Parental investment, potential reproductive rates, and mating system in the strawberry dart-poison frog, *Dendrobates pumilio*

**Abstract** We studied the effect of relative parental investment on potential reproductive rates (PRRs) to explain sex differences in selectivity and competition in the dart-poison frog *Dendrobates pumilio*. We recorded the reproductive behavior of this species in a Costa Rican lowland rainforest for almost 6 months. Females spent more time on parental care than males, and ‘time out’ estimates suggest that PRRs of males are much higher than those of females, rendering females the limiting sex in the mating process. Males defended territories that provide suitable calling sites, space for courtship and oviposition, and prevent interference by competitors. Male mating success was highly variable, from 0 to 12 matings, and was significantly correlated with calling activity and average perch height, but was independent of body size and weight. Estimates of opportunity for sexual selection and variation in male mating success are given. The mating system is polygamous: males and females mated several times with different mates. Females were more selective than males and may sample males between matings. The discrepancy in PRRs between the sexes due to differences in parental investment and the prolonged breeding season is sufficient to explain the observed mating pattern i.e., selective females, high variance in male mating success, and the considerable opportunity for sexual selection.

**Key words** Potential reproductive rates · Parental investment · Territoriality · Sexual selection · *Dendrobates pumilio*

**Introduction**

The concept of parental investment has been used to explain sex differences in mating competition found in many animal reproductive systems (Trivers 1972). Emlen and Oring (1977) synthesized the evolution of animal mating systems, parental investment, sexual selection, resource defense, and environmental factors into a unified theory. They argued that when one sex becomes a limiting factor (e.g., due to high parental investment), the result is increased intrasexual competition among members of the opposite sex. A more recent approach introduced the concept of potential reproductive rates (PRRs, measured as the maximum number of independent offspring that parents can produce per unit time) in relation to the direction of mating competition (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). The PRR is inversely (but not exclusively) related to parental investment. Recently, it has been suggested that the costs of reproduction can be measured empirically as the parent’s ‘time out’, a principal component of PRR, which in turn relates directly to the operational sex ratio (OSR, the ratio of males to females ready to mate; Kvarnemo and Ahnesjö 1996). In this model, ‘time out’ is the processing time for a given reproductive event and ‘time in’ is the time spent on mate acquisition (Parker and Simmons 1996). The ratios of ‘time out’ are sufficient to predict the direction of mating competition: the sex with the lower ‘time out’ or the higher PRR competes more intensely for mates, whereas the sex with the higher ‘time out’ can afford to be selective and choose high-quality mates without loosing mating opportunities (Kvarnemo and Ahnesjö 1996; Parker and Simmons 1996).

Selective females and competing less selective males have been reported in several studies investigating the...
behavior of neotropical poison frogs (Dendrobatidae) (Summers 1989; Roithmair 1992, 1994). The inequality of relative parental investment and variance in male quality have been identified as factors causing sexual selection in this group (Summers 1992a,b). Two studies suggest that female mate choice is the reason for variance in male mating success and that male territoriality is associated with competition for females (Roithmair 1992, 1994). The direction of mating competition has not yet been analyzed in terms of PRR or OSR in these frogs. This study analyzes the mating system of Dendrobates pumilio within the framework of the above-mentioned concepts. The social behavior of D. pumilio seems particularly interesting, because males are territorial and their parental care is minimal, whereas females perform most duties associated with the care of offspring (Weygoldt 1980; McVey et al. 1981).

We test the following hypotheses about the mating system of D. pumilio. First, due to differences in parental investment, ‘time out’ of female D. pumilio will be greater than male ‘time out’ and, therefore, females are the sex with the lower PRR and are limited as mates. Second, because of their lower PRR, females are more selective about mates than males, and female choice may lead to variance in male mating success and polygyny in successful males. Finally, male territorial behavior is related to competition for access to females.

Methods

The study organism

The strawberry dart-poison frog D. pumilio is a member of the neotropical family Dendrobatidae. Its distribution ranges from Nicaragua to Panama on the Atlantic coast (Myers and Daly 1983) where it inhabits lowland forests and fruit plantations (McVey et al. 1981; Donnelly 1989b). Populations vary in color, color pattern, density, body size, and calls (Myers and Daly 1983). Populations in Costa Rica are colored orange to red with red, black, or blue hind limbs. The aposematic coloration indicates the defensive function of toxic skin alkaloids in D. pumilio (Myers and Daly 1983).

The courtship of D. pumilio is complex, prolonged, and involves tactile, visual, and acoustic stimuli (Limerick 1980; Zimmermann and Zimmermann 1988). Oviposition is terrestrial (Limerick 1980) and fertilized eggs are hydrated by the male. After hatching, tadpoles are transported to water-filled axils of bromeliads (only one tadpole per axil) by the female frogs and are subsequently fed with insects (Limerick 1980; Weygoldt 1980, 1987).

Males are territorial and females are not (Bunnell 1973; McVey et al. 1981). Males’ advertisement calls are used for mate attraction and spacing and are characterized by a high sound intensity. Courtship calls consume less energy and are used in short-range and tactile interactions between the sexes (Zimmermann 1990).

Adult D. pumilio are sexually monomorphic in color (except throat), have a mean snout-vent length (SVL) of 2.14 cm and a mean weight of 0.93 g (Prohl 1997a).

In Hitoy Cerere, D. pumilio is very common and reaches large areas without records. The centers of all quadrants in which a male called were connected to obtain the limits of his territory.

The data were analyzed using the software package Statistica 5.0. The distribution of data was assessed from visual analysis of box-and-whisker plots. For some variables (e.g., mating success) the box-and-whisker plots revealed a skewed distribution and outliers. For this reason, nonparametric descriptive statistics were generally used. A correlation analysis (Pearson product-moment) and a multiple-regression model (stepwise forward-selection procedure) were used to explain the effects of male traits on male mating success.

Data analyses

The density of both sexes within the study area was determined from population estimates using the Peterson method (Krebs 1989) comparing the observed individuals between two sample periods once each month from July to November. One sample period combined the observations of 2 successive days and was separated from the second sample period by at least 1 week. In December, the activity was very low so that the majority of the frogs could not be found (Prohl 1997a). To determine if the sex ratio differed from a 1:1 ratio, we used the chi-square test.

The total calling activity of each male was calculated by adding up all hours when a male called at least once. A territory is defined as the calling area of one male, used exclusively and defended from male intruders. The territory size was calculated using the modified minimum-area method (Harvey and Barbour 1965) which eliminates large areas without records. The centers of all quadrants in which a male called were connected to obtain the limits of his territory.

The reproductive cycle of an individual is divided between being ready to mate (‘time in’) and not being ready to mate (‘time out’). ‘Time out’ is the time devoted to gamete production, mating, and parental care. It was calculated for both sexes of D. pumilio using the technique proposed by Parker and Simmons (1996). The technique considers a series of special cases according to the degree of male parental investment and number of males and females involved in one reproductive event. Since the production of one
clutch in our species involves just one male and one female and male parental care is low, we used a slightly modified approach from ‘case 1’ including male parental care and egg mortality. Thus, we added the means of the duration of the observed reproductive activities not compatible with mate searching. These are mating and egg attendance for the males and production of clutches, mating, and tadpole transport for the females.

The calculation of the opportunity for sexual selection on male reproductive success followed the modification by Kluge (1981) of the models developed by Wade and Arnold (1980). According to these models the index of the opportunity for sexual selection $I_S$ is the variance of male mating success $S^2$ divided by the square mean of male mating success $X^2$. This index and the coefficient of variation on male mating success are given for comparisons with other species (Table 2).

**Results**

Population density and territoriality

The calculation of population density indicates that 9–12 males (mean = 11, n = 5) and 6–12 (mean = 9, n = 5) females resided in the study area. The sex ratio did not differ significantly from 1:1 (chi-square test: $P > 0.4$ for each month). Because several animals stayed only some days in the area, however, a total of 29 females and 20 males were recorded within the study period.

Six males either did not call or called for less than 3 days and left the study area after a short time. These males were not considered as territorial. They did not differ from territorial males regarding color, SVL ($t = 0.30$, $P = 0.77$), or weight ($t = 0.74$, $P = 0.47$). The remaining 14 males defended territories using them as calling site, courtship area, and oviposition site (Fig. 1) from 13 days to the entire study period (172 days, mean = 128 days, n = 14 males). Territories were defended against conspecific calling intruders with calls ($n = 13$) and fights ($n = 4$) which were always won by the residents. Territory centers, where males were predominantly found, contained vegetation structures (e.g., vines, stilt roots, and buttresses) which males used as calling sites: 70% of calling activity occurred from elevated calling perches. Tadpole-rearing sites (bromeliads) were located outside the territories and were not defended by males. Female home ranges exceeded the limits of the study area (Pröhl 1997b).

Differences in male traits, mating, and reproductive success

Individual males differed considerable in their territorial and mating behavior. Thus, we found great variation in calling activity among territorial males ranging from 5 to 291 h [median = 145.5, interquartile range (Iqr) = 169, n = 14 males]. The median individual perch height varied from 5 to 79 cm (median = 26, Iqr = 27, n = 14 males) and territory size from 1 to 24.5 m$^2$ (median = 11, Iqr = 10, n = 14).

Mating frequency and reproductive success of males were also highly variable. Only territorial males were observed mating. The two most successful males mated 12 times, the other males mated between 0 and 5 times (median = 1.5, Iqr = 5, n = 14 males) (Fig. 1). Male calling activity and average perch were highly correlated with mating success and explained 86% of the variation in male mating success in a multiple-regression model (Table 1). Territory size and number of days present showed lower correlations, and SVL and weight did not correlate nor did they enter the regression model (Table 1). Moreover, reproductive success, defined as the number of hatched tadpoles (Median = 0, Iqr = 3, n = 14, respectively) was highly correlated with mating success ($r = 0.81$, $P < 0.001$). The 22 hatched tadpoles were from ten clutches which belonged to four males.

Females visited males with higher mating success more frequently than less successful ones. The number of females found in a territory and the visiting frequency (Fig. 1) were both significantly correlated with mating success ($r = 0.66$, $P = 0.010$, n = 14; $r = 0.84$, $P < 0.001$, n = 14, respectively). Estimates of the opportunity for sexual selection based on variance in male mating success are presented in Table 2.

Courtship behavior and mating system

All courtships and ovipositions took place during the morning in the territory of the resident male. The mean duration of a mating was 1.5 h (mean = 89 min, SD = 37 min, n = 33) and mean clutch size was 4.6 eggs (range: 3–7 eggs, SD = 1.06, n = 37) (Pröhl 1997a,b). A total of 9 males and 14 females mated. Females visited up to four territories before and between matings (Appendix 1). In 36 of 42 matings (42 observed matings + 2 clutches found = evidence for 44 successful matings) it was possible to identify the mating female. In 11 unsuccessful courtships, the females rejected the male

![Fig. 1 Territorial boundaries of male Dendrobates pumilio. Male 17 settled after male 1 disappeared from the study area (n = number of matings a male achieved; number of different females that visited the territory/total number of female visits to the territory)](image-url)
Table 1 Summary of correlation and multiple-regression analysis for male mating success and variables (male traits) potentially affecting the mating success. Because of a skewed distribution, the dependent variable was square root transformed for the regression model. Minimum F to enter the model was 4.0. Variables with a nonsignificant effect (P > 0.05) were omitted from the model.

<table>
<thead>
<tr>
<th>Dependent variable</th>
<th>Explanatory variable</th>
<th>Simple correlation</th>
<th>Multiple regression model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Male mating success</td>
<td>Calling activity</td>
<td>0.79, 0.0008</td>
<td>0.75, 0.0027, 0.86, &lt;0.001</td>
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<td></td>
<td>Average perch height</td>
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<td>0.57, 0.400</td>
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<td>Territory size</td>
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<tr>
<td></td>
<td>Number of days present</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Snout-vent length</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>Weight</td>
<td>0.06, 0.85</td>
<td></td>
</tr>
</tbody>
</table>

Table 2 Calculation of the opportunity for sexual selection in male Dendrobates pumilio (according to Wade and Arnold 1980; Kluge 1981).

Mean of male mating success $X_m = 3.14$
Variance of male mating success $S_m^2 = 17.36$
Intensity of sexual selection $I_m = S_m^2 / X_m^2 = 1.76$
Coefficient of variation of male mating success $CV = 132.6$

and left the territory. On only two occasions did the male stop calling during the courtship, although females seemed to be willing to court. The difference between 11 female to 2 male courtship stops is significant (chi-square = 6.2, df = 1, P = 0.01). Prior to the matings, females had been courted by the same (n = 5) or another male (n = 4), they had mated with the same (n = 15) or another male (n = 3), or they had neither mated nor courted (n = 9). Female-female aggression was never observed even in the presence of a calling male (n = 8).

One of the most successful males (M2, Fig. 1) mated with at least five different females, while females mated with one to three males (Appendix 1). However, females also mated with males outside the study area. Eight females returned to the same male and mated with him repeatedly, e.g., F19 and M8 mated six times until tadpole transport (Appendix 1). The two most successful males were observed to mate once with two (M8) and once with three females (M2) in succession. In contrast, the average observed interval between two matings of a female was 4.4 days (range = 3–7 days, n = 8).

Parental investment and calculation of ‘time out’

While both sexes provide parental care, females spend more time raising the offspring. To demonstrate this, we calculated ‘time out’ for both sexes of our species. For these calculations, we took into account that only 12% of the eggs survived and if so, lasted on average 12 days until tadpole hatching. Because of high egg mortality and small clutch size, a female must produce eight eggs and a pair must mate twice to obtain one hatched tadpole.

Since males moistened their clutches once a day, which on average took 10 min (0.17 h, n = 8), males ‘time out’ to rear one offspring, Gm, is $2 \times 1.5$ h (two matings) + 12 × 0.17 h (to moisten one clutch during 12 days) = 5 h.

Because the average clutch size was 4.6 eggs and the average interval between two successive matings of a female was 4.4 days we conclude that the production of one egg takes approximately 1 day. Furthermore, the mean duration of tadpole transport to waterfilled bromeliads was 3 h (range 2.0–4.5 h, n = 4 completely observed tadpole transports). Development until metamorphosis of two tadpoles lasted 43 and 46 days, respectively. Because the mothers of these tadpoles had a second tadpole at the same time, tadpole rearing of only one tadpole may cost 22–23 days. This is consistent with the observation that the females provided each tadpole with unfertilized eggs five times ($5 \times 4.6 = 23$ eggs corresponding to approximately 23 days of egg production).

Hence, female ‘time out’, Gf, is: 8 days (egg production) + 2 × 1.5 h (matings) + 3 h (tadpole transport) + 22 days (tadpole rearing) = 30 days + 6 h.

It follows that the ratio female ‘time out’ to male ‘time out’, Gf/Gm, is 366/5 h = 73.2.

It is evident that mating, egg attendance, and tadpole transport are negligible compared to egg production for clutches and tadpole rearing. This calculation did not consider the time for sperm replenishment because it is not known. But even if we assume that sperm replenishment takes 1 or more days, male ‘time out’ should be much smaller than female ‘time out’ or, in other words, male PRR is much greater than that of the female.

Discussion

In this study ‘time out’ of females was higher than ‘time out’ of males providing evidence that male PRR is greater than female PRR (Clutton-Brock and Vincent 1991; Parker and Simmons 1996). Behavioral observations support empirical measures of the PRR: male
D. pumilio can mate in succession on different days or even on the same day with different females and guard several clutches at the same time (personal observation), whereas females can only mate every few days and do not mate during tadpole rearing \((n = 4\) tadpole-rearing females). This intensive maternal investment clearly illustrates the increase in an offspring’s chance of survival at the cost of the parent’s ability to invest in other offspring (sensu Trivers 1972).

As the adult sex ratio did not seem to deviate from unity, the unequal PRR of the sexes generates a male-biased OSR, the main determinant of mating competition (Kvarnemo and Ahnesjö 1996). In the case reported here, the sex with the smaller parental investment is the predominant competitor because the discrepancy in parental investment strongly determines the inequality in PRR. Other factors than parental investment that may affect PRR and OSR are temperature, food, and nest site availability (Bush 1993; Kvarnemo and Ahnesjö 1996) but were not analyzed in our study.

It has been argued that variance in mating success alone is not necessarily evidence for the operation of sexual selection (Koenig and Albano 1986; Sutherland 1987). Nevertheless, it should give an estimate of the maximum opportunity for sexual selection and has been applied for comparisons of mating systems between and within amphibian species (Ryan 1985; Sullivan et al. 1995). Measures of the opportunity for sexual selection \(I_S\) on male reproduction and the coefficient of variation of male mating success in *D. pumilio* (Table 2) fall within the range calculated by Kluge (1981) for a number of species with a prolonged breeding season \((I_S; \text{range } 0.5–3.0 \text{ (outlier 13.6)}, \text{median } = 1.7; \text{CV: range } 72.9–286.6, \text{median } = 134)\). In anurans, a male-biased OSR is often associated with a prolonged breeding season and leads to high values of \(I_S\) and sometimes high levels of polygyny (Sullivan et al. 1995) and our results are consistent with these findings.

Furthermore, three criteria for identifying sexual selection (Koenig and Albano 1986) seem to apply to *D. pumilio*. (1) Both intrasexual competition and mate choice are given. As in many frog species, territoriality represents a form of intrasexual competition and has evolved toward defense of calling sites for mate attraction, and areas involved in courtship and mating rather than defense of feeding areas (Mathis et al. 1995; Pröhl 1997b). In turn, females seem to sample males before and between mating and may interrupt courtships. This behavior suggests female selectivity. (2) There is variance in some fitness measurements such as mating and reproductive success. (3) Mate choice acts on specific characters that might provide reproductive advantages over other individuals of the same sex. Energetically expensive calls in frogs seem to be such a character, e.g., louder calls, longer calls, and higher calling activity are attractive to females in many amphibians and other groups (Ryan 1985; Roithmair 1992; review in Halliday and Tejedo 1995).

The mating system of *D. pumilio* is best described as sequential polygamy (Davies 1991) comprising sequential and simultaneous polygyny and sequential polyandry, with male and female parental care. This mating system is associated with a prolonged breeding season due to a tropical environment where the constant availability of water and food allows females to produce clutches continuously. The same mating system was found in *D. histrionicus* (Silverstone 1973) and may be true for all dendrobatids of the *histrionicus* group sharing the same parental-care pattern (Myers et al. 1984; Zimmermann and Zimmermann 1988; review in Sullivan et al. 1995). In general, dendrobatids show great variability in mating patterns ranging from species with exclusively male or female parental care, through biparental care, to temporal pair bonding (Weygoldt 1987; Summers 1992b; Caldwell 1997). In some species with territorial males and male parental care (*D. auratus* and *D. leucomelas*), both sexes are competitive with respect to access to mates, although females are more selective (Summers 1989, 1992a). Those studies showed that apart from relative parental investment, variation in mate quality affects the direction of mating competition and that choice and competition, in contrast to the situation in *D. pumilio*, need not necessarily be opposite sex roles (Owen and Thompson 1994). The mating system variability in dendrobatids may reflect adaptations to different environments but may also be the result of sexual conflict ending up in deception and reproductive parasitism (Caldwell 1997; Summers and Amos 1997).

This study was conducted during only 6 months. We observed three males 3 years later still defending their territory on the study area (H. Pröhl, unpublished data) and assume that the observed mating success represented between 20 and 50% of lifetime mating success. Long-term research would be an essential complement to this study, because lifetime reproductive success is a more accurate indicator of fitness, to estimate differences between individuals and the significance of sexual selection as an evolutionary force (Sullivan et al. 1995).

The theoretical predictions outlined in the introduction concerning differences in PRR between the sexes, competition for mates, selectivity for mates, variance in male mating success, and the function of territoriality were confirmed. A new, unpredicted component of the mating system is polyandry, which can be attributed to short intervals between clutch production and female mate choice.

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