

FIELD STUDIES ON REPRODUCTIVE BEHAVIOUR IN TWO DART-POISON FROG SPECIES (*EPIPEDOBATES FEMORALIS*, *EPIPEDOBATES TRIVITTATUS*) IN AMAZONIAN PERU

MARGARETE E. ROITHMAIR

Institut für Zoologie, Universität Wien, A - 1090 Wien, Althanstr. 14, Austria

Present Address: Research Centre for Biosystematics & Ecology, Academy of Sciences, Kegelgasse 27/2, A-1030 Wien, Austria

The reproductive behaviour of two syntopic dendrobatid species, *Epipedobates femoralis* and *Epipedobates trivittatus* were studied in two separate field studies in Amazonian Peru. Males of both species defended territories against calling conspecifics; females were not territorial. Pair-formation, courtship, and mating took place in the territories of the males. Females entered territories and approached calling males who attempted to lead females to oviposition sites. Females rejected males during courtship by leaving males or refusing nest sites. Males never rejected females. Brood care was performed by males only. The reproductive behaviour of the two species varied in length and pattern of courtship, oviposition behaviour and male brood-care behaviour.

INTRODUCTION

Neotropical frogs of the family Dendrobatidae are particularly promising subjects for ethological studies because of their conspicuous appearance, diurnal habits, and their complex reproductive and social behaviour. Dendrobatids deposit their eggs on land and the tadpoles are transported to aquatic sites on the back of a parent, except in *Colostethus stepheni* where the tadpoles develop in terrestrial nests (Junca, 1989; Lima, 1992). All species studied to date demonstrate elaborate courtship behaviour and parental care (e.g. Crump, 1972; Weygoldt, 1980a,b; Zimmermann, 1990). Male and/or female territoriality and aggressive behaviour have been reported in several species (e.g. McVey, Zahary, Perry & McDougal, 1981; Wells, 1980a,b; Summers, 1989; Roithmair, 1992, 1994).

Courtship may be viewed as an exchange of signals to provide information about the potential mate (Wells, 1977), possibly including cues for the females' mate selection and information for males about the receptivity of females. In frogs, courtship usually starts with the male advertising his position and trying to persuade a female to mate with him rather than with his neighbouring competitor. Advertisement calls of male frogs are reported to serve as a cue for female mate choice (e.g. Gerhardt, 1991). Information for males about the receptivity of females could be especially important in dendrobatids because of their terrestrial and prolonged breeding habits with receptive as well as non-receptive females entering the territories of males (Wells, 1977). In dendrobatids, brood care is assumed to be the "initial condition" (Maynard Smith, 1977), because larval transport is essential for the survival of the offspring, which would die if they were not carried to a suitable environment for development (Weygoldt,

1987). This situation creates perhaps a more sophisticated courtship and mating system in which both partners attempt to obtain as much information about the other as possible.

In previous papers, I have described my field observations on the social behaviour of the dart-poison frogs, *Epipedobates femoralis* and *Epipedobates trivittatus*. Main emphasis centered on male territorial behaviour and the interrelation between territoriality and mating success in males (Roithmair, 1992, 1994). In this paper I report on my results concerning the reproductive behaviour of these two dart-poison frogs. The main objective is to describe in detail the behavioural patterns of courtship, mating and brood care as shown by the two species in the field, thus providing a basis for comparison.

MATERIALS AND METHODS

STUDY AREA

Both species were studied at the Panguana biological station located on the lower Rio Lullapichis (approx. 9°35' S, 74°48' W) in lowland Amazonian Peru. The site is situated in a primary rain forest at an elevation of 260 m. The wet season ran from September/October to March/April. Annual precipitation ranged from 2000 to 2600 mm, and the mean annual temperature was 25°C.

STUDY SUBJECTS

Epipedobates femoralis (Boulenger, 1883) and *Epipedobates trivittatus* [Spix, 1824; taxonomy of both species following Myers (1987)] are diurnal inhabitants of the forest leaf litter. Calling activity of the frogs began about August/September (i.e. before the onset of the wet season) and ended about February/March. Males of both species have two types of calls:

an advertisement call for long-range communication (Schlüter, 1980; Hödl, 1983) and a courtship call of a lower sound intensity for short-range communication (Weygoldt, 1980a; Roithmair, 1994). There is no significant difference in the sound pressure levels of calls of conspecific males in either species (Hödl, 1983; Roithmair, 1994). During these studies, *E. trivittatus* males mostly called in the mornings between 04.40 and 09.00 hr, and *E. femoralis* males called the most in the afternoons between 14.00 and 18.00 hr. In both species females are slightly larger than males. In *E. femoralis*, the snout-vent length (SVL) of adult males averaged 26.8 mm ($n = 55$); average SVL of females measured 27.5 mm ($n = 33$). The skin of *E. femoralis* is non-toxic (Daly, Myers & Whittaker, 1987). *Epipedobates femoralis* is a feeding generalist, taking as prey mainly ants and termites in proportions not significantly different from those in the leaf litter (Toft, 1980). In *E. femoralis*, activity ceased completely during the dry season and adult frogs could neither be seen nor heard. In *E. trivittatus*, average SVL of adult males measured 39.3 mm ($n = 27$); SVL of adult females measured 43.6 mm ($n = 65$). The skin of *E. trivittatus* is toxic (Daly *et al.*, 1987). This frog is considered to be a feeding specialist actively searching for prey, mostly ants (Toft, 1980). *Epipedobates trivittatus* could be seen throughout the entire year, however, only very few frogs could be heard in the dry season; one unmarked male was found carrying tadpoles in July. None of the frogs in the study group showed reproductive activity during the dry season.

FIELD METHODS

Observations were made on both species for the duration of two reproductive periods. *Epipedobates femoralis* was studied from August 1985 to February 1987, and *E. trivittatus* from October 1988 to January 1990.

Two study areas were marked off in separate and undisturbed forest patches: one was 625-720 m² (*E. femoralis*), and the other about 3300 m² (*E. trivittatus*). I visited the study area mornings and afternoons for a total of 300 observation days for the *E. femoralis* study, and for a total of 407 observation days for the *E. trivittatus* study. The surface structures of the two different study sites did not change in the two years of the respective study. All frogs captured in the study area were measured to the nearest 0.1 mm (snout-vent length). A detailed sketch of the dorsal and lateral pattern of each frog was made to enable individual recognition without handling. In *E. trivittatus*, toe-clipping was not necessary for marking since the highly variable dorsal pattern (see Silverstone, 1976) permitted reliable individual recognition up to three meters distance without handling. In *E. femoralis*, all adult frogs were toe-clipped to ensure identification since the individual pattern (i.e. dorsolateral stripes) was not as easily distinguishable as in *E. trivittatus*.

Toe-clipping did not appear to impede the frogs' normal behaviour and toe regeneration was never detected. In both species frogs were sexed by the presence of two vocal slits (longitudinal folds) on the throat of males. Frogs smaller than 24.5 mm (in *E. femoralis*) or smaller than 33.0 mm (in *E. trivittatus*) and lacking vocal slits could not be sexed externally and were regarded as juveniles. My usual procedure was to locate all calling males within the study area during the first hour of observation. Then I slowly moved through the area or sat quietly in one spot and observed interactions between individuals. Locations of all individuals were marked with small, numbered plastic tags attached to the vegetation and recorded on a map. For methods of estimating territory size and maps of territories see my previous papers (Roithmair, 1992, 1994).

DATA ANALYSES

The data were analyzed with product-moment correlation using the STATS 2.1 software program. The distribution of the data was checked for normality by applying the Kolmogoroff-Smirnov test using the STATGRAPHICS 2.0 software program. The 10% level was used to determine difference from normality; \bar{x} and SD are given for normally distributed samples, otherwise median and interquartile ranges (*iqr*) are used.

RESULTS

BRIEF DESCRIPTION OF SOCIAL BEHAVIOUR

In *E. femoralis*, 81 adult frogs (55 males, 26 females) were marked. In *E. trivittatus*, 92 adult frogs (27 males, 65 females) were recorded in total. Males of both species established territories using the advertisement call as a cue for spacing and marking their territories. Females, juveniles and non-calling males were not territorial and could enter a territory and move around freely without evoking aggression. In both species, territory sites could be occupied by different males in succession. Size and shape of the territories varied for each resident. A total of 44 *E. femoralis* males were regarded as territorial. They established 18 territories during the first wet season and 16 territories during the second wet season. In *E. trivittatus*, 20 territorial males established 14 territories during the first wet season and seven during the second wet season.

In *E. femoralis*, territory sizes ranged from 0.25 to 26 m², and in *E. trivittatus*, territory sizes varied between 4 and 156 m². In both species territory size was positively correlated with the number of days with calling activity of the owner and length of residence. Successful males (i.e. males mating at least once) maintained significantly larger territories and called on more days than unsuccessful males (i.e. no mating). SVL of males did not influence mating success (for details see Roithmair 1992, 1994).

REPRODUCTIVE BEHAVIOUR

Courtship. In *E. femoralis*, I observed six complete courtships and one only partially, and in *E. trivittatus* I observed 17 courtships leading to oviposition. In both species, pair formation, courtship, and mating always took place within the territories of the males. Females entered the territories and approached calling males. I observed a few females of *E. trivittatus* nudging the male to initiate courtship. Vocally inactive males were ignored by conspecific females in both species. As soon as a male detected the presence of a female he started to lead her to an oviposition site. In most cases, the nest

site was hidden under dead leaves on the forest floor or, occasionally in *E. trivittatus*, in fallen palm-leaf sheaths (Table 1). In neither species was the length of the courtship march influenced by the size of the resident's territory (product-moment correlation: $r = -0.58$, $t = 1.43$, NS in *E. femoralis*; $r = -0.19$, $t = 0.76$, NS in *E. trivittatus*).

Males of both species were not able to distinguish between a non-calling conspecific male or female. In either case the territorial males commenced courtship by emitting courtship calls and their subsequent activity was determined by the behavioural response of the other frog. Males never rejected a female. In unsus-

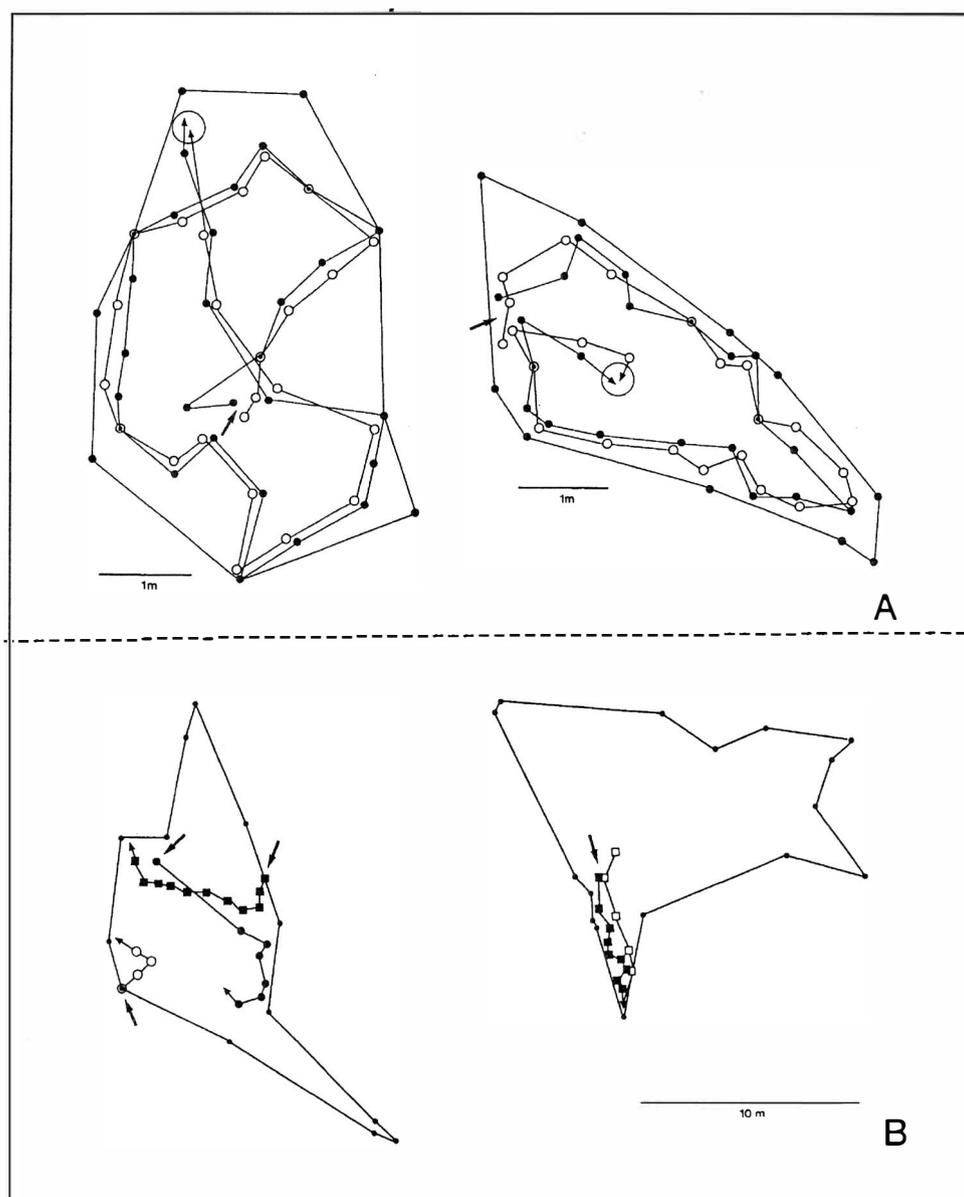


FIG. 1. Courtship behaviour of *Epipedobates femoralis* (A) and *Epipedobates trivittatus* (B) in the field. The males led the females to oviposition sites within their territories. A: Arrows = start of courtship march; dots = males; small circles = females; large circles = symbol of nest sites. B: In the case of multiple matings of the resident only the male is drawn, symbols of courtship marches are different. Full squares = first courtship march; full circles = second one; open circles = third one. Large arrow = start of courtship march; full squares = males; open squares = females; points of small arrow(s) indicate location of nest sites.

cessful courtships (i.e. courtships not leading to mating) females either did not follow at all (but orientated themselves towards the courting male), or stopped following the courting male, or refused the male-chosen nest site. After a female had rejected a resident she left the territory. If a courtship sequence was disturbed by me the pair hid under leaves starting again with courtship after a few minutes. In *E. femoralis* 89 unsuccessful courtships were observed (59 in the first season and 30 in the second). When faced with unwilling partners, males of *E. femoralis* immediately switched from courtship calls to normal advertisement calls and ceased attempting to lead females to a nest site. The average duration of these unsuccessful courtships was 20 min (range: 4 - 47 min, SD = 10.58; $n = 25$). In *E. trivittatus*, nine out of a total of 48 unsuccessful courtships (= 19 %) were due to the female refusing the nest site. The females ($n = 8$; one female refused the nest sites of two males) followed the male to the nest site, entered the nest and left it almost immediately. Duration of these mating attempts ranged from 23 - 96 min ($\bar{x} = 61.33$, SD = 25.75; $n = 9$). Except for one case where the male-chosen palm-leaf sheath was full of water, the refused nest sites seemed (to the observer) as suitable for egg development as the sites accepted by females. On two occasions, the male tried without success to clasp the female leaving the nest.

In *E. femoralis*, females stayed at least two days before mating in the male's territory where they were courted daily by the residents. During this premating presence, however, the female followed the courting male only over a short distance and disappeared under leaves within the territory. *Epipedobates femoralis* females, who signaled their interest in mating by constant phonotactic approach, were led by the male in a roundabout trip throughout the territory. The males hopped along the boundaries of their territories, but never left them. Regularly they gave courtship calls. The females followed quickly behind, sometimes hopping to the same spot, which the male occupied a few minutes before. The distance between the two mates never exceeded 50 cm, and averaged 20-40 cm (Fig. 1A). If a female lost sight of her mate, she was unable to locate him without the help of advertisement calls. Towards the end of the courtship march the male started to crawl under leaves and into rolled leaves. The entire courtship lasted from 95 to 225 min, beginning with the first reaction of the male (i.e. turning towards the female, emitting courtship calls) and ending when both partners entered the nest and the male stopped calling (Table 1).

In *E. trivittatus*, only two of 17 paired females stayed one or two days in the territory prior to mating. Fifteen females were never seen in their mating territory before courtship and mating. *Epipedobates trivittatus* courtships never lasted longer than 68 min, the shortest was 12 min (Table 1). The males led the

	<i>E. femoralis</i>	<i>E. trivittatus</i>
No. matings	7	17
Premating presence of female in male territory	2.4(2-4)days	0+(0-2)days
Courtship duration (min)	157.2(95-225)	32.7(12-68)
Stay in nest (min)	male 13(7-18) female 37.8(18-60)	79(29-187) 133.5*(43-1440*)
Total duration of courtship and mating(min)	170.2(111-232)	113.1(58-209)
Nest site	old leaves	old leaves: $n=14$ palm-leaf sheath $n=3$

TABLE 1. Description of courtship and mating behaviour of *Epipedobates femoralis* and *Epipedobates trivittatus*. Mean or median (+) values and ranges (in parentheses) are given. Courtship start = the first reaction of male to female and vice versa; courtship end = male and female stay in the nest and male stops calling; mating end = male leaves the nest. * = the overnight stay of females in the nest is estimated at 1440 min (=24hr)

females in a roughly straight line to an oviposition site (Fig. 1B). Courtship calls were not given regularly. In one case they were entirely absent and in two cases given only once. Females of *E. trivittatus* were able to locate mates by courtship calls. *Epipedobates trivittatus* males did not demonstrate nest-searching behaviour, such as looking under leaves or crawling inside palm-leaf sheaths. During one courtship, a male was interrupted twice in his attempts to lead a female to an oviposition site. Finally, on the third attempt he led her to a nest site which was nearly at the same distance and in the same direction as the former trials.

Mating. Matings occurred in the early morning starting between 06.05 and 06.35 hours in *E. femoralis* and between 04.57 and 06.30 hours in *E. trivittatus*. In both species more than 60% of all recorded matings occurred in November and December.

In *E. femoralis*, seven matings were recorded. No male or female was observed to mate twice. In *E. trivittatus* 17 matings were performed by 11 males: eight males mated once, two males mated twice. One male defended a territory in both rainy seasons and mated three times in the first season and twice in the second. The clutches were always laid in different nest sites (Fig. 1B). No *E. trivittatus* females were observed to mate more than once. In both species, the males en-

tered the nest site first and the females always left after the males.

Epipedobates femoralis males continued to give courtship calls; when both partners were in the nest and in the proper position the males ceased calling. The male sat behind the female without body contact (number of observations = 4). I could not determine the exact moment of fertilization, but I presume it took place almost simultaneously with egg deposition, since males left the clutch two to four minutes after egg deposition staying in the nest for seven to 18 min. The average number of eggs laid was 26. Afterwards, the females slowly turned around one or two times, than sat motionless on the clutch and finally left after approximately 40 min (Table 1).

In *E. trivittatus* cephalic amplexus was performed. Fertilization occurred after egg deposition. Accidentally, I disturbed a pair during mating. Both frogs left the nest, and since the laid eggs neither changed their colour nor developed, I assume, they were not fertilized. The average number of eggs per clutch was 40. The pairs stayed much longer in the nests than *E. femoralis*: the males remained up to three hours in the nests and 30% of the females stayed with their clutches the whole day and the following morning, thus very probably stayed overnight (Table 1).

In neither of the two species were correlations found between clutch size and (a) female body size (product-moment correlation: $r = 0.26$, $t = 0.61$, NS in *E. femoralis*; $r = 0.58$, $t = 1.01$, NS in *E. trivittatus*) or (b) male body size (product-moment correlation: $r = 0.48$, $t = 1.23$, NS in *E. femoralis*; $r = 0.03$, $t = 0.13$, NS in *E. trivittatus*) or (c) size of male territory (product-moment correlation $r = -0.18$, $t = 0.40$, NS in *E. femoralis*; $r = -0.05$, $t = 0.19$, NS in *E. trivittatus*).

Brood Care. In both species, brood care was performed by males only. After mating, females left the territories and neither visited their clutches nor carried tadpoles.

Males of *E. femoralis* were never found within their nests attending their clutches. They either returned only to transport their offspring or for very short visits unnoticed by the observer (see also Weygoldt, 1980a). Males continued to call during embryonic development, except for the first two days after mating (Table 2). They did not use calling sites next to their clutches. Males of *E. trivittatus* attended their clutches three to nine times during embryonic development (Table 2). I did not observe them moistening or cleaning their clutches; they just sat quietly beside the clutches, touching them with one side of the body. One *E. trivittatus* male had two clutches at the same time in his territory for two days, until one clutch was destroyed by fungus. After mating, males stopped calling for 1 - 22 days (median = 4, $iqr = 5$, $n = 17$). Throughout the period of embryonic development, six males continued to call and three males ceased calling entirely. Males never called while in the nest. No correlation was found between the number of surviving

		<i>E. femoralis</i>	<i>E. trivittatus</i>
No. clutches		7	17
Eggs/clutch		26.3(24-30)	39.7(26-51)
Tadpoles/clutch		13.86(0-23)	17.71(0-41)
Tadpoles transported		19.4(16-23)	33.4(22-41)
Behaviour of the resident (=father) until tadpole transport	Days calling	8.4(5-10)	3 ⁺ (1-11)
	Days courting other females	0 ⁺ (0-2)	0 ⁺ (0-2)
	Days attending the clutch	0	5.78(3-9)
Transport of clutches on x th day after mating		14.2 (12-16; n=5)	17.9 (15-18; n=9)
Destruction of clutches on x th day after mating		1st,2nd (n=2)	3.6 (2-7; n=8)

TABLE 2. Description of clutches and brood-care behaviour of *Epipedobates femoralis* and *Epipedobates trivittatus*. Mean or median (+) values and ranges (in parentheses) are given. *calculated from data of successful development only: =number of tadpoles moving in the clutch, counted one day before transport.

larvae and number of paternal visits to the clutch in *E. trivittatus* (product-moment correlation: $r = -0.19$, $t = 0.51$, NS).

In *E. femoralis*, development until larval uptake lasted 12 to 16 days, averaging 14 days. In *E. trivittatus*, eggs developed into larvae in 15 to 22 days, averaging 18 days. Two of seven *E. femoralis* clutches and eight of 17 clutches of *E. trivittatus* were destroyed by fungus, fly larvae or heavy rainfalls within one to seven days (Table 2).

I never was able to observe individually marked males taking up tadpoles nor did I capture marked males while carrying tadpoles. Outside the study area, all frogs captured with tadpoles on their back were males ($n = 9$ in *E. femoralis*; $n = 11$ in *E. trivittatus*). Usually, after rainfall the clutches were missing in the study area. No water sites were recorded inside of male territories. *Epipedobates femoralis* males required no more than half a day to transport their offspring to water sites, since they were found calling in the morning and the afternoon of the day of transport. *Epipedobates trivittatus* males stopped calling for at least one day and up to 40 days after clutch transport. However, one male transported 24 tadpoles on one day and returned

to carry the remaining eight tadpoles of the same clutch on the following day.

Except for this one case in *E. trivittatus*, tadpoles of one clutch were transported all at once. In *E. femoralis*, the average number of tadpoles transported by individually known males was 19 (range = 16 - 23, SD = 2.42, $n = 5$); in *E. trivittatus* the number of tadpoles (carried at once) averaged 33 (range = 22 - 41, SD = 5.31, $n = 8$; calculated from the number of tadpoles moving before the clutch was transported). When the transport of the last clutch was completed or if the clutch was destroyed, residents either deserted their territories immediately ($n = 1$ in *E. femoralis*; $n = 3$ in *E. trivittatus*) or maintained residency calling for up to 24 days ($n = 6$ in *E. femoralis*; $n = 9$ in *E. trivittatus*).

DISCUSSION

The basic patterns of courtship are similar in both dart-poison frog species studied: males tried to attract females by advertisement calling, the females approached residents and were courted by the males who attempted to lead the females to oviposition sites. While advertisement calls are directed towards all females as a signal of male sexual activity (besides the function of a signal to competitors of male readiness to defend a specific territory), courtship calls rather are signals to an individual female in the vicinity. Males of *E. femoralis* or *E. trivittatus* were not immediately able to distinguish the sex of a silent conspecific, or differentiate a non-receptive or unwilling female from a female ready to mate. After courting for a short time, however, males were able to decide if it paid continuing with courtship or stopping it. Thus, courtship behavioural patterns of females appear to provide males with sufficient valuable information about female physiological conditions.

Epipedobates femoralis courtships lasted, on average, nearly five times longer than those of *E. trivittatus*. However, if the duration of courtship and time spent in the nest by both partners were added, then courtship lasted only one and half times longer in *E. femoralis* (Table 1). In *E. trivittatus*, females entering a male-chosen nest site sometimes decided not to mate at all and left the nest immediately. Presumably, females ovulated in the nest during cephalic amplexus considering the prolonged stay of both partners in the nest. Perhaps the tactile stimulus is necessary for ovulation. I suppose that female *E. femoralis* needed the time of courtship to reach the proper physiological condition. To deposit a clutch and to fertilize it, the mating pair required only a few minutes in the nest (Table 1). The courtship calls regularly given by *E. femoralis* males may serve as acoustic stimuli to females, since the calls did not provide cues for orientation. Since females *E. femoralis* never refused a nest site, a male followed continuously and without hesitation by a female could be "confident" that this female would mate with him and be ready for oviposi-

tion. Thus, the long courtship duration in *E. femoralis* is suggested to serve as well to assure the male of the female's willingness and readiness to mate. Furthermore, *E. femoralis* males spent additional time searching for a nest site during courtship. The absence of this searching behaviour in *E. trivittatus* and the observation that one *E. trivittatus* male repeatedly led a female to the same spot in the same direction, suggest that males have chosen a nest site previous to the start of a single courtship trip.

Although females of both species were observed to sample males and males mating successfully defended larger territories and called on more days than unsuccessful males (Roithmair, 1992, 1994), the time of the female's decision with which male to mate was different in the two species. *E. femoralis* females "had made up their minds" when engaging in the final prolonged courtship in the morning, whereas *E. trivittatus* females were able to delay their decision until the last possible moment, i.e. before performing cephalic amplexus. I suppose neither the duration nor the performance of courtship (e.g. number of courtship calls, shape of trip through the territory) were decisive factors in the female mate choice in either species. Although it seems possible that *E. trivittatus* females could use nest site quality to choose mates, one would expect a higher percentage of unsuccessful courtships due to nest site refusal (see also Roithmair, 1992, 1994).

In dendrobatid species where both sexes defend territories, courtship may serve to overcome the aggressive tendencies of the partner (Dole & Durant, 1974; Wells, 1980a, b). In the two species studied here, however, any non-calling frog could enter a territory without evoking aggression. In *Dendrobates auratus* and *D. leucomelas*, active courtship of males by females may be performed in order to prevent males from multiple mating, which infers costs to the female in terms of reduced offspring survival (Summers, 1989, 1990, 1992). Although *E. trivittatus* males mated polygynously, no male attended two clutches or carried tadpoles of two clutches simultaneously to the same water site. Courtship initiation by some *E. trivittatus* females was rather to draw the male's attention to the female's presence and females never remained in their mates' territory after mating. Intra-female aggression was observed only once (Roithmair, in press).

Brood care behaviour in anurans may increase their reproductive success (e.g. McDiarmid, 1978; Townsend, Stewart & Pough, 1984) and may involve defence against other frogs and egg predators, provision of skin secretions to inhibit fungal growth, and provision of moisture to prevent desiccation (Salthe & Mecham, 1974; Wells, 1981). In *E. trivittatus*, paternal care did not involve special behavioural patterns such as cleaning or watering the eggs and defence of clutches against egg predators never was observed. Although cannibalism never was observed and causes of clutch

destruction were always explicable, males never called in or near their nests, as if to avoid attraction of predators to the nest site. The most essential contribution to the survival of the offspring in dendrobatids is to transport the larvae to a water site, requiring the presence of at least one parent to perform it. The behaviour of staying with or repeatedly returning to the clutch, as demonstrated by *E. trivittatus*, may be regarded as the easiest way to ensure that the parent can relocate the nest site (Weygoldt, 1987). Consequently, *E. femoralis*' behaviour of returning to the clutch only for larval transport, would be a derived behavioural pattern of brood care that requires site memory.

In both species studied here, only males carried tadpoles (see also Aichinger, 1991). Since females always left the nest after males, they would be pre-disposed to care for the offspring, i.e. to engage in egg attendance and larval transport (Dawkins & Carlisle, 1976). Presumably, the possibility of the male to desert first is outweighed by the association with the offspring by the territorial sex (i.e. the male) and the combination of territoriality and external fertilization, enabling assurance of paternity (Trivers, 1972; Ridley, 1978; Gross & Shine, 1981). In addition, remains the simple question, of whether a female would be able to find her clutch again. Although females may have information about the extensions of various territories (Roithmair, 1992, 1994), the degree of their familiarity with their mate's territory remains unknown and presumably is less than that of the resident male.

A summary of the behavioural patterns of *Epipedobates femoralis* and *Epipedobates trivittatus* demonstrated in courtship, mating, and brood care (for detailed explanation see results), are shown in Tables 3-5.

<i>E. femoralis</i>	<i>E. trivittatus</i>
<i>Unsuccessful courtships</i>	
no nest-site refusal	19% due to nest-site refusal
<i>Successful courtships</i>	
females in territory at least 2 days before mating	rare premating presence
males lead females around territory	a roughly straight line to nest site
never shorter than 95min (\bar{x} = 157min)	never longer than 68min (\bar{x} = 32min)
regular courtship calls	courtship calls not obligatory
nest-site searched towards end of courtship	nest-site chosen previously?

TABLE 3. Summary of courtship behaviour.

<i>E. femoralis</i>	<i>E. trivittatus</i>
males (n = 7) stayed in nests 13min ($= \bar{x}$)	males (n = 11) stayed in nests 79min ($= \bar{x}$)
simultaneous fertilization and egg deposition	fertilization after egg deposition
females left nests after 38min ($= \bar{x}$)	70% females left nests after 110min ($= \bar{x}$) and 30% stayed overnight
females always left nests after males	
\bar{x} number of eggs:26	\bar{x} number of eggs:40
no correlation between male or female body size and clutch size	
no males mated twice	27% males mated more than once
females never mated twice	

TABLE 4. Summary of nesting and mating.

<i>E. femoralis</i>	<i>E. trivittatus</i>
males did not attend clutches	males attended clutches
no correlation between territory (= clutch) defence and hatching success	no correlation between clutch attendance (= no. of visits) and hatching success
53% hatching success (= eggs laid/transported tadpoles)	45% hatching success
tadpoles were carried to water by males	
females neither visited their clutches nor carried tadpoles	

TABLE 5. Summary of brood care.

ACKNOWLEDGEMENTS

I thank C. Vasquez and his family for their help in Peru, my parents for supporting my way of life, Professor Friedrich Schaller for steady encouragement and fruitful discussions, Günther Gollmann and Walter Hödl for their valuable comments on earlier drafts of the manuscript, J. Plant for correcting my English, and Christian Listabarth for living with me in South America and Vienna. Financial support was provided by the "Bundesministerium für Wissenschaft und Forschung", the "Theodor-Körner Fonds", and the Austrian "Fonds zur Förderung der wissenschaftlichen Forschung" (P7314).

REFERENCES

- Aichinger, M. (1991). Tadpole transport in relation to rainfall, fecundity and body size in five species of poison-dart frogs from Amazonian Peru. *Amphibia-Reptilia* **12**, 49-55.
- Crump, M. L. (1972). Territoriality and mating behavior in *Dendrobates granuliferus* (Anura: Dendrobatidae). *Herpetologica* **28**, 195-199.
- Daly, J. W., Myers, Ch. W. & Whittaker, N. (1987). Further classification of skin alkaloids from Neotropical poison frogs (Dendrobatidae), with a general survey of Toxic/Noxious substances in the amphibia. *Toxicon* **25**, 1023-1095.
- Dawkins, R. & Carlisle, T. R. (1976). Parental investment, mate desertion and a fallacy. *Nature* **262**, 131-132.
- Dole, J. W. & Durant, P. (1974). Courtship behavior in *Colostethus collaris* (Dendrobatidae). *Copeia* **1974** 988-990.
- Gerhardt, H. C. (1991). Female mate choice in treefrogs: static and dynamic acoustic criteria. *Anim. Behav.* **42**, 615-635.
- Gross, M. R. & Shine, R. (1981). Parental care and mode of fertilization in ectothermic vertebrates. *Evolution* **35**, 775-793.
- Hödl, W. (1983). *Phylllobates femoralis* (Dendrobatidae): Rufverhalten und akustische Orientierung der Männchen (Freilandaufnahmen). Begleitveröffentlichung zum Film C 1788 d. BHWK Wien; *Wiss. Film Nr. 30*, 12-19.
- Junca, F. A. (1989). Biología reproductiva de *Colostethus marchesianus* e *Colostethus* sp. (Amphibia: Anura: Dendrobatidae). In *Resumos XVI Congresso Brasileiro de Zoologia*, **64**. Christoffersen, M. L. & Amorim, D. S. (Eds). Joao Pessoa, Paraíba.
- Lima, A. P. (1992). Effects of prey size and foraging mode on the ontogenetic change in the feeding niche of *Colostethus stepheni* (Anura, Dendrobatidae). Unpubl. PhD. thesis, Manaus, Brasil.
- Maynard Smith, J. (1977). Parental investment: A prospective analysis. *Anim. Behav.* **25**, 1-9.
- McDiarmid, R. W. (1978). Evolution of parental care of frogs. In *The development of behavior: Comparative and evolutionary aspects*, 127-147. Burghardt G. M. & Beckoff M. (Eds). New York: Garland.
- McVey, M. E., Zahary, R. G., Perry, D. & Macdougall, J. (1981). Territoriality and homing behavior in the poison dart frog (*Dendrobates pumilio*). *Copeia* **1981**, 1-8.
- Myers, C. W. (1987). New generic names for some neotropical poison frogs (Dendrobatidae). *Papéis Avulsos Zool., S. Paulo* **36**, 301-306
- Ridley, M. (1978). Paternal Care. *Anim. Behav.* **26**, 904-932.
- Roithmair, M. E. (1992). Territoriality and male mating success in the dart-poison frog, *Epipedobates femoralis* (Dendrobatidae, Anura). *Ethology* **92**, 331-343.
- Roithmair, M. E. (1994) Male territoriality and female mate selection in the dart-poison frog, *Epipedobates trivittatus* (Dendrobatidae, Anura). *Copeia* **1994**, 107-115.
- Salthe, S. N. & Mecham, J. S. (1974). Reproductive and courtship patterns. In *Physiology of the Amphibia* (Vol. 2), 209-521. Lofts, B. (Ed). New York: Academic Press.
- Schlüter, A. (1980). Bioakustische Untersuchungen an Dendrobatiden in einem begrenzten Gebiet des tropischen Regenwaldes von Peru (Amphibia: Salientia: Dendrobatidae). *Salamandra* **16**, 149-161.
- Silverstone, P. A. (1976). A revision of the poison-arrow frogs of the genus *Phylllobates* Bibron in Sagra (Family Dendrobatidae). *L. A. Nat. Hist. Mus. Sci. Bull.* **27**, 1-53.
- Summers, K. (1989). Sexual selection and intra-female competition in the green poison-dart frog, *Dendrobates auratus*. *Anim. Behav.* **37**, 797- 805.
- Summers, K. (1990). Paternal care and the cost of polygyny in the green dart-poison frog. *Behav. Ecol. Sociobiol.* **27**, 307-313.
- Summers, K. (1992). Mating strategies in two dart-poison frogs: a comparative study. *Anim. Behav.* **43**, 907-919.
- Toft, C. A. (1980). Feeding ecology of thirteen syntopic species of anurans in a seasonal tropical environment. *Oecologia* **45**, 131-141.
- Townsend, D.S., Stewart, M. M., & Pough, F. H., (1984). Male parental care and its adaptive significance in a neotropical frog. *Anim. Behav.* **32**, 421-431.
- Trivers, R. L. (1972). Parental investment and sexual selection. In *Sexual selection and the descent of Man 1871 - 1971*, 136-179. Campbell, B. (Ed). Chicago: Aldine.
- Wells, K. D. (1977). The courtship of frogs. In *The reproductive biology of amphibians*, 233-262. Taylor, H. & Guttman, S. I. (Eds). New York: Plenum Press.
- Wells, K. D. (1980a). Behavioral ecology and social organization of a dendrobatid frog (*Colostethus inguinalis*). *Behav. Ecol. Sociobiol.* **6**, 199-209.
- Wells, K. D. (1980b). Social behavior and communication of a dendrobatid frog (*Colostethus trinitatus*). *Herpetologica* **36**, 189-199.
- Wells, K. D. (1981). Parental behavior of male and female frogs. In *Natural selection and social behavior: Recent research and new theory*, 184-197. Alexander, R. D. & Tinkle, D. W. (Eds). Newton, Mass.: Chiron Press.
- Weygoldt, P. (1980a). Zur Fortpflanzungsbiologie von *Phylllobates femoralis* (Boulenger) im Terrarium

- (Amphibia: Salientia: Dendrobatidae). *Salamandra* **16**, 215-226.
- Weygoldt, P. (1980b). Complex brood care and reproductive behavior in captive poison-arrow frogs, *Dendrobates pumilio* O. Schmidt. *Behav. Ecol. Sociobiol.* **7**, 329-332.
- Weygoldt, P. (1987). Evolution of parental care in poison dart frogs (Amphibia: Anura: Dendrobatidae). *Z. Zool. Syst. Evolutionsforsch.* **25**, 51-67.
- Zimmermann, E. (1990). Behavioral signals and reproduction modes in the neotropical frog family Dendrobatidae. In *Fortschritte der Zoologie (Vol.38): Biology and Physiology of Amphibians*, 41-60. Hanke, W. (Ed.). Stuttgart, New York: Gustav Fischer Verlag.

Accepted: 25.10.93