Sex differences in polymorphic body coloration and dorsal pattern in Darwin's frogs (*Rhinoderma darwinii*)

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We demonstrate that Darwin's frogs (*Rhinoderma darwinii*) show sex differences in dorsal pattern and body coloration. Males possessed higher variability than females, which were mainly brown; two dorsal patterns and a green body colour were found exclusively in males. Males at different reproductive stages differed significantly in body colour and dorsal pattern; brooding males were characterized by being greener. Females, which were almost exclusively brown, were mostly found on brown substrates, whereas males were distributed across brown, green and brown/green substrates. An association between body and substrate coloration suggests crypsis to reduce predation risk.

Key words: Chile, gender, microhabitat, polymorphism, temporal variation

INTRODUCTION

"The reason behind *Rhinoderma*'s variation is as big as the mysteries that surround its strange reproduction."
(Hellmich, 1932)

Body colour and pattern constitute adaptive evolutionary characters, representing a compromise between the selective forces of natural and sexual selection (Endler, 1978, 1986; Andersson, 1994). When a selective pressure such as predation favours crypsis, colour polymorphism (Tordoff, 1980; Endler, 1988) and individual colour change (Waring, 1963; Heinen, 1994) are suggested as alternative solutions to background matching or outline disruption in an environment consisting of spectrally heterogeneous microhabitats (Stevens & Cuthill, 2006). Sexual selection can shape these visual cues, because colour traits can also function in mate recognition and mate choice, thereby selecting traits such as mimetic coloration (Jiggins et al., 2001), bright coloration (Maan & Cummings, 2009), or own coloration (Summers et al., 1999), contributing to reproductive isolation between individuals of different coloration (Jiggins et al., 2001). Sexual dimorphism in coloration can be linked to sexual niche-partitioning (Shine, 1989); for example, in *Hyperolius argus*, green males may be better camouflaged in breeding ponds where they vocalize to attract females (Hayes, 1997). For *Hyla luteocellata*, it has been suggested that when a pair is in amplexus the different striping patterns meld to form the illusion of one large frog (Rivero, 1969).

More than 225 anuran species are polymorphic in colour and/or pattern, and 25 of these have been described as sexually dimorphic (Hoffman & Blouin, 2000). An anuran species that shows polymorphic cryptic coloration and pattern is Darwin's frog (*Rhinoderma darwinii*). Its body coloration is polymorphic and varies from brown to green. The colour polymorphism is widely recognized (Gay, 1848; Jiménez de la Espada, 1875; Werner, 1898; Krieg, 1924; Wilhelm, 1927; Cei, 1962; Kilian, 1965; Crump, 2002; Busse, 2003), but the pattern polymorphism was only analysed by Werner (1898) and later rectified by Kilian (1965). A correlation between background body coloration was reported by Wilhelm (1927) and Kilian (1965), leading to substrate and body colour matching (Crump, 2002). Body coloration is also influenced by temperature (Kilian, 1965; Crump, 2002).

Rhinoderma darwinii is generally characterized by small size (0.4–3.2 cm), a nasal prolongation, a bird-like tweet, and males that brood their offspring after hatching in their vocal pouch until completion of metamorphosis. Darwin's frogs are preyed on by visual predators such as understory birds (Rhynocryptidae) and snakes (*Philodryas*). *Rhinoderma darwinii* is endangered (Young et al., 2001), and its current decline can be linked to chytridiomycosis and habitat destruction (Úbeda et al., 2008; Bourke et al., 2010). Its preferred habitat is cool temperate rainforest (Valdivian forest), which is threatened by conversion to plantations of introduced species (Neira et al., 2002).

The aim of the present study was to analyse the relationships between colour/pattern polymorphisms and individual and habitat characteristics in order to explore the roles of sexual selection and/or natural selection in the evolution of polymorphisms in Darwin's frogs.

MATERIALS AND METHODS

Individuals were sampled between November and February (late spring and summer) 2008 in Vergara Hot Springs (HS; 39°23´S,71°23´W), central Chile, near Coñaripe (Fig. 1). The study area was located in the Araucanian mountain range, in the Andean patagonic forest vegetation region (Gajardo, 1994). The Vergara HS is at an altitude of 850 m, and is characterized by temperate rainforest (Valdivian forest), with trees such as *Nothofagus dombeyi* and *Saxegothea conspicua* and shrubs such as *Chusquea* sp. and *Drymis andina*. It is private property used as selective timberland.

For four months, the study area was systematically surveyed. Four plots of 50 × 50 m were set out. Each

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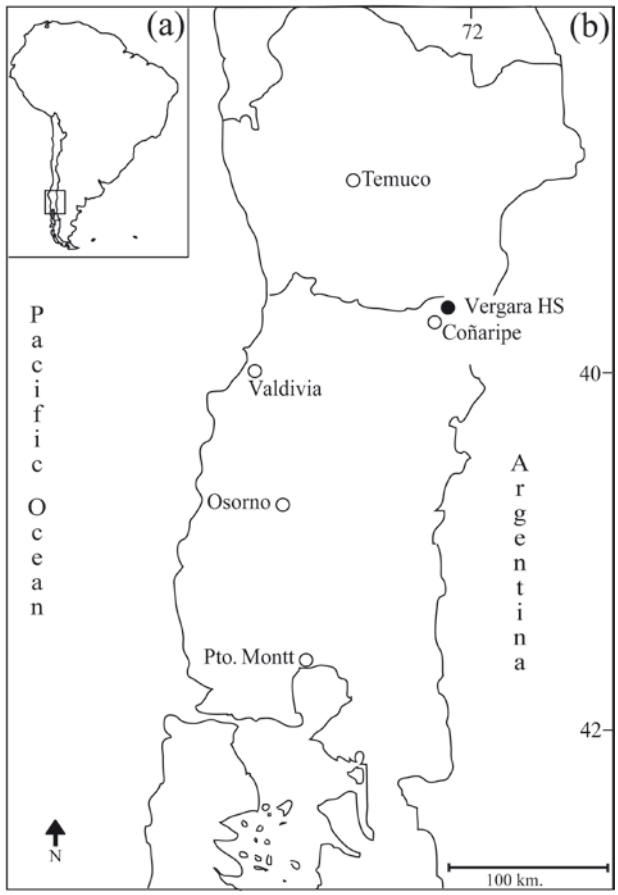

Fig. 1. a) Global location of study area. b) The location of the study area, Vergara Hot Springs (HS) (filled circle), and cities for geographic reference.

plot was surveyed for *R. darwinii* for 30 minutes each day by two people, between five and six times each month. For each individual caught, sex (assessed by the presence or absence of a vocal pouch and body shape) and body size (snout–vent and tibia length to the nearest 0.1 mm, measured using a caliper) were recorded. The dorsal body colour and dorsal pattern was documented by taking a digital picture. Individuals were also photographed ventrally in order to identify them by their unique ventral pattern; each individual was only considered once in a given month.

Microhabitat characteristics were recorded within a circle 2 m in diameter around the individual; substrate colour (green, brown, light brown, reddish brown, orange brown, beige, brown and green), abiotic conditions (temperature and humidity using a thermohygrometer), bottom coverage and the presence or absence of vegetation types (leaf litter, herbaceous plants, shrubs, mosses, logs, branches, bamboo, climbing plants and mud) were considered. Since most individuals were found in more than one type of bottom coverage, we had a total of 278 records corresponding to 121 frogs.

The data were analysed using SPSS 11.0.1. As the data were not normally distributed, non-parametric statistics were applied to analyse whether individual and microhabitat characteristics and time affected dorsal pattern and body colour frequencies. *P*-values given are two-tailed throughout and values <0.05 were considered statistically significant.

RESULTS

Dorsal patterns

Five dorsal patterns were distinguished in the study area (Fig. 2). The two most commonly found patterns were "double V" (Fig. 2a), resembling a reticulated venation pattern in a leaf blade, and "bamboo leaf" (Fig. 2b), resembling the parallel veins in a leaf blade of bamboo. The three further patterns were "complete green" (Fig. 2c, uniformly coloured green), "white forelimbs" (Fig. 2d, possessing white or yellowish forelimbs in addition to one of the other patterns) and "stained" (Fig. 2c, entailing a green covering on a brown body, especially in the anterior middle part of the dorsum).

Females and immatures had mainly the "double V" pattern (Table 1). The "complete green" and "stained" patterns were exclusively found in males, and were especially frequent in brooding males (Table 1). The relative abundance of the pattern morphs differed significantly between sexes and male reproductive stages (Table 1).

The different pattern morphs were found at similar microhabitat temperatures (Kruskal Wallis test, χ^2=6.936, df=4, *P*=0.139) and humidities (χ^2=7.214, df=4, *P*=0.125) (see also Electronic Appendix 1). Mean body size (measured as snout–vent length and tibia length) was not significantly different between pattern morphs (snout–vent length, χ^2=6.079, df=4, *P*=0.193; tibia length, χ^2=2.126, df=4, *P*=0.713) (see also Electronic Appendix 1). This was also true when analysed separately for males and females (females: snout–vent length, χ^2=0.529, df=2, *P*=0.768; tibia length, χ^2=0.075, df=*2*, *P*=0.963; males: snout–vent length, χ^2=7.219, df=2, *P*=0.125; tibia length, χ^2=8.345, df=2, *P*=0.080).

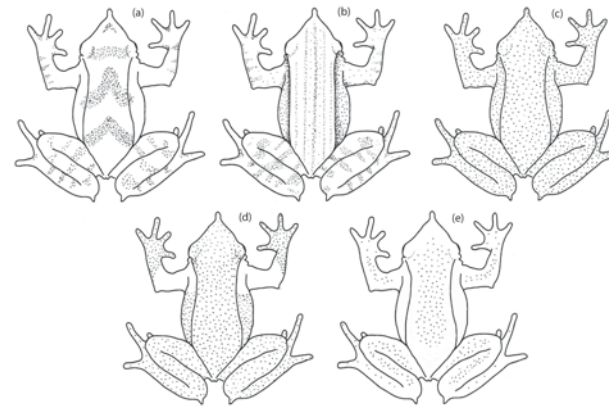

Fig. 2. Dorsal pattern morphs in the *Rhinoderma darwinii* population. a) "double V", b) "bamboo leaf", c) "complete green", d) "white forelimbs", e) "stained".

Table 1. Distribution of dorsal pattern and body colour morphs with respect to sex/age in Darwin's frogs (relative numbers in bracket); NSA: not sexually active. *P*-values based on Fisher exact probability tests for differences in frequency distribution are given.

Sex/age		Dorsal pattern					Body colour			
		Double V	Bamboo leaf	Complete green	White forelimbs	Stained	Brown	Green	Brown/ green	Total
Females		22 (68.8)	7 (21.9)	0	3 (9.4)	0	31 (96.9)	0	1 (3.1)	32
Males	NSA	7 (53.8)	3 (23.1)	2 (15.4)	0	1 (7.7)	7 (53.8)	1 (7.7)	5 (38.5)	13
	Calling	1 (33.4)	0	0	2 (66.7)	0	1 (33.3)	0	2 (66.7)	3
	Brooding	9 (25.7)	10 (28.6)	13 (37.1)	1 (2.9)	2 (5.7)	5 (14.3)	14 (40.0)	16 (45.7)	35
	Total	17 (33.3)	13 (25.5)	15 (29.4)	3 (5.9)	3 (5.9)	13 (25.5)	15 (29.4)	23 (45.1)	51
Non adults		25 (65.8)	13 (34.2)	0	0	0	32 (84.2)	2 (5.3)	4 (10.5)	38
Total		64 (52.9)	33 (28.1)	15 (12.4)	6 (5.0)	3 (2.5)	76 (62.8)	18 (14.9)	27 (22.3)	121
Between sexes				$P<0.001$				$P<0.001$		
Between male classes				$P<0.05$				$P<0.05$		

Body coloration

Three colour morphs, "brown", "green", and "brown/green", could be distinguished (Fig. 3). The most abundant body colour was brown (62.8%), especially in females and immatures (frequencies of 96.9% and 84.2%, respectively, Table 1). Males showed larger colour variability than females. Most green and brown/green individuals were males (88.9% and 81.5%, respectively), with the proportion of brooding males being 77.8% and 59.3% of all green and brown/green individuals, respectively (Table 1).

The sexes and the different male reproductive stages differed significantly as to the relative abundance of the body colour morphs (Table 1). There were no significant associations between colour morphs and abiotic conditions (Kruskal Wallis tests, temperature: $\chi^2=2.393$,

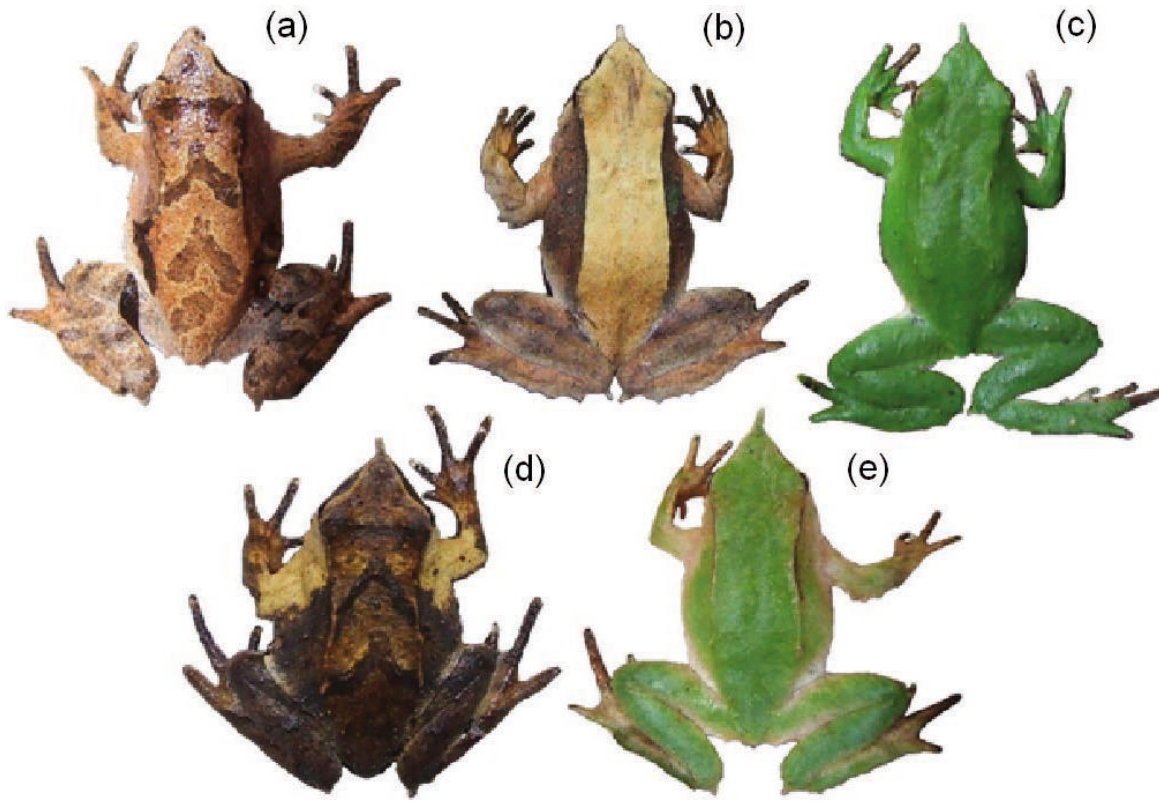

Fig. 3. Colour and dorsal pattern morphs in *Rhinoderma darwinii*. a) "Double V", b) "bamboo leaf", c) "complete green", d) "white forelimbs", e) "stained". Colour morphs were "brown" (a, b, d), "brown/green" (e), and "green" (c).

Table 2. Temporal distribution of dorsal pattern and body colour morphs in Darwin's frogs. *P*-values based on Fisher exact probability tests for differences in frequency distribution are given.

		All individuals								Males							
		Dorsal pattern					Body colour			Dorsal pattern					Body colour		
Months	Substrate colour	Double V	Bamboo leaf	Complete green	White forelimbs	Stained	Brown	Green	Brown/green	Double V	Bamboo leaf	Complete green	White forelimbs	Stained	Brown	Green	Brown/green
November	Brown	5	1	0	0	0	6	0	0	0	1	0	0	0	1	0	0
	Green	1	0	1	0	0	0	1	1	0	0	1	0	0	0	1	0
	Brown/green	4	4	4	0	0	7	4	1	1	1	4	0	0	1	4	1
December	Brown	11	1	2	1	0	12	2	1	3	0	2	0	0	2	2	1
	Green	1	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0
	Brown/green	1	2	1	0	0	3	1	0	1	0	1	0	0	1	1	0
January	Brown	11	8	1	1	1	16	2	4	2	4	1	1	1	3	2	4
	Green	3	2	4	0	1	3	4	3	1	1	4	0	0	0	4	3
	Brown/green	11	3	1	0	0	8	2	5	4	1	1	0	0	1	1	4
February	Brown	6	3	1	1	0	8	1	2	2	1	1	0	0	2	1	1
	Green	3	4	0	1	0	3	1	4	1	2	0	1	1	1	0	3
	Brown/green	7	5	0	2	1	9	0	6	1	2	0	1	1	0	0	5
Between months (substrates pooled)		*P*=0.285					*P*=0.064			*P*=0.199					*P*<0.05		
Between months (morphs pooled)		*P*<0.05								*P*=0.228							

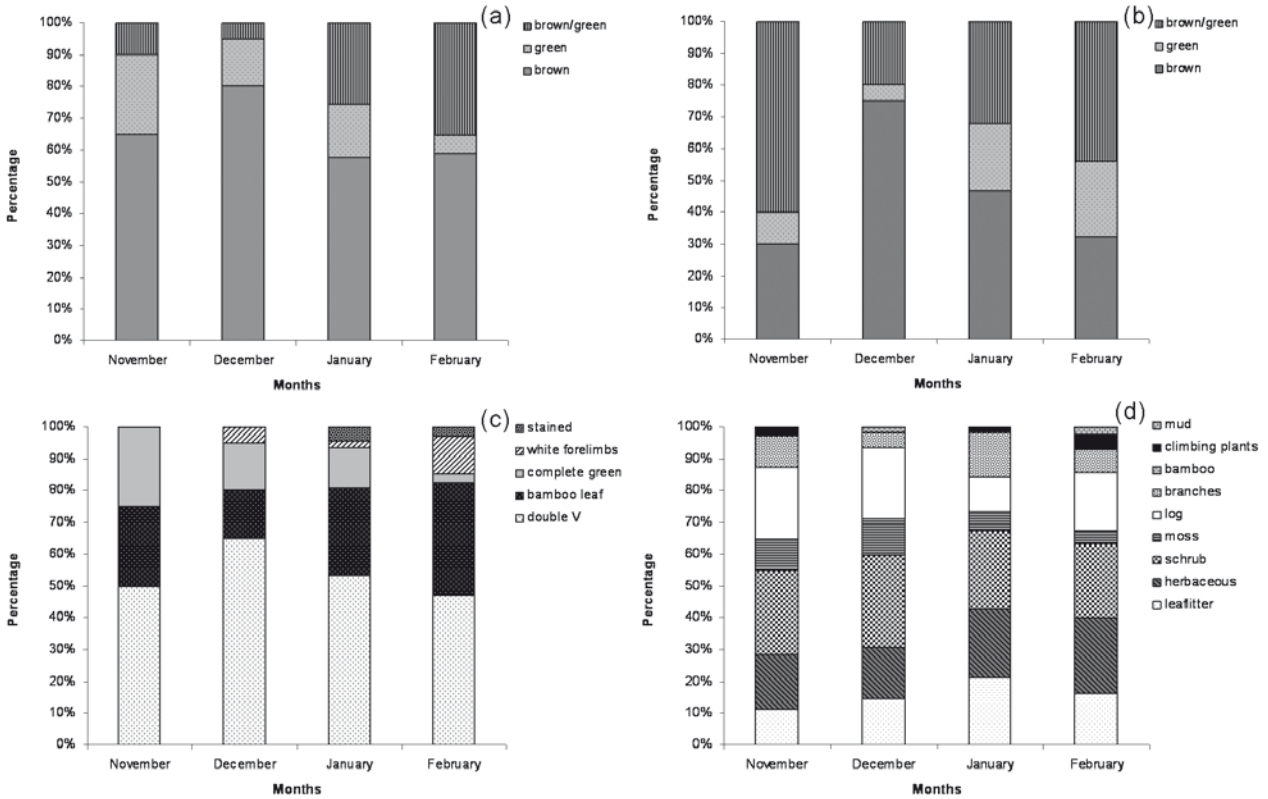

Fig. 4. Changes (%) across study months in a) body colour morphs (brown, green, brown/green), b) substrate colour (brown, green, brown/green), c) dorsal pattern morphs (double V, bamboo leaf, complete green, white forelimbs and stained), d) bottom coverage (leaf litter, herbaceous plants, shrubs, mosses, logs, branches, bamboo, climbing plants, mud).

Table 3. Abundance (relative numbers in brackets) of dorsal pattern and body colour morphs of Darwin's frogs with respect to substrate colour and bottom coverage. *P*-values based on Fisher exact probability tests for differences in frequency distribution are given.

		Substrate colour			Bottom coverage								
		Brown	Green	Brown/ green	Leaf litter	Herbs	Shrubs	Mosses	Logs	Branches	Bamboo	Climbing plants	Mud
Dorsal pattern morph	Double V	33 (61.1)	8 (38.1)	23 (50.0)	39 (53.4)	23 (69.7)	4 (28.6)	13 (44.8)	36 (50.7)	20 (46.5)	1 (50.0)	5 (50.0)	0
	Bamboo leaf	13 (24.1)	6 (28.6)	14 (30.4)	19 (26.0)	6 (18.2)	7 (50.0)	8 (27.6)	20 28.2)	15 (34.9)	1 (50.0)	3 (30.0)	3 (100.0)
	Complete green	4 (7.4)	5 (23.8)	6 (13.0)	8 (11.0)	4 (12.5)	2 (14.3)	7 (24.1)	11 (15.5)	5 (11.6)	0	2 (20.0)	0
	White fore-limbs	3 (5.6)	1 (4.8)	2 (4.3)	6 (8.2)	0	1 (7.1)	1 (3.4)	3 (4.2)	1 (2.3)	0	0	0
	Stained	1 (1.9)	1 (4.8)	1 (2.2)	1 (1.4)	0	0	0	1 (1.4)	2 (4.7)	0	0	0
		Between pattern morphs P=0.557			Between pattern morphs P=0.577								
Body colour	Brown	42 (55.3)	5 (27.8)	7 (25.9)	43 (24.9)	23 (13.3)	8 (4.6)	19 (11.0)	47 (27.2)	25 (14.5)	2 (1.2)	4 (2.3)	2 (1.2)
	Green	7 (9.2)	6 (33.3)	8 (29.6)	9 (20.0)	5 (11.1)	2 (4.4)	8 (17.8)	12 (26.7)	7 (15.6)	0	2 (4.4)	0
	Brown/green	27 (35.5)	7 (38.9)	12 (44.4)	21 (35.0)	5 (8.3)	4 (6.7)	2 (3.3)	12 (20.0)	11 (18.3)	0	4 (6.7)	1 (1.7)
		Between colour morphs P<0.01			Between colour morphs P=0.472								

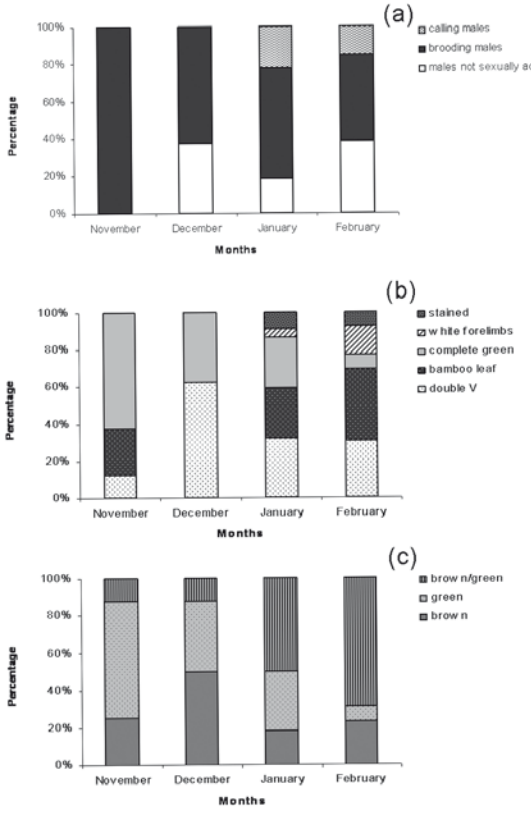

Fig. 5. Changes (%) across study months in a) male reproductive activity, b) male body colour morphs and c) male dorsal pattern morphs.

df=2, P=0.302; humidity: χ^2=1,704, df=2, P=0.427) or body measurements (snout–vent length: χ^2=0.921, df=2, P=0.631; tibia length: χ^2=0.005, df=2, P=0.997, see Electronic Appendix 1).

Relationship between pattern and colour morphs

The patterns "double V", "bamboo leaf" and "white forelimbs" were significantly positively associated with brown and brown/green colour morphs (Fisher exact probability test, P<0.001; see Electronic Appendix 2). Frogs with the "complete green" dorsal pattern all belonged to the green body colour morph, and the "stained" frogs were brown/green.

Temporal colour and pattern frequency variation

The frequency of the dorsal pattern and body colour morphs varied between the four months of study (Figs 4 and 5; Table 2), but the relative abundance of the respective morphs did not significantly differ (Fisher exact probability test, P=0.245 and 0.209 for dorsal pattern morphs and colour morphs, respectively; Electronic Appendix 3). In both sexes the pattern morph distribution was not significantly different among months (Fisher exact probability test, P=0.351 and 0.199 for females and males, respectively), as was the colour morph distribution in females (Fisher exact probability test, P=1.00). In males, the colour morph distribution was significantly different among

Table 4. Substrate colour choice (relative numbers in brackets) by male and female Darwin frogs. *P*-values based on Fisher exact probability tests for differences in frequency distribution are given. NSA = not sexually active.

		Brown	Green	Brown/ green	Total
Sex	Females	22 (68.8)	0 (0.0)	10 (31.3)	32
	Males	19 (37.3)	13 (25.5)	19 (37.3)	51
		$P<0.001$			
Males	NSA	8 (61.5)	1 (7.7)	4 (30.7)	13
	Brooding	10 (28.6)	11 (31.4)	14 (40.0)	35
	Calling	1 (33.3)	1 (33.3)	1 (33.3)	3
		$P=0.205$			

months (Fig. 5, Table 2, Fisher exact probability test, $P<0.05$; see also Electronic Appendix 3).

Colour matching

Body colour was associated with substrate colour; brown individuals in particular were significantly associated with brown substrates (Table 3). Females were predominantly present on brown substrates, whereas males were more evenly distributed across substrates (Table 4). Body colour morphs and dorsal pattern morphs were, however, not significantly different across bottom coverage types (Table 3). The distribution of frogs across the substrate colours also differed between months (Table 2, Fisher exact probability test, $P<0.05$).

Microhabitat choice

Sexes showed significantly different substrate colour choices (Table 4, Fisher exact probability test, $P<0.001$). Only males (particularly brooding individuals) were found on green substrates, which were non-significantly warmer (15.3 °C) than brown (14.6 °C) and brown/green substrates (14.5 °C; Kruskal Wallis test, $\chi^2=0.976$, df =2, $P=0.613$). Different substrate colours also had similar humidities ($\chi^2=2.206$, df =2, $P=0.332$).

The most frequent bottom coverage on which frogs were found was shrubs (Fig. 4c), where 22.4–29.0% of frogs were found each month. The distribution of frogs across bottom coverage types was significantly different among months (Pearson $\chi^2=38.313$, df=24, $P<0.05$). November and December were characterized by the presence of individuals under or next to logs, and in January and February individuals were mostly found in areas with leaf litter and herbaceous plants. In February diverse bottom coverage was used (Fig. 4c).

DISCUSSION

We have described for the first time differences in the frequency of body coloration and dorsal pattern in relation to substrate choice and sex in Darwin's frogs. Brooding males in particular showed greater variability in body colours and dorsal patterns than females. Males were greener, and the patterns "complete green" and "stained" were exclusively restricted to males. Females were only found on brown and brown/green substrates, while males also occurred on green substrates. The body colour differences between the sexes thus coincided with differences in microhabitat choice. One reason for the almost exclusive occurrence of brooding males on green substrates may be that lighter colours enable a higher metabolic rate (Wente & Phillips, 2003). Alternatively, brooding males may select greener substrates because these are warmer, accelerating tadpole development (Werner & Glennemeier, 1999; Skelly et al., 2002); however, further studies are needed to investigate whether statistically non-significant temperature differences have an effect. The body colour and pattern differences between the sexes may be further explained by sexual selection, with green being advantageous in male–male competition or attractiveness to females. Sexual selection by female choice has previously been described in this species (Busse, 2003). Females exhibited kick-off behaviour towards small males, increasing the chances of mating success for larger males. In the present study, Darwin's frogs matched their substrate colour, suggesting crypsis to reduce predation risk. This agrees with a previous description of the distribution of *R. darwinii* by Crump (2002) in a population in the south of Chile (Melimoyu, 44°S, 73°W). Darwin's frogs are active in the daytime and preyed upon by visually hunting predators such as birds and snakes. In the example of *Pseudacris regilla*, green and brown morphs were also more frequently found in green and brown microhabitats, respectively (Morey, 1990).

We identified five types of dorsal patterns. Three types matched with those described by Werner (1898) and Kilian (1965). "Double V" was also previously described by Krieg (1924) and Wilhelm (1927); "bamboo leaf" and "complete green" refer to "lateralis" and "unicolor" in Kilian (1965). The previously described patterns "picta" (Werner, 1898) and "complete brown" (Kilian, 1965) were absent in the present study. Our new pattern, "white forelimbs", was present in individuals possessing the "complete green", "bamboo leaf" and "double V" patterns; we therefore assume that it may be regulated by a cofactor that is expressed together with the other patterns. Individual *R. darwinii* are, however, also able to change from "double V" and "bamboo leaf" via the appearance of green spots to "stained" and "complete green" (predominantly males; Bourke et al., 2011). This suggests that "double V" and "bamboo leaf" are possibly inherited patterns which are able to change into "stained" and "complete green" in males.

Body colour and dorsal pattern morph frequencies changed over time, predominantly due to changes in the number of brooding males and their coloration. The number of brooding males decreased during the study period, while the number of calling males increased. Between November and December there were almost no individuals on green substrates, and individuals were darker, often found under shrubs. Thus body colour and dorsal pattern

frequencies and microhabitat choice were correlated with season and breeding activity.

The seasonal body colour change in *R. darwinii* may be explained by microhabitat change (Janvier, 1935). Other anuran species have previously been reported to vary in colour depending on breeding season and male reproductive activity. In *Mannophryne trinitatis*, males that are not calling or defending calling sites assume a cryptic brown coloration, and when calling they turn black and attack other males (Wells, 2007). In *Hyla elaechroa* and *H. pseudopuma*, males turn brighter during the breeding season (Savage, 2002), whereas in red-spotted newts (*Notophthalamus viridescens*) body background coloration changes with habitat (Davis & Grayson, 2007). We found for the first time that body colour and pattern morph frequencies were related to sex, season and male reproductive activity in *R. darwinii*. The colour polymorphism seemed environmentally plastic, potentially regulated by natural selection through substrate matching in order to avoid predation by visual predators and/or different microhabitat use by the sexes. Males exhibited a larger variability of body colours and patterns than females, which may be linked to sexual selection.

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