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Territorial and vocal behaviour in a captive dart-poison frog, *Epipedobates tricolor* Boulenger, 1899 (Anura: Dendrobatidae)

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ABSTRACT. Territorial and vocal behaviour of captive dart-poison frogs, *Epipedobates tricolor*, were studied in captivity. Most adult males (10 out of 13) showed territorial behaviour, while there was no indication of female territoriality. Territorial males defended sites with vocal and aggressive behaviour against male intruders. The residents' aggressive behaviour consisted of chases, physical combat and vocalizations. Only male frogs were observed producing sounds. Males vocalized more often in the morning than in the evening and they preferred to call from elevated perches. Females and non-calling males mainly stayed on the ground surface, although in the afternoon females were often observed visiting male territories

KEY WORDS: Frogs, Dendrobatidae, Epipedobates, territoriality, aggression, vocalization.

INTRODUCTION

Territorial species defend areas, coincident with or included within their home range. Territoriality is best understood in the context of resource competition; the defence of space is a surrogate for the defence of resources located within that space (DONNELLY 1989a, 1989b). A "resource" can be roughly defined as any environmental factor that enhances reproductive success, and that is in limited supply, relative to the number of potential users (STAMPS, 1998). To date, territorial behaviour has been described in an enormous array of animals, including anemones, molluscs, insects, spiders, fish, amphibians, reptiles, birds and mammals. Territorial behaviour among anurans has been reported in numerous families. MARTOF (1953) described the spacing phenomenon in green frogs (*Rana clamitans* Latreille, 1801), while territorial defence has also been documented in tree frogs (e.g. MARTINS et al., 1998), dart-poison frogs (e.g. SUMMERS, 2000), glass frogs (e.g. GREER & WELLS, 1980), pipids (e.g. ÖSTERDAHL & OLSSON, 1963), Madagascan poison frogs (e.g. HEYING, 2001), leptodactylids (e.g. STEWART & RAND, 1991), and several other anuran families.

All dendrobatid species studied to date have been reported to be territorial (e.g. SEXTON, 1960; CRUMP, 1972; BUNNELL, 1973; ZIMMERMANN, 1990; ROITHMAIR, 1992, 1994; SUMMERS, 2000). Previous research has reported male and / or female territoriality in dart-poison frogs (SEXTON, 1960; WELLS, 1980a, 1980b; ROITHMAIR, 1992, 1994). Vocalizations play a fundamental role in dendrobatid behaviour. Male territorial frogs call to attract receptive females and to space territories. BUNNELL (1973) showed in the strawberry dart-poison frog (*Dendrobates pumilio* Schmidt, 1857) that the playback of a recorded call would provoke approach of a territorial male.

In this paper we studied the territorial and vocal behaviour in the Ecuadorian dart-poison frog *Epipedobates tricolor* under captive conditions. Until now little was known about the territorial behaviour of this species (but see ZIMMERMANN & RAHMANN, 1987). We addressed the following questions: (1) how is territoriality being displayed? (2) which sex is territorial? (3) do both sexes produce calls and when do they call? and (4) what places are preferred for calling?

MATERIAL AND METHODS

Study species and housing

Epipedobates tricolor is a small (males: 22.6 mm; females: 24.6 mm) diurnal dart-poison frog from south western Ecuador (SILVERSTONE, 1976). All individuals used in this study were captive-bred. Animals were fed daily

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with calcium- and vitamin-enriched Drosophilae. Colour patterns in *E. tricolor* vary between individuals, and we were able to recognise individuals based on variation in the striping patterns. The research was carried out under captive conditions. Twenty-two individuals (13 males and 9 females) were randomly divided over four standardized terraria. Two of these terraria contained two males and two females, one terrarium contained six males and two females and the fourth terrarium had three individuals of both sexes. To exclude possible influences of the number of territorial males in the same terrarium, the number of males should be kept as constant as possible. For practical reasons this was, however, not always possible. The terraria were made of glass and measured 0.5 m x 0.5 m x 0.5 m. The back and side walls were coated with rock-like brown-coloured polystyrene. Each terrarium had four elevated perches (0.02 m^2/perch). Both side walls contained one perch, while the back wall contained two perches placed at different heights. A small cave, made of brown-coloured polystyrene, was placed on top of every perch. A black film roll canister was placed in every cave as well as on the ground surface. In captivity, dart-poison frogs will use these plastic canisters as oviposition places (WALLS, 1994). Two small bromeliads were placed on the ground surface and one bromeliad was placed on top of each cave. In our results we will refer to the term 'perch' to indicate the perch with the cave and the bromeliad on top of it. Humidity was kept at a high level (75% relative air humidity) by using a centrifugal pump that pumped a constant flow of water across circa 30% of the total back wall surface area. All terraria were placed in a blacked out room with controlled lighting (12:12schedule) and temperature (circa 24°C) conditions.

Observations

Five morning and five afternoon observations were carried out for all terraria. During each observation every terrarium was observed for half an hour, and this was done for five days. This gives us a total observation time of 300 minutes per frog. The 'morning' observations started at a minimum of half an hour after lights turned on. 'Afternoon' observations started a maximum of three hours before lights turned off. For recording spacing behaviour, we used a scan sampling method (ALTMANN, 1974): every minute, we recorded the exact place of each frog in the terrarium. Call behaviour was recorded every time it occurred. Advertisement calls are loud trilling calls, making them easy to recognise and quantify. Each call consists of a series of rapidly repeated notes (see Fig. 1).

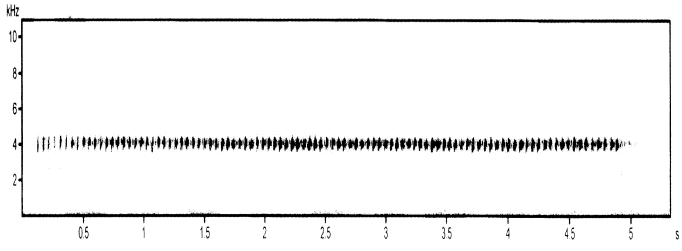

Fig. 1. – Advertisement call of a representative male frog.

Social behaviours different from space occupation and call behaviour were also continuously recorded.

Statistical analyses

Data were analysed using the statistical software programs STATISTICA (StatSoft, 1997), SPSS/PC (SPSS, 1986) and SAS (SAS INSTITUTE, 1989), following procedures outlined in SIEGEL (1956) and SOKAL & ROHLF (1981). The average proportion of the total time spent on an elevated perch, during, separately, the morning and afternoon was first calculated for each individual frog. Using SAS procedure, we carried out a two-way ANOVA (mixed ANOVA-model with period (morning and afternoon) and sex (male and female) as fixed factors, and individual as random factor, to compare proportions between all individuals. Individual was put as a random factor in the model because we used repeated measures of the same individual (morning and afternoon), because the observations are not independent. As a result, the number of degrees of freedom was adjusted by the ANOVA-model using sattertwaite formulas (see LITTELL et al., 1996). The model first tested if there was a significant interaction between period and sex. If this was the case we tested, for each separate period, if there were significant differences between the sexes, using t-statistic. Similarly we tested, for both sexes, if there were significant differences between the morning and the afternoon observations. Means and standard errors were calculated by using the statistical program SPSS. To determine if there were differences in calling activity between morning and afternoon observations, we used a paired, non-parametric Wilcoxon-test, performed in SPSS. Possible relations between the proportion of time that frogs occupied elevated areas and the call activity were tested by a Spearman Rank correlation, using STATISTICA. In all analyses, average values were calculated for each period for each individual to avoid problems with pseudo-replication. To satisfy the assumptions required for parametric statistics, proportions were subjected to arcsine square-root transformation. Two-tailed statistics were used with alpha set to 0.05.

RESULTS

Perch occupation

When comparing the proportion of time spent on a perch, a two-way ANOVA revealed a significant period x sex interaction effect, indicating that differences between the sexes depend on the observation period (two-way ANOVA, $F_{1,20}=8.20$, $p=0.0096$). During the morning observations, males spent significantly more time on elevated perches than did females (t-test, N=22, $p=0.006$; Fig. 2). During the afternoon observations there was no significant difference between the sexes (t-test, N=22, $p=0.22$; Fig. 2). The proportion of time males spent on a perch did not differ significantly between morning and

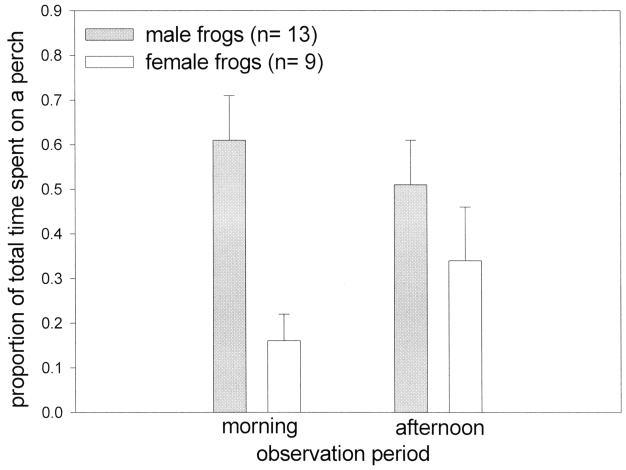

Fig. 2. – Proportion of total time (mean ± SE) spent on a perch by males and females during morning and afternoon observation periods.

afternoon observations (t-test, N=13, p=0.12; Fig.2). By contrast, females spent significantly more time on elevated perches during the afternoon than in the morning (t-test, N= 9, p= 0.029; Fig. 2). Calling males (N=10) visited 1.02 ± 0.09 (range: 0 to 4; median=1) different perches per observation period (30 minutes) whereas females visited 0.32 ± 0.08 (range: 0 to 2; median=0) different perches per observation period. Considering the entire observation period (300 minutes) calling males were observed visiting 3.10 ± 0.31 (range: 1 to 4; median=3) different perches.

Calling behaviour

Only male frogs were observed producing calls. Ten males produced a total of 2036 calls during the entire observation period. Three males were never observed calling during the entire study period.

These 'silent' males also occupied an elevated perch significantly less often than did the calling males (t-test, N=13, p=0.004; Fig. 3). Two out of three silent males were housed in the terrarium with eight individuals, the other male was housed in the terrarium with six individuals. Males produced 0 to 7 calls per minute, although one male exceeded this range and called 0 to 10 times per minute. Male frogs called significantly more during the morning observations than during the afternoon observations when they only called sporadically (Wilcoxon test, N=10, p=0.0051; Fig. 4). During the morning observations, males also called significantly more on elevated perches than on the ground surface (Wilcoxon test, N=10, p=0.025; Fig. 4). During the morning observations there was a significant positive relationship between the proportion of time spent on a perch and the average number of calls produced per hour (Spearman rank correlation coefficient=0.584, N=13, p=0.036; Fig. 5), while during the afternoon observations this relationship was not significant (Spearman rank correlation coefficient=0.377, N=13, p=0.20). Calling males were always spaced at a minimum distance of 10 cm from each other.

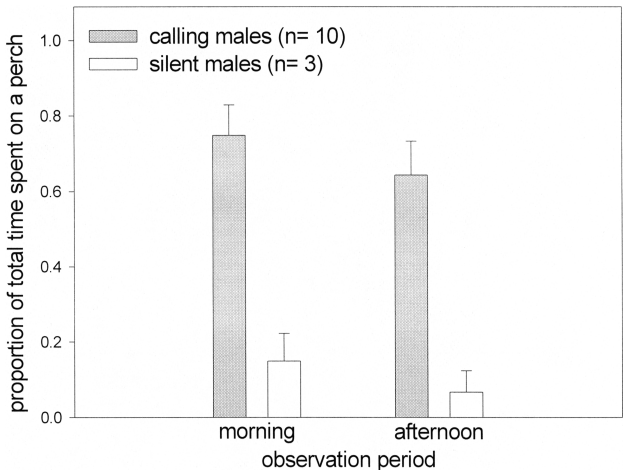

Fig. 3. – Proportion of total time (mean ± SE) spent on a perch by silent and calling males during morning and afternoon observation periods.

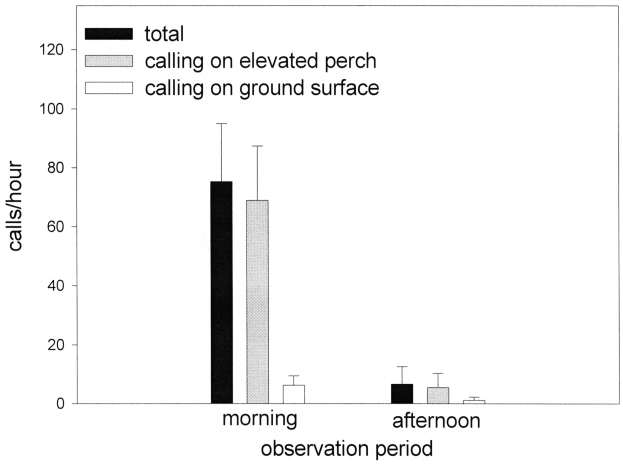

Fig. 4. – Mean number of calls produced per hour (mean ± SE) by males calling on an elevated perch and calling on the ground surface.

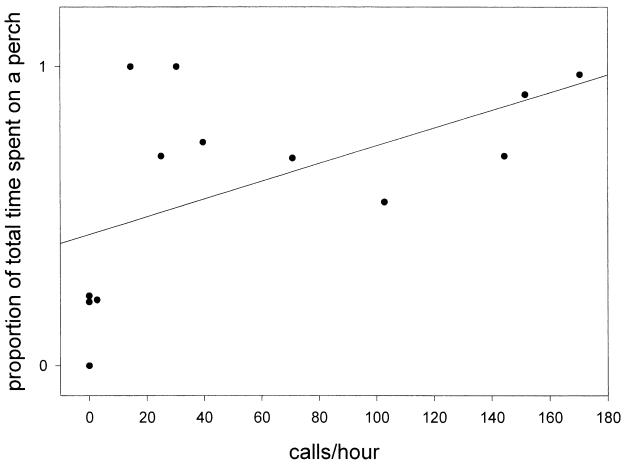

Fig. 5. – Relationship between the proportion of the total time spent on a perch and mean number of calls produced per hour by male frogs (N=13) during morning observations.

Aggressive behaviour

Only male-male aggression was observed. We observed a total of 18 aggressive conflicts, involving 10 different male – male combinations. They all occurred when a male entered the elevated perch (cave or bromeliad; see materials and methods) of a calling male. Both males then adopted an erect posture, with their front legs splayed out and rigid. The males leapt almost simultaneously at one another. They clashed, then embraced, standing upright on their hind limbs for a fraction of a second. After this encounter they circled one another, and came together again. Each frog tried to get behind its opponent so that he could jump on his back and press him downwards.

DISCUSSION

This is one of the few studies, carried out under captive conditions, explicitly designed to examine territorial behaviour in a dendrobatid species. Previous research has shown that male strawberry dart-poison frogs aggressively defend territories under captive conditions (BAUGH & FORESTER, 1994). Our data revealed that only males were territorial and produced calls. In the morning males spent significantly more time on elevated perches than did female frogs. During the afternoon, perch occupation did not differ significantly between the sexes. Field studies have shown that the occupation of elevated perches could be an indicator of territorial behaviour in many of the leaf-litter-living dendrobatid frogs (CRUMP, 1972; ROITHMAIR, 1992; GRAVES, 1999). Three males that were never observed calling spent significantly less time on elevated perches than did the other males. Moreover, we have never observed aggressiveness in or towards these 'silent' males. These observations indicate that these males were not territorial, and it is possible that they were not sexually active during the observation periods. Another explanation might be that they may act like satellite males (e.g. HOWARD, 1978; PERRILL et al., 1978; FORESTER & LYKENS, 1986), and play a 'making the best of a bad job'-strategy although we have never observed this behaviour during our study. Perhaps the presence of high quality males (e.g. males with a high call repetition rate) may influence the potential calling behaviour of these males. When we exclude the data of these three non-territorial males, we also find a significant intersexual difference in perch occupation for the afternoon observations: males spent significantly more time on elevated perches than did females (t-test, N= 19, p= 0.023). During the morning observations females mainly stayed on the ground surface, whereas during the afternoon they spent significantly more time on elevated perches. At the moment it is unclear why females behaved that way. Perhaps females mainly show mating behaviour in the afternoon (personal observations).

Most calling behaviour was observed during the morning periods. Other studies on dendrobatid calling behaviour (CRUMP, 1972; GRAVES, 1999) also found a maximum call activity during morning observations. By contrast, ZIMMERMANN & RAHMANN (1987) found in captive *E. tricolor* that sexually active males called from dawn to dusk throughout the whole day, with a peak in calling activity just before and after noon. However, their results were based on a single individual.

For the morning observations, we found a positive correlation between perch occupation and intensity of calling behaviour, indicating that males on an elevated perch call more than individuals on the ground surface. We did not find such a correlation for the afternoon observations, probably due to the low number of calls observed during this period (Fig. 3). GRAVES (1999) monitored activity patterns in two dendrobatid frogs, and found in the strawberry dart-poison frog that calling males become active earlier in the morning than females or silent males. He also found that, just after sunrise, a smaller number of individuals were active, but a larger proportion were on elevated perches, compared to later in the day (GRAVES, 1999).

Most of the calling males only visited one perch during each observation period (30 minutes). However when considering the entire observation period, most calling males were observed visiting three to four different perches, indicating that they did not occupy the same perch every day. During a night control we noticed that all frogs slept in the bromeliads on the ground surface. Perhaps, every morning males have to compete again for territories. This may also explain the intensive calling behaviour during the morning hours. In our terraria we made all elevated perches had the same surface area and had only one potential oviposition place, though they were not all at the same height (see materials and methods). As we can see in the results it might be interesting in a future experiment to include the height of an oviposition place as a quality factor, and to examine which males (call characteristics, morphological measurements)will obtain which perches. Aggressive behaviour occurred when calling males entered the elevated perch of a resident. Similar behaviour has been described in other dendrobatid species (DUELLMAN, 1966, CRUMP, 1972; SUMMERS, 2000). We have never observed aggression towards females and silent males. Furthermore we have never observed female-female aggression, as described in some other dendrobatid species (SUMMERS, 1989).

Our data about calling behaviour, perch occupation and aggressive behaviour show that in this small Ecuadorian frog, most males are probably territorial. They defend elevated areas, with potential oviposition places, by means of aggressive and vocal behaviour towards other calling males. Calling is probably used for spacing territories and attracting receptive females, although further experimental work is necessary to demonstrate this. This study further indicates that territorial behaviour in dart-poison frogs can be studied under captive conditions because males seem to behave normally in captivity.

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