

Costs and benefits of temporary egg desertion in a rocky shore frog with male-only care

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Abstract

Egg attendance imposes costs on parents, including decreased food intake and increased mortality risks. By concentrating parental activities when egg predation is greater and abiotic conditions are less stressful, parents may decrease these costs. Here, we quantify the costs and benefits of temporary egg desertion in the frog *Thoropa taophora*, whose males care for eggs on rocky shores. We tested hypotheses on the effect of the period of the day (day vs. night) and breeding site (exposed vs. protected from sunlight) on the frequency of temporary desertion, water loss, and egg predation. Using naturalistic observations, we show that parental males deserted their clutches more often during daytime and in exposed sites. Using a field experiment with agar models simulating adult males, we show that water loss was greater during daytime and in exposed sites. Finally, using field observations and a male removal experiment, we show that male presence improves egg survival and that egg predation was higher during the night, with no effect of breeding site. Because the main egg predators are conspecifics, which are mostly inactive when parental males are not attending their clutches, the costs

of temporary desertion in terms of egg loss are relatively low when compared with the benefits related to decreased exposure of parental males to stressful abiotic conditions. In conclusion, we predict that temporary offspring desertion should be found especially among ectotherms, when periods of harsher environmental abiotic conditions for the parents are coincident with periods of low offspring demand for protection against predators.

Significance Statement

To take care of eggs is costly for the parents because they are exposed to predators or stressful environmental conditions. In order to avoid these costs, parents may leave the eggs temporarily unattended. Although temporary egg desertion has been reported for many species, the selective forces favoring its evolution are still poorly understood. Here, we investigated the costs and benefits of temporary egg desertion in a frog whose males care for eggs on rocky shores, an extreme environment for animals with permeable skin. Our findings lead us to conclude that temporary egg desertion should evolve when periods of harsher environmental conditions for the parents are coincident with periods of low offspring demand for protection against predators.

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Introduction

One of the most widely spread forms of post-ovipositional care among ectotherms is egg attendance, in which one or both parents remain with the eggs at a fixed location after egg laying (Crump 1995; Smiseth et al. 2012). Egg attendance usually increases offspring survival as a consequence of

parental protection against harsh environmental conditions, predators, and pathogens, as well as by providing the necessary conditions for proper egg development (Smiseth et al. 2012). Despite the benefits enjoyed by the offspring, egg attendance typically imposes costs on parents, including increased exposure to predation and/or stressful abiotic conditions, decreased food intake, increased energy expenditure related to parental activities, and decreased mating rates (Trivers 1972; Clutton-Brock 1991). Therefore, understanding the evolution and maintenance of parental care requires a comprehensive knowledge of its fitness consequences not only to the offspring but also to the parents providing the care (Alonso-Alvarez and Velando 2012; Klug et al. 2013).

Temporary egg desertion is a behavior that may reduce the costs associated with egg attendance when parents abandon the offspring for short periods of time. This strategy has already been reported for several animal groups, including arthropods (Zink 2003; Machado et al. 2004; Chelini and Machado 2012), fish (Rangeley and Godin 1992), and frogs (Chen et al. 2007; Cheng and Kam 2010), with either female-only or male-only parental care. In such cases, the parent is expected to concentrate parental activities when the probability of egg predation is greater or when environmental conditions are less stressful for them to perform egg attendance. During the period of egg desertion, the parent can (i) seek shelter or occupy other microhabitats, thus reducing their exposure to predators and stressful abiotic conditions, and (ii) seek food, thus reducing the foraging costs of parental care. Therefore, the behavior of temporary egg desertion decreases the total amount of energy allocated to egg attendance, potentially increasing the net benefits for the parents if predation pressure on eggs during the temporary parental absence is not severe.

Anuran amphibians are ideal organisms for studying the costs and benefits of temporary egg desertion for at least two main reasons. First, egg attendance is very common in this group, occurring in 17 of 27 families (Crump 1996; Wells 2007). When present, egg attendance is crucial to offspring survival and mainly consists of prevention of egg dehydration and protection against pathogens and predators (Crump 1996; Wells 2007). Second, because amphibians have permeable skin and are susceptible to dehydration, the activities of most species are restricted to the nocturnal period (Wells 2007). Egg attendance is no exception and, in many species, parents abandon their eggs during the day, returning to attend them only at dusk (Williams 1975; McDiarmid 1978; Wells 1981; Chen et al. 2007). Temporary egg desertion during the day and egg attendance at night may allow parents to avoid physiological costs related to water stress during the hottest periods of the day and also to reduce the risk of being attacked by visually oriented predators, such as birds and some snakes. On the other hand, temporary egg desertion imposed by stressful abiotic conditions may increase offspring mortality by diurnal egg predators, including a wide variety of arthropods and

vertebrates. To our knowledge, however, only a few studies have taken advantage of these features to investigate the costs and benefits of temporary egg desertion in the group (e.g., Chen et al. 2007; Cheng and Kam 2010).

Here, we used the frog *Thoropa taophora* (Anura: Cycloramphidae) as a study system to quantify the costs and benefits of temporary egg desertion. The eggs of *T. taophora* are deposited predominantly in films of freshwater flowing on the surface of outcrops and rocky shores (Giaretta and Facure 2004; Fig. 1), an extreme environment for anurans, where exposure to sunlight can impose severe physiological costs to parental individuals. Egg attendance is performed exclusively by males (Fig. 1c–f) and occurs primarily at night. During daytime, most of the clutches seem to be abandoned by the males, who take shelter in rock crevices or other microhabitats that probably provide protection against dehydration (Giaretta and Facure 2004). Based on the available information about the natural history of *T. taophora* and on parental care theory, we tested three hypotheses. First, the frequency of temporary egg desertion should be higher during the day than during the night, especially in open areas, because exposure to sunlight on rocky shores would impose severe physiological costs to parental males. Second, temporary egg desertion should minimize water loss to males during the day, especially when males are attending eggs in open areas exposed to sunlight. Finally, if stressful abiotic conditions on the rocky shore indeed impose physiological costs to parental males, the benefits of temporary desertion during daytime should be higher than the eventual costs in terms of egg predation. However, since egg attendance is expected to increase offspring survival, the number of eggs consumed by predators during daytime should be higher than during the night, and the intensity of predation should be higher in open areas, where parental males are expected to desert for longer periods during daytime.

Materials and methods

Study system

T. taophora is endemic to the Atlantic Forest and occurs only in the state of São Paulo, southeastern Brazil (Feio et al. 2006; Fitzpatrick et al. 2009). Adults and juveniles feed on a wide variety of invertebrates and have high tolerance to salinity (Sazima 1971; Abe and Bicudo 1991; Brasileiro et al. 2010). The reproductive activity is greatest from December to February, which coincides with higher temperatures and greater rainfall (Giaretta and Facure 2004). Oviposition occurs in films of freshwater flowing on the surface of outcrops and rocky shores, where the development of tadpoles also occurs (Fig. 1c–f). Embryonic development lasts from 4 to 6 days and, after hatching, the tadpoles feed by scraping algae from the rocky substrate (Fig. 1b), but they may also cannibalize

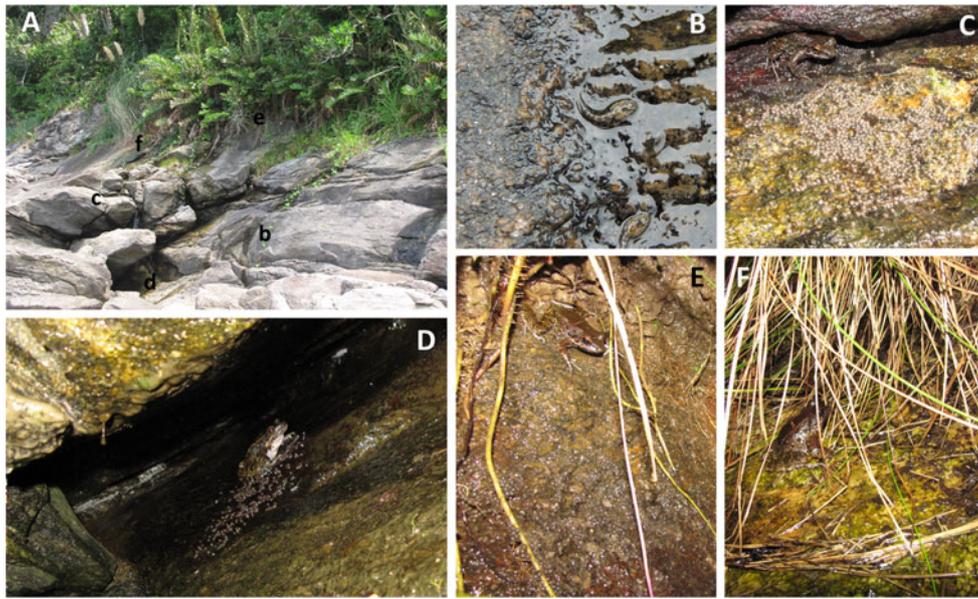


Fig. 1 **a** General view of a rocky shore in southeastern Brazil. Letters in *small case* refer to specific microhabitats used as breeding sites by the frog *T. taophora*; each micro-habitat is illustrated in a photo of same letter. **b** Two tadpoles scraping algae on a film of freshwater flowing on the surface of the rocky shore. **c–f** Males caring for clutches in two types of

breeding sites: exposed to sunlight, such as **c** open areas in the rocky shore without any cover and **f** areas partially covered with sparse vegetation (dark eggs are in the *right*, under the grass); and protected from sunlight, such as **d** rock crevices and **e** areas permanently shaded by dense vegetation (brownish eggs are in the *bottom left corner*)

eggs (Giaretta and Facure 2004). Males exclusively perform egg attendance, actively defending their clutches against potential predators, such as conspecifics and ants (Facure and Giaretta 2009). Many males, however, temporarily abandon their eggs during daytime, when they take refuge in vegetation or crevices between rocks (Giaretta and Facure 2004).

Study site

We conducted the study on Toque-Toque Grande Beach (23°49'55"S; 45°30'53"W) in the municipality of São Sebastião, northern coast of the state of São Paulo. The climate is warm and humid, with average monthly temperatures ranging from 26.2 to 28.2 °C and average monthly rainfall ranging from 89.6 to 178.6 mm in the summer months (December to February). For behavioral observations and experiments, we sampled one rectangular plot (approximately 600 m²) of rocky shore crossed by strips of flowing freshwater (Fig. 1a).

Identification of breeding sites and individuals

We conducted seven visits to the study site, one every month between September 2012 and March 2013. The duration of each visit ranged from 10 to 20 days, for a total of 91 days of fieldwork. During each visit, we identified active breeding sites as those where we found clutches of *T. taophora*. We classified these breeding sites ($n=30$) into one of two categories: (a) exposed to sunlight, including open areas without any cover or only partially covered by sparse vegetation, such as

herbs and grass ($n=18$; Fig. 1c, f); and (b) protected from sunlight, including rock crevices or areas permanently shaded by dense vegetation, such as shrubs and small trees ($n=12$; Fig. 1d, e). Moreover, we photographed and measured all individuals we found (102 males and 62 females) for snout-vent length (SVL) using digital calipers (to the nearest 0.01 mm). Given that *T. taophora* shows great inter-individual variation in size and color patterns, we were able to use photographs and SVL as complementary means of identifying the individuals.

Frequency of temporary egg desertion

To quantify the natural frequency of temporary egg desertion by male *T. taophora*, we monitored 34 clutches for a period of 3 to 5 days, which corresponds to 50–83 % of the maximum period of embryonic development for the species (Giaretta and Facure 2004). We performed periodic inspections of each clutch at regular 1-h intervals, totaling a minimum of 30 and a maximum of 84 inspections per clutch (median = 53 inspections per clutch). Given the impossibility of inspecting clutches continuously for 24 h, we alternated periods of eight consecutive hours of inspection with periods of eight consecutive hours of rest. Thus, we conducted inspections from 2200 to 0600 hours (between the 1st and the 2nd sampling days), from 1400 to 2200 hours (during the 2nd sampling day), from 0600 to 1400 hours (during the 3rd sampling day), and so on for the clutches that we followed for more than 3 days. We divided the surveys into two time periods: day (from 0600 to

1800 hours) and night (from 1800 to 0600 hours). We removed two males from the analyses (see below) because they completely abandoned their clutches after manipulation.

During each inspection, we recorded the presence or absence of parental males at the breeding sites (snapshot sampling sensu Altmann 1974). Because males show aggressive responses towards intruders even when they are far from their clutches (Giaretta and Facure 2004; RCC, personal observation), we considered that a male was absent (i.e., not attending the eggs) only when he was further than 50 cm away from the clutch. We stress, however, that in more than 90 % of the censuses, males were observed on their clutches (Fig. 1d) and, in the remaining censuses, males were mostly found up to 30 cm from their clutches, generally facing the eggs, in typical guarding posture (Fig. 1c, e, f).

Benefits of temporary egg desertion: decreased water loss

To evaluate a possible benefit of temporary egg desertion related to the mitigation of stressful abiotic conditions faced by parental males, we conducted an experiment to estimate water loss during January 2014. In the experiment, we used agar models that dehydrate similarly to animals with fully permeable skin (Spotila and Berman 1976; Navas and Araújo 2000). Although the agar models do not have physiological mechanisms of water retention, we assume that the water loss they experienced during the experiment is proportional to the actual loss experienced by *T. taophora* males on the rocky shore. Moreover, the agar models used here emulate the natural water retention posture of frogs, with arms and legs close to the body (following Navas and Araújo 2000).

First, we built a mold of dental alginate using a sacrificed adult *T. taophora* male (mass = 15.0 g, SVL = 56.7 mm). We then used this mold to make 160 agar models (concentration = 30 g/L; Rowley and Alford 2009) and stored them in refrigerated water at 4 °C for up to 4 days prior to the field experiments, in order to maintain their form and keep them hydrated. Immediately before the beginning of the experiment in the field, we weighed each agar model on a digital electronic scale (Gehaka AG200) to the nearest 0.001 g. Then, we placed a single agar model either at a protected site or at an exposed site. Whenever possible, we used sites that had already been used as an oviposition site during the breeding season ($n = 30$; 18 exposed and 12 protected); otherwise, we selected sites that were as similar as possible to the sites actually used and where we found males vocalizing during previous nights ($n = 10$; 2 exposed and 8 protected). To minimize water exchange between the agar models and the substrate, we placed them on an impermeable plastic surface (Rowley and Alford 2009).

Different models were exposed on the rocky shore for a 3-h period during the day (between 0700 and 1000 hours or between 1200 and 1500 hours) or a 3-h period during the night (between 1800 and 2100 hours or between 0300 and 2400

hours). In each period, we used 20 models placed in exposed sites and 20 models placed in protected sites, measuring the relative air humidity and the substrate temperature at the time of the initial placement of the model and at intervals of 30 min using a hygrometer (Alla 910.15 CHP) and a digital infrared thermometer (Minipa MT-350), respectively. At the end of each exposure period, we weighed each model again using the same digital scale. Finally, we estimated water loss from the difference between the initial weight and the final weight of each agar model. Throughout the duration of the experiment, no rainy or cloudy period was recorded in the study site.

Costs of temporary egg desertion: increased egg predation

To estimate natural predation on eggs, we followed 25 of the 34 clutches used to estimate the frequency of temporary egg desertion described above (see “Frequency of temporary egg desertion”). We photographed each clutch daily, once early in the morning (0600 hours) and once early in the evening (1800 hours), during a period of three to five consecutive days. We used the photographs to count the number of eggs in each clutch during each time period, which allowed us to quantify diurnal and nocturnal predation as the total number of eggs that disappeared from each clutch. In order to increase our confidence that missing eggs have been consumed by predators and not simply have hatched, we estimated egg predation in each clutch only until the eclosion of the first tadpoles.

We also conducted a male removal experiment to quantify the intensity of predation on the eggs during the day and during the night in clutches laid only in exposed breeding sites. We divided males into two experimental groups. In the male removal group, we selected 18 males with newly laid eggs and removed them from their respective clutches for 48 h. We maintained the removed males in coolers in the laboratory throughout the duration of the experiment and monitored egg mortality of their unattended clutches in the field. At the end of the experiment, we returned each male to its respective breeding site. In the control group, we recorded the mortality of the eggs in 15 clutches kept under natural conditions in which males were removed and immediately replaced close to their respective clutches. We photographed the clutches twice every day (0600 and 1800 hours) throughout the duration of the experiment to estimate total egg predation in the two experimental groups. Because our experiment involved focal animals and focal clutches under field conditions, we were unable to record data blind.

In order to identify egg predators under both natural conditions and throughout the experiment, we conducted continuous observations during 5 min at regular intervals of 1 h in every sampled clutch ($n = 58$ clutches; total sample of 192 h). During each observation period, we recorded all events of egg predation. We also positioned a video camera (Sony DCR-SR85 with nightshot mode) directed towards 15 active

breeding sites where males were not removed to continuously record their clutches. We recorded videos during 23 nights and 20 days during the 7 months of fieldwork for a total of 236 h of footage. Video recording of each clutch took a maximum duration of six consecutive hours and was performed without the interference of the researcher being in the vicinity of the breeding site.

Statistical analyses

To test our hypotheses on the costs and benefits of temporary egg desertion in *T. taophora*, we used a model selection approach (Burnham and Anderson 2002) applied to linear models (LMs) and generalized linear mixed-effects models (GLMMs). In this framework, we compared a null model with alternative models that incorporated the effect of time period (day vs. night), breeding site (exposed vs. protected), and their interaction, in order to quantify their relative fit to the observed data.

In the first analysis, we tested the assumption that abiotic conditions are more stressful during daytime and in exposed breeding sites. We considered the temperature on the substrate surface and the air humidity at each location where we placed the 160 agar models, averaged over the seven consecutive measurements within the 3-h sampling period (as described above in “Benefits of temporary egg desertion: decreased water loss”), as the response variables in LMs. We expected that the model including the additive effect of time period and breeding site to be the most plausible, with higher temperatures and lower humidity during the day and in exposed sites.

In the second analysis, we considered the number of inspections when a male was absent in comparison to the total number of inspections conducted at his clutch for each time period (as described above in “Frequency of temporary egg desertion”) as the response variable. In this case, we built GLMMs assuming that errors follow a binomial distribution. Given that each clutch provided repeated measures (day and night) and some males attended different clutches over consecutive months, we included clutch identity and male identity as random variables in all GLMMs.

In the third analysis, we considered the water loss of each agar model in each time period (as described above in “Benefits of temporary egg desertion: decreased water loss”) as the response variable. Because the initial weight varied among the agar models, but we were not interested in the effect of such variation, we included this information as a co-variable in the LMs evaluated in this analysis.

In the fourth analysis, we considered the number of eggs consumed under natural conditions in each time period in comparison to the total amount of eggs initially present in each clutch before the observation trials (as described above in “Costs of temporary egg desertion: increased egg predation”)

as the response variable (with binomial error distribution). We also included clutch identity and male identity as random variables in the GLMMs. According to our hypotheses, we expected that the models including the interaction between time period and breeding site to be the most plausible, explaining the variation in the (i) frequency of temporary egg desertion, (ii) water loss in the agar models, and (iii) intensity of egg predation under natural conditions.

Finally, we also built alternative GLMMs according to which egg predation rate under experimental conditions should not depend on any predictor variable (null model) or should depend on experimental group, time period, as well as the additive and interactive effects between these two variables. We considered the number of eggs consumed in each day, in comparison to the total number eggs present initially in each experimental clutch (as described above in “Costs of temporary egg desertion: increased egg predation”), as the response variable (with binomial error distribution). Given that we analyzed the data for each day independently, we included the sampled day nested within clutch identity as random variables in the GLMMs. We expected that the model including the interaction between experimental group and time period to be the most plausible.

We implemented all models using the package *lme4* (Bates et al. 2015) in the software R 3.2.1 (R Development Core Team 2015) and used the small sample size bias-corrected version of Akaike Information Criterion (AIC_c) to rank and calculate the relative weight of all models fitted to the data. We computed the difference in those indexes between the model with the lowest value and all other models in the ranking (Burnham and Anderson 2002) using the package *bbmle* version 1.0.17 (Bolker and R Development Core Team 2014).

Results

Abiotic conditions

As would be expected, mean temperature on the substrate surface was higher in exposed sites than in protected sites and higher during the day than during the night (Table 1, Fig. 2). Moreover, air humidity was lower during the day than during the night, but showed no difference between exposed and protected breeding sites (Table 1, Fig. 2). Although more complex models presented $\Delta AIC_c \leq 2.0$ (Table 1), the simplest models among the equally plausible ones are nested within the more complex ones. Thus, the additional parameters should be considered uninformative due to its poor explanatory power, as extensively pointed out elsewhere (Burnham and Anderson 2002; Arnold 2010). Therefore, our interpretation of the results will be based on the simplest models within the interval up to $\Delta AIC_c = 2.0$ (see Table 1).

Table 1 Results of model selection used to investigate variation in temperature and humidity conditions in the sampled area, as well as male temporary egg desertion, water loss in agar models simulating adult frogs, and egg predation rate (both under natural and experimental conditions) in the frog *T. taophora*

Model	<i>K</i>	<i>AIC_c</i>	ΔAIC_c	Weight
Mean temperature on the substrate surface				
<i>Time period × breeding site</i>	5	799.0	0.0	0.655
<i>Time period + breeding site</i>	4	800.4	1.4	0.317
Time period	3	805.3	6.3	0.027
Breeding site	3	913.1	114.1	<0.001
Null	2	914.5	115.5	<0.001
Mean relative air humidity				
<i>Time period</i>	3	1163.6	0.0	0.510
<i>Time period + breeding site</i>	4	1164.5	0.9	0.310
<i>Time period × breeding site</i>	5	1165.6	2.0	0.179
Null	2	1257.4	93.8	<0.001
Breeding site	3	1258.8	95.2	<0.001
Frequency of temporary egg desertion ^a				
<i>Time period × breeding site</i>	6	400.8	0.0	0.972
Time period + breeding site	5	407.9	7.1	0.027
Time period	4	429.2	28.4	<0.001
Breeding site	4	621.9	221.1	<0.001
Null ^b	3	645.2	244.4	<0.001
Water loss in agar models ^c				
<i>Time period × breeding site</i>	6	152.0	0.0	0.640
<i>Time period + breeding site</i>	5	153.1	1.1	0.359
Time period	4	173.3	21.3	<0.001
Breeding site	4	199.7	47.7	<0.001
Null ^b	3	213.2	61.2	<0.001
Eggs predation rate—natural conditions ^a				
<i>Time period</i>	4	1237.4	0.0	0.698
Time period + breeding site	5	1239.9	2.5	0.210
Time period × breeding site	6	1241.5	4.1	0.091
Null ^b	3	2684.3	1446.9	<0.001
Breeding site	4	2686.6	1449.2	<0.001
Eggs predation rate—experimental manipulation ^d				
<i>Experimental group × time period</i>	6	2945.8	0.0	0.999
Experimental group + time period	5	3107.9	162.1	<0.001
Time period	4	3131.7	185.9	<0.001
Experimental group	4	6287.1	3341.3	<0.001
Null ^e	3	6313.2	3367.4	<0.001

The symbols + and × represent additive and interactive effects between variables, respectively. Most plausible models are indicated in italics

AIC_c Akaike Information Criterion, *K* number of parameters, ΔAIC_c difference between the *AIC_c* value of each model and the *AIC_c* value of the most plausible model, *Weight AIC_c* weight of each model

^a Models consider the random effects of male and clutch identities

^b Null model includes no fixed effects of time period (day vs. night) and breeding site (exposed vs. protected)

^c Models consider the initial weight of the agar model as a co-variable

^d Models consider the random effects of sampling day nested within clutch identity

^e Null model considers no fixed effects of time period (day vs. night) and experimental group (control vs. male removal)

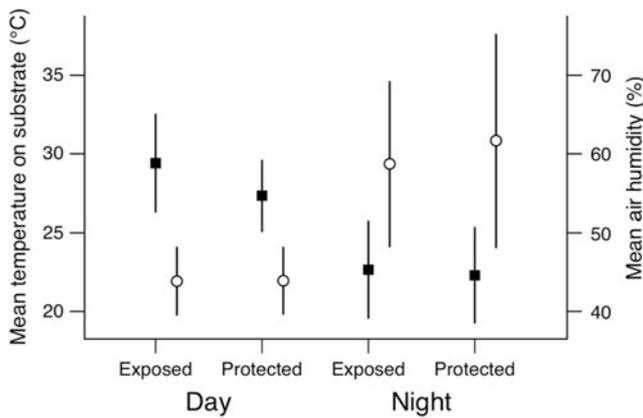


Fig. 2 Mean temperature of the substrate surface and mean air humidity observed during the day and during the night in sites exposed to or protected from direct sunlight in the study area. *Solid squares* represent averaged values for temperature and *open circles* represent averaged values for humidity in each site. In both cases *vertical lines* represent the standard deviation

General characterization of the clutches

We found 67 clutches of *T. taophora* in the 30 breeding sites identified over the course of the study period. The median number of eggs per clutch was 451 eggs (range=140–1746 eggs, $n=55$ clutches) and the median time of embryonic development was 4 days, ranging from 3 to 6 days ($n=27$ clutches). Paternal care lasted the entire period of embryonic development, and occasionally extended to the tadpoles up to 2 days after hatching ($n=11$ clutches). Some females added eggs to 1-day-old clutches ($n=7$), promoting a marked increase in the number of eggs in these clutches from 1 day to another. We excluded these clutches from the analysis of egg predation (see below) because we were unable to determine accurately the number of eggs that disappeared. In all other clutches used in the analysis, we are confident that no egg was added after the first day because we did not detect any increase in the number of eggs, and the photographs we took twice a day did not indicate the presence of early laid eggs.

Frequency of temporary egg desertion

Parental males deserted their clutches much more often during daytime. The median proportion of the inspections for which they were absent from their clutches during the day was 0.937 (range=0–1), whereas the median proportion during the night was only 0.103 (range=0–0.714). Moreover, regardless of the time period, the median proportion of temporary egg desertion in clutches deposited in exposed breeding sites was 0.545 (range=0–1), whereas in protected breeding sites it was only 0.083 (range=0–0.657). In fact, male egg attendance was modulated by the interaction between time period and breeding site: males attending eggs in exposed sites increased their

temporary egg desertion during daytime more than parental males in protected sites (Table 1, Fig. 3).

Benefits of temporary egg desertion: decreased water loss

Great variation was found in the proportional water loss in the agar models used to simulate adult frogs under natural conditions. Both the model including the additive effect between time period and breeding site and the model including their interaction were equally plausible to explain the variation on the proportional water loss in agar models (Table 1). As mentioned before, however, we will only interpret the simplest model, since it is likely that the interaction term is simply a variable with poor explanatory power added to the additive model (Burnham and Anderson 2002; Arnold 2010). Thus, among agar models with similar initial weight, regardless of the breeding site, the water loss was greater during the day than during the night (Fig. 4). Moreover, regardless of the time period, agar models of similar initial weight lost more water when placed in exposed sites than in protected sites (Fig. 4).

Costs of temporary egg desertion: increased egg predation

Despite males' temporary egg desertion during the day and frequent attendance during the night, egg predation was higher during the night. The median proportion of eggs consumed in non-manipulated clutches observed in the field at night was 0.372 (range=0.039–0.781), whereas the median proportion during the day was 0.105 (range=0.006–0.419). Breeding site had no effect on the intensity of egg predation (Table 1; Fig. 5a). We observed the same pattern among experimental clutches, in which control clutches suffered higher egg predation during the night than during the day (Fig. 5b). However, this difference was greater among clutches of the male

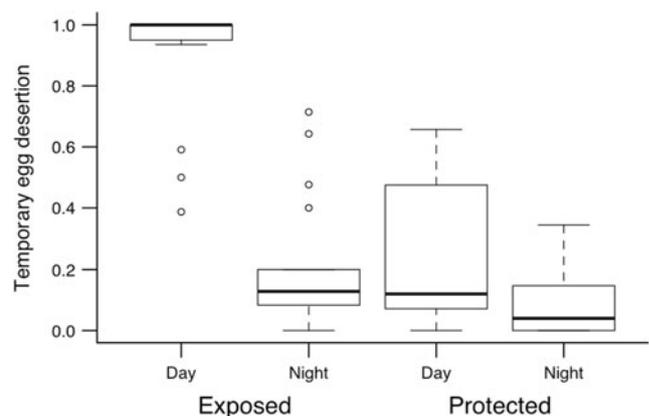


Fig. 3 Proportion of inspections when parental males of the frog *T. taophora* were absent from their clutches in sites exposed to sunlight (during the day and during the night) and in sites protected from sunlight (also during the day and during the night). *Horizontal lines* represent the median value observed in each dataset, *boxes* represent the quartiles, *vertical lines* represent the range, and *circles* represent outliers

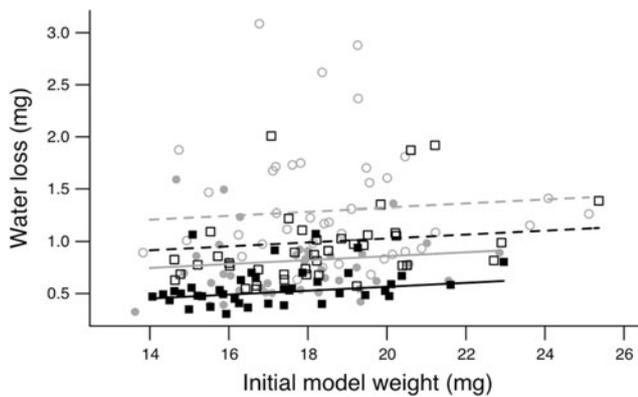


Fig. 4 Correlation between water loss and the initial weight of each agar model used to simulate adult males of the frog *T. taophora*. *Solid symbols* represent water loss observed during the night, and *open symbols* represent data observed during the day. Similarly, *solid lines* represent the relationship between water loss and initial weight during the night predicted by the best model, and *dashed lines* represent the prediction for the day. *Gray circles* represent water loss observed in sites exposed to sunlight, and *black squares* represent observed data in sites protected from sunlight. Similarly, *gray and black lines* represent predicted values in sites exposed or protected from sunlight, respectively

removal group, in which parental males were absent all the time (Fig. 5b). Thus, egg predation in experimental clutches was determined by the interaction between experimental groups and time period (Table 1; Fig. 5b).

We recorded 232 events of predation on eggs, most of them at night (Table 2). The main predators were conspecifics, including adults, juveniles, and tadpoles (Table 2). However, we have never recorded any event of filial cannibalism, and we also never observed parental males consuming eggs from other clutches during periods of temporary desertion. On only eight occasions we recorded heterospecifics consuming eggs, and all cases occurred during the day (Table 2). Workers of the ant *Pachycondyla striata* (Formicidae: Ponerinae) caused a drastic reduction in the number of eggs in four clutches of the male removal group, sometimes consuming the entire clutch in a period of 4 to 6 h.

Besides the events of predation on eggs, we also recorded four events of predation on parental males by the snake *Liophis miliaris* (three during the night and one during the day); all of them in exposed sites. Moreover, one parental male was attacked and consumed by the rocky shore crab *Geograpsus lividus* (Decapoda: Grapsidae) during the day in a protected site. In general, the frequency of predation on parental males was low, so it is not possible to infer any trend related to the period of the day or type of breeding site.

Discussion

Here, we investigate the costs and benefits of temporary egg desertion by a rocky shore frog with male-only parental care. Our results show that water loss is greater during daytime and

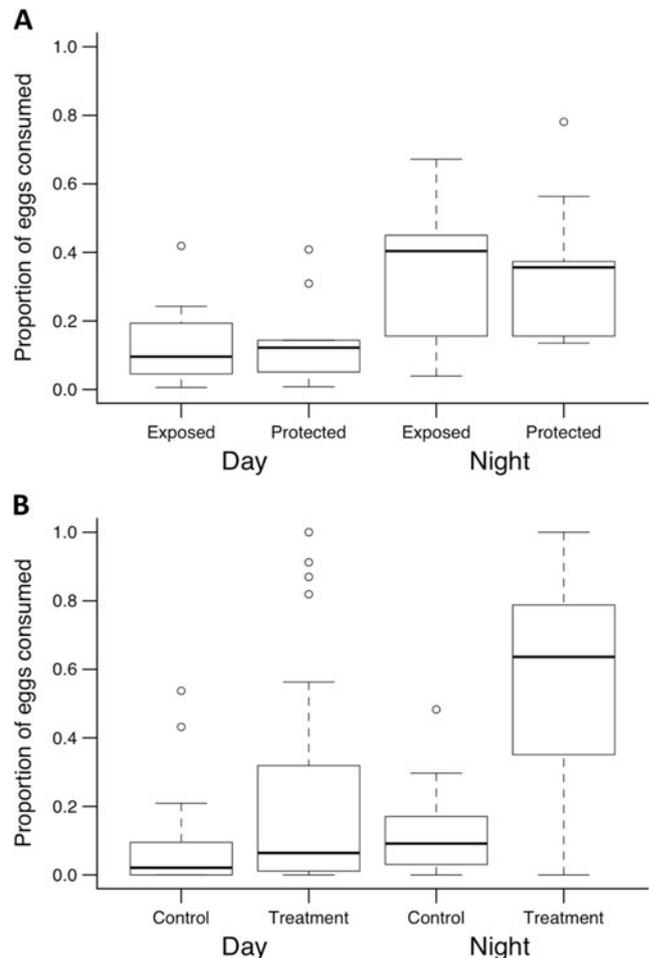


Fig. 5 Proportion of eggs initially present in clutches of the frog *T. taophora* that were consumed by predators. **a** Results obtained under natural conditions, depicting the observed data in sites exposed to sunlight (during the day and during the night) and in sites protected from sunlight (also during the day and during the night). **b** Results obtained under experimental conditions, depicting the observed predation on clutches in which parental males were either removed (i.e., treatment group) or maintained (i.e., control group). Data are divided into two time periods: day and night. *Horizontal lines* represent the median value observed in each dataset, *boxes* represent the quartiles, *vertical lines* represent the range, and *circles* represent outliers

in exposed sites. In accordance, the frequency of temporary egg desertion exhibited by males is considerably higher during daytime and in breeding sites exposed to direct sunlight. Indeed, virtually no male remained attending a clutch in exposed sites during daytime. Despite the high frequency of diurnal egg desertion, we demonstrate experimentally that the intensity of egg predation is higher during the night. Moreover, the presence of the parental male is crucial for egg survival because unattended clutches are almost entirely preyed upon, mostly by conspecifics. Below, we discuss each of these results and explore their broad implications in terms of parental care and male reproductive success.

In environments where temperature and humidity show great variation throughout the day, the physiological costs

Table 2 Predators and frequency of predation on eggs of the frog *T. taophora* during the day and during the night

Predators	Number of predation events	
	Day	Night
Anura: Cycloramphidae		
<i>Thoropra taophora</i> (n = 232)		
Adult males (n = 149)	15	134
Adult females (n = 28)	1	27
Juveniles (n = 49)	42	7
Tadpoles (n = 6)	6	0
Serpentes: Colubridae		
<i>Liophis miliaris</i> (n = 2)	2	0
Hymenoptera: Formicidae		
<i>Pachycondyla striata</i> (n = 4)	4	0
Crustacea: Grapsidae		
<i>Geograpsus lividus</i> (n = 2)	2	0
Total	72	166

of parental care are likely to be high, especially for species sensitive to dehydration (Requena et al. 2013). Anurans have low resistance to cutaneous water loss and dehydrate quickly when exposed to direct sunlight (Spotila and Berman 1976; Shoemaker 1992). When compared to actual values of water loss for frog species, the results reported here for daytime (mean \pm SD = 14.3 \pm 5.9 mg/cm²/h according to the allometric equation by McClanahan and Baldwin 1969) are high enough to compromise vital functions of individual frogs (Shoemaker 1992). Therefore, we suggest that *T. taophora* males interrupt parental activities in exposed sites during daytime primarily as a response to the risk of dehydration. As with amphibians, harvestmen are sensitive to water loss (Santos 2007), and the frequency of temporary egg desertion of parental individuals is also usually higher during daytime (Chelini and Machado 2012) or during the drier periods of the year (Machado et al. 2004). Therefore, because abiotic conditions modulate the physiological costs paid by parental individuals, we argue that these conditions exert great influence in the evolution and the extent of temporary offspring desertion in terrestrial ectotherms.

A common function of offspring attendance is protection against egg predators (Smiseth et al. 2012). Therefore, we initially predicted that eggs would be more vulnerable to predatory attacks during temporary desertion, and the cost of parental absence would include the partial loss of offspring (frogs: e.g., Chen et al. 2007; Cheng and Kam 2010; arthropods: e.g., Zink 2003; Chelini and Machado 2012). Contrary to our prediction, the frequency of predatory attacks upon the clutches of *T. taophora* is more intense at night, when the frequency

of egg attendance by males is higher than during daytime. These predatory attacks are accomplished mainly by conspecific adults, which are active only at night (Giaretta and Facure 2004). As an alternative to our prediction, it is possible that males simply adjust the intensity of parental care to temporal variations in egg predation risk. Parents of the convict cichlid fish *Cichlasoma nigrofasciatum*, for instance, decrease foraging activities and increase defensive behaviors in the presence of predators (Rangeley and Godin 1992). However, if egg predation risk alone determines the intensity of male care in *T. taophora*, we would expect no interaction between the frequency of temporary egg desertion and the type of breeding site. The fact that males in protected sites attend their eggs during daytime whereas males in exposed sites abandon their eggs during the same period reinforces the notion that harsh abiotic conditions play an important role determining the intensity of male care (see also Delia et al. 2013 and references therein). The relative importance of abiotic conditions and egg predation in determining how individuals allocate caring activities over time remains to be explored in more details, and species showing behavioral flexibility in the frequency of offspring attendance are ideal models to investigate this question.

The results of our field experiment indicate that the cost of temporary egg desertion in terms of offspring mortality in *T. taophora* would be greater during the night because unattended clutches are almost entirely preyed upon by conspecifics. During daytime, cannibalism upon unattended clutches is less frequent probably because conspecific adults are mostly inactive, hidden in protected places to avoid dehydration. During the night, however, temperature and humidity conditions on the rocky shore are milder, so that parental males can remain near their eggs during this period (even in exposed sites) and non-parental adults can wander around to forage. Despite the constant presence of parental males, nocturnal egg predation is higher because juvenile and mainly adults of *T. taophora* are able to overcome parental protection and cannibalize eggs. Similar results have also been reported for the gladiator harvestman *Neosadocus maximus* (Arachnida: Opiliones) and the maritime earwig *Anisolabis maritima* (Insecta: Dermaptera), in which some predators, including conspecifics, were able to displace attendant females and consume a great quantity of eggs (Miller et al. 2011; Chelini and Machado 2012). Nonetheless, the number of eggs that survive in the presence of the parent is far greater than that which survive in their absence. In situations where egg mortality in the absence of parental care is high, the benefits of protection to the offspring may outweigh the costs, thus favoring the maintenance of parental care (Klug et al. 2013). Based on the information obtained in this study, we suggest that the main current role of parental care in *T. taophora* is the protection of the eggs against predation imposed by conspecifics. In

fact, cannibalism has long been regarded as one of the main selective forces favoring the evolution and maintenance of egg attendance in a wide variety of animals (Wilson 1975).

For many species with terrestrial oviposition, egg attendance may also mitigate adverse environmental conditions, for instance, by protecting the eggs from desiccation (frogs: e.g., Delia et al. 2013; Poo and Bickford 2013; giant waterbugs: e.g. Smith 1997). Although *T. taophora* males temporarily abandon their eggs, no clutch was found dehydrated during our fieldwork. We argue that the films of freshwater flowing on the surface of the rocky shore may prevent egg dehydration during daytime, allowing males to be absent from their clutches without condemning their offspring to death by dehydration. Given that sources of freshwater are limited along the shore, suitable breeding sites are aggressively defended by males and shared by ovipositing females (Giaretta and Facure 2004; Muralidhar et al. 2014; this study). However, egg cannibalism by recently hatched tadpoles may have important implications for both male and female reproductive success. When juveniles do not cannibalize eggs, males can attend clutches composed of eggs laid by females at different moments, as observed in several fish and arthropods with male-only care (Stiver and Alonzo 2009; Requena et al. 2013). When juveniles cannibalize eggs, though, asynchronous oviposition events may impose mortality costs to eggs added later to the clutches (Manica and Johnstone 2004). Consequently, females should avoid laying eggs with males attending a clutch, thus limiting the opportunities for male multiple mating. We suggest that the low frequency of eggs added to 1-day-old clutches of *T. taophora* reported here (ca. 10 % of all clutches) was the result of females avoiding males who already had eggs in later stages of development. As previously recorded for some dendrobatid frogs (Summers and Tumulty 2013), egg cannibalism by tadpoles may impose costs for polygyny in *T. taophora* and may have favored synchrony between consecutive oviposition events among females.

Although temporary offspring desertion has been reported for several taxa (e.g., Rangeley and Godin 1992; Zink 2003; Machado et al. 2004; Chen et al. 2007; Cheng and Kam 2010; Chelini and Machado 2012), the selective forces favoring the evolution and maintenance of this behavioral strategy are still poorly understood. As reported here, males of *T. taophora* exhibit temporary egg desertion during daytime and in breeding sites exposed to direct sunlight, where physiological stress due to water loss is more intense. Since the main egg predators are conspecific adults, which are mostly inactive when parental males are not attending their clutches (probably due to similar tolerance limits), the costs of temporary desertion in terms of egg loss are relatively low when compared with the benefits related to decreased exposure of parental males to stressful abiotic conditions. This is also the case of some harvestman species in which parents leave their eggs temporarily

unattended (e.g., Machado et al. 2004; Requena et al. 2009; Chelini and Machado 2012). As a general prediction, therefore, we propose that temporary offspring desertion should be found when periods of harsher environmental abiotic conditions for the parents are coincident with periods of low offspring demand for protection against predators.

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Compliance with ethical standards

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Conflict of interest All authors declare that they have no competing interests.

Ethical approval All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Author's contribution RCC, GM, and CAB conceived the idea and designed the sampling and the experimental methods. RCC collected the data. GSR analyzed the data. RCC, GM, CAB, and GSR equally contributed to writing and revising the manuscript.

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