

## Original Article

## Amphibians' response to the lunar synodic cycle—a review of current knowledge, recommendations, and implications for conservation

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The way in which amphibians respond to the geophysical changes brought about by the lunar synodic cycle is a neglected area of their ecology, but one which has recently generated interest. Knowledge of how amphibians respond to lunar phase is of intrinsic interest and also may be important for conservation and monitoring of populations. We surveyed the literature on amphibians' responses to the lunar cycle and found 79 examples where moon phase in relation to amphibian behavior and ecology had been studied, across diverse amphibian taxa. Of the examples reviewed, most of them show some type of response to lunar phase, with only a few species being unaffected. We found that there is no significant difference between the numbers of species which increase, and those that decrease activity or reproductive behavior (including calling) during a full moon. The responses to the lunar cycle can not be generalized across taxonomic group, but instead are highly species specific and relate directly to the species' ecology. The primary reasons for changes in amphibian behavior in response to the lunar cycle appear to be temporal synchronization of breeding and predator avoidance. Responses to changes in prey availability, facilitation of visual signalling and use of lunar cues in navigation and homing are less prevalent but merit further investigation. Comparisons between studies are hampered by differences in field and analytical methods; we therefore make a number of recommendations for future collection and analysis of data related to lunar phase. **Key words:** amphibians, circular statistics, light, lunar cycle, moon phase, predator avoidance, reproductive synchronization. [*Behav Ecol*]

## INTRODUCTION

Recently, there has been interest in the way in which lunar cycles affect amphibians, with reports suggesting that the lunar synodic cycle influences breeding and behavior in a number of amphibian species (Deeming 2008; Grant et al. 2009; Yetman et al. 2011). While the influence of environmental variables such as temperature and rainfall on behavior and population counts is widely recognized (Wells 2007), relatively few studies have addressed the possible impact of lunar cycles.

That moon phase should influence amphibian behavior is unsurprising, as light levels can vary by nearly 2 orders of magnitude throughout the course of the lunar cycle (Campbell et al. 2008), providing a significant source of temporal environmental heterogeneity likely to affect nocturnal animals. Gravitational and magnetic changes also occur regularly with the lunar cycle, such that gravitational forces peak twice per cycle (at new and full moons) and the geomagnetic field peaks during the moon's third quarter (Stolov 1965; Bell and Defouw 1966). Despite this, however, and although it was shown in the 1960s that ovulation in several species of tropical anurans was linked to the lunar cycle (Church 1960a, 1960b, 1961), the topic has since been largely neglected. Here, we review the literature that (either quantitatively or descriptively) describes

lunar-mediated behavior in amphibians, and discuss the possible adaptive significance of such behavior. We also make recommendations to improve comparability between future studies of amphibian ecology by accounting for lunar cycles in study design, and by correct analysis of lunar cycle data.

## EVIDENCE FOR LUNAR-MEDIATED BEHAVIOR

There are very few studies which set out to investigate the influence of moon phase on amphibians. Most studies (such as that of Byrne [2002] and Byrne and Roberts [2004]) note the effects of lunar phase, while studying other aspects of amphibian ecology. Typically, reports of amphibians being affected by the lunar cycle are qualitative and have not been statistically validated. This is particularly the case in older papers, or papers that are primarily natural history accounts of species, such as Duellman's (1967) study of Costa-Rican hylid frogs. This lack of quantitative studies makes a rigorous meta-analysis impossible; however, we do present some statistical tests on the data collected (carried out using Minitab 13 and Oriana 3), which must be cautiously interpreted, bearing in mind the limitations and qualitative nature of much of the data.

Systematic literature searches revealed 79 examples of amphibian behavior, where moon phase was recorded, arising from 47 publications. These included 20 examples of amphibians showing a positive response to the full moon, by increasing activity or calling, 30 showing a negative response, 17 where amphibians were unaffected by moon phase, and

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Table 1

Summary of literature concerning lunar mediated responses in amphibians\*

Type of response	Number of species	Species
<b>REPRODUCTIVE ACTIVITY</b>		
Migration or breeding linked to full moon	6	<i>Crinia georgiana</i> , [1][2] <sup>a</sup> ; <i>Duttaphrynus</i> ( <i>Bufo</i> ) <i>melanostictus</i> (ovulation) [3][4]; <i>Ingerophrynus</i> ( <i>Bufo</i> ) <i>biporcatus</i> [4]; <i>Bufo bufo</i> [5]; <i>Rana temporaria</i> [5]; <i>Pyxicephalus adspersus</i> [6]
Migration or breeding linked to new moon	1	<i>Fejervarya</i> ( <i>Rana</i> ) <i>cancrivora</i> [7]
Migration or breeding unaffected by moon phase	3	<i>Ambystoma californiense</i> [8]; <i>Epidalea</i> ( <i>Bufo</i> ) <i>calamita</i> [9]; <i>Duttaphrynus</i> ( <i>Bufo</i> ) <i>melanostictus</i> (spermatogenesis) [3][4]
Males call more, or for longer under increased moonlight	11	<i>Ptychadena stenocephala</i> [10]; <i>Phrynomantis</i> ( <i>Bufo</i> ) <i>aspera</i> [11]; <i>Cophixalus ornatus</i> [12]; <i>Smitisca sila</i> [13][14]; <i>Acris crepitans</i> [15]; <i>Ingerophrynus</i> ( <i>Bufo</i> ) <i>biporcatus</i> [4][11]; <i>Megophrys montana</i> [11]; <i>Dendropsophus bipunctatus</i> [16]; <i>Hypsiboas albomarginatus</i> [16] <sup>b</sup> ; <i>Adenomera</i> ( <i>Leptodactylus</i> ) <i>bokermanni</i> [16] <sup>b</sup> ; <i>Kassina senegalensis</i> [17] <sup>c</sup>
Males call more, or for longer under decreased moonlight (including full moon avoidance)	21	<i>Hyla cinerea</i> [15]; <i>H. versicolor</i> [18]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>hemiphys</i> [18]; <i>A. cognatus</i> [18]; <i>Rana pipiens</i> [18]; <i>Rana sylvatica</i> [18]; <i>Pseudocris</i> ( <i>Hyla</i> ) <i>crucifer</i> [19]; <i>Hyla squirella</i> , [20]; <i>Scinax</i> ( <i>Hyla</i> ) <i>boulengeri</i> [21]; <i>S. elaeochroa</i> [21]; <i>Dendropsophus</i> ( <i>Hyla</i> ) <i>eberratus</i> [21]; <i>D. phlebodes</i> [21]; <i>Tlalocohyla</i> ( <i>Hyla</i> ) <i>loquax</i> [21]; <i>Smitisca baudini</i> [21]; <i>S. phaeota</i> [21]; <i>S. puma</i> [21]; <i>Agalychnis</i> ( <i>Phyllomedusa</i> ) <i>callidryas</i> [21]; <i>A. saltator</i> [21]; <i>Leptodactylus mystacinus</i> [16]; <i>Rhacophorus achantharrhena</i> [22]; <i>Engystomops</i> ( <i>Physalaemus</i> ) <i>pustulosus</i> [23] <sup>d</sup>
Male calling is unaffected by moon	11	<i>Cophixalus ornatus</i> [24]; <i>Austrochaperina robusta</i> [24]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>woodhousii</i> [18]; <i>Spea bombifrons</i> [18]; <i>Pseudacris maculata</i> [18]; <i>Hypsiboas</i> ( <i>Hyla</i> ) <i>boans</i> [25]; <i>Rana clamitans melanota</i> [26]; <i>Dendropsophus anceps</i> [16]; <i>D. minutus</i> [16]; <i>D. seniculus</i> [16]; <i>Physalaemus signifer</i> [16]
Mate choice affected by moon phase	2	<i>Engystomops</i> ( <i>Physalaemus</i> ) <i>pustulosus</i> [27]; <i>Hyperolius marmoratus</i> [28]
<b>NON REPRODUCTIVE ACTIVITY</b>		
Animals using moon for orientation, navigation, homing	3	<i>Ichthyosaura</i> ( <i>Triturus</i> ) <i>alpestris</i> [29] <sup>e</sup> <i>Acris gryllus</i> [30]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>fowleri</i> [31]
Animals not using moon for orientation, navigation, homing	2	<i>Rana pipiens</i> [32]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>boreas</i> [33][34]
Foraging / Locomotion / abundance increased at full moon	3	<i>Litoria</i> sp [42]; <i>Eleutherodactylus martinicensis</i> [43]; <i>Pyxicephalus adspersus</i> [6]
Foraging / Locomotion / abundance increased at new moon (including full moon avoidance)	8	<i>Lissotriton vulgaris</i> [35]; <i>Triturus cristatus</i> [35]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>americanus</i> [36]; <i>Hoplobatrachus occipitalis</i> [37]; <i>Leiopelma hamiltoni</i> [38]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>fowleri</i> [39]; <i>Ambystoma opacum</i> (larvae) [40]; <i>Hypsiboas leptolineatus</i> [41]
Foraging / Locomotion / abundance unaffected by moon	3	<i>Rana clamitans melanota</i> [26]; <i>Eleutherodactylus augusti</i> [44]; <i>Phaeognathus hubrichti</i> [45]
Ambiguous cases	5	<i>Lissotriton</i> ( <i>Triturus</i> ) <i>vulgaris</i> [5]; <i>Triturus cristatus</i> [5]; <i>Lissotriton</i> ( <i>Triturus</i> ) <i>helveticus</i> [5]; <i>Anaxyrus</i> ( <i>Bufo</i> ) <i>houstonensis</i> [46]; <i>Bufo bufo</i> [47]

<sup>a</sup>Another study (Smith et al. 2003) found the number of males in the chorus was not affected by the lunar cycle.<sup>b</sup>Close to significance at  $P=0.06$ .<sup>c</sup>Territorial, not mating call on a full moon.<sup>d</sup>When bat predators present.<sup>e</sup>Could be an artefact of the testing arena.

1. Byrne and Roberts 2004; 2. Byrne 2002; 3. Church 1960a; 4. Church 1961; 5. Grant et al. 2009; 6. Yetman et al. 2011; 7. Church 1960b; 8. Loredó et al. 1996; 9. Sinsch 1988; 10. Amiet 1974; 11. Iskandar 1998; 12. Brooke et al. 2000; 13. Da Silva Nunes 1988; 14. Tuttle and Ryan 1982; 15. Granda et al. 2008; 16. Abrunhosa et al. 2006; 17. Fleischack and Small 1978; 18. Johnson and Batie 2001; 19. Forester and Lykens 1986; 20. Taylor et al. 2007; 21. Duellman 1967; 22. Harvey et al. 2002; 23. Tuttle et al. 1982; 24. Hauselberger and Alford 2005; 25. Magnusson et al. 1999; 26. Baker and Richardson 2006; 27. Rand et al. 1997; 28. Backwell and Passmore 1990; 29. Diego-Rasilla et al. 2005; 30. Ferguson et al. 1965; 31. Ferguson and Landreth 1966; 32. Dole 1972; 33. Gorman and Ferguson 1970; 34. Tracy and Dole 1969; 35. Deeming 2008; 36. Fitzgerald and Bider 1974; 37. Kühn et al. 1987; 38. Newman 1990; 39. Ferguson 1960; 40. Hassinger and Anderson 1970; 41. Hiert and Moura 2010; 42. Brown and Shine 2002; 43. Jaeger and Hailman 1976; 44. Goldberg and Schwalbe 2004; 45. Bakkegard 2002; 46. Swannack et al. 2009; 47. Llusia et al. 2010. Literature was searched systematically in May 2011, using ISI Web of Knowledge (<http://wok.mimas.ac.uk/>), Google Scholar ([www.google.com](http://www.google.com)), Amphibiaweb ([www.amphibiaweb.org](http://www.amphibiaweb.org)) and JSTOR (<http://www.jstor.org/>).

12 examples that were ambiguous or related only to mate choice, navigation, and homing (Table 1). Leaving out the 5 ambiguous cases, there were significantly more examples of amphibian behavior being affected, rather than unaffected by lunar phase ( $N = 72$ ,  $df = 1$ ,  $\chi^2 = 16.06$ ,  $P < 0.001$ ). Even

allowing for non-presentation of negative results, this implies that lunar-related behavior in amphibians is considerably more prevalent than previously supposed.

Families Bufonidae, Ranidae, Salamandridae, and Hylidae were the most frequently represented in the dataset. Within

these families, 71% of studies reported a response to lunar cycles, and there was no significant difference between families in the prevalence of lunar responses (Chi-squared test:  $N = 43$ ,  $df = 3$ ,  $\chi^2 = 1.06$ ,  $P = 0.79$ ). Comparison with other families was not possible due to small sample size.

### The adaptive significance of lunar-mediated behaviors

Some of amphibians' responses to the lunar cycle are likely to be adaptive, and here we look at the evidence for the adaptive nature of amphibians' response to lunar phase. Again, we are hampered by a lack of rigorously recorded studies, and many purely qualitative or anecdotal observations. The following discussion is therefore speculative, and we hope it will stimulate further research and more stringent testing of hypotheses related to lunar phase in amphibians.

Animal behavior is the result of a complex balance of costs and benefits; animals act to maximize their foraging efficiency and reproductive output, while minimizing their predation risk (Dill 1987; Sih 1994; Grafe 1997; Kie 1999; Akre and Ryan 2011). The adaptive nature of lunar-mediated behavior is therefore likely to vary within and between species, with location and habitat, and with prevailing environmental conditions, as species are expected to behave differently with regard to moon phase, depending on their unique ecology. Additionally, many responses to the lunar cycle may arise as consequences of other behavior.

#### Predator avoidance

Lunar-related predator avoidance may depend on a number of factors, including whether the visual acuity of predator and prey is similar. For example, visual nocturnal predators (e.g., owls) may be at an advantage under increased light levels (Clarke 1983), but if changes in illumination affect both visual predator and prey equally, there will be no net change in predation risk (Rand et al. 1997). Nonvisual nocturnal predators such as bats (which use echolocation; Surlykke and Kalko 2008), carnivorous mammals (which use visual and olfactory cues) or snakes (which use olfactory, thermal, and vibrational cues, as well as visual ones; Vincent et al. 2005) may be at a disadvantage at full moon if their amphibian prey can visually detect and avoid them. For diurnal predators, full moon can provide opportunities to hunt crepuscular or nocturnal prey, due to increased light levels at dusk (Watanuki 1986). Overall, the relative advantages to prey and

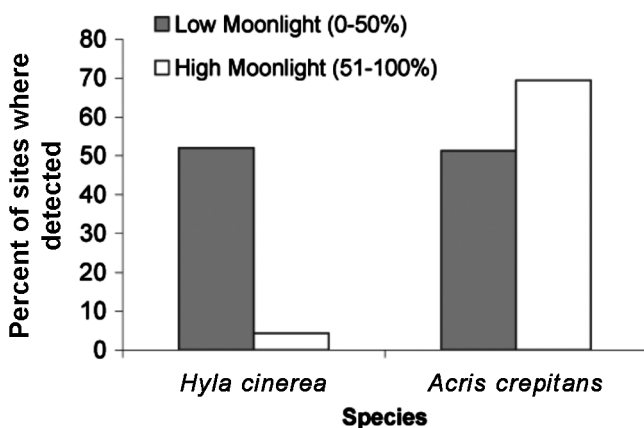
predators under different levels of moonlight depend on the combination of senses used by prey and predator, the range of vision under which each best operates, and consequently whether a particular level of moonlight gives predator or prey a visual advantage. Each amphibian species has a range of illumination under which it can see best, and in some species this range may be very narrow, and much wider in others (Jaeger and Hailman 1976, 1981; Buchanan 1992, 2006), so relative advantage is likely to be highly species specific.

The behavior of conspecifics and other competitors further complicates the picture (Daly et al. 1992). Many amphibians, for example, prey on insects and are in turn preyed on by a range of carnivores and omnivores. All 3 categories (insect prey, amphibian predator, and top predator) will therefore be involved in a multiparty game situation, the outcome of which is difficult to predict and depends on the relative costs and benefits, which will vary with the game situation (Seligmann et al. 2007). For this reason, behavior in relation to lunar cycles may be difficult to predict.

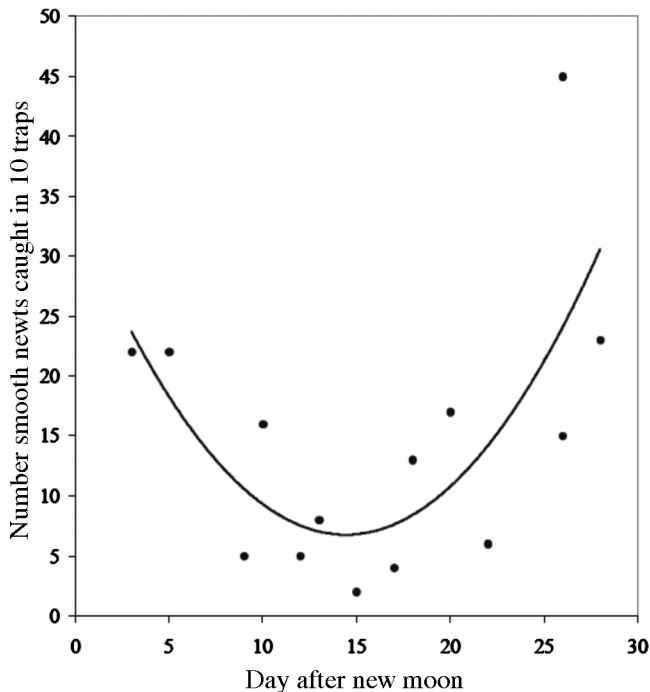
A number of amphibian behavioral responses to the lunar cycle have been attributed to predator avoidance, including changes in the timing or intensity of calling (Taylor et al. 2007; Granda et al. 2008), foraging, and other activity outside the breeding season (Fitzgerald and Bider 1974), departure from breeding ponds (Deeming 2008), and visual signaling/mate choice (Backwell and Passmore 1990; Rand et al. 1997).

Calling is important in most anurans as an advertisement for reproduction, but can make them conspicuous to predators, so the timing, duration, and location of displays should be evolutionarily optimized to maximize reproductive success, while minimizing energetic cost and predation risk (Brooke et al. 2000). Calling is the best documented behavior type in relation to lunar cycles (43 of our 79 examples, Table 1), and illustrates the diversity of responses exhibited by different taxa. Many anurans confine calling to the darker parts of the lunar cycle; for *Hyla cinerea*, for example, calls are detected less frequently in call surveys under increased lunar illumination (Granda et al. 2008; Figure 1), while the squirrel treefrog (*Hyla squirella*) either stops calling on moonlit nights, or calls from concealed sites (Taylor et al. 2007). Predator avoidance has been suggested as the reason for this behavior (Taylor et al. 2007; Granda et al. 2008). Conversely, however, some species increase calling during full moon. *Acris crepitans*, for example, calls more in moonlight (Granda et al. 2008; Figure 1). *Acris crepitans* is a small and cryptically colored frog, which has high frequency, rapidly extinguished calls, making it difficult for both visual and auditory predators to locate, and Granda et al. (2008) speculate that it may call during periods of high moonlight to avoid acoustic interference by the calls of the other frogs, of which there are several sympatric species.

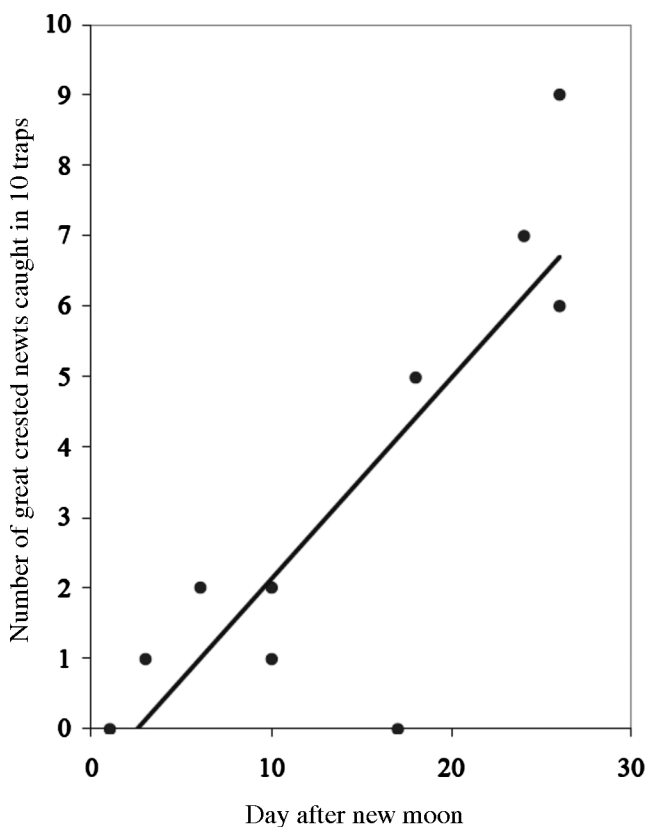
Because calling behavior is often associated with breeding, it is difficult in many cases to discriminate whether the species concerned are responding to lunar cycles due to predator avoidance, or because they are using lunar cues to aid breeding synchronization. Few studies explicitly investigate predator avoidance with respect to lunar cycles. Two studies relating calling behavior to bat predation are exceptions to this, but reveal differing responses to lunar illumination, although both responses indicate that moonlight helps these amphibians to detect their predators. The túngara frog *Engystomops (Physalaemus) pustulosus* and the hyliid treefrog *Smilisca sila* are both preyed on by bats. On clear and moonlit nights, túngara frogs reduce calling when bats arrive, whereas on cloudy moonless nights there is little change in chorusing behavior (Tuttle et al. 1982; Ryan 1985). Conversely, *S. sila* call for longer, and from more open sites on moonlit nights (Da Silva Nunes 1988), and when moonlight is simulated



**Figure 1**  
High moonlight is associated with increased calling by *Hyla cinerea* ( $\chi^2 = 17.87$ ,  $df = 1$ ,  $P < 0.001$ ) and with decreased calling by *Acris crepitans* ( $\chi^2 = 3.91$ ,  $df = 1$ ,  $P = 0.048$ ). From Granda et al. (2008).



**Figure 2**  
Number of smooth newts (*L. vulgaris*) caught in 10 bottle traps is significantly associated with days after new moon ( $F = 9.98$ ,  $P = 0.003$ ). From Deeming (2008).



**Figure 3**  
Number of great crested newts (*T. cristatus*) caught in 10 bottle traps is higher just prior to the new moon (Spearman's ranked correlation,  $R = 0.788$ ,  $P = 0.007$ ). From Deeming (2008).

these frogs increase both the frequency and complexity of calls compared with low light conditions (Tuttle and Ryan 1982).

Other examples of lunar adapted behaviors also show a diversity of response to the lunar cycle. Activity (number of frogs encountered per night) of several frogs of the genus *Litoria* is significantly greater on illuminated nights, possibly as an adaptation to predation by snakes. Snakes are a partially olfactory predator and may well be at a relative disadvantage to their visually oriented prey under increased illumination around the full moon (Brown and Shine 2002). Activity in brighter lunar phases as an adaptation to snake predation has been observed in other taxa (Bouskila 1995), and as snakes are major amphibian predators (Wells 2007) this may be a common response. *Hyla squirella*, however, is also preyed on by snakes and avoids the full moon (Taylor et al. 2007); the difference in response may be due to several factors, including the relative risk from different predator types, or other aspects of the frogs' ecology. The examples of frogs preyed on by bats and snakes discussed above underline the varied and species-specific responses to the lunar cycle, even in animals with similar predators.

The American toad *Anaxyrus* (*Bufo*) *americanus* exhibits reduced locomotor activity during full moon phases outside the breeding season (Fitzgerald and Bider 1974). Similarly, captures (in bottle traps) of *Lissotriton* (*Triturus*) *vulgaris* and *Triturus cristatus* during spring were highest around the new or waning moon, respectively (Deeming 2008, Figures 2 and 3). In Deeming's (2008) study, bottle traps had their openings facing toward the pond, and were therefore likely to have trapped only newts leaving the pond, so it is assumed that this reflects nonbreeding behavior (departures) rather than breeding arrivals. These moonlight avoidance behaviors may be an antipredator adaptation. Although decreases in activity in brighter moon phases are often attributed to predator avoidance (e.g., Fitzgerald and Bider 1974; Deeming's 2008), this is rarely explicitly tested and there are alternative explanations for lunar-phobic behavior in amphibians such as moonlight being outside the optimum range for visual foraging or other activity. This may be particularly true for species that are highly nocturnal with a limited optimum visual range (Buchanan 2006).

Two examples show that variation in predation risk across the lunar cycle can affect mate choice in amphibians, and therefore may affect reproductive success. Female reed frogs *Hyperolius marmoratus* prefer simulations of males calling from elevated perches surrounded by upright vegetation rather than open ground at the full moon, but showed no such preference when ambient light levels were lower (Backwell and Passmore 1990). Female túngara frogs (*Engystomops pustulosus*) are more willing to respond to calls from males when conditions are dark (Rand et al. 1997), possibly because they are safer from visual predators at this time. This is in contrast to males of this species which are additionally at risk from acoustic predators (bats) and consequently call more in high illumination (Rand et al. 1997). It has also been shown experimentally that light may influence mate choice through perceived predation risk. Baugh and Ryan (2010) showed, using acoustic playback, that female Túngara frogs (*E. pustulosus*) are more likely to commit to initial mate choices, even with lower quality males when light levels increase, which is attributed to trade-offs between perceived predation risk and choosiness. The question of how moonlight impacts on visual display and mate choice in amphibians merits further research.

Despite an intuitive assumption that amphibians might avoid activity at full moon in order to reduce predation risk, the evidence does not support this view and we have found



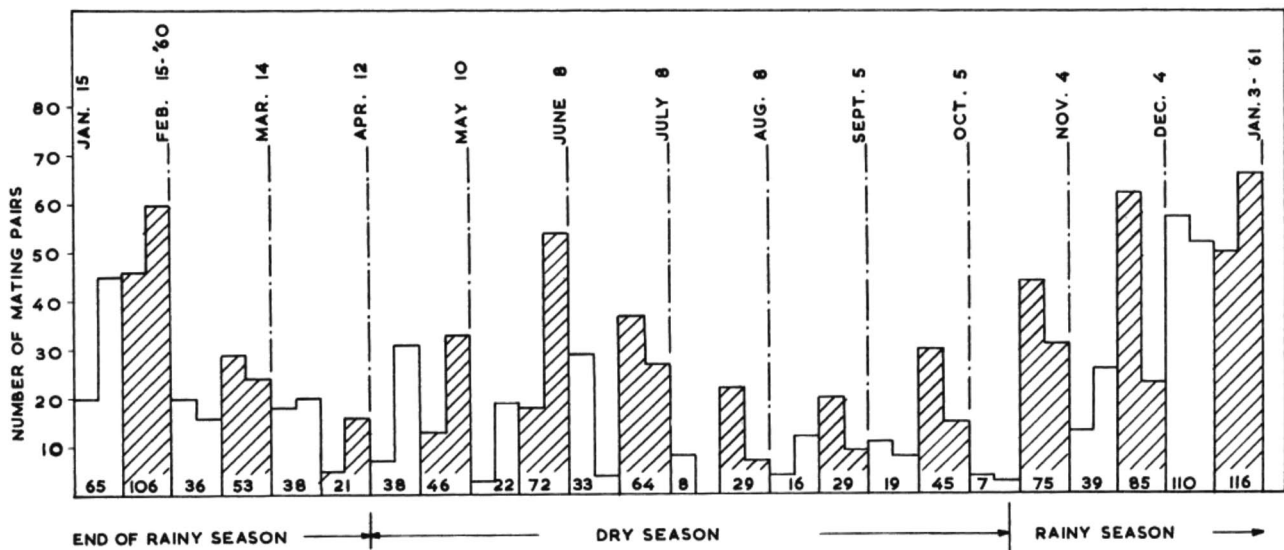


Figure 4

Number of *B. melanostictus* in amplexus in different lunar quarters in Bandung, Java in 1960. From Church (1961). The waxing moon is represented by shaded areas and the vertical dotted lines denote the full moon. More animals were in amplexus as the moon waxed. Actual numbers of counted animals in amplexus are given at the base of the graph. Mann-Whitney analysis  $P < 0.05$  (Deeming, 2008).

no significant difference in the number of studies showing increased, versus decreased, activity during brighter moon phases (either for all studies [20 show an increase, 30 show a decrease; Chi-squared test:  $N = 50$ ,  $df = 1$ ,  $\chi^2 = 2.0$ ,  $P = 0.16$ ] or for calling behaviour in isolation [11 show an increase, 21 show a decrease; Chi-squared test:  $N = 32$ ,  $df = 1$ ,  $\chi^2 = 3.1$ ,  $P = 0.08$ ]). Although strong inference cannot be made from this test due to the inclusion of qualitative and anecdotal reports, it nonetheless suggests that the intuitive belief that bright moonlight phases are more risky for amphibians is

incorrect. Again, differing responses to the lunar cycle by amphibians reflect the highly species-specific nature of the costs and benefits associated with nocturnal activity under different levels of illumination.

#### Reproductive synchronization

Reproductive synchronization serves to maximize reproductive success, by maximizing the pool of available breeding adults (Shapiro et al. 1993; Tsukamoto et al. 2003) and by reducing predation risk through “predator dilution/satiation” (Ims 1990). Predator dilution or satiation can exert protective effects for breeding adults in the short term (Ims 1990), as well as enhancing recruitment by resulting in predator satiation later in the life cycle, through synchrony of larvae or metamorphs (Omori 1995).

Use of the lunar cycle to synchronize reproduction in amphibians was first suggested in the 1960s, for *Duttaphrynus* (*Bufo*) *melanostictus* in Java and Indonesia (Church 1960a, 1961) and *Ingerophrynus* (*Bufo*) *biporcatus* in Bali (Church 1961). In these tropical habitats, temperature and humidity vary little throughout the year, food is always available, and toads breed all year round. Ovulation in *D. melanostictus* (measured by destructively sampling the ova) was associated with the full moon (Church 1960a), and amplexus was more common when the moon was waxing (Church 1961; later statistically validated by Deeming 2008; Figure 4), while in Bali, more *I. biporcatus* females were found in the water when the moon was waxing.

Lunar-synchronized reproduction in amphibians is not again discussed in the literature until some 40 years later. Various studies then report lunar phase effects, in Europe, Africa, and Australia. For example, large arrival and amplexus events (common toad, *Bufo bufo*), and large spawning events (*B. bufo* and common frog, *Rana temporaria*), are more frequent around full moon at a variety of European sites (Grant et al. 2009; Figure 5). In the African giant bullfrog, *Pyxicephalus adspersus*, spawning is more prolonged when there is a full moon (Yetman et al. 2011). In Australia, correlations are recorded with frequency of mating and activity level (increased near full moon in the Australian quacking frog, *Crinia georgiana* Byrne 2002), male density, operational

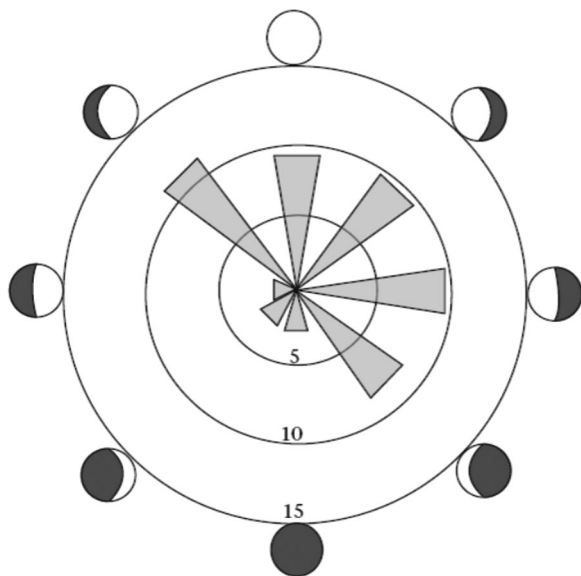


Figure 5

Frequency of large spawn events in relation to lunar phase in *Bufo bufo* and *Rana temporaria* at Marston Pond, UK over a 10-year period: 1978–1987. More large spawn events occurred around the full and waning moon and very few large spawn events occurred around the new moon. Rao's spacing test: toads  $U = 180$ ,  $N = 38$ ,  $P < 0.001$ , and frogs  $U = 84$ ,  $N = 12$ ,  $P = 0.02$ . From Grant et al. (2009).

sex ratio, and number of females in a chorus (negatively correlated with days since a full moon in *C. georgiana*; Byrne and Roberts 2004). Byrne and Roberts (2004) showed that most of the variation in male density and the number of females in a chorus was explained by lunar phase and rainfall, but it should be noted that Smith et al. (2003) found that variation in male chorus attendance of *C. georgiana* at a nearby site was explained by temperature, the number of females in the chorus and date, and there was no significant correlation with rainfall or moon phase; the reason for the difference is unclear.

A mechanism by which lunar synchrony might be controlled is described for rabbitfish (a group of fish species in the genus *Siganus*), where lunar light inhibits the production of melatonin by the pineal gland, which in turn influences the secretion of reproductive hormones, thereby synchronizing reproduction (Takemura et al. 2006). In lunar-synchronized fish, spawning may be synchronized to the full, new, or both moons, and species within the same family may spawn at different species-specific lunar phases (Takemura et al. 2004). Similarly in amphibians, although most of the examples cited above show synchronization around the full moon, there are exceptions; Church (1960b, in Java) found more *Fejervarya* (*Rana*) *cancrivora* with mature ova around the new moon. Hormone-mediated light-entrained ovulation in amphibians, should this exist, is therefore likely to be a proximate, but not ultimate cause of lunar-synchronized reproduction.

While reproductive synchronization provides a potential explanation of the adaptive nature of lunar responses, the available evidence does not allow differentiation of this from other possible explanations, including avoidance of acoustic or olfactory predators (as discussed above), the necessity of light for mate choice or other activities, or the behavior may simply be a consequence of lunar involvement in orientation to breeding sites. A response to variations in lunar light may also have evolved as a by-product or covariate of another physiological or molecular mechanism, which has persisted in the absence of negative selection pressure.

#### Visual signaling

There are many examples of visual signaling in amphibians (Hödl and Amézquita 2001), which have been reported across a range of anuran taxa including hylids (Amézquita and Hödl 2004; Gomez et al. 2009), dendrobatids (Summers et al. 1999), ranids (Hirschmann & Hödl 2006; Hettyey et al. 2009), leptodactylids (Rosenthal et al. 2004), and arobmatids (De Luna et al. 2010). The purpose of visual signals includes courtship display (Halliday 1974; Taylor et al. 2007, 2010; Vasquez and Pfennig 2007), territorial display (Amézquita and Hödl 2004), and warning potential predators (Hödl and Amézquita 2001). Despite the widespread use of visual signals in amphibians, the majority of the literature discussing visual signaling in nocturnal amphibians does not address the possible influence of the varying light levels caused by the lunar cycle on signaling behavior. Byrne (2002) suggested that the importance of light in mate choice might explain the increased frequency of mating of *C. georgiana* around full moon, but this was not explicitly tested.

Given the variability in amphibian visual acuity at different levels of illumination (Jaeger and Hailman 1976), and the relatively common use of visual signaling, the possibility that lunar light aids mate choice in some groups, or affects visual signaling in other contexts, is an interesting area for future research. One interesting example suggests that moonlight could influence visual signaling for the purposes of territorial defense and spacing in amphibians; the African frog *Kassina senegalensis* gives a territorial call (which is distinct from its mating call) only on full moon nights when males are spaced

less than 1 m apart (Fleischack and Small 1978). Presumably, moonlight helps these frogs detect the presence of other males in close proximity.

#### Foraging

Amphibian predation success is likely to reflect both prey availability and prey detectability, both of which may be influenced by lunar light. Buchanan (1998) points out that amphibians detect prey by primarily visual means and can do so at very low light intensities. Amphibians are thought to have an optimal range of light intensities for foraging (Hailman and Jaeger 1976) so the considerable changes in light intensity caused by the lunar cycle will surely affect amphibians' foraging ability in species-specific ways, although there is no literature concerning this.

Insects form a major component of amphibian diet (Wells 2007), and there are numerous reports of insects changing activity with the lunar cycle (although evidence is contradictory and may be at least partially due to artifacts caused by light traps; Nowinszky 2004). It therefore seems likely that variation in amphibian activity with lunar cycles will also reflect changes in prey availability. Only 2 examples of lunar-mediated amphibian behavior appear to be a response to prey availability, however, and both are somewhat ambiguous.

Fowler's toads (*Anaxyrus* [*Bufo*] *fowleri*) in Mississippi, USA, congregate around streetlights to feed on insects; fewer toads congregate when the moon is full and the sky clear (Ferguson 1960). Research was conducted outside the breeding season, so the movements described are unlikely to relate to reproduction. Potential predators in the area were controlled by the human population, so it seems unlikely to be a direct response to predation, although an evolved but now redundant avoidance response to predators cannot be ruled out. It seems probable that fewer toads congregate to feed on clear moonlit nights because fewer insects are attracted to streetlights when the contrast between streetlight and ambient (lunar) light is less.

The larvae of the marbled salamander (*Ambystoma opacum*) rise to the surface of the water in response to rapid decreases in illumination such as that seen at a lunar eclipse (Hassinger and Anderson 1970). This may be a response to prey availability, as many species of plankton (on which larvae feed) are known to move vertically upward in response to decreases in lunar illumination (Alldredge and King 1980; Gliwicz 1986). However, other reasons for the behavior cannot be ruled out.

Response to the lunar cycle as a means of maximizing foraging effectiveness appears to be relatively rare in amphibians, perhaps because predation and reproduction are much stronger selection pressures. Alternatively this may be an understudied aspect of amphibian foraging behavior, either because it is difficult to separate the maximization of foraging effectiveness from antipredator behavior, or because amphibians are generally studied during their breeding season when they are more conspicuous and the terrestrial stages of life are less well studied.

#### Navigation, orientation, and homing

Lunar cues influence navigation, orientation, and homing in some amphibian species, such as *Acris gryllus* (Ferguson et al. 1965), *Anaxyrus* (*Bufo*) *fowleri* (Ferguson and Landreth 1966), and *Ichthyosaura* (*Triturus*) *alpestris* (Diego-Rasilla et al. 2005), while others such as *Rana pipiens* (Dole 1976) and *Anaxyrus* (*Bufo*) *boreas* (Tracy and Dole 1969; Gorman and Ferguson 1970) move randomly with respect to lunar cues. Lunar influence on navigation may be related to cyclic changes in the Earth's magnetic field, which fluctuates according to the synodic cycle, peaking at the third quarter (Stolov 1965; Bell

and Defouw 1966). Some amphibian species use magneto-reception in navigation, orientation, and homing, detecting very small shifts in magnetic intensity. Examples include the Eastern red-spotted newt *Notophthalmus viridescens* (Phillips 1986a, 1986b; Phillips et al. 1995, 2002; Deutschlander et al. 1999b; Fischer et al. 2001); the Alpine newt *Ichthyosaura alpestris* (Diego-Rasilla et al. 2005), bullfrog tadpoles *Rana catesbeiana* (Freake and Phillips 2005), and larval Iberian green frogs *Pelophylax (Rana) perezi* (Diego-Rasilla and Phillips 2007). Detection of lunar modulation of geomagnetism is suggested by the avoidance of the third quarter by newts *L. vulgaris*, *L. helveticus*, and *T. cristatus*, when arriving at 2 separate breeding sites in Wales and Hampshire, UK (Grant et al. 2009) (although orientation behavior was not investigated as part of this study). The mechanism of magnetoreception has been shown to be a light-dependent process, as both urodeles and anuran tadpoles shift their response to magnetic fields by 90° in long-wavelength light (Phillips and Borland 1992; Deutschlander et al. 1999, 1999b). Although light-dependent magnetoreception is not completely understood, this suggests a potential interaction between lunar light, magnetoreception, and amphibian orientation behavior.

## Recommendations

Synthesizing and comparing the results of different studies on behavioral responses to the lunar cycle is difficult, as different investigators use different methods, and study different behavioral traits. Most studies described here were designed for other purposes and mention the effect of lunar phase as a minor point, or they are natural history accounts of species, which are anecdotal rather than quantitative. In order to achieve a better understanding of lunar-related behaviors, a more consistent and quantitative approach is required.

## Recording data

Animals may react directly to ambient light levels, or, alternatively, changing light levels may regulate an endogenous rhythm (Neumann 1981). When endogenous periodic rhythms are established in a species, they continue even when the animal is isolated from its natural environment or held in constant conditions. Usually, these rhythms are entrained at intervals by an external factor, termed a "Zeitgeber" (Anders 1982). To distinguish between endogenous rhythms and direct responses it is necessary to study the animals during a lunar eclipse and note changes in behavior (Donati et al. 2001), or to keep the animals under constant conditions and see if the rhythm persists (Rahman et al. 2000). There

are examples of both types of response in the literature (e.g., Wikelski and Hau 1995; Donati et al. 2001), but in most cases this difference is not discussed.

Of the quantitative studies available, some consider moon phase or number of days since a full moon as independent variables, regardless of whether the moon had risen or was obscured by cloud (Byrne 2002; Byrne and Roberts 2004; Deeming 2008; Grant et al. 2009); others use an index based on the probable light levels from the moon, by, for example, considering the period as moonless, or dark if the moon has not yet risen, or cloud cover was 100% (Johnson and Batie 2001; Brown and Shine 2002; Granda et al. 2008). While both are valid approaches, the effects they are able to detect differ. Using an index of probable light levels will not pick up endogenous lunar rhythms, as these will continue on days when the moon is obscured by cloud or has not yet risen (Grant et al. 2009). Considering only lunar phase without regard for light levels will miss effects that are directly due to variations in light intensity. We recommend that field studies of amphibians record both light levels and lunar phase, as well as cloud cover, moon rise and set times, and moon's visibility. The phase of the moon can also be calculated retrospectively using data from the United States Naval Observatory Astronomical Applications service (<http://www.usno.navy.mil/USNO/astronomical-applications>).

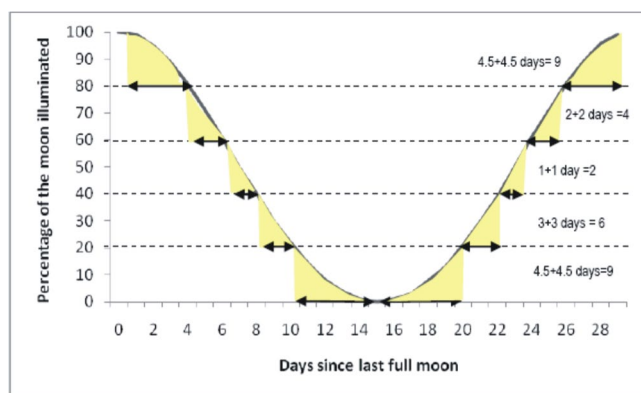
Where studies used visual means to locate amphibians, the question of bias arises as amphibians may be more visible, rather than more active or abundant in brighter moon phases. Some studies take this into account, and detail the steps that were taken to minimize this bias (such as Byrne and Roberts 2004; Grant et al. 2009), whereas in other studies this issue is not addressed (e.g., Brown and Shine 2002).

## Analyzing data

Lunar phase is quantified in a variety of ways, including percentage of the moon illuminated, days to the nearest full moon, or days since full moon. This can lead to subtle differences in interpretation, and in some cases to serious statistical flaws.

Values recording the percentage (or fraction) of the moon illuminated (PMI values) reflect the proportion of the moon's surface which is visible and thus reflecting light from the Sun. This value is increasingly being used in the ecological literature (e.g., Fernandez-Duque et al. 2008; Orrock et al. 2004; Lang et al. 2006). Because the moon passes more quickly through intermediate phases and spends longer in the new and full phases, there is a serious statistical bias associated with using PMI in categorical tests. Using data from the US Naval Oceanography Portal (<http://www.usno.navy.mil/USNO/astronomical-applications/data-services/frac-moon-ill>) for January 30, 2010 to February 28, 2010, we plotted PMI on each theoretical day of a lunar month (Figure 6).

It can be clearly seen that in a lunar month there are more days when the moon is 0–20% and 80–100% illuminated (9 days in each group) than days when the moon is in intermediate phases (6 days in the 21–40% group, 2 days in the 41–60% group, and 4 days in the 61–80% group) (Figure 6). If one is counting, for example, breeding events occurring in relation to PMI, breeding is less likely in intermediate phases because there are fewer days available for breeding. To illustrate this we constructed a theoretical model of amphibian breeding events, assuming an equal distribution of 1 breeding event per day, on each day of the lunar cycle, and tested for a difference between the numbers of breeding events in 5 equal categories using PMI as the categorical independent variable (categories were 0–20%, 21–40%, 41–60%, 61–80%, and 81–100% illuminated). This analysis produces a highly significant (and clearly incorrect) result (Chi-squared test:  $N = 30$ ,  $df = 4$ ,  $\chi^2 = 63.3$ ,  $P < 0.001$ ). Analyzing the same data using "days since last full



**Figure 6**  
Nonlinearity of the lunar cycle with respect to days since a full moon.



moon” as the categorical independent variable (categories are “days since last full moon”: 0–5, 6–11, 12–17, 18–23, and 24–29) gives a nonsignificant outcome with both Chi-squared test ( $N = 30$ ,  $df = 4$ ,  $\chi^2 = 0$ ,  $P = 1.0$ ) and the Rayleigh test (a circular goodness of fit test:  $N = 30$ ,  $Z = 0$ ,  $P = 1.0$ ). The results obtained by Swannack (2007, 2009) which showed that the endangered Houston toad, *Anaxyrus (Bufo) houstonensis* does not breed when the moon is 51–60% (males) or 71–80% (females) illuminated, gives the impression that breeding does not occur in intermediate lunar phases: this conclusion may be incorrect due to uncorrected bias, although the paper does not discuss this explicitly. It is recommended that in moon phase studies, if PMI is to be used, a correction is applied to account for the fact that the moon does not spend equal numbers of days in full, new, and intermediate stages. Lunar light, being directly proportional to PMI on clear nights will be subject to the same bias and this should be taken into account.

As an alternative to PMI, the number of days to the nearest (past or future) full moon can be used as a predictor in linear regression (days are therefore numbered 0–15). This approach overcomes the statistical bias associated with the differing speed of passage through lunar phases. This measure and PMI are both, however, subject to another issue in relation to interpretation. There is no differentiation between the first and second halves of the lunar cycle, so the first and last quarter moons will both have the same value (approximately 50% illuminated/day 7). Equally, the days just before and after a full moon will both have values of 90–99% (days 0, 1, 2) etc. Direct effects relating to the symmetric cycles of lunar illumination would therefore be adequately described, but effects due to lunar-mediated variations in asymmetric cycles such as geomagnetism would not. Additionally, events where a lunar stage (e.g., full moon) acts as a trigger for an event which occurs subsequently (and not at the equally illuminated but preceding stage of the cycle) will also be obscured.

Finally, “days since last full moon” can be used as an independent variable (0–29), effectively distinguishing the waning and waxing phases of the moon, and giving 2 different values for the same level of illumination. In this case, circular statistics should be used. Linear regression or correlation is often applied to this measure (e.g., Deeming 2008), but because moon phase is a circular variable with an arbitrary or undefined origin, linear regression will incorrectly treat day 0 and 29 of the lunar cycle as outliers, not taking into account the wrapping of the scale (Hussin 2007). We therefore recommend that circular-linear regression be used for moon phase studies in amphibians, using days since last full moon as an independent variable, which can be combined with other linear variables in a multiple regression approach, as demonstrated in deBruyn and Meeuwig (2001). Alternatively, if using a categorical independent variable, circular goodness of fit tests (Batschelet 1981) can be applied (e.g., Grant et al. 2009).

## IMPLICATIONS FOR AMPHIBIAN CONSERVATION

As well as being of intrinsic interest, the results of this study have implications for the monitoring and conservation of amphibians. Many long-term studies of amphibian diversity and population dynamics do not consider lunar phase or even record it as a variable. As the phase of the moon may have a considerable effect on the number of active or calling amphibians, long-term monitoring studies carried out on the same calendar date each year but at differing lunar phases may give misleading results about the true size of breeding populations. Additionally, where responses to the lunar cycle are driven by light levels, high levels of ecological light pollution (Longcore and Rich 2004) may disrupt normal behavior, by negatively affecting synchronization of breeding populations, making

animals more vulnerable to predation or interfering with mate choice and visual signaling. This type of disruption is more likely in areas of high ecological light pollution such as the United States of America and Western Europe. Indeed, Taylor et al. (2007) report that the squirrel treefrog (*Hyla squirella*) stops calling, or calls from areas concealed within vegetation in light polluted areas, as well as around the time of the full moon. Light pollution, therefore, has the capacity to act as a “perpetual full moon” (Longcore and Rich 2004, p. 196) which may alter amphibians’ behavior in a variety of ways.

Finally, the inclusion of moon phase as an additional variable in predictive models of amphibian breeding or activity may produce better-fitting, more accurate models. In the light of catastrophic declines in amphibian populations (Houlahan et al. 2000), population monitoring, and research into factors that influence behavior (in particular where behavior impacts on recruitment or mortality) are critical, and we encourage biologists to take lunar phase into account when planning field studies.

## SUMMARY

Changes in amphibian behavior in relation to the lunar cycle are widespread, both geographically and taxonomically. The way in which amphibians respond to lunar cycles cannot be generalized by taxonomic group or region, but instead appears to relate directly to species’ ecology. In the same genus, such as *Hyla* or *Bufo*, both positive and negative responses to the full moon are observed, and we therefore conclude that lunar-related behavior in amphibians is highly species specific. Although not all behavior related to the lunar cycle is adaptive in nature, there is evidence of the lunar cycle being used by amphibians for the purposes of maximization of reproductive success and predator avoidance, the final outcome of which is likely to be a trade-off between sometimes conflicting selection pressures. Lunar cues may also be used by some species to maximize foraging effectiveness, orientation/homing toward the breeding site, navigation, visual signaling and mate choice; these may prove interesting areas for further study. In particular, the gravitational and magnetic changes occurring in relation to the lunar cycle and their effects on amphibians have not been well studied. Large-scale studies on the effects of moon phase on amphibians across different taxa, latitudes and mating systems are lacking and we encourage further research in this area.

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