

# Contrasted influences of moon phases on the reproduction and movement patterns of four amphibian species inhabiting different habitats in central Italy

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**Abstract.** Many studies have provided evidence that prey adjust their behaviour to adaptively balance the fitness effects of reproduction and predation risk. Nocturnal terrestrial animals should deal with a range of environmental conditions during the reproductive season at the breeding sites, including a variable amount of natural ambient light. High degrees of illumination are expected to minimize those behaviours that might increase the animal detection by predators. Therefore, under habitat variable brightness conditions and in different ecosystems, the above mentioned behaviours are expected to depend on the variation in predation risk. Although moon effects on amphibian biology have been recognized, the direction of this influence is rather controversial with evidences of both increased and depressed activity under full moon. We tested in four nocturnal amphibian species (*Hyla intermedia*, *Rana dalmatina*, *Rana italica*, *Salamandrina perspicillata*) the effects of different (i) light conditions and (ii) habitats (open land vs. dense forest) on the reproductive phenology. Our results showed that the effects of the lunar cycle on the study species are associated with the change in luminosity, and there is no evidence of an endogenous rhythm controlled by biological clocks. The habitat type conditioned the amphibian reproductive strategy in relation to moon phases. Open habitat breeders (e.g., ponds with no canopy cover) strongly avoided conditions with high brightness, whereas forest habitat breeders were apparently unaffected by the different moon phases. Indeed, for all the studied species no effects of the moon phase itself on the considered metrics were found. Rather, the considered amphibian species seem to be conditioned mainly by moonlight irrespective of the moon phase. The two anurans spawning in open habitat apparently adjust their oviposition timing by balancing the fitness effects of the risk to be detected by predators and the reproduction.

**Keywords:** amphibians, Mediterranean, moon cycles.

One of the most significant decisions to make by an organism during its life is surely when, where, and how, to reproduce, being such decision-making more crucial under the threat of predation (Baugh and Ryan, 2010). Indeed, predation is by far one of the most impor-

tant selection pressures acting on the evolution of reproduction strategies in preys (Burk, 1982; Lima and Dill, 1990). The risk of predation is seldom constant but varies in time and space, shaping prey behaviour accordingly. Indeed, many studies have provided evidence that prey adjusts its behaviour to adaptively balance the fitness effects of reproduction and predation risk (reviewed in Lima, 1998).

Nocturnal terrestrial animals have to deal with a range of environmental conditions during the reproductive season at the breeding sites, including a variable amount of natural ambient light (i.e. moonlight) reaching the ground. For nocturnal animals, high degrees of illumination are expected to minimize those behaviours that might increase their detection by visually oriented predators (Lima and Dill, 1990). Therefore, under habitat variable condi-

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tions (i.e. light at the ground during the moon cycle) and in different ecosystems, the above mentioned decision-making processes may depend on a suite of selective pressures, including the variation in predation risk. Although moon effects on amphibian biology have been recognized (Church, 1960a, 1960b; Byrne et al., 2002; Grant et al., 2009, 2013; Vignoli and Luiselli, 2013), the direction of this influence is rather controversial with evidences of both increased activity (Tuttle and Ryan, 1982; Grant et al., 2009; Yetman and Ferguson, 2011), and depressed activity (Church, 1960b; Fitzgerald and Bider, 1974; Grant et al., 2009; Vignoli and Luiselli, 2013) under the full moon. Anurans may be able to respond directly to changing moonlight (antipredator and/or foraging behaviours; Kotler et al., 2001), or may present an endogenous cycle with lunar periodicity (Ralph, 1956).

The differences in moonlight intensity between new moon and full moon phases is on average 6-10 times (0.1-1 lux, see Bunning and Moser, 1969; Clarke, 2004), hence even in undisturbed sites (e.g. with no lighting pollution), the alternation between full and new moon phase may determine a huge variation in surface lightning intensity. A recent study (Vignoli and Luiselli, 2013) has demonstrated a direct effect of the moonlight on anuran spawning activity, pointing out that two species reproducing in open habitats synchronize their breeding activity (oviposition) with the synodic moon cycle by avoiding the moonlit nights. In addition, these anurans did not show any endogenous rhythm related to moon cycle, being their behaviour influenced by the light condition determined by both moon phases and cloud cover.

In the present study, we tested in four species of nocturnally reproducing amphibians the effects of different (i) light conditions (moonlight reaching the ground) and (ii) habitats (open land vs. dense forest) on the temporal dynamics of reproductive activity. More specifically, we aim at answering to the following key question: is there any moon-phase-related difference

in the reproductive biology and/or movement patterns of the considered species in contrasted habitat types (i.e., open land vs. dense forest)? Since the moonlight facilitates the vision likely more in open lands than in dense forests, we would expect that under full moon the risk of visually-oriented predation should be higher in open lands than in forested areas (Lima and Dill, 1990). Consequently, we hypothesize that the moon light variation exerts a higher influence on reproductive activity of amphibians inhabiting open lands than in forested areas (as evidenced by Rothermel and Semlitsch, 2002 for juvenile amphibians dispersal). However, the occurrence of non-visually oriented predators may complicate these expected patterns.

Four species of amphibians living in Central Italy were considered in the analyses. Populations of two frogs species were studied at the Mercareccia pool, Canale Monterano (190 m a.s.l.; 42°7'41.02"N, 12°2'45.91"E) in the Regional Natural Reserve of Monterano (Province of Rome, Italy). In this site the breeding amphibian community consists of six species (two salamanders and four anurans), among which we selected the two anurans characterized by open water-oviposition: the Italian tree frog, *Hyla intermedia* Boulenger, 1882 and the agile frog, *Rana dalmatina* Bonaparte, 1841 (Vignoli et al., 2007b). Samples were collected over an area of five hectares within an abandoned tuff quarry hosting two lentic semi-permanent ponds fed predominantly by rainfall (see Vignoli et al., 2007a for the description of this area). At the Insugherata Reserve site, where at least six species were recorded (one salamander, five anurans), we selected the two amphibians breeding in dense wooded habitat: the spectacled salamander *Salamandrina perspicillata* (Savi, 1821) and the Italian stream frog *Rana italica* Dubois, 1987. The Insugherata Natural Reserve (80 m a.s.l.; 41°57'37.40"N, 12°25'46.97"E) is a natural area inside Rome. The reproductive site of both species consists in a very small valley of about three hectares in surface area, with mesic woodland dominated by *Castanea sativa* and *Ostrya carpinifolia*, along a short perennial stream, tributary of the Fosso dell'Acqua Traversa, which is an affluent of the Tiber River. The Reserve, which covers an area of about 700 hectares, is a mosaic of weed cultivations, pastures, thermophilic woodlands, and small marshes with riparian hygrophilic woodlands (see Della Rocca et al., 2005 for the description of this area). At the Monterano site, the study ponds were surveyed periodically over one year (2007) with a survey effort of three samplings per week in late winter and spring when *R. dalmatina* and *H. intermedia* have their activity peaks (see Vignoli et al., 2007a, 2007b, 2009). For comparison, we used also the data in Luiselli and Vignoli (2013) referring to the same species in the same site for the years 2001-2003. As regards to amphibian samplings, at each visit, we checked all the clutches oviposited the night

before as a proxy of frog spawning activity, assuming that to one clutch corresponds one mating pair (Paton and Harris, 2010; Vignoli and Luiselli, 2013). The embryo stage (Gosner, 1960) and the degree of egg jelly capsule hydration (an indirect measure of the time elapsed by eggs into water) was used to recognize whether each egg mass had been deposited the day before the sampling (estimated precision:  $\pm 1$  day) or in previous dates (Vignoli and Luiselli, 2013). In the analyses we used the number of mating pairs per night as a descriptor of anuran activity (Vignoli and Luiselli, 2013), this reproductive phase being among those subjected to the highest predation risk (Olson, 1989). For each sampling we recorded the moon phase and the cloud cover, this latter retrospectively from a weather stations sited few kilometres far from the site (Monte Virginio). At the Insugherata site, we monitored the reproductive stream from 2005 to 2010. As concerns *S. perspicillata*, the study period extended from February 2005 to May 2007. For *R. italica* the daily observations were carried out in spring (end of February-end of May) in 2008-2010. All the considered *S. perspicillata* individuals were females (see Vignoli et al., 2010 for a method to distinguish sexes in vivo), because only females are aquatic during the oviposition phase (Angelini et al., 2007). Adult frogs were always sighted in water and were observed while mating on several occasions. In order to correlate salamander and frog activities to the moon phase, we considered only the newly arriving individuals to the stream, hence those moving to the reproductive site because we judged that the influence of the moon on salamander and frog activity, if there is any, should mainly affect the movement to reach the brook, i.e. the time with the highest exposition to potential predators. In fact, during the oviposition, both *S. perspicillata* and *R. italica* remain under stones into the water and their localization by predators is not dependent on night lightning (Della Rocca et al., 2005; Vignoli pers. obs.). In particular, for *S. perspicillata* the time spent into the water by females (and the moment they leave the oviposition site) is strictly related to the salamander weight (proportional to egg number) (Della Rocca et al., 2005), hence the time at which individuals abandon the brook could reflect intrinsic requirements (end of the time for oviposition) rather than ecological constraints (predation risk). We devised different reproductive phenology descriptors for the study species (i.e. number of clutches for the species at the Monterano site, and movement activity toward the reproductive site for amphibians at the Insugherata site), because for each case we considered the reproductive activity (migration, breeding, oviposition) with the higher threat by the exposition to predation. In both the study sites, we measured the light amount reaching the ground under full moon and new moon phases by using a luxmeter (Lafayette DT-8820). In the open habitat (Monterano site), the light measured at the ground under clear sky condition was (mean  $\pm$  SD)  $0.02 \pm 0.1$  lux ( $n = 4$ ) and  $0.12 \pm 0.3$  lux ( $n = 5$ ) respectively under new and full moon phases. With clouds covering the sky, no statistically significant differences can be detected between moon phases in terms of moonlight amount reaching the ground ( $U = 3.00$ ;  $p = 0.513$ ; Mann-Whitney  $U$ -test). In the wooded habitat, the moonlight filtered by the

dense canopy did not reach the ground at all (0.00 lux) irrespectively of lunar phase and cloud cover.

In order to analyse amphibian phenology data by means of circular statistics, we coupled data on reproductive activity with lunar periodicity, assigning to each sampling date a value in the range 0-29, where 0 represents the full moon. Then, we converted lunar day values to angles, by dividing the length in days of the lunar cycle ( $n = 29.5$ ), and after this we multiplied the result obtained by  $360^\circ$  (Grant et al., 2009). In order to assess whether amphibian reproductive activity follows the lunar cycle, we used Rao's spacing test (Batschelet, 1981), an equivalent of non-parametric test of classic statistics, because phenological data did not show normal distribution. For all the study species we tested our  $H_1$  hypothesis that reproductive activity follows lunar periodicity against the  $H_0$  hypothesis that reproductive events are randomly spaced throughout the lunar cycle. For those species exhibiting a lunar periodicity in their reproductive activity, we tested the datasets for a specific angle using alternatively four expected means (the four quarters of the synodic lunar cycle) by means of V-test for testing data distribution against a specified angle (Batschelet, 1981). Moreover, we analysed the study species at the open land habitat site taking into account also the sky conditions (cloudy or clean). Therefore we tested the datasets considering all the cloudy nights as falling during new moon (low light lunar phase) in order to test the influence of the moonlight irrespectively of the moon phase (Vignoli and Luiselli, 2013). All circular data were analysed using the software Oriana 2.0 (<http://www.kovcomp.co.uk/oriana/>, Kovach Computing Services, Anglesey, UK), all test being two tailed and alpha set to 0.05.

In total, we analyzed 97 *H. intermedia* clutches, 59 *R. dalmatina* clutches, 325 *R. italica* individuals, and 452 *S. perspicillata* females. Overall, our analyses on raw data revealed that reproductive activity patterns were significantly related to lunar periodicity in only one species (*R. dalmatina*) (table 1). Both the species inhabiting dense wooded habitat did not show any relation of activity (i.e. approach to the reproductive site) with lunar synodic cycle (table 1). When in the analyses also the cloud cover is taken into account, *H. intermedia* clutch distribution apparently concentrated around the moon phase with the lowest ambient light level (table 1). The same was true for *R. dalmatina*.

As regards to *H. intermedia*, the analysis performed on the raw data showed a low concentrated clutch distribution with the mean vector falling at the end of the waning gibbous moon phase (fig. 1A). On the other hand, the distribution pattern revealed by the analysis considering

data on cloud cover presented an apparent concentration in moon phases with low moonlight condition. As for *R. dalmatina*, the distribution of the clutches concentrated around new moon phase (fig. 1D). However, it should be noted that when data on cloud cover are not considered, the bulk of the observations felt just before and after the new moon (fig. 1A). Both *R. italica* and *S. perspicillata* showed overdispersion of sightings, and this fact impeded reliable calculation of some statistics of interest (fig. 1E-F).

Before discussing our results, it is necessary to state that we have analyzed data that were not collected every day as should be preferable for moon phase correlations, and also for a relatively short time span.

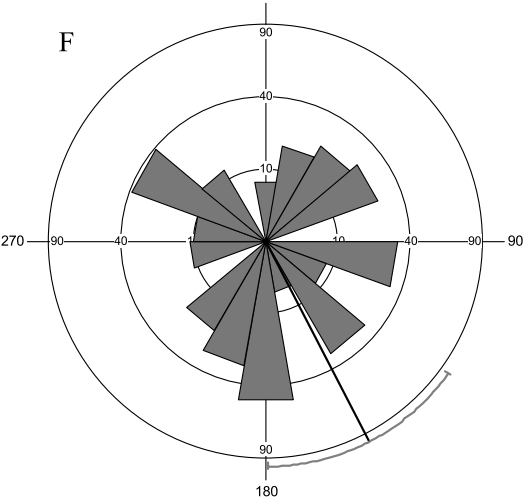
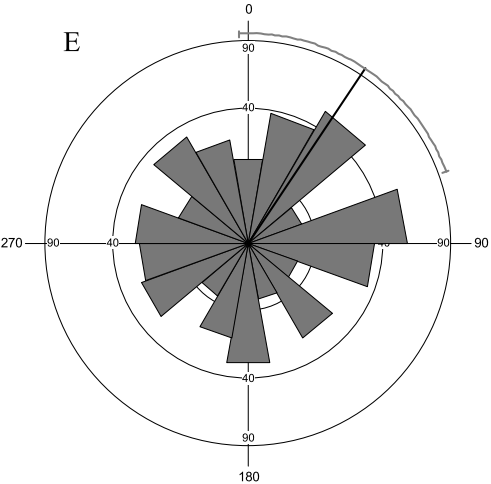
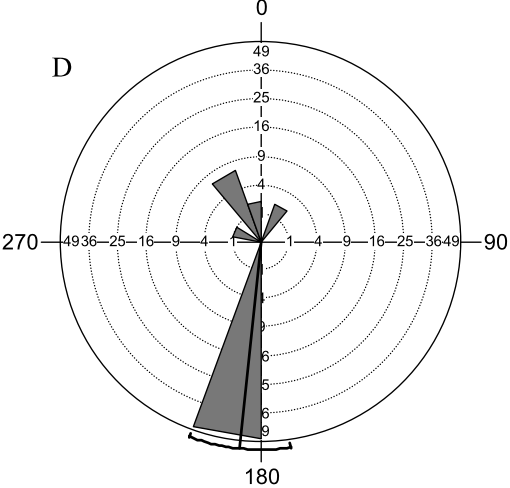
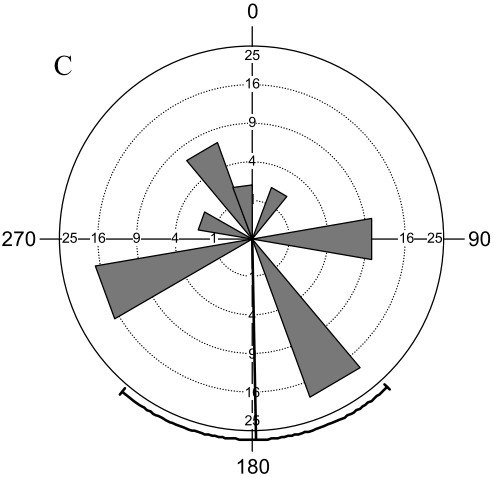
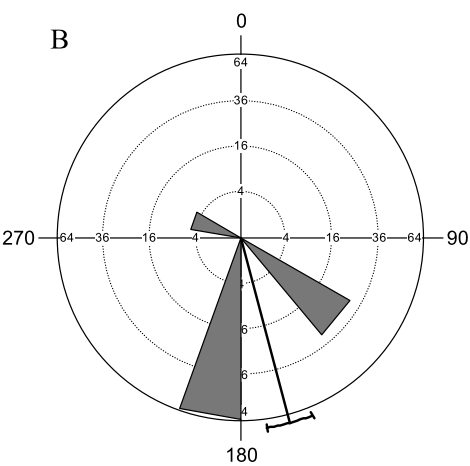
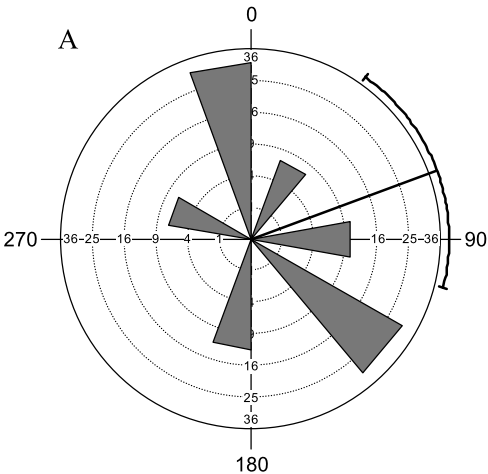
The effects of the moon on animal biology have been widely recognised in several groups (i.e.: Farbridge and Leatherland, 1987; Bentley et al., 2001; Naylor, 2001). Our results showed that the effects of the lunar cycle on the study

species are associated with the change in luminosity, and there is no evidence of an endogenous rhythm controlled by biological clocks (in accordance with Vignoli and Luiselli, 2013). Indeed, we found that the reproductive strategy of the study species in relation to moon phases was conditioned by the habitat type, with the various species from contrasting habitats (i.e.: open vs. wooded habitats) behaving differently. That is: (i) open habitat breeders (e.g.: ponds with no canopy cover in the surroundings in our study case) strongly avoided ambient conditions with high levels of lighting on ground surface; and (ii) forest habitat breeders were apparently unaffected by the different moon phases, showing inconsistent activity patterns randomly different among years. In this latter case, it should be considered that we include an anuran and a salamander species among the forest habitat breeders, thus differences more than just habitat type can be responsible for the patterns ob-

**Table 1.** Synopsis of the circular statistics for the metric distribution in four species of amphibians at two localities in Mediterranean Central Italy. The statistical tests refer to whether or not clutches are laid uniformly over the lunar cycle (Rao spacing test) and whether or not clutch distribution have a mean angle (expected mean 180°) (V test) (Batschelet, 1981). For *H. intermedia* and *Rana dalmatina*, the column \* showed the analysis taking into consideration also the cloud cover (see Methods).

	<i>S. perspicillata</i>	<i>R. italica</i>	<i>H. intermedia</i>	<i>H. intermedia</i> *	<i>R. dalmatina</i>	<i>R. dalmatina</i> *
Number of observations	452	325	97	97	59	59
Mean vector ( $\mu$ )	33.7°	152.7°	69.6°	165.1°	179.1°	186.1°
Length of mean vector (r)	0.13	0.16	0.23	0.82	0.25	0.63
95% C.I. ( $\pm$ ) for $\mu$	6.1°-61.4°	125.9°-179.4°	35.2°-104.1°	158.0°-172.2°	137.6°-220.5°	171.8°-200.3°
Concentration	0.27	0.33	0.47	3.15	0.51	1.66
Circular variance	0.86	0.84	0.77	0.18	0.75	0.36
Circular standard deviation	114.7°	109.0°	98.1°	35.9°	96.1°	54.56°
Rao's spacing test (U)	336.903	335.631	334.021	348.866	311.186	329.492
Rao's spacing test (p)	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
V test (V; exp. mean 180.00°)	-0.112	0.145	-0.08	0.794	0.177	0.632
V test (u)	-3.365	3.708	-1.12	11.055	2.667	6.864
V test (p)	1	0.0001	0.868	<1E-12	8.68E-08	2.64E-12

**Figure 1.** Circular plots showing the distribution of the used metric for the study species. (A) Distribution of *Hyla intermedia* clutches at Monterano site. (B) The same data in A with cloud cover information (see Methods). (C) Distribution of *Rana dalmatina* clutches at Monterano site. (D) The same data as in C with cloud cover information. (E) Frequency of occurrence (N individuals) of *Salamandrina perspicillata* females approaching reproductive site during 2005-2007 at Insugherata site. (F) Frequency of occurrence (N individuals) of *Rana italica* individuals approaching reproductive site in 2008-2010 at Insugherata site. In circular plot the area of each wedge represents the number of sampling unit occurring in the various lunar sub-phases. Concentric dotted lines represent the scale for the sampling unit of the various metrics used (numbers only on the top axis). Black ray indicates the mean vector ( $\mu$ ) and the external black curved line represents 95% confident intervals (in grey if the statistic was unreliable). 0° = full moon; 180° = new moon.



served. At a closer inspection, the plots would reveal for all the studied species no effects of the moon phase itself on the considered metrics. Rather, amphibians seem to be conditioned mainly by moonlight irrespective of the moon phase. At the Insugherata site, under the canopy of the wooded habitat, *S. perspicillata* and *R. italica* movement behaviour is clearly conditioned by neither moon phase nor cloud cover as expected, because at night no light filtered through the dense foliage. At Monterano site, since a night during full moon coupled with cloudy weather produces the same amount of light at the ground as a night under new moon, the two anurans spawning in open habitat apparently adjust their oviposition timing by balancing the fitness effects of the risk to be detected by predators and the reproduction (Lima, 1988; Vignoli and Luiselli, 2013). In other amphibian species, however, activity seems to be reduced during the new moon phases, and the calling activity by males can increase during the full moon, when however the potential predators are not visually oriented (for instance, bats; reviewed in Grant et al., 2013).

It is possible that the different evolutionary trajectories between salamanders and frogs have shaped their reproductive phenologies, thus partially explaining the differences observed in this study. However, we included in the study two species which are phylogenetically related (*R. dalmatina* and *R. italica*), and also these species confirmed the pattern described above, despite the different metrics applied.

As concerns the open habitat breeders, the observed behavioural responses might result from both natural selection through selective removal of the individuals failing to exhibit this behavioural pattern become predated, and a prey learning to respond to predation risk in a temporal threat-sensitive manner. Many prey species have been shown to respond to predators in a threat-sensitive manner, that is, with an intensity that matches the level of threat they are exposed to (Helfman, 1989). *Hyla intermedia* spawns in spring when it is actively pre-

dated by night by several animals (mainly the snake *Natrix natrix*; Luiselli et al., 2005). On the contrary, *Rana dalmatina* reproduces in winter when many potential predators of amphibians are not active (i.e.: snakes), it mates underwater, and remains underwater during most of its permanence at the reproductive site. It is hence likely that its avoidance of full moon phase for mating activity reflects both a low contingent predation risk and/or a phylogenetically fixed behaviour. In this regard, it should be noticed that several predators, and for instance snakes, may also use olfactory cues to find their prey (e.g., Brown and Shine, 2002). It is also noteworthy that experimental studies have revealed that mating in light and dark conditions may have comparable reproductive payoffs, with displaying in the dark being not detrimental and may even be advantageous if predation risk is reduced at night (Denoel and Doellen, 2010).

Our suggestion that the predation risk shapes the response of amphibians to moon phases by habitat type in relation to the intensity of light arriving on ground is indirectly supported by a recent experimental study (Campbell et al., 2008). In this latter study, the authors showed an habitat shift due to antipredatory behaviour also in a snake (*Boiga irregularis*), which selected more covered habitats during full moon phase. Although moonlight influence on nocturnal visually oriented predator/prey relationships has been widely proposed (i.e. Blair, 1943; Metzgar, 1967; Vickery and Bider, 1981), very few studies confirmed the effect of moon illumination on prey's vulnerability (Clarke, 1983). Further experimental studies involving also predators (for instance, snakes; Luiselli et al., 2005; and owls; Jaksic et al., 1982) in the study system could clarify if the patterns observed can be unequivocally interpreted as an adaptive anti-predator response.

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