.022)	0.351-0.42 (0.386 ± 0.024)	0.344-0.394 (0.381 ± 0.021)	0.332-0.392 (0.364 ± 0.02)	0.363-0.422 (0.385 ± 0.017)
0.044-0.055 (0.049 ± 0.005)	0.051-0.062 (0.055 ± 0.003)	0.037-0.057 (0.044 ± 0.008)	0.051-0.067 (0.061 ± 0.005)	0.045-0.073 (0.053 ± 0.01)
0.12-0.142 (0.128 ± 0.006)	0.115-0.14 (0.128 ± 0.008)	0.105-0.125 (0.115 ± 0.01)	0.113-0.145 (0.125 ± 0.01)	0.105-0.135 (0.115 ± 0.01)
0.085-0.1 (0.09 ± 0.005)	0.082-0.1 (0.09 ± 0.003)	0.08-0.094 (0.089 ± 0.006)	0.08-0.1 (0.087 ± 0.006)	0.077-0.1 (0.087 ± 0.007)
0.108-0.128 (0.12 ± 0.006)	0.101-0.12 (0.11 ± 0.006)	0.096-0.118 (0.111 ± 0.009)	0.1-0.12 (0.111 ± 0.006)	0.1-0.115 (0.11 ± 0.006)
0.254-0.265 (0.26 ± 0.004)	0.237-0.275 (0.26 ± 0.015)	0.248-0.277 (0.261 ± 0.011)	0.238-0.27 (0.256 ± 0.011)	0.251-0.281 (0.266 ± 0.011)
0.235-0.267 (0.253 ± 0.012)	0.247-0.288 (0.264 ± 0.012)	0.248-0.272 (0.262 ± 0.01)	0.231-0.25 (0.24 ± 0.006)	0.245-0.271 (0.255 ± 0.007)
1.49-2.022 (1.822 ± 0.21)	1.42-2.25 (1.82 ± 0.257)	1.545-1.744 (1.621 ± 0.76)	1.5-3.0 (2.5 ± 0.474)	1.316-2.0 (1.684 ± 0.214)
1.0-1.615 (1.406 ± 0.183)	1.06-1.9 (1.4 ± 0.245)	1.184-1.625 (1.412 ± 0.18)	1.06-1.5 (1.22 ± 0.135)	1.0-1.4 (1.211 ± 0.132)
1.17-1.84 (1.5 ± 0.24)	1.25-1.64 (1.42 ± 0.131)	1.1-1.53 (1.344 ± 0.155)	1.05-1.7 (1.4 ± 0.177)	1.093-1.674 (1.362 ± 0.166)
0.34-0.467 (0.431 ± 0.03)	0.367-0.464 (0.428 ± 0.032)	0.411-0.471 (0.442 ± 0.027)	0.393-0.462 (0.423 ± 0.026)	0.381-0.473 (0.42 ± 0.028)

(168D) or Robin's Egg Blue (93) male with darker throat (Fig. 6).
Remarks: These frogs were very abundant in some areas of Loma Partida Island.
Specimens examined: PANAMA: Bocas del Toro: Loma Partida Island, 9°10'37.2"N, 82°12'30.7"W, 20 m: SMF 86610-16.

Cerro Brujo (Locality 6 in Fig. 1)
Colouration in life: Dorsal surfaces of head, body and limbs Indigo (73); Vandike Brown (221), uniform or with Jet Black (89) spots; venter Venetian Blue (168B); females with Light Sky Blue (168D) throat, males with darker throat (Fig. 7).
Colour after ten months in preservative: Dorsal surfaces of head, body solid dark greyish; venter grey blue; limbs black.
Remarks: The series was collected during daytime in a mature secondary forest and in disturbed areas. Most frogs were found on the ground, one was observed climbing a tree ten meters above the ground.
Specimens examined: PANAMA: Bocas del Toro: Cerro Brujo, 9°11'16.4"N, 82°11'25.4"W, 10 m: SMF 85329-37.

Fig. 5. *Oophaga pumilio* from Isla Popa (Locality 4 in Fig. 1), Bocas del Toro, Panama.

Fig. 6. *Oophaga pumilio* from Isla Loma Partida (Locality 5 in Fig. 1), Bocas del Toro, Panama.

Río Uyama (Locality 7 in Fig. 1)
Colouration in life: Dorsal ground colour dirty white with large Sayal Brown (223C) blotches that have the tendency to form stripes; venter Light Sky Blue (168D) with large black blotches.
Colour after six months in preservative: Dorsal surfaces of head, body dark greyish to brown, with the white areas scarcely visible; venter almost black with white blotches scarcely visible; limbs brown or black (Fig. 8).
Remarks: This series was collected in the late morning at the egde and within a mature secondary forest. Most frogs were found on the ground, one was observed climbing a tree

Fig. 7. *Oophaga pumilio* from Cerro Brujo (Locality 6 in Fig. 1), Bocas del Toro, Panama.

two meters above the ground. At Río Uyama we observed one population of *O. pumilio* with red dorsum with black spots and blue legs in very close vicinity (more or less 800 m) to the black and white populations described here.
Specimens examined: PANAMA: Bocas del Toro: Río Uyama; 9°08'55"N, 82°19'28"W, 35 m; SMF 85321-28.

Quebrada la Gloria (Locality 8 in Fig. 1)
Colouration in life: Dorsal surfaces of head and body Orange Yellow (18) or Olive Yellow (52), rarely Light Sky Blue (168D), with Sepia (119 or 219) or Sayal Brown (223C) blotches that have the tendency to form stripes, dorsal and ventral surfaces of limbs as well as ventral surfaces of head and body Light Sky Blue (168D) with Sepia (219) blotches; some individuals with ventral colour same as dorsum; males with darker throat (Fig. 9).
Specimens examined: PANAMA: Bocas del Toro: Quebrada la Gloria (9 km SW from Chiriquí Grande Road): SMF 86626-30.

Kusapin (Locality 9 in Fig. 1)
Colouration in life: Dorsal surfaces of head and body uniform red; in SMF 86608 frontal and parietal region suffused with Pratt's Rufous (140); upper surfaces of forelimbs same colour as dorsum or brown; in SMF 86609 forelimbs Scarlet (14), hands Raw

Fig. 8. *Oophaga pumilio* from Río Uyama (Locality 7 in Fig. 1), Bocas del Toro, Panama.

Fig. 9. *Oophaga pumilio* from Quebrada la Gloria (Locality 8 in Fig. 1), Bocas del Toro, Panama.

Fig. 10. *Oophaga pumilio* from Kusapin (Locality 9 in Fig. 1), Comarca Ngöbe Bugle, Panama.

Fig. 11. *Oophaga pumilio* from about 2 km SW mouth of Río Krikamola (Locality 10 in Fig. 1), Comarca Ngöbe Bugle, Panama.

Umber (223) and fingers Sky Blue (168C) suffused with Raw Umber (223); dorsal surfaces of hind limbs same colour as upper surfaces or darker; posterior surfaces of hind limbs brown to dark brown; lips Sky Blue (168C) or coloured as dorsum; tympanum brown to black or same colour as dorsum; upper edge of tympanum usually bordered by a thin black stripe, about two times the tympanum length; transition of colours in flanks (red to sky blue) with dark flecks in some individuals; ventral surfaces of head and body and limbs uniform Sky Blue (168) in females, male with Medium Plumbeus (87) throat; some specimens with dark flecks on dorsum and flanks (Fig. 10).

Colour after six months in preservative: Dorsal surfaces of head, body solid dark greyish; venter almost black; limbs dark brown, regions of ellbows and knees brown.
Remarks: The series was collected during daytime on the floor in a mature secondary forest on a hill near Kusapin town.
Specimens examined: PANAMA: Comarca Ngöbe Bugle: Kusapin, 9°10'54.9"N, 81°53'22.1"W, 81 m: SMF 86584-94.

Rio Krikamola (Locality 10 in Fig. 1)
Colouration in life: dorsal surfaces of head and body uniform Leaf Green (146)

to Parrot Green (260) or with Jet Black (89) flecks; upper surfaces of limbs brown, Blue Black (90) or same colour as dorsum; tympanum Jet Black (89) (usually only at lower part) or same colour as dorsum; ventral surfaces of head and body uniform Olive Yellow (52) to Lime Green (159), usually with black spots, rarely with Sky Blue (168C) blotches; male with darker throat; ventral surfaces of limbs grey blue or dark blue; lips coloured as venter (Fig. 11).

Colour after seven months in preservative: Dorsal surfaces of head and body solid dark greyish, some specimens keep their black spots on dorsum and flecks in the venter; limbs dark brown; venter grey.

Remarks: The series was collected during daytime in a wetland forest, most specimens were found climbing on trees at less than two meters above the ground.

Specimens examined: PANAMA: Comarca Ngöbe Bugle: Kankintú, Río Krikamola, 8°58'38.6"N, 81°55'01.7"W, 7 m: SMF 86564-73.

Comparisons

Our study documented several distinct phenotypes of colouration and pattern that are highly correlated geographically. On the contrary, variation in morphometric characters studied is comparatively small among these populations. All morphometric characters show largely overlapping ranges among most populations (Table 1). In respect of the morphometric characters examined, the Popa population (Locality 4 in Fig. 1) is the most distinctive one. In several characters (FAL/SVL, HAL/SVL, 3TD/3TW) it has barely or non-overlapping ranges with the other populations. The series from Bastimentos (Locality 2 in Fig. 1) has the highest average values for FAL/SVL and HAL/SVL indicating that these frogs possess relative long hind feet and toes, although the ranges of these characters do overlap to some degree with the other populations.

Discussion

Oophaga pumilio exhibits a distinctive pattern of phenotypic variation which is highly correlated geographically; even several phenotypically distinct populations occur in sympatry or parapatry (Myers & Daly 1983, Summers et al. 2003, Saporito et al. 2007). This includes examples of distinct populations in close proximity without any obvious physiographic barriers that show no evidence of hybridization in terms of colouration. In the area of Almirante an abrupt transition is found between a population consisting of a black and white morph and red morph with blue legs (Summers et al. 2003). In the area of Chiriquí Grande, three distinct phenotypes meet and abrupt transitions are reported between them: a population consisting of a black and yellow morph, one with a red dorsum and bluish flanks, and one with a green ground colour (Myers & Daly 1983, Summers et al. 2003, this study). We can interpret these abrupt transistions as evidence of lack of or remarkably reduced gene flow. Nevertheless, minimal gene flow may exists since at Pueblo Nuevo and at Chiriquí Grande we found individuals that appear to be intermediate in colouration between those populations (Fig. 12).

Daly & Myers (1967: 973) stated that for *O. pumilio* "a static subspecies concept does not seem well suited to the dynamics of the situation". However, the descriptions of the phenotypes by these authors agree well with our observations indicating that over the course of at least four decades the phenotypic pattern had remained stable. The underlying mechanisms and barriers that prevent mixing of the phenotypes in the natural populations are poorly understood. It is known that females of *O. pumilio* preferentially choose mates of their own colour morph (Siddiqi et al. 2004). Under captive conditions it has been observed that certain males of *O. pumilio,* i.e. red with blue legs, display courtship behavior (mating calls) only towards females of their own phenotype but not towards populations from Bastimentos Island (G. Var-

gas pers. comm). In accordance with this, Siddiqi et al. (2004) provided evidence that the colours displayed by the various colour morphs are effective visual signals, not only to potential predators but also to conspecifics, making sympatric speciation driven by sexual selection possible. Thus, colouration may be important in maintaining the identities of the various populations (Siddiqi et al. 2004). Fisher's runaway process of sexual selection is potentially an important force generating character divergence between closely related populations (Pomiankowski & Iwasa 1998). Captive cross-breeding experiments in *O. pumilio,* including several populations from the Bocas del Toro Islands and mainland, demonstrated that frogs of different colours morphs can produce fertile offspring. However, the survival rates of offspring were relatively low (Summers et al. 2004). These observations are supported by the fact that breeding success appeared to be higher if only captive frogs from the same geographical origin were put together (Salewski 2005).

Perhaps in contrast to all these observations, molecular genetic studies based on mtDNA data indicated that the studied populations are phylogenetically closely related and most probably are members of the same species (Summers et al. 1997, 2003). Summers et al. (2004) suggested that colour pattern is under single locus control with dominance, whereas colouration may be under polygenic control, or may represent a single locus system with incomplete dominance.

Most of the phenetically distinct populations described in the present study have very restricted geographical distributions. Ignoring the distinctness of these populations presents a latent threat to them in the light of the ongoing alterations and contaminations of their habitats.

Acknowledgements

Collecting and export permits were provided by Yariela Hidalgo, Autoridad Nacional del Ambiente (ANAM), Panama City. Querube D. Fuenmayor, Panama City, provided valuable assistance with acquisition of these permits. Meike Piepenbring, Botanisches Institut J.W. Goethe-Universität, Frankfurt, provided logistic support for our studies in Panama and was instrumental in enabling Abel Batista and Marcos Ponce to visit Frankfurt, for a three months research stay. We thank Pedro Caballero (Director of Istituto de Ciencias Ambientales y Desarrollo Sostenible) and Boris E. Sanjur, Facultad de Ciencias Naturales y Exactas de la Universidad Autónoma de Chiriquí (UNACHI), David, Panama, for their support. This paper is based on part upon work supported by the Deutscher Akademischer Austauschdienst (DAAD) to Abel Batista and to Gunther Köhler through the Partnership Program between the J.W. Goethe-Universität Frankfurt am Main, and the Facultad de Ciencias Naturales y Exactas der Universidad Autónoma de Chiriquí (UNACHI), David, Panama. We are grateful to Alfred A. Schmidt for his financial support of this study. We thank Marcos Ponce, José Torres and Ramon Luna for field assistence, Rigoberto Lopez for guide and facilities at his farm at Cerro Tebata, Alicia Cáceres for her support to Abel Batista in this work. We appreciate the help and comments by Stefan Lötters and two anonymous reviewers who significantly improved this paper.

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Manuscript received: 29 November 2006

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