MATING AND AGGRESSIVE BEHAVIOUR IN DENDROBATID FROGS FROM CORCOVADO NATIONAL PARK, COSTA RICA: A COMPARATIVE STUDY

by

KYLE SUMMERS[1]
(Department of Biology, East Carolina University, Greenville, NC, USA 27858 and
Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama)

(Acc. 19-IV-1999)

Summary

1. Mating and aggressive behaviour was observed in four species of dendrobatid frogs in Corcovado National Park, Costa Rica: *Colostethus nubicola*, *Colostethus talamancae*, *Phyllobates vittatus* and *Dendrobates granuliferus*.

2. Males of both species of *Colostethus* were more likely to respond to call playbacks than male *P. vittatus* or *D. granuliferus*. Male *D. granuliferus* were less likely to be found calling than males of the other species. Conspecific male-male aggression was observed in *P. vittatus*, but not in the other species.

3. Females were more active during courtship in *P. vittatus*. Female-female aggression was observed on one occasion in *P. vittatus*. Females were more likely to reject males than the reverse in all species.

4. These observations suggest that sexual conflict occurs in *P. vittatus*, but not in *C. nubicola* or *C. talamancae*.

Introduction

Theoretical and empirical research indicates that several different factors can cause sexual selection to act on males and females. The most important of

---

[1] I thank K.D. Wells, A.G. Kluge, R.D. Alexander, R. Wrangham, A.S. Rand, B. Hazlett, M. Daly and two anonymous reviewers for comments on previous versions of this manuscript, and L. Gilbert for discussion and advice at Sirena Biological Station. I thank the Costa Rican National Parks Service for research and marking permits. Special thanks to C. Housel for assistance in the field. Funding for this research was provided by the Smithsonian Tropical Research Institute.

these is probably the degree of asymmetry in the amount of time and effort each sex typically invests in producing offspring (Trivers, 1972; Clutton-Brock & Parker, 1992; Arnold & Duvall, 1994, Johnstone *et al.*, 1996). Asymmetry between the sexes in the typical amount of parental investment favors competition by the sex investing less to mate with multiple members of the sex investing more. It also raises the cost of selectivity in the sex investing less, causing members of this sex to be less choosy about mating (Johnstone *et al.*, 1996).

The degree of variation in mate quality between individuals of one sex also has an important effect on sexual selection on the opposite sex (Petrie, 1983; Owens & Thompson, 1994; Johnstone *et al.*, 1996). Variation in quality in one sex favors selectivity in the opposite sex. When the typical parental effort provided by each sex is similar, variation in quality in one sex also favors competition for the highest quality mates by members of the opposite sex.

If there is potential variation in the amount of parental investment provided by an individual of one or both sexes, then conflict between the sexes over the allocation of parental resources is also a potential source of sexual selection (Trivers, 1972; Davies, 1989; Summers, 1989, 1992b). When members of one sex vary in the quality or quantity of parental investment they provide for their offspring as a function of the number of mates they have (and the number of offspring they consequently invest in), then sexual selection favors aggressive mate guarding and selectivity about mating in the opposite sex.

These factors are not independent and all of them may influence the nature and intensity of sexual selection acting on males and females in a particular species. Nevertheless, each produces specific selection pressures that are not predicted by the others alone.

Studies of species within the family Dendrobatidae (poison frogs and their non-toxic close relatives) have revealed complex patterns of aggression, courtship, mating and parental behaviour (*e.g.* Wells, 1977, 1978, 1980a, b, 1981; Weygoldt, 1987; Zimmerman & Zimmermann, 1988).

Within the genus *Dendrobates*, comparisons of males and females within species with male parental care, and comparisons between species with male and female parental care, suggest that potential variability in the quality of male parental care leads to female-female aggression (Summers, 1989, 1990, 1992a). This aggression occurs because females suffer a cost when their mates mate with other females and care for their offspring (Summers, 1989, 1990), leading to intersexual and intrasexual conflict over the allocation of male parental care.

Competition between females may also occur because of sex role reversal, as proposed by Trivers (1972). Dendrobatid frogs have been proposed as possible examples of sex role reversal (*e.g.* Trivers, 1972; Ridley, 1978; Wells, 1978). In order for sex role reversal to occur, average levels of male parental care must be so expensive that receptive males become rare relative to receptive females in the population (Wells, 1981). The reproductive success of females would then be limited by their ability to find mates, and females would actively court and compete for multiple mates (Trivers, 1972).

Intersexual conflict over the allocation of parental investment by males can cause mate guarding and female aggression (see above). This can occur without sex role reversal, and hence can provide an alternative explanation for female-female aggression (Summers, 1989, 1992b). I will call this the sexual conflict hypothesis, to be consistent with descriptions of similar phenomena in other species (*e.g.* Davies, 1989). Conflict occurs both between males and females and between females under this hypothesis.

This study compares the mating and aggressive behaviour of three species of dendrobatid frogs with paternal care, *Phyllobates vittatus*, *Colostethus talamancae* and *Colostethus nubicola*, and one species with primarily maternal care, *Dendrobates granuliferus*. In *D. granuliferus*, females carry tadpoles to pools in plant leaf axils (phytotelmata), and then return periodically to each pool to feed the tadpole with infertile eggs. In contrast, male parental care in this species is restricted to brief periodic egg attendance, involving movement and moistening of the eggs (Meyer, 1992; van Wijngaarten & Bolanos, 1992).

There have been several field studies of mating and aggressive behaviour in *Colostethus* (*e.g.* Wells, 1980a, b). *Colostethus nubicola* has male parental care, in which the entire clutch of tadpoles is carried to a small stream and released (Wells, 1981). Parental care appears to be carried out by males in the population of *C. talamancae* surveyed in this study. Males and females are sexually dimorphic (males have a dark throat and chest, whereas the underside of females is white), and so can be distinguished in the field. Males were seen carrying clutches of tadpoles on seven occasions (including three marked, resident males who were seen calling on many occasions). On two occasions males were observed to carry the tadpoles to small streams (the other five males were not followed). However, females have been observed carrying tadpoles in a different population of *C. talamancae* in Panama (K.D. Wells, pers. comm.).

There have been no published field studies of behaviour in *P. vittatus*, or any other species in the genus *Phyllobates*, although research has been carried out on captive animals (*e.g.* Zimmermann & Zimmermann, 1985). As in other species of *Phyllobates*, males of *P. vittatus* carry multiple tadpoles on their back from the leaf litter to water (Silverstone, 1976). Field collections of tadpoles suggest that this species utilizes small pools that occur in treeholes and fallen leaf petioles (Silverstone, 1976).

In this paper, comparisons among these four species are used to investigate the degree to which the behaviour of males and females in *P. vittatus*, *C. talamancae* and *C. nubicola* depart from expectations derived from the sexual conflict and sex role reversal hypotheses.

The following predictions are derived from the sexual conflict and the sex role reversal hypotheses, respectively. The sexual conflict hypothesis predicts that:

1) Males will compete for females in species with male parental care.
2) Females in species with male parental care will compete for males more frequently and intensely than females in species with female parental care.
3) Females in species with male parental care will compete for a single male through aggressive mate guarding; they will associate with a male and attempt to prevent other females from mating with that male.
4) Females will be more selective about mating than males in species with male parental care.
5) Males in species with male parental care will be moderately more selective about mating than males in species with female parental care.

The sex role reversal hypothesis predicts that:

1) Females will compete for males more frequently and aggressively than males compete for females in species with male parental care.
2) Females in species with male parental care will compete for males more frequently and intensely than females in species with female parental care.
3) Females in species with male parental care will compete for multiple males as mates.
4) Males will be more selective than females about mating in species with male parental care.
5) Males in species with male parental care will be highly selective about mating compared to males in species with female parental care.

Methods

The study was carried out near the Sirena Biological Station, in Corcovado National Park, on the Osa Peninsula, in Costa Rica, Central America. The research was conducted during July and August, 1989. Field observations were made between 0800 and 1700 hrs, in lowland wet tropical forest.

Observations on *P. vittatus*, *C. nubicola* and *C. talamancae* were made in two study plots: a 22 by 42 m plot on the south side of a shallow stream (this plot will be referred to as plot 1a), and an 8 by 60 m plot that followed the contours of a ravine created by a narrow stream (this plot will be referred to as plot 1b). These plots were approximately 60-70 m apart, and were located approximately seven km east of the Sirena Biological Station, near the Pavo River on the trail to the Los Patos ranger station. Plot 1a was marked with red flags at two meter intervals, to form a rectangular grid. In plot 1b, flags were placed at one meter intervals down the length of the ravine, and flags were placed at two meter intervals to the north and south of the stream (on the sides of the ravine). Flags in both plots were numbered, and were used to record the location of each marked individual each time it was sighted.

These two study plots differed in the number of resident males (see below) of each species present. Six resident male *C. talamancae* and three resident male *C. nubicola* were observed in plot 1a, whereas no *P. vittatus* were seen in plot 1a frequently enough to be classified as residents. In contrast, no *C. talamancae* or *C. nubicola* males were found in plot 1b (although males were found just outside the site, above the banks of the ravine). There were nine resident male *P. vittatus* in plot 1b.

Observations on *D. granuliferus* were made in two plots along Skyline Trail, approximately five km southeast of the Sirena Biological Station. Both plots were located on a hillside near the top of a ridge, approximately 200 meters apart. Plot 2a (22 by 27 m) was marked with flags in the same fashion as plot 1b. The outline of plot 2b (17 by 17 m) was marked, but flags were not used to form a grid within the plot. Seven resident male *D. granuliferus* were found in plot 2a, and eight in plot 2b.

Observations were carried out by searching the study areas and recording where and when individual frogs were sighted, and the behaviour they were engaged in when seen. Unmarked frogs seen during searches of each plot were caught, measured (snout-vent length), and marked.

Identification of individuals using natural markings was not possible, so they were given two types of identification mark. A unique combination of colored beads was tied around the waist of each frog when it was first captured, using cotton thread soaked in paraffin or waxed dental floss. This procedure allowed identification of each individual from a distance, without the need for recapture. Each frog was also toe-clipped in a unique pattern, to allow identification in case the identifying beads were lost.

During searches of the study areas, I attempted to identify (or capture and mark if unmarked) each individual sighted. The location of each individual observed in plot 1a, plot 1b and plot 2a was estimated to the nearest square meter, to allow comparisons of nearest neighbor distances among frogs in these plots.

Estimates of home range location and size were made by plotting the locations of all sightings of each individual on a map (on graph paper) of each study site that was marked with a grid (plots 1a, 1b and 2a). A rough estimate of home range was made by drawing a line connecting the outermost sighting locations of each male, to form a polygon. Home range sizes were estimated by summing the square meter blocks (and proportions thereof) enclosed by each polygon. Nearest neighbor distances and average distances among all resident males were calculated in two ways: 1) from the center of each male's home range polygon (estimated by eye), and 2) from the nearest edges of each male's home range polygons.

Physical aggression (seen almost exclusively in *P. vittatus*) was characterized by wrestling, with each frog attempting to grasp the other from behind and push it down onto the substrate. Face to face grappling also occurred, in which both frogs attempted to push each other backwards. In males, such grappling was accompanied by calling.

For the purpose of analysis, males who were recaptured after at least ten days, and were seen in the same area on at least four different days, were considered to be territorial residents. Only residents were used in the analysis of calling behaviour.

Calls were played at the areas where males were captured in order to determine how responsive they were to intrusions by other males. Due to equipment failure and weather conditions, calls were not played at each male's area every time that area was visually scanned. The word 'trial' will be used to denote only instances when the area was visually scanned and calls were played.

Calls were recorded from single calling males in the field using an Audio-Technica microphone (model AT9400) and a General Electric cassette tape recorder (model 3-5016D). Calls were played at the areas occupied by marked males for 1 minute (from the edge of the area they were caught in), and presence or absence of a response within five minutes of the playback (calling back and/or moving toward calls) was recorded. Calls were played at the frogs with a General Electric model 3-5016D, or model 3-5300B cassette tape recorder. The volume setting was placed at the highest level with the smaller model (model 3-5300B), and at three quarters of full volume for the larger model, which yielded sound levels that sounded equivalent to me when played at a distance of one meter.

I was unable to control the distance from the frog at which calls were played exactly, because I did not always know where the frog was at the start of the playback. However, all cases in which frogs seen to be present did not respond to calls were within the maximum distance at which frogs responded on other occasions. Hence, it is unlikely that a male's lack of response when he was known to be present was a result of inability to perceive the stimulus. If two or more individuals were observed interacting, then the search was interrupted and the individuals were observed until the end of the interaction.

The criteria used to classify the terminations of female-male encounters were as follows: A female was considered to have rejected a male if she courted him and then moved away from or did not respond to him while he continued to call to her, follow or stroke her. A female was considered to have ignored a male if she moved away or did not respond when he approached or called to her, followed or stroked her. The reciprocal occurrences were taken as evidence for a male rejecting or ignoring a female, respectively. The 'Separate' category refers to instances when the male and female separated without clear rejection by either party.

Statistical analyses were performed with StatView (Abacus Concepts, 1992). The residuals were examined for homogeneity of variances and departures from normality when parametric ANOVAs were used. Statistical comparisons between the calling behavior of males of different species were made by calculating the relevant percentage for each male (*e.g.* the percentage of trials in which a male responded to calls over the course of the study) and then averaging across males within each species to obtain a species level parameter.

Results

Male aggression

Resident males of all three species were seen repeatedly near the area where they were first captured (within a few meters). The density of resident males within the grid, and estimates of home range size and nearest neighbor distances are given in Table 1.

Average home range sizes appeared to differ between the species (Table 1). The variances for average home range size among species were not homogeneous, so a Welch's test (a one-way ANOVA robust to non-homogeneity of variances) was used. This test revealed significant differences in home range size ($N = 25, p < 0.02$), but post-hoc tests are not available to determine which means are significantly different. There were no significant differences among resident males of each species in the average distance to the nearest neighbor, measured from the center of each resident male's home range (Welch's test, $N = 25, p = 0.415$), or from the edge of the home range (Welch's test, $N = 25, p = 0.193$). There were no significant differences among species in the average distance between resident males (for all possible pairwise comparisons), whether calculated from the center of each male's home range (one-way ANOVA, $N = 75$, df = 3, $F = 0.467, p = 0.707$), or from the edge of each male's home range (one-way ANOVA, $N = 75$, df = 3, $F = 0.848, p = 0.472$).

Males of all species usually responded aggressively when calls were played at them, by either calling at the recorder, moving toward it, or both. Males of each species engaged in calling bouts, in which males calling near each other (within 5 m) would call alternately. Male *P. vittatus* were seen fighting with other males in their areas ($N = 6$ fights). Male *C. talamancae* were not seen fighting with other males of their own species, although one male *C. talamancae* was observed attacking a male *C. nubicola*, apparently in response to his call. *Dendrobates granuliferus* males were not observed fighting, but physical aggression between males has been reported previously in this species (Goodman, 1971; Crump, 1972). These observations suggest that males of *P. vittatus*, *C. talamancae* and *D. granuliferus* are territorial.

In order to assess the intensity of competition for mates among males of the different species, I compared three aspects of calling behaviour and one aspect of physical aggression between species.

TABLE 1. *Estimates of population parameters for the resident males of four species of poison frogs in this study*

Species	Plot	Density	Home range	Nearest N1	Nearest N2	Dist 1	Dist 2
P. vittatus	Plot 1b	$0.019/m^2$	$6.0 \pm 7.0\ m^2$	5.6 ± 3.4 m	2.1 ± 3.8 m	17.1 ± 10.8 m	14.0 ± 11.2 m
C. talamancae	Plot 1a	$0.007/m^2$	$13.1 \pm 4.4\ m^2$	4.5 ± 0.8 m	0.4 ± 0.6 m	14.9 ± 7.4 m	10.13 ± 7.3 m
C. nubicola	Plot 1a	$0.003/m^2$	$5.8 \pm 2.9\ m^2$	9.0 ± 10.0 m	6.7 ± 9.4 m	16.6 ± 10.3 m	13.7 ± 9.7 m
D. granuliferus	Plot 2a	$0.012/m^2$	$2.8 \pm 1.4\ m^2$	10.1 ± 8.0 m	7.8 ± 7.8 m	19.2 ± 12.3 m	16.0 ± 11.7 m
D. granuliferus	Plot 2b	$0.028/m^2$	–	–	–	–	–

Abbreviations are as follows: Density: the number of resident males per square meter on each plot; Home range: a minimum estimate of the average home range size in each species (see methods); Nearest N1: the average nearest neighbor distance between resident males, calculated from the center of each resident male's home range; Nearest N2: the average nearest neighbor distance between resident males, calculated from the edge of each resident male's home range. Dist 1: the average distance between resident males of each species, calculated from the center of each male's home range. Dist 2: the average distance between resident males of each species, calculated from the edge of each male's home range. The mean plus or minus one standard error is shown for each value.

(1) The percentage of trials in which the male responded to calls when observed: the percentage of trials in which a male responded to calls when he was known to be present (*i.e.* the male was observed in his territory before calls were played) was taken as a measure of a male's willingness to defend his territory against intruders, which in turn should correlate with the intensity of competition over mates. A male was considered to have responded aggressively if he either called back in response to the playback, or moved toward the calls (apparently searching for the calling intruder). The data for this parameter were non-normally distributed, so a Kruskal-Wallis analysis of variance was used. This analysis showed no significant differences between males of the three species in the percentage of calls to which they responded when known to be present (Kruskal-Wallis test, $N = 32, H = 2.173, p = 0.537$).

(2) The percentage of trials in which a male responded to calls played at his area: males may compete for females by remaining alert and available in their territories, and differences in the probability of response to calls could reflect differences between species in the importance of attracting females, and hence differences in the intensity of competition for females among males of different species. For the comparisons, I only used data from trials which occurred up to the last date the male was seen in his territory, and hence known to be still alive.

There were significant differences between species in the proportion of trials in which males responded to calls (Fig. 1, One-way ANOVA, $N = 32$, df $= 3$, $F = 5.77$, $p < 0.005$). Post-hoc multiple comparison tests using Fisher's PLSD revealed that *C. nubicola* and *C. talamancae* males were significantly more likely to respond than either *P. vittatus* males and *D. granuliferus* males, although the more conservative Bonferroni/Dunn post-hoc tests revealed significant differences only between *C. nubicola* and two other species: *P. vittatus* and *D. granuliferus*.

(3) The percentage of samples in which the male was found calling when present: one way of competing for females may be for males to spend more time calling when they are in their territories, trying to attract females. I recorded whether or not a male was calling from his territory when I approached it, before calls were played, as a measure of the time that males were putting into advertising their territories (presumably to attract females as well as to warn males). I calculated the number of samples in which a male was found calling in his territory divided by the total number of samples in

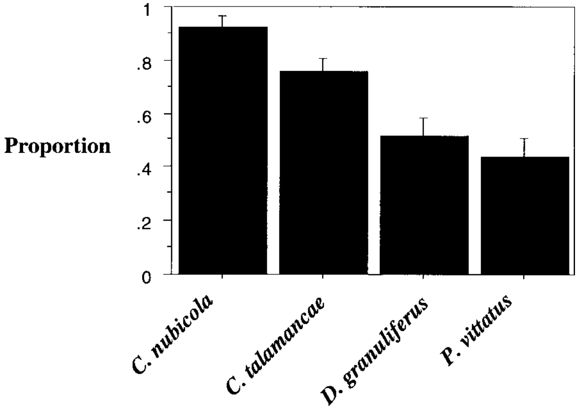

Fig. 1. The proportion of trials in which resident males responded to calls played at their territories.

which the male was seen in his territory. This ratio was used as an estimate of the probability that a male would be calling to attract females at any time that he was in his territory, and compared between species.

The ANOVA revealed overall significant differences among species (Fig. 2, one-way ANOVA, $N = 32$, df $= 3$, $F = 13.342$, $p < 0.0001$). There were significant differences only between *D. granuliferus* and the other three species, all of whom were more likely to be found calling than *D. granuliferus*. Differences were significant with both Fisher's PSLD and Bonferonni/Dunn post hoc tests.

(4) Frequency of fights: the number of bouts of physical aggression between males was taken as an indicator of the intensity of male-male competition for mates. The frequency of aggression was measured as the number of bouts per hour of observation. Physical aggression was seen between *P. vittatus* males on six occasions (0.05 fights per hour of observation in plot 1a and 1b). *Colostethus nubicola*, *C. talamancae* or *D. granuliferus* males were never observed fighting with conspecifics.

Female competition

Female-female competition was observed on only one occasion in any of the four species. Two female *P. vittatus* fought for 40 minutes for a calling male in plot 1b. The male followed the females while they wrestled, calling. Unfortunately, the male moved away and hid near the end of the fight (I may have startled him by moving too close), and so when the two females

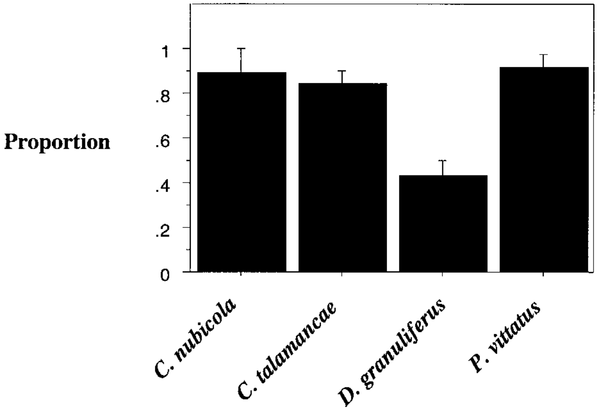

Fig. 2. The proportion of samples in which resident males were found calling in their territories.

separated I captured them both without determining which one would have remained with the male.

Female-male associations

Females were seen less frequently than males, and appeared to hide or flee more readily than males in all four species. Females were observed associating with the same male more than once only in *P. vittatus*: female QFP27 was seen fighting for male QMP17 on August 17th, and was then seen courting with the same male in the same area three days later. Female QFP18 was seen courting with male QMP3 on the 23rd of July and the 11th of August, and was seen in that male's area on three other occasions over a 25 day period. This female was not observed in any other area.

Courtship and selectivity

Encounters between male and female *P. vittatus* were observed on 24 occasions, and the encounter termination was observed in 18 of these cases (Table 2). The male called at the female in each case. Females followed and actively courted males by stroking, nudging, or climbing on them on eleven occasions. Females were significantly more active in tactile stimulation than males in this species (Wilcoxon signed ranks test, $N = 22$, $z = -2.341$, $p < 0.05$). Nevertheless, female *P. vittatus* typically rejected males after courting them actively (Table 2).

TABLE 2. *The results of observed encounter terminations in three species of dendrobatids*

	C. talamancae	*P. vittatus*	*D. granuliferus*
Female rejects	1 (33%)	11 (61%)	1 (12%)
Female ignores	2 (66%)	5 (28%)	7 (87%)
Separate	0	2 (11%)	0

Behavioral categories are described in the methods section.

Encounters between male and female *C. talamancae* were observed on only three occasions (Table 1). Courtship was seen during one encounter. The courtship lasted five and one half hours, but did not result in oviposition. During the courtship, the female followed the male occasionally, but was otherwise inactive or involved in foraging. The male called repeatedly throughout the entire courtship, and performed several different postural displays repeatedly, involving crab-like sideways walking back and forth in front of the female, arching of the dorsum and raising of the hind quarters, and exaggerated inflating and deflating of the body with air.

Encounters between male and female *D. granuliferus* were seen on 17 occasions, and the encounter termination was observed in eight of these cases (Table 2). Males approached and called at females during all encounters. Females usually ignored males when approached. No encounters were seen between *C. nubicola* males and females.

Table 2 shows the results of all cases for which the encounter terminations were observed, for each species. Oviposition was not observed in any species. Females rejected or ignored males in all or almost all encounters in each species, whereas males were not observed to reject or ignore females in any species. The sample sizes for *D. granuliferus* and *C. talamancae* were too small for statistical analysis, but females were significantly more likely to ignore or reject males than the reverse in *P. vittatus* (X^2 test, $N = 16$, $X^2 = 10.667, p = 0.0011$).

Discussion

Calling and life history

The data on calling behaviour revealed several unexpected results; *P. vittatus*, *C. talamancae* and *C. nubicola* were all more likely to be found calling than

D. granuliferus. This result was completely unexpected, and the reason for it is unknown. It is possible that *D. granuliferus* males were more likely to detect the approach of the observer and stop calling, and hence less likely to be found calling.

Colostethus nubicola and *C. talamancae* males were significantly more likely to call back when calls were played at their areas than the other two species of dendrobatids, suggesting that males of these species of *Colostethus* are spending more time above the leaf litter and available on their territories. In a further comparison of *C. talamancae* and *P. vittatus*, I recorded the number and species (*P. vittatus* or *C. talamancae*) of all calls heard during a two minute period, every fifteen minutes during the searches of plot 1a and 1b during the second half of the field study. Significantly more *C. talamancae* calls were heard in both plot 1a (Fig. 3, Wilcoxon signed ranks tests, $N = 7$, $z = -2.371$, $p < 0.05$) where *C. talamancae* was more abundant, and in plot 1b (Fig. 3, Wilcoxon signed ranks tests, $N = 8$, $z = -2.313$, $p < 0.05$), where *P. vittatus* was more abundant.

There are several possible explanations for these results. One possibility is that males of the two species of *Colostethus* are spending more time advertising because they invest less in paternal care, and hence have more time to advertise. This hypothesis does not fit with the observation that *C. talamancae* and *C. nubicola* males responded more frequently than *D. granuliferus* males, which perform less parental care.

Another possibility is that males of the two species of *Colostethus* are less vulnerable to predation, but this hypothesis contradicts the fact that *Colostethus* are much less toxic than either *Phyllobates* or *Dendrobates* (Myers & Daly, 1983).

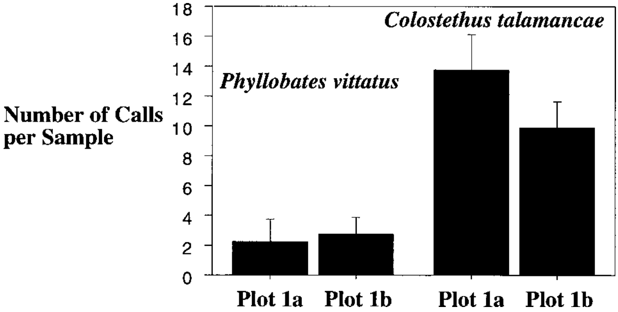

Fig. 3. The average number of calls per sample for *C. talamancae* and *P. vittatus*, in Plot 1a and 1b.

Another possibility is that males of the two species of *Colostethus* are not subject to guarding by their mates, whereas *Dendrobates* males (in species with male parental care), are, and *Phyllobates* males may be (see below). However, this hypothesis does not explain why *C. talamancae* and *C. nubicola* males were more likely to respond in a given trial than *D. granuliferus* males, a species with primarily female parental care in which there is no evidence for mate guarding by females.

It is also possible that males of *C. nubicola* and *C. talamancae* are more strongly territorial than males of *P. vittatus* or *D. granuliferus* because they are defending different resources. It is not clear what such resources would be, however, and strong territorial behaviour has not been found in other species of *Colostethus* with male parental care (*e.g. C. trinitatis*, Wells, 1980a).

Finally, it is possible that males of the two species of *Colostethus* spend more time calling because they face a different life history tradeoff than males in *Phyllobates* and *Dendrobates*. Males in these two species are highly toxic, and hence are unlikely to suffer much mortality through predation. Captive specimens of *Dendrobates auratus*, another highly toxic species, have been found to live over 20 years in captivity (C. Toft, pers. comm.). *Colostethus* are relatively non-toxic, and high levels of predation by snakes have been reported for at least one species (Sexton, 1960).

If predation rates on *Colostethus* are high, but relatively independent of time spent advertising for mates, then male *Colostethus* might profit by spending as much time as possible advertising for mates during the breeding season. *Dendrobates* and *Phyllobates*, on the other hand, might face a different life history tradeoff: if males of this species typically survive over many breeding seasons, then it may pay males to take a more conservative, opportunistic strategy with respect to advertising for mates.

This hypothesis predicts that territorial males in the highly toxic *Dendrobates* and *Phyllobates* species will tend to be older than their counterparts in *Colostethus*. This prediction could be tested by using skeletochronology to estimate the age of individuals captured in the field.

Sexual conflict in Phyllobates and Colostethus

Phyllobates vittatus was the only species in which males were observed fighting, although a *C. talamancae* was seen attacking a male *C. nubicola*, and *D. granuliferus* males have been observed fighting in two other field studies (Goodman, 1971; Crump, 1972). Resident *P. vittatus* males had larger home ranges than *D. granuliferus* resident males, and smaller nearest neighbor distances (Table 1), although the nearest neighbor differences were not statistically significant. These results suggest that *P. vittatus* males might be more likely to encounter neighboring males, making aggressive interactions more likely. The fact that *P. vittatus* males were observed fighting more often suggests that they are at least as aggressive as *D. granuliferus* males. The results of the call playbacks did not indicate that *D. granuliferus* males are more aggressively territorial than *P. vittatus* males. For *P. vittatus*, this contradicts a prediction of the sex-role reversal hypothesis, but is consistent with the sexual conflict hypothesis.

Female-female competition for mates was observed in *P. vittatus* but not in either species of *Colostethus* or in *D. granuliferus*. The patterns of association between some males and females in *P. vittatus* were consistent with the prediction of mate guarding by females derived from the sexual conflict hypothesis, in that one female was seen courting with a male she had fought for several days previously, and another female was seen courting with the same male twice over a period of three weeks. These observations, although small in number, are similar to more extensive observations of female mate guarding in two species of *Dendrobates* with male parental care, *Dendrobates auratus* (Summers, 1989) and *Dendrobates leucomelas* (Summers, 1992a).

Females were not observed associating more than once with the same male in either species of *Colostethus* or in *D. granuliferus*. Females courted males actively in *P. vittatus*, but were not seen to do so in either *Colostethus* or *D. granuliferus*. For *P. vittatus*, this observation is consistent with both the sexual conflict and sex role reversal hypotheses.

The results of the encounter terminations show that females frequently rejected or ignored males in all three species for which encounter data were available, whereas males were not observed to reject or ignore females in any of the species. These data are consistent with the prediction from the sexual conflict hypothesis that females will be more selective than males about mating.

Overall, the data from the observations on *P. vittatus* are consistent with predictions derived from the sexual conflict hypothesis, although the small sample size of the observations makes further research necessary before firm conclusions can be reached.

In contrast, the lack of female-female aggression in either species of *Colostethus*, and the limited data on male-female association patterns in *C. talamancae*, do not support the prediction of mate guarding by females derived from the sexual conflict hypothesis. There was no evidence that females of either species of *Colostethus* associate with a particular male and attempt to prevent other females from mating with him. The data also did not support the prediction of intense female-female aggression and high male selectivity about mating derived from the sex-role reversal hypothesis. These results are consistent with observations on the mating behaviour of females in other species of *Colostethus* with male parental care (Wells, 1980a, 1981).

The explanation for the lack of female competition over males in this genus may be related to the nature of parental care in this group. *Colostethus* usually deposit their tadpoles in streams, rather than in the small pools of water (*e.g.* in treeholes) which are used by species of *Dendrobates* with male parental care. In species of *Dendrobates* with male parental care, the use of small pools may mean that polygyny imposes an important cost on offspring survivorship through either cannibalism or reduced growth rates of tadpoles (Summers, 1990). This cost may not exist for *Colostethus* females whose mates mate with other females, because of the difference in the nature of the tadpole deposition site. Furthermore, *Colostethus* males carry all the tadpoles in a clutch to water at once, whereas males in *Dendrobates* carry one tadpole at a time. Hence, the amount of time, per tadpole, taken to find a deposition site, may be higher in *Dendrobates*, and this might also cause polygyny to impose a higher cost on tadpole survivorship in *Dendrobates*.

Although members of the genus *Phyllobates* typically carry all tadpoles from a clutch at once (Zimmermann & Zimmermann, 1985), *P. vittatus* has been reported to use mainly small pools (Silverstone, 1976). If males deposit tadpoles from more than one mate in the same pool, this may lead to cannibalism or competition between half-sibs, and hence females might experience a cost of polygyny. This would be consistent with the observations of female-female competition and active courtship by females reported here.

References

Arnold, S.J. & Duvall, D. (1994). Animal mating systems: a synthesis based on selection theory. — Amer. Nat. 143, p. 317-348.

Clutton-Brock, T.H. & Parker, G.A. (1992). Potential reproductive rates and the operation of sexual selection. — Quart. Rev. Biol. 67, p. 437-456.

Crump, M.L. (1972). Territoriality and mating behaviour in *Dendrobates granuliferus* (Anura: Dendrobatidae). — Herpetologica 28, p. 195-198.

Davies, N.B. (1989). Sexual conflict and the polygamy threshold. — Anim. Behav. 38, p. 226-234.

Goodman, D.E. (1971). Territorial behaviour in a neotropical frog, *Dendrobates granuliferus*. — Copeia 1971, p. 365-370.

Johnstone, R.A., Reynolds, J.D. & Deutsch, J.C. (1996). Mutual mate choice and sex differences in choosiness. — Evolution 50, p. 1382-1391.

Meyer, E. (1992). Erfolgreiche nachzuct von *Dendrobates granuliferus* Taylor, 1958. — Herpetofauna 14(76), p. 11-21.

Myers, C.W. & Daly, J.W. (1983). Poison frogs. — Sci. Amer. 248, p. 120-133.

Owens, I.P.F. & Thompson, D.B.A. (1994). Sex differences, sex ratios and sex roles. — Proc. R. Soc. B 258, p. 151-156.

Petrie, M. (1983). Mate choice in role-reversed species. — In: Mate choice (P. Bateson, ed.). Cambridge University Press, Cambridge, p. 167-179.

Ridley, M. (1978). Paternal care. — Anim. Behav. 26, p. 904-932.

Sexton, O.J. (1960). Some aspects of the behaviour and of the territory of a dendrobatid frog, *Prostherapis trinitatis*. — Ecology 41, p. 107-115.

Silverstone, P.A. (1976). A revision of the poison-arrow frogs of the genus *Phyllobates* Bibron in Sagra (family Dendrobatidae). — L.A. Nat. Hist. Mus. Sci. Bull. 27, p. 1-53.

Summers, K. (1989). Sexual selection and intra-female competition in the green poison-dart frog, *Dendrobates auratus*. — Anim. Behav. 37, p. 797-805.

— — (1990). Paternal care and the cost of polygyny in the green dart-poison frog, *Dendrobates auratus*. — Behav. Ecol. Sociobiol. 27, p. 307-313.

— — (1992a). Mating strategies in two species of dart-poison frog: a comparative study. — Anim. Behav. 43, p. 907-919.

— — (1992b). Dart-poison frogs and the control of sexual selection. — Ethology 91, p. 89-107.

Trivers, R.L. (1972). Parental investment and sexual selection. — In: Sexual selection and the descent of man 1871-1971 (B. Campbell, ed.). Aldine, Chicago, p. 136-179.

van Wijngaarden, R. & Bolanos, F. (1992). Parental care in *Dendrobates granuliferus* (Anura, Dendrobatidae), with a description of the tadpole. — J. Herpetol. 26, p. 102-105.

Wells, K.D. (1977). The social behaviour of anuran amphibians. — Anim. Behav. 25, p. 666-693.

— — (1978). Courtship and parental behaviour in a Panamanian poison-arrow frog (*Dendrobates auratus*). — Herpetologica 34, p. 148-155.

— — (1980a). Social behavior and communication of a dendrobatid frog (*Colostethus trinitatis*). — Herpetologica 36, p. 189-199.

— — (1980b). Behavioral ecology and social organization of a dendrobatid frog (*Colostethus inguinalis*). — Behav. Ecol. Sociobiol. 6, p. 199-209.

— — (1981). Parental behaviour of male and female frogs. — In: Natural selection and social behaviour (R.D. Alexander & D.W. Tinkle, eds). Chiron Press, New York, p. 184-197.

Weygoldt, P. (1987). Evolution of parental care in dart poison frogs (Amphibia: Dendrobatidae). — Zeit. Zool. Syst. Evol.-forsch. 25, p. 51-67.

Zimmermann, H. & Zimmermann, E. (1985). Zur Fortpflanzungsstrategie des Pfeilgiftfrosches *Phyllobates terriblis* Myers, Daly & Malkin, 1978. — Salamandra 21, p. 281-297.

— — & — — (1988). Ethotaxonomie und zoographische Artenggruppenbildung bei Pfeilgiftfröschen (Anura: Dendrobatidae). — Salamandra 24, p. 125-160.