ORIGINAL ARTICLE

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# Clutch loss affects the operational sex ratio in the strawberry poison frog *Dendrobates pumilio*

**Abstract** Both modelling and field data from three breeding seasons show that an environmental factor, clutch loss (CL), affects the operational sex ratio (OSR) and therefore male mating frequency in strawberry poison frogs. Clutch loss affects the length of reproductive cycles of both sexes: with increasing clutch losses, males spend proportionately more time than females in parental investment activities. Because of this, males spend relatively less time in the mating pool, i.e. exhibit proportionately more "time-out" than females in comparison to a situation with low or no clutch loss. Hence, clutch loss leads to a less male-biased OSR, coupled with a decrease in the opportunity for sexual selection. Furthermore, this study resolves an apparent paradox, the negative correlation between mating frequency and reproductive success (=number of produced tadpoles) of individual males in one breeding season. Clutch loss decouples the correlation between mating frequency and reproductive success because females re-enter the mating pool when they lose their offspring. However, clutch loss diminishes the reproductive output. Similar consequences of clutch loss on the OSR may be true for many species where both sexes reproduce frequently in one breeding season.

**Keywords** Clutch loss · Operational sex ratio · Sexual selection · Poison frog · *Dendrobates pumilio*

## Introduction

The intensity of mating competition and sexual selection is thought to be primarily determined by the operational sex ratio (OSR; Emlen and Oring 1977; Kvarnemo and Ahnesjö 1996). The OSR is the ratio of fertilizable females to sexually active males at the site and time when mating occurs, i.e. the number of females to number of males currently in the mating pool (Emlen and Oring 1977). If the adult sex ratio in the population is 1:1, sexual differences in parental investment (Trivers 1972; Clutton-Brock and Vincent 1991) can determine the extent of bias in the OSR. The OSR is biased towards the sex with lower time costs associated with gamete production and parental care because this sex can spend more time in the mating pool, and is therefore relatively more available than the sex with the higher reproductive time costs. The sex with lesser time costs competes for mates while the sex with the higher time costs faces less competition for mates, but is often choosy in selecting mates (Trivers 1972; Clutton-Brock and Vincent 1991). Because, in most species, females invest more time and energy in their progeny than males, the OSR is typically male biased (Clutton-Brock and Parker 1992; Kvarnemo and Ahnesjö 1996).

The OSR may fluctuate in space and time within the same species or population (Breitburg 1987; Kruse 1990; Bush 1993). Environmental factors such as resource abundance (food: Gwynne and Simmons 1990; Kvarnemo and Simmons 1998; nest sites: Almada et al. 1995; Forsgren et al.1996; Pröhl 2002), temperature (Kvarnemo 1994; Ahnesjö 1995), and higher mortality in one sex than in the other (Forsgren et al. 2004) can influence the OSR.
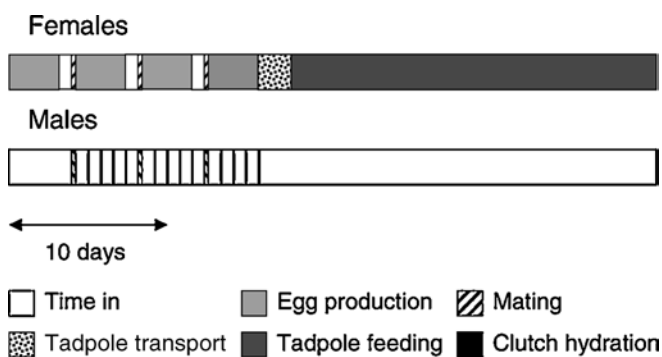
An additional factor that has been proposed to be critical to the OSR is clutch loss during the care-giving period (Kvarnemo and Ahnesjö 1996). After predation or parasitism of the brood, a parent should become sexually receptive on a faster time scale than they would if no clutch loss occurred. This effect should be different on the sexes if they differ in time expenditure for parental care, and therefore should alter the proportions of males to females in the mating pool. This, in turn, should influence the average and variance in mating frequency of the limited sex. However, so far no efforts have been made to explain quantitative changes in durations of parental care activities as a result of clutch predation.

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In this study, I examine how clutch loss affects the population OSR in strawberry poison frogs, *Dendrobates pumilio*. Strawberry poison frogs inhabit tropical lowland rainforests of Central America. Males are aggressive, hold long-term territories and compete for females (Pröhl and Hödl 1999). In contrast, females choose between territorial males, undergoing long courtship sequences before oviposition (Pröhl and Hödl 1999; Pröhl 2003). The mating system is polygamous: males and females mate with several partners during one breeding season (Pröhl 2002). After oviposition, males moisten the eggs to prevent desiccation. However, most of the eggs die. Major sources of egg mortality are parasitic flies (Phoridae), fungus infestation, and depredation by leeches (H. Pröhl, unpublished data). After the fertilized eggs develop into tadpoles, females transport up to four tadpoles individually to water-filled leaf axils and feed them with unfertilized eggs until metamorphosis (Weygoldt 1980; Brust 1993). If females lose their eggs, they continue mating with the same or other males. During tadpole rearing, females do not mate. Instead, they use all their eggs for feeding their young.

To summarize, males stay in the mating pool most of time, only interrupted by the mating process itself and by egg moistening. In contrast, females only enter the mating pool when they have produced enough eggs for a clutch and have no tadpoles to feed (Fig. 1). Since females invest much more time in parental care than males, the OSR is strongly male biased (Pröhl and Hödl 1999). Because I found that male mating success and clutch loss varied between years, I calculated the influence of varying clutch loss on OSR, i.e. the time that both parents provided for gamete production, mating activity and parental care by using a technique from Clutton-Brock and Parker (1992) and Parker and Simmons (1996). Finally, I related changes in the OSR to variation in mating and reproductive success and the intensity of sexual selection.

## Females

## Males

10 days

☐ Time in     ▨ Egg production     ▨ Mating
▨ Tadpole transport     ■ Tadpole feeding     ■ Clutch hydration

**Fig. 1** Schematic representation of the reproductive cycle of the two sexes of *Dendrobates pumilio*. The time where the sexes are available for mating ("time in") is *white*; the times they are occupied with reproductive activities ("time out") are *grey* or *patterned*. It is assumed that one female mates with the same male several times until the tadpoles from the first clutch hatch, i.e. all four eggs of the first clutch develop into tadpoles. The time for tadpole-rearing is underrepresented (showed for one tadpole only) because of space limits. Only approximate time estimates are shown for "time in" because the real "time in" is not known

## Methods

### Field observations

I investigated the behavioural ecology of strawberry poison frogs in one population at Hitoy Cerere Biological Station, Costa Rica, in a study area located in a primary rainforest during the breeding seasons in 1993 (143 days), 1996 (88 days) and 1997 (91 days). I observed territorial (i.e. calling and spacing) and mating behaviour during the morning hours when reproductive activity was highest, usually from 0700 to 1200 hours. I measured the mating success of individual males, followed the survival of eggs into tadpoles in every breeding season and observed parental-care activities ad libitum (see Pröhl 1997, 2002; Pröhl and Hödl 1999, for description of the study area and detailed methodology).

### Estimation of time for parental investment

Clutton-Brock and Parker (1992) and Parker and Simmons (1996) divided the reproductive cycle of an animal into "time in" and "time out". "Time in" ($S_f$ for females, $S_m$ for males) is the time present in the mating pool (i.e. time spent searching, attracting or waiting for a mating), while "time out" ($G_f$ for females, $G_m$ for males) is the processing time for a given reproductive event including time for gamete production, mating activity and parental care (Parker and Simmons 1996). Thus "time out" measures the time costs of parental investment. Consequently, the bias of the OSR can be deduced from "time out" measurements: when the sex ratio is equal, the OSR is biased towards the sex with the smaller "time out". As follows, the bias in the OSR, the direction and intensity of competition for mates, and the opportunity for sexual selection should be correlated with the degree of disparity in "time out" between the sexes (Clutton-Brock and Vincent 1991; Parker and Simmons 1996).

The data used here are based on the behaviour observations from all 3 study years (see Pröhl and Hödl 1999; H. Pröhl, unpublished data). According to these data: (1) average clutch size is 4 eggs (mean±SD=4.2±1.2, $n$=121 clutches). (2) The average time between two matings for a female is 4 days: the production of one clutch takes 3 days and females enter the mating pool on the 4th day during the course of which mating takes place. Thus, on average a female produces one egg per day. (3) A mating lasts 1.5 h. (4) Clutch moistening lasts 10 min and is performed once a day. (5) Time to hatching takes on average 12 days (range 10–13 days). (6) The transport of one tadpole takes 3 h (or 12 h for four tadpoles). (7) Rearing of one tadpole with unfertilized eggs until metamorphosis takes 22 days (or 88 days for four tadpoles). Individual tadpoles receive the same total amount of unfertilized eggs whether reared in isolation or a group, but these are distributed over a longer time period when several tadpoles are present. The "time out" of females ($G_f$) is the sum of time for egg production+time for mating+time for tadpole transport+time for tadpole

rearing, while the "time out" for males ($G_m$) is the time for mating+time for clutch hydration (Table 2).

I modified our original calculation of "time out" for *D. pumilio* (Pröhl and Hödl 1999) by taking into account that reproductive activities of both sexes take place almost exclusively during the morning hours (Brust 1993; Pröhl 1997; Haase and Pröhl 2002). To get more realistic values of female and male "time out", for the model presented here, I assume that reproductive activity takes place during only 6 h of a day, i.e. maximum "time out" of a day is set as 6 h. For simplicity, I further assume that either all eggs of a clutch die or all eggs survive. This assumption is based on my observation that in most cases clutch mortality affected all eggs (see Results). Because females produce a clutch on average every 4 days, mating takes place two additional times before tadpole transport (Fig. 1). Furthermore, on average, clutches disappeared on the 3rd day after oviposition (mean±SD=2.9±1.4 days, *n*=56 observations of total clutch loss), which implies that males moisten their clutches on average two times before they lose them.

## Statistical methods

I used *t*-tests to compare the mating frequencies between years with higher and lower clutch loss. The relationship between mating frequency and reproductive success (number of tadpoles produced by one male) was analysed with a contingency table analysis for comparing multiple proportions, and following a Tukey-type test for multiple comparisons (Zar 1999), as well as Spearman rank correlation coefficients.

## Results

### Clutch loss and mating frequency

The average male mating frequency and clutch loss differed between the study periods. Clutch loss (CL) was higher in 1997 than in 1993 and 1996 (Table 1). In most cases (*n*=99, or 81.8% of clutches), CL was complete, i.e. all eggs of one clutch died or disappeared at the same time. The average male mating frequency was approximately twice as high in 1997 than in 1996 and 1993, whereas differences in average reproductive success between years were much smaller (Table 1). The average male mating fre-

quency did not differ significantly between 1993 and 1996 (two-tailed *t*-test: *t*=−0.63, *df*=27, *P*=0.53), but was significantly higher in the year with higher clutch loss (1997) compared to the years with lower clutch loss (one-tailed *t*-test: *t*=−2.05, *df*=37, *P*=0.023). Moreover, the ratio between observed mating frequency and reproductive success differed significantly between the years (contingency table analysis for comparing multiple proportions: $\chi^2$=15.37, *df*=2, *P*<0.001). A Tukey-type test for multiple comparisons revealed significant differences between 1997 and the other 2 years, but not between 1993 and 1996 (1993 vs 1996: *q*=1.29, *P*>0.5; 1993 vs 1997: *q*=4.03, *P*<0.025; 1996 vs 1997: *q*=5.50, *P*<0.001). Mating frequency and reproductive success were positively correlated in the years with lower clutch loss (Spearman rank correlation; 1993: $r_s$=0.81, *n*=14 males, *P*<0.001; 1996: $r_s$=0.85, *P*<0.001, *n*=15) and negatively correlated in the year with higher clutch loss (1997: $r_s$=−0.68, *P*=0.03, *n*=10). Furthermore, the opportunity for sexual selection (calculated as variance in male mating frequency divided by the square of mean male mating success according to Wade and Arnold 1980; Arnold and Wade 1984) was higher in 1993 and 1996 than in 1997 (Table 1). The adult sex ratio did not deviate from the 1:1 ratio in either of the years (Pröhl and Hödl 1999; Pröhl 2002).

### Influence of clutch loss on female and male "time out"

From the observation that male mating frequency was higher in the year with higher clutch loss, I presumed that females become relatively more available as mating partners when clutch loss increases. For that reason, I tested the hypothesis that clutch loss affects the OSR, by modelling the influence of clutch loss on male and female "time out" and calculating their ratio $G_f/G_m$. When there is no clutch loss and assuming the time estimates of reproductive events described in the methods section, production of four surviving offspring (resulting from one oviposition) results in a much higher female than male "time out". Consequently the $G_f/G_m$ ratio is high (Table 2), thereby pointing to a strong male-biased OSR.

As outlined above, most of the embryos die and, as a consequence, females must produce more eggs, both sexes must mate more often and males must moisten their clutches repeatedly in order to produce surviving young. Including clutch loss as a variable affecting the OSR, "time out" for the production of a clutch with four eggs, mating

**Table 1** Descriptive statistics of clutch loss (*CL*), opportunity for sexual selection ($I_s$=variance in male mating frequency divided by the square of mean male mating frequency), mating frequency and reproductive success of male strawberry poison frogs in three study periods in Hitoy Cerere, Costa Rica. Mating frequency and reproductive success are calculated as number of matings or number of tadpoles achieved per male and observation day
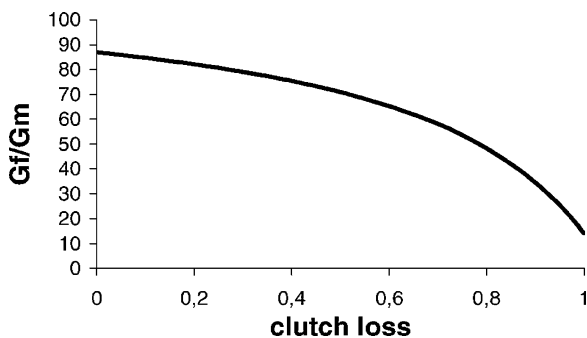
|  | % CL | $I_s$ | Mating frequency | | | Reproductive success | | | N (# of males) |
|---|---|---|---|---|---|---|---|---|---|
|  |  |  | Mean | SD | Total | Mean | SD | Total |  |
| 1993 | 88.0 | 1.76 | 0.026 | 0.033 | 44 | 0.011 | 0.021 | 21 | 14 |
| 1996 | 87.5 | 1.48 | 0.036 | 0.045 | 33 | 0.018 | 0.035 | 17 | 15 |
| 1997 | 94.9 | 1.08 | 0.068 | 0.07 | 62 | 0.013 | 0.019 | 11 | 10 |

**Table 2** Calculation of female "time out" ($G_f$) and male "time out" ($G_m$) and the sexual "time out" ratio ($G_f/G_m$) for the production of four (dependent) offspring resulting from one clutch, based on average measurements for reproductive activities (see text and Fig. 1) in a population of Costa Rican strawberry poison frogs, with and without considering the effect of clutch loss (*CL*). Note that in one reproductive cycle, egg production and mating take place two additional times between the first mating and tadpole transport (Fig. 1). This is because females do not stop to produce and lay eggs until tadpole transport. Two examples for the effect of clutch loss are given. The relative different changes in $G_f$ and $G_m$ are due to the fact that most of male "time out" (mating and clutch hydration) takes place before the time point clutch loss occurs (*cP*), whereas most of female "time out" (tadpole transport and tadpole-rearing) takes place after *cP*

| Reproductive activities | Egg production (♀) | Mating (♂, ♀) | Clutch hydration (♂) | Tadpole transport (♀) | Tadpole rearing (♀) | $G_f$ (♀) | $G_m$ (♂) | $G_f/G_m$ (♀, ♂) |
|---|---|---|---|---|---|---|---|---|
| Without CL | $3\times6h^a+(2\times3\times6h^a)$ | $1.5 h+(2\times1.5 h)$ | $12\times0.17 h$ | $4\times3 h$ | $4\times22\times6 h^a$ | 598.5 h | 6.5 h | 91.5 |
| With CL | | | | | | | | |
| 1. CL=88% (1993/1996) | $[3\times6 h/(1-0.88)]$ $+(2\times3\times6 h)$ | $[1.5 h/(1-0.88)]$ $+2\times1.5 h$ | $[2\times0.17 h/(1-0.88)]$ $+[10\times0.17 h]$ | $4\times3 h$ | $4\times22\times6 h$ | 741.5 h | 20.0 h | 37.0 |
| 2. CL=95% (1997) | $[3\times6 h/(1-0.95)]$ $+(2\times3\times6 h)$ | $[1.5 h/(1-0.95)]$ $+2\times1.5 h$ | $[2\times0.17 h/(1-0.95)]$ $+[10\times0.17 h]$ | $4\times3 h$ | $4\times22\times6 h$ | 969 h | 41.5 h | 23.3 |

[a]Note that the maximum "time out" for 1 day is 6 h

and the first 2 days of clutch hydration have to be divided by the proportion of surviving clutches (1−CL, Table 2). The proportion of surviving clutches is inversely related to the number of times reproductive activities have to be repeated. For instance, if clutch loss is 0.8, then clutch survival is 0.2 and both sexes have to engage in five matings to produce four surviving tadpoles. "Time out" for the additional two matings, tadpole transport, tadpole rearing and 10 days of clutch hydration remain the same because these activities take place only when embryos survive, e.g. they do not have to be repeated.

By incorporating clutch loss as a parameter, female and male "time out" duration increases (Table 2) with increasing clutch loss. Interestingly, although female $G_f$ increases more in absolute time than $G_m$, the decreasing ratio $G_f/G_m$ reveals that female "time out" increases relatively slower than male "time out" (Fig. 2). This decline becomes most pronounced when clutch loss exceeds 80%, i.e., at values observed in nature (Fig. 2). For example, by inserting the values of clutch loss observed in nature, the change in "time out" from 1993/1996 to 1997 is relatively higher for males (107%) than for females (31%, Table 2). Because of the relative different changes in "time out" of the sexes, increasing clutch loss should result in less and less male-biased OSRs.



**Fig. 2** Ratio of female "time out" ($G_f$) to male "time out" ($G_m$) of *D. pumilio* as a function of clutch loss

## Discussion

My study provides evidence that the time invested in parental investment ("time out") is affected by the environmental factor clutch loss in both sexes of the strawberry poison frog. Clutch loss increases "time out" of both sexes because some reproductive activities have to be performed repeatedly when eggs are eaten by predators or attacked by parasites. Hence, the whole reproductive cycle lengthens. Male "time out" increases relatively quicker under the influence of clutch loss than female "time out". This is because tadpole-rearing presents the largest part of female "time out" and this reproductive activity is only carried out when embryos survive: in the case of clutch loss, females continue to mate (within the same reproductive cycle) until they have tadpoles, i.e. females become relatively more available in the mating pool. Since the $G_f/G_m$ ratio declines, i.e. females become relatively more available as mates, the OSR becomes less male biased (Parker and Simmons 1996). However, it is important to mention that female "time out" is always much larger than male "time out", i.e. the OSR always remains male biased (Table 2).

The ultimate explanation for why male "time out" is relatively more affected than female "time out" is found in the distribution of parental investment before and after the critical time point (*cP*) at which eggs die or survive. Parental activities, which happen before *cP*, have to be repeated when the clutch disappears until one clutch develops into tadpoles; parental activities that happen after *cP* are only performed once in each completed reproductive cycle. In this study, males performed 74% of their "time out" before and 26% of their "time out" after *cP*. Meanwhile, for females it is 10% and 90% of "time out", respectively. Consequently, when clutch loss occurs, males have to repeat most of their parental activities (74%) whereas females must only repeat a small proportion (10%) of their parental activities. Thus, under the influence of clutch loss, changes in male "time out" are more dramatic than those in female "time out".

Similar to clutch loss, the premature death of tadpoles during the feeding period should result in a changing "time out" ratio between the sexes. The effect of tadpole death on the OSR should also depend on $cP$. When death occurs shortly after tadpole transport, the outcome is similar to that described, because females would enter the mating pool quickly and would not perform most of their "time out" (i.e. tadpole feeding). In contrast, when death occurs near metamorphosis, both parents would have to start the entire reproductive cycle from the beginning and repeat (almost) 100% of their parental activities. Hence, the closer $cP$ lies towards the end of the reproductive cycle, the less the "time out" ratio deviates from a situation without clutch or tadpole loss. Yet, because tadpole development is difficult to observe in my study area, I have no empirical data that would corroborate the assumption that tadpole predation is severe and varies between reproductive periods.

Climatic conditions are likely to exert an indirect effect on egg survival and the OSR through their influence on predator population dynamics, or directly affect the OSR through regulating reproductive activities of both sexes. For example, casual observations of an unidentified snail species predating heavily upon frog eggs were made in the exceptionally warm and rainy El Niño year (1997) at the Caribbean slope of Costa Rica (H. Pröhl, unpublished data). Temperature and precipitation themselves are positively correlated with reproductive activity in the strawberry poison frog (Pröhl 1997) and some other anurans (e.g. Aichinger 1987; Donnelly and Guyer 1994). Temperature also influences the brooding or clutch-guarding time of males and/or egg synthesizing time and clutch size of females in several species of ectotherms (Kruse 1990; Bush 1993; Kvarnemo 1994; Ahnesjö 1995). This may be also true for *D. pumilio*. In one study of maternal brood care on Isla Bastimentos (Panama), females produced a slightly higher number of eggs per day (mean=0.65) and tadpoles received a higher number of eggs during their development (mean=27.7; Brust 1993) than in Hitoy Cerere. I assume that this difference in egg synthesizing rate is due to higher temperatures in Bastimentos (H. Pröhl, unpublished data).

My results further indicate that the relationship between mating frequency and reproductive success is not a simple one. In the years when clutch loss was lower, mating and reproductive success of individual males were positively correlated. By contrast, in 1997, individual mating and reproductive success were negatively correlated. This observation demonstrates that, although a less male-biased OSR leads to higher male mating frequency, on average, and reduced sexual selection (as estimated by the index of opportunity for sexual selection), this does not always result in the production of more tadpoles for individual males (Table 1). Similar interplays between offspring survival, mating frequency and OSR might be found in other animal groups where the loss of the brood leads to repeated reproduction of females in the same breeding season (birds: Major 1991; Verhulst and Hut 1996; insects: Tallamy and Denno 1982; Martinez et al. 1996). Also, filial cannibalism by caring male fish has been proposed to causes shifts

in the OSR (Smith and Wootton 1995; Kvarnemo et al. 1998; Manica 2002; Neff 2003) but there is disagreement about the direction of the shift (Kvarnemo 1998; Smith and Wootton 1998), and no efforts have been made to quantify the influence of clutch loss on time spent with parental investment and length of reproductive cycles in these study systems.

In summary, the presented data provide evidence that the influence of an environmental factor on male fitness components varies temporally. Through the direct effect on the reproductive success of both sexes, clutch loss differentially affects the time for parental investment of the sexes, thereby altering the OSR, male mating frequency, and the opportunity for sexual selection.

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