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The lunar cycle: a cue for amphibian reproductive phenology?

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Lunar cycles give rise to cues that can be recognized by animals, including changes in light intensity, geomagnetism and gravity. Many environmental variables affect reproductive timing in amphibians and we tested the hypothesis that lunar cycles provide one of the cues for amphibian breeding phenology. For several species of anurans, the number of individuals arriving, amplexed or spawning at breeding sites in Italy and the U.K. were recorded each day over several breeding seasons. Data on various aspects of reproductive phenology were also collated from the published literature, for several anuran and urodele species. Large arrival, amplexus and spawning events were more frequent around the full moon than the new moon in anurans, although the date that the first spawn was observed showed no lunar periodicity. Anurans could be responding directly to lunar light, or could have a lunar-synchronized endogenous cycle. First sightings and peak arrivals of urodeles occurred more frequently around new and full moons, but less frequently during the third quarter of the lunar cycle, while departure dates did not show lunar periodicity. Newts could be using gravitational and/or geomagnetic changes related to the lunar cycle to time their arrivals. Synchronization of reproduction in this way may function to maximize spawning success by ensuring the temporal and spatial proximity of breeding adults, or by reducing predation on individuals. Few studies of amphibian breeding phenology consider lunar phase and our results have important implications for the prediction of amphibian mass movements and conservation strategies.

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The position of the Moon in relation to the Earth and the Sun gives rise to several cycles that occur at regular intervals. The lunar synodic cycle (full moon to full moon) has an average length of 29.5 days and causes a number of environmental changes that can be perceived by animals, such as the brightness of lunar light and gravitational changes, with maximum gravitational pull occurring when the Moon and Sun are aligned (at periods of new and full moons). Geomagnetic fields are also modulated by the lunar cycle, and these changes can be detected and are used as navigational or temporal cues by animals (Phillips 1986; Lohmann & Willows 1987; Fischer et al. 2001).

Many marine animals take advantage of cues from the 29.5-day lunar cycle to synchronize their reproduction. This may protect adults, eggs and larvae from predation (by diluting predation risk or by using tidal currents to disperse or protect larvae), or maximize spawning success by ensuring the largest number of animals are in

reproductive condition and in one place at the same time (Takemura et al. 2004). Lunar periodicity in marine animals is not necessarily tidally mediated; some marine animals respond specifically to lunar light (Takemura et al. 2004). Many fish show lunar synchronization which is not influenced directly by tides, for example, rabbitfish, *Siganus guttatus*, held in tanks continue to spawn at a species-specific lunar phase (Rahman et al. 2000). Mummichog, *Fundulus heteroclitus*, show semilunar synchronized spawning in habitats where there is no tidal stimulus (Hines et al. 1985).

In addition to marine animals, various terrestrial birds and mammals have reproductive cycles linked to lunar phase (Cowgill et al. 1962; Erkert 1974; Archibald 1976; Dixon et al. 2006). Lunar periodicity of reproduction has also been reported in amphibians. The Javanese toad, *Bufo melanostictus*, ovulates on or near a full moon (Church 1960a) and lunar phase significantly affects both frequency of mating and activity level in the frog *Crinia georgiana* (Byrne 2002). Fitzgerald & Bider (1974) reported reduced locomotory (but not necessarily reproductive) activity in the toad *Bufo americanus* during full moon phases.

In anuran species with short breeding seasons, often called explosive breeders (Wells 1977, 2007), females arrive at the breeding site synchronously, either at the same time as or shortly

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after males, which actively compete for females. In contrast, prolonged breeders are characterized by males calling to attract females, often defending territories (Wells 1977, 2007). Explosive and prolonged breeding represent two extremes along a continuum of mating strategies. Although rainfall and temperature can be good predictors of reproductive activity in amphibians (Oseen & Wassersug 2002) these variables alone do not explain the high degree of synchronization that occurs in explosive breeders. In some studies of anurans, particularly *B. bufo*, rainfall was not found to influence the arrival of toads at the breeding site (Gittins 1983; Reading 1998). Indeed, this has led several authors to conclude that there may be a large endogenous component to amphibian breeding phenology. Sinsch (1988) found that the timing of *Bufo bufo* migration was fairly independent of climatic factors and concluded that endogenous components may make up a larger part of the variation in migration timing than normally supposed. Wells (1979) made similar observations in the explosive breeding *Bufo typhonius* and suggested that an endogenous cycle interacts with an environmental cue in this species to produce highly synchronous breeding. Moon phase is an often overlooked environmental cue that could affect reproductive timing, and in this study we tested the hypothesis that periodicity in the breeding phenology of amphibians reflects periodicity in the lunar cycle. We analysed various parameters related to reproductive activity for a range of species, sites and years. For anurans, these parameters included (1) large arrival events (days on which more than 10% of the total in each year arrived), (2) large amplexus events (days on which more than 2% of the annual total number of mating pairs were observed), (3) large spawning events (days on which more than 10% of the annual total of spawning individuals were observed) and (4) first evidence of spawn. For urodeles, parameters included (1) first sighting, (2) peak (mode) arrival dates, and (3) median departure dates.

METHODS

General Methods

We collected data from three sites: San Ruffino Lake, Italy, Llandrindod Wells, U.K. and Marston Pond, U.K. In all cases, individuals were located by sight during transects surveyed on foot using powerful torches (flashlights). In all three surveys the torches used were considerably brighter than the ambient moonlight, minimizing bias caused by animals being more visible on a full moon. At San Ruffino Lake the torch used was an Energizer Halogen, at Llandrindod Wells a Clulite CL1, and at Marston Pond an Ever-Ready, all of which had a brightness between 5×10^3 and 5×10^6 lx. For comparison, light levels are around 10^{-3} lx on a clear night with a full moon and 10^{-5} lx in overcast starlight (Buchanan 1993). At all three study sites, we noted little or no deviation in amphibian movement towards the water on the approach of surveyors or illumination. The San Ruffino site is in a rural and undeveloped area and the part of the lake that was surveyed is free from artificial illumination. Llandrindod Wells Lake is in a semirural area, and Marston Pond is in an urban area, where artificial lighting is higher. Unfortunately, as the data were analysed retrospectively, the level of artificial light at the sites was not quantified.

Study Sites and Site-specific Methods

San Ruffino Lake

San Ruffino Lake, Monte San Martino, Italy ($43^{\circ}00'4''N$, $13^{\circ}23'4''E$) supports large breeding populations of *B. bufo*, and smaller numbers of *Rana klepton hispanica* living in mixed

populations with *Rana bergeri* (klepton indicating that this frog is a fertile hybrid). *Rana bergeri* and *R. kl. hispanica* were treated as a single species in this study as they are virtually impossible to distinguish in the field, being morphologically almost identical (Vignoli et al. 2007), and are referred to as *R. bergeri* below. Treefrogs, *Hyla intermedia*, were also present at the site but were excluded from analysis because of the small numbers encountered on land.

A transect 2.5 km long on one side of the lake was surveyed once by R.G. each evening at dusk during the breeding season (April to June), for 40 nights in 2006 and 44 nights in 2007. The time taken to survey the transect was approximately 1.5 h. To reach the breeding site, the amphibians had to cross a pale-coloured lakeside path approximately 1.5 m in width, on which the animals could be clearly seen. Individuals were difficult to see as they entered the undergrowth at the side of the path, so only animals crossing the path were counted, thereby minimizing differences in detection probability caused by the changing intensity of lunar light. Individuals on land around the perimeter of the lake were counted as they moved towards the water and categorized by species and as single or amplexed in 2006, and additionally by sex in 2007.

Marston pond

Marston Pond, Oxford, U.K. ($51^{\circ}46.2'N$, $1^{\circ}41.1'W$) supported breeding populations of *B. bufo* and *Rana temporaria*, but may no longer be an amphibian breeding site. The circumference of the pond was patrolled each night for around 2 h from dusk by T.R.H. during the breeding season (March and April) from 1978 to 1987 (*B. bufo*) and 1979–1985 (*R. temporaria*) with the exception of 1984. As the pond was shaded by trees and bushes, the moon was not bright enough to detect animals without artificial illumination, so it is unlikely that the changing moonlight intensity biased the results. Numbers of males and females arriving at the breeding site (on land) and the number of spawning pairs (in water) of *B. bufo* and *R. temporaria* were recorded. The date of the first spawn observed was also recorded from 1977 to 1987 (*B. bufo*) and in 1977 and 1980–1984 (*R. temporaria*). The length of the breeding season varied between 8 and 42 days for *B. bufo*, and between 18 and 23 days for *R. temporaria*.

Llandrindod Wells Lake

Llandrindod Wells Lake, Wales, U.K. ($52^{\circ}14'0''N$, $3^{\circ}22'8''W$) supports a large population of *B. bufo*. A complete circuit of the lake, 1 km in circumference, was walked each night of the breeding season (March and April) in 2000 and 2001 by E.A.C. and repeated every half hour from dusk until arrival numbers declined for three consecutive circuits, to below 20 individuals for at least two circuits and below 10 for the final circuit. Numbers of single males, females and amplexed pairs were recorded. The time taken for the survey was variable but was typically 2 h from dusk. Animals were clearly visible as they crossed a wide metalled path or a road surrounding the lake, so changes in moonlight intensity were unlikely to have influenced detection probability at this site. The length of the breeding season was 55 days in 2000 and 49 days in 2001.

Literature Search

Data on significant reproductive events, such as the date on which the first amphibian was sighted or the date on which the first spawn was laid, are widely available in published literature. Data on reproductive events were obtained from various research papers, and previously unpublished data on newt arrivals were supplied by E.A.C. (for details of data collection methods, see Chadwick et al. 2006). The criteria for inclusion of published data

were as follows: the study showed clearly either consecutive daily arrivals for each year, or the dates of significant reproductive events over a number of years, either as raw data or in a form that could be easily estimated with a reasonable degree of accuracy (i.e. to within 2–3 days). We excluded data that showed weekly or monthly arrivals totals, that combined arrival and departure totals, or that averaged totals over a number of years, and data where the exact dates of the study were not given. Five published studies were used involving three urodele and six anuran species. Table 1 shows a numbered list of all data sources used in this study; these are referred to by study number in the following analyses.

Study Species and Breeding Biology

Of the anuran species studied here, *Bufo boreas*, *B. bufo*, *Rana cascadae* and *R. temporaria* are explosive breeders, where males engage in scramble competition for females, the sex ratio is male biased and breeding is highly synchronized (Beebee & Griffiths 2000; Blaustein et al. 2001). *Bufo calamita* has a more prolonged breeding season, and calls to attract females (Beebee & Griffiths 2000). *Rana bergeri* and *R. kl. hispanica* are mainly aquatic frogs that are often found in mixed populations of which *R. bergeri* is usually the most numerous, *R. kl. hispanica* being a hybridogenetic frog, which depends on *R. bergeri* for its reproduction (Lanza et al. 2007). *Rana esculenta* is also a highly aquatic pool frog.

The three newt species included in this study (*Lissotriton* [previously *Triturus*] *vulgaris*, *L. helveticus* and *Triturus cristatus*) were all studied in the U.K. where breeding migrations occur over a protracted period between January and April (Beebee & Griffiths 2000). The three newts studied here often share the same habitat.

All the species studied here are spring breeders and the literature suggests that emergence from overwintering sites and breeding migrations are largely constrained by climate. Geographical variation in climate can cause considerable variation in breeding phenology. For *R. cascadae* and *B. boreas*, emergence occurs following snowmelt (Corn 2003) and other species seem to be largely constrained by temperature (Reading 1998).

Table 1
The source of data used in this investigation

Study number	Source	Period	Site	Species	Data used
1	Unpublished R.G.*	2006–2007	San Ruffino, Italy	<i>Rana bergeri</i>	N arriving
1	Unpublished R.G.*	2006–2007	San Ruffino, Italy	<i>Bufo bufo</i>	N arriving
2	Unpublished T.R.H.*	1978–1987	Oxford, England	<i>Bufo bufo</i>	N arriving
2	Unpublished T.R.H.*	1978–1987	Oxford, England	<i>Rana temporaria</i>	N arriving
2	Unpublished T.R.H.*	1978–1989	Oxford, England	<i>Bufo bufo</i>	First spawn
2	Unpublished T.R.H.*	1979–1983	Oxford, England	<i>Rana temporaria</i>	First spawn
3	Unpublished E.A.C.*	2000–2001	Llandrindod Wells, Wales	<i>Bufo bufo</i>	N arriving
4	Blaustein et al. 2001	1982–1989	Oregon, U.S.A.	<i>Rana cascadae</i>	First spawn
4	Blaustein et al. 2001	1982–1989	Oregon, U.S.A.	<i>Bufo boreas</i>	First spawn
5	Beebee 1995	1978–1994	Sussex, England	<i>Rana temporaria</i>	First spawn
5	Beebee 1995	1978–1994	Sussex, England	<i>Bufo bufo</i>	First spawn
5	Beebee 1995	1978–1994	Sussex, England	<i>Rana esculenta</i>	First spawn
5	Beebee 1995	1978–1994	Hampshire, England	<i>Bufo calamita</i>	First spawn
5	Beebee 1995	1978–1994	Sussex, England	<i>Lissotriton vulgaris</i>	First sighting
5	Beebee 1995	1978–1994	Sussex, England	<i>Lissotriton helveticus</i>	First sighting
5	Beebee 1995	1978–1994	Sussex, England	<i>Triturus cristatus</i>	First sighting
6	Tryjanowski et al. 2003	1978–2002	Western Poland	<i>Rana temporaria</i>	First spawn
6	Tryjanowski et al. 2003	1978–2003	Western Poland	<i>Bufo bufo</i>	First spawn
7	Unpublished E.A.C.	1981–1987, 1997–2005	Llysdyman, Wales	<i>Lissotriton vulgaris</i>	N arriving
7	Unpublished E.A.C.	1981–1987, 1997–2005	Llysdyman, Wales	<i>Lissotriton helveticus</i>	N arriving
7	Chadwick et al. 2006	1981–1987, 1997–2005	Llysdyman, Wales	<i>Lissotriton vulgaris</i>	Median departure
7	Chadwick et al. 2006	1981–1987, 1997–2005	Llysdyman, Wales	<i>Lissotriton helveticus</i>	Median departure
8	Unpublished E.A.C.†	1981–1987, 1997–2005	Llysdyman, Wales	<i>Lissotriton vulgaris</i>	Peak arrival
8	Unpublished E.A.C.†	1981–1987, 1997–2005	Llysdyman, Wales	<i>Lissotriton helveticus</i>	Peak arrival
9	Gittins et al. 1980	1978	Llandrindod, Wales	<i>Bufo bufo</i>	N arriving

Studies were carried out by R. A. Grant (R. G.), T. R. Halliday (T. R. H.) and E. A. Chadwick (E. A. C.).

* See text for details of methods.

† See Chadwick et al. (2006) for details of methods.

Breeding migrations vary considerably in terms of distance travelled. The pool frogs *R. bergeri* and *R. esculenta* hibernate in the water and *B. calamita* and *R. cascadae* overwinter at or adjacent to the breeding sites, so these species do not make extensive breeding migrations (Beebee & Griffiths 2000). Some individuals of *R. temporaria* overwinter in the pond and others migrate (Verrell & Halliday 1985). However, *B. bufo* is largely terrestrial and may overwinter in refugia up to 1200 m from the breeding site (Sinsch 1988).

Moon Phase Data

We obtained the dates of full moons from the US Naval Observatory Astronomical Applications Department (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>) for midnight at Universal Time (GMT). Moon phase is independent of the geographical position of the observer.

No account was taken of the actual light levels at the breeding sites, moon rise or set times, the moon's angle of declination, other lunar cycles (such as the 18.6-year nodal cycle which may affect biota, Archibald 1977) or whether or not the moon was visible on a given night. This was because most of the data were collected before the current hypothesis was proposed.

Derived Data

For each of the recorded reproductive 'events' (e.g. first spawn or sighting), we counted the days since full moon (DFM) and thereby assigned DFM values from 0 to 29 to each date, where 0 represents the full moon. To facilitate graphical presentation of the data, the DFM values were grouped into eight lunar phases (Fig. 1), which we used to plot circular histograms, with the length of the bar representing the frequency of reproductive events occurring (see Results). The circular histograms show the actual frequencies of reproductive events and therefore the scales vary depending on the value of *N* in each case.









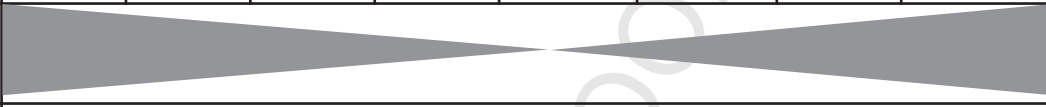


Lunar phase	Full moon	Waning gibbous	3rd quarter	Waning crescent	New moon	Waxing crescent	1st quarter	Waxing gibbous
	1	2	3	4	5	6	7	8
								
Days since full moon (DFM)	28,29, 0,1	2,3,4,5	6,7,8	9,10,11,12	13,14,15,16	17,18,19,20	21,22,23	24,25,26,27
N in category	4	4	3	4	4	4	3	4
Illumination								
Gravitational pull								
Geomagnetic fields								

Figure 1. The eight moon phases and their geophysical effects. The lunar effect on geomagnetism was adapted from Stolov (1965) and Bell & Defouw (1966).

The number of anuran arrivals recorded at the breeding sites on each day was expressed as a percentage of the total observed population for each species, in each year and for each site (% arrivals), so that data from different years could be pooled. We assigned DFM values to dates on which more than 10% of the total arrived, more than 10% of males or females arrived and more than 10% of the total were spawning (Marston Pond only), and the dates on which more than 2% of the total amplexed pairs were observed at the other two sites.

Statistical Analysis

We analysed the data for correlation with lunar phase. Most of the data were collected before the current hypothesis was proposed, thereby reducing the likelihood of observer bias. We converted DFM values to angles ($^{\circ}$) by dividing by 29.5 (the length, in days, of the lunar cycle) and then multiplying by 360° so that the data could be analysed using circular statistics. To assess whether reproductive events showed lunar periodicity, we analysed data using Rao's spacing test (Batschelet 1981), unless otherwise specified. Rao's spacing test is more powerful and robust than many other circular goodness-of-fit-tests, and is able to analyse bimodal and multimodal distributions, whereas other tests, such as the Rayleigh test and Watson's U^2 are not (Bergin 1991). Rao's spacing test is robust even at small sample sizes, but also shows a low frequency of type I errors when analysing data that show no pattern. The only cases where Rao's spacing test fails are in distributions that show directional avoidance (Bergin 1991). Where data appeared to be unimodal, we also used the Rayleigh test for departure from randomness, and where this produced a different outcome from Rao's test, the Rayleigh test statistic is also presented. The null hypothesis that reproductive events would be equally or randomly spaced throughout the lunar cycle was tested for each data set. All data were analysed using the circular statistics software Oriana 2.0 (<http://www.kovcomp.co.uk/oriana/>, Kovach Computing Services, Anglesey, U.K.). Oriana 2.0 does not give exact P values for Rao's spacing test, but provides the test statistic U . For nonsignificant

results Oriana gives P as a range; this is presented as provided. For significant P values Oriana uses the form $P < 0.05$ or $P < 0.01$. To find more precise values for significant results, we used an expanded table of P values for Rao's spacing test (Russell & Levitin 1995), which includes P values greater than 0.001 for $U = 1-220$. Where P is given for a range of U we take the conservative approach of rounding U values down; this potentially overestimates P and therefore provides a conservative estimate of significance.

The sample sizes in this study consist of the number of days on which the reproductive event (e.g. large spawn event, large arrival event) occurred; however, the actual sampling units are individuals, or pairs of animals. While this could be statistically problematic, the fact that on all days more than one individual or pair arrived means that the bias in this case would be towards type II error, and the significant results observed in this study can be deemed trustworthy.

Another possible source of statistical error may come about through multiple testing (when there are a large number of tests, some will reach significance from chance alone, Cross & Chaffin 1982); this is discussed below.

RESULTS

Large Arrival Events

For most anurans tested large arrival events occurred around the full moon (studies 1,2,3,9; Table 1, Fig. 2). Large arrival events of *B. bufo* at Marston Pond occurred primarily in phases 1 and 8 (around the full moon; males: $U = 171$, $N = 40$, $P = 0.003$; females: $U = 188$, $N = 44$, $P < 0.001$). At Llandrindod Wells, all *B. bufo* large arrival events occurred in phases 6–8 (the waxing to full moon; males: $U = 226$, $N = 5$, $P = 0.006$; but note $U > 220$ so P is overestimated; females: $U = 202$, $N = 6$, $P = 0.016$). At San Ruffino, the two large *B. bufo* arrival events occurred on days 0 and 1 of the lunar cycle (full moon, phase 1). The three large arrivals of *R. bergeri* occurred on days 0, 3 and 5 of the lunar cycle (on, and just after, the full moon, phases 1 and 2), but no statistical tests were carried out

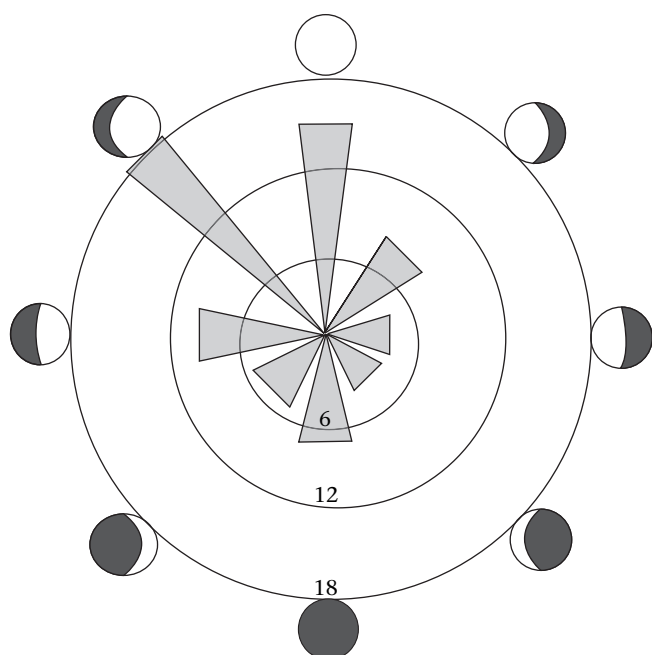


Figure 2. Large arrival events: frequency of occurrence in each moon phase, for *B. bufo*, *R. temporaria* and *R. bergeri* at Marston Pond, San Ruffino Lake and Llandrindod Wells Lake. See Fig. 1 for moon phases.

owing to the small sample size. Conversely, *R. temporaria* arrivals were uniformly spaced with respect to moon phase (males: $U = 118$, $N = 15$, $P = 0.5–0.9$; females: $U = 125$, $N = 25$, $P = 0.1–0.5$).

Large Amplexus Events

Amplexed pairs at San Ruffino Lake and Llandrindod Wells Lake were seen more frequently around the time of the full moon (studies 1,3; Table 1). When total numbers of amplexed pairs at the sites were counted, 90% of those recorded at Llandrindod Wells Lake, and 84% of those recorded at San Ruffino Lake occurred in phases 1, 2, 7 and 8 (around the full moon). Most large amplexus events (>2% of the total) occurred in phases 1, 7 and 8 at Llandrindod Wells and phases 1 and 2 at San Ruffino. There were no large amplexus events in moon phases 3, 4 or 5 (the new moon) in any of the 4 years over which data were collected, at either site (Fig. 3). Statistical tests on the number of large *B. bufo* amplexus events occurring showed that this was a significant effect at San Ruffino, ($U = 233$, $N = 12$, $P < 0.001$) and close to significance at Llandrindod Wells ($U = 160$, $N = 12$, $P = 0.096$). With the Rayleigh test, the data from Llandrindod Wells were significant ($Z = 4.9$, $N = 12$, $P = 0.005$).

Large Spawning Events

Large spawning events at Marston Pond from 1978 to 1987 occurred more frequently around and soon after the full moon, with 75% of large spawning events occurring in phases 8, 1, 2 and 3 (study 2; Table 1, Fig. 4). This was significant for toads ($U = 180$, $N = 38$, $P < 0.001$) and for frogs ($U = 184$, $N = 12$, $P = 0.02$).

First Spawn

First spawn dates occurred uniformly throughout the lunar month (studies 2,4,5,6; Table 1, Fig. 5). Table 2 shows the statistical outcomes of tests on the first spawn data.

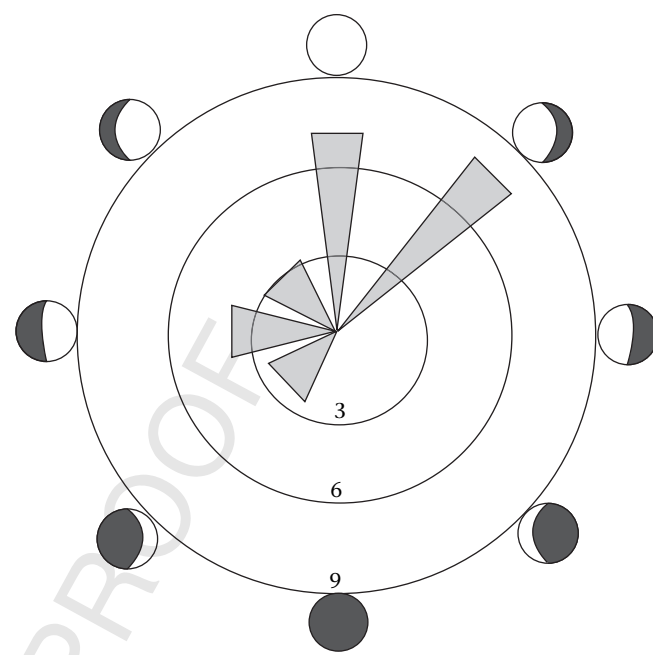


Figure 3. Large amplexus events: frequency of occurrence in each moon phase for *B. bufo* at Llandrindod Wells Lake and San Ruffino Lake. See Fig. 1 for moon phases.

First Sighting

First sightings in Sussex (study 5; Table 1) were most commonly made in phase 2 of the lunar cycle (just after a full moon) and in phases 5–8 (the new and waxing moon). In phases 3 and 4 there were no first sightings of any species of these newts in any of the 17-year study period (Fig. 6). This difference was significant for *L. helveticus* ($U = 186$, $N = 16$, $P = 0.006$), but not for *T. cristatus* ($U = 150$, $N = 17$, $P = 0.1–0.5$) or *L. vulgaris* ($U = 144$, $N = 16$, $P = 0.1–0.5$).

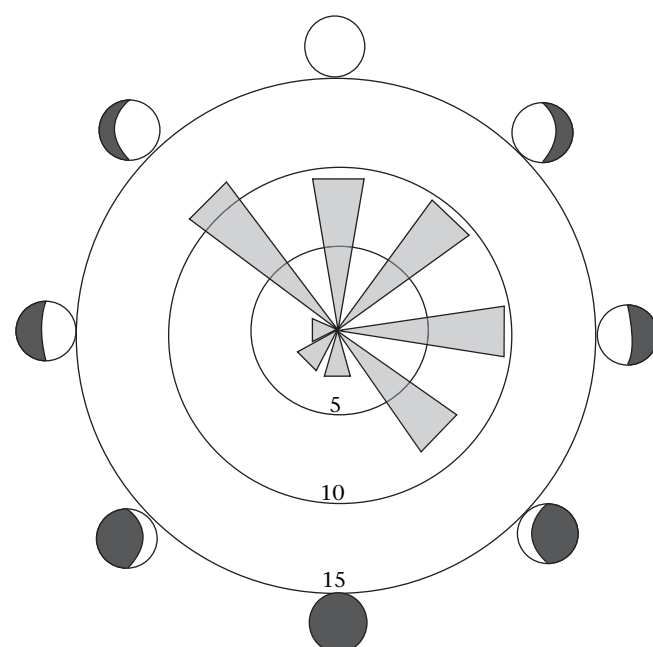


Figure 4. Large spawning events: frequency of occurrence in each moon phase for *B. bufo* and *R. temporaria* at Marston Pond. See Fig. 1 for moon phases.

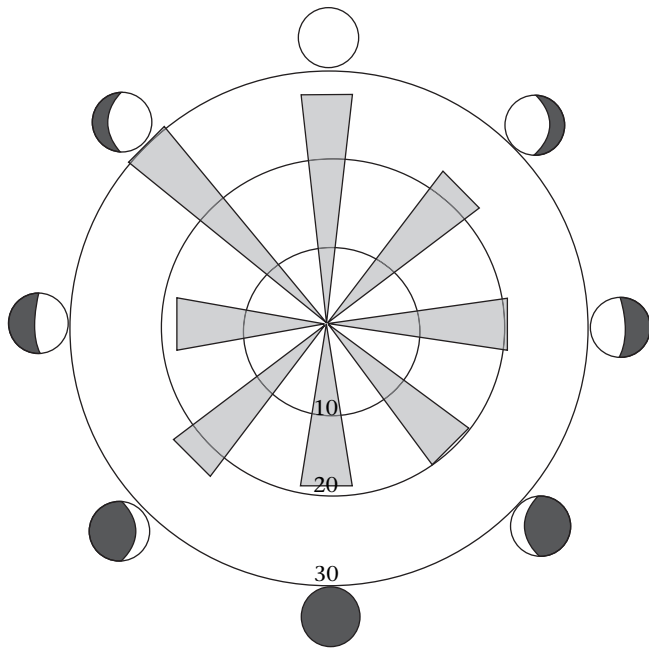


Figure 5. First spawn: frequency of occurrence in each moon phase for six anuran species at eight sites, as listed in Table 2. See Fig. 1 for moon phases.

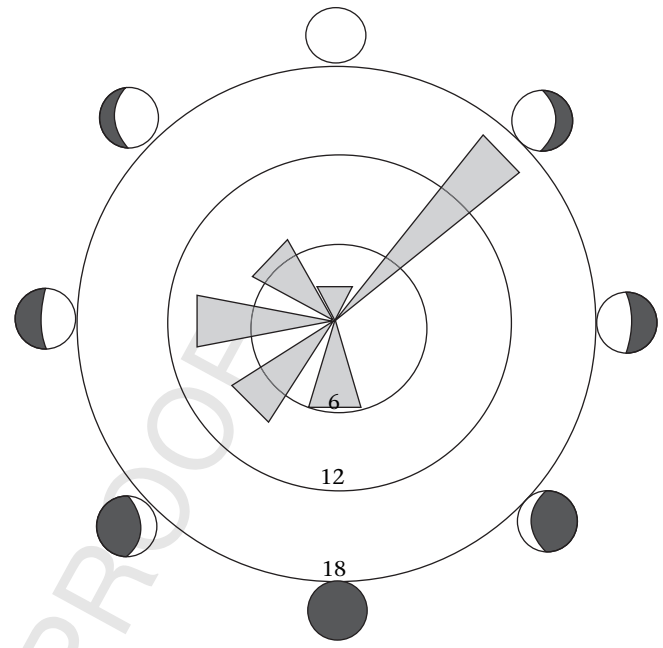


Figure 6. First sighting: frequency of occurrence in each moon phase for *L. vulgaris*, *L. helveticus* and *T. cristatus* in Sussex, U.K. See Fig. 1 for moon phases.

Peak (Mode) Arrivals

Peak (mode) arrival dates at Llysdyndy Pond (study 8; Table 1) occurred most frequently around the full moon (phase 1) and the new moon (phases 5 and 6). Few peak arrival dates occurred during the moon's third quarter (phase 3) (Fig. 7). When the modal values of males and females were analysed together for *L. vulgaris* the outcome was significant ($U = 168$, $N = 30$, $P = 0.017$); however, when the sexes were analysed separately the outcome was not significant for males ($U = 125$, $N = 15$, $P = 0.5–0.9$) or females ($U = 131$, $N = 15$, $P = 0.1–0.5$). For *L. helveticus* the outcome was not significant, whether analysed together or separately (males: $U = 137$, $N = 15$, $P = 0.1–0.5$; females: $U = 119$, $N = 15$, $P = 0.5–0.9$).

Departure Dates

There was no significant difference in the frequency of median departure dates from Llysdyndy Pond occurring in each moon phase for the two newt species studied (*L. helveticus*: males: $U = 107$, $N = 15$, $P = 0.5–0.9$; females: $U = 96$, $N = 15$, $P = 0.9–0.95$; *L. vulgaris*: males: $U = 119$, $N = 12$, $P = 0.5–0.9$; females: $U = 125$,

$N = 12$, $P = 0.5–0.9$; study 7; Table 1, Fig. 8). The median was used for departures rather than the mode, as mode departure dates were not informative, newt departures being highly multimodal.

Bonferroni Correction for Multiple Testing

Of the 35 tests presented in this study, 10 showed significance, where only two would be expected by chance. Following Bonferroni correction for multiple testing (Abdi 2007), three of the data sets tested (arriving and spawning toads at Marston Pond and large amplexus events at San Ruffino) remained significant ($P < 0.001$).

Table 2
Results of Rao's spacing test for periodicity in first spawn dates

Species and location	N	Rao's spacing test (U)
<i>Rana temporaria</i> , western Poland	18	102***
<i>Bufo bufo</i> , western Poland	18	117**
<i>Bufo boreas</i> , Lost Lake, Oregon, U.S.A.	14	113**
<i>Rana cascadae</i> , Site 1, Oregon, U.S.A.	14	133*
<i>Bufo boreas</i> , Three Creeks Lake, Oregon, U.S.A.	15	113**
<i>Bufo boreas</i> , Todd Lake, Oregon, U.S.A.	15	137*
<i>Rana cascadae</i> , Todd Lake, Oregon, U.S.A.	16	121**
<i>Bufo bufo</i> , Marston Pond, U.K.	10	113**
<i>Rana temporaria</i> , Marston Pond, U.K.	6	82**
<i>Rana esculenta</i> , Sussex, U.K.	16	154*
<i>Rana temporaria</i> , Sussex, U.K.	14	130*
<i>Bufo calamita</i> , Hampshire, U.K.	16	146*

* $P = 0.1–0.5$; ** $P = 0.5–0.9$; *** $P = 0.9–0.95$.

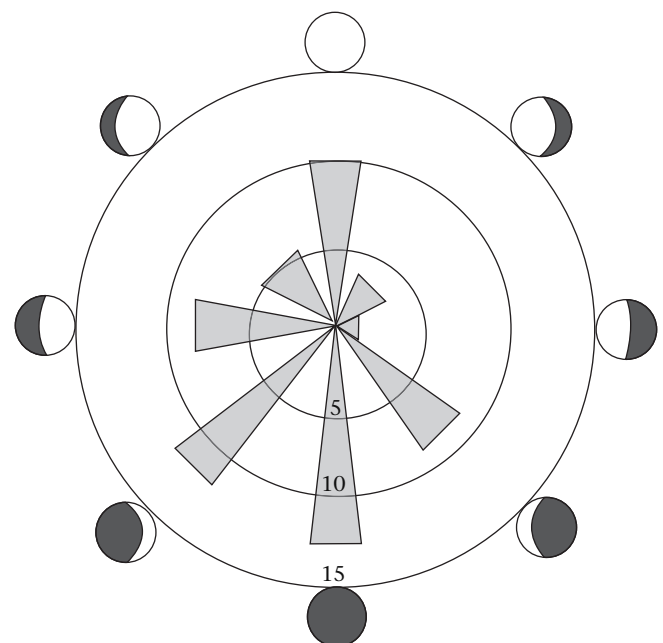


Figure 7. Peak (mode) arrival: frequency of occurrence in each moon phase for *L. vulgaris* and *L. helveticus* at Llysdyndy pond, Wales, U.K. See Fig. 1 for moon phases.

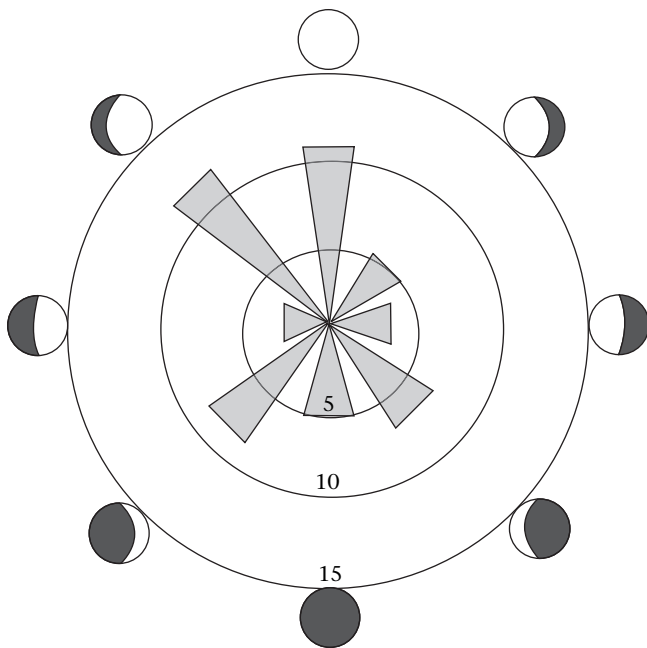


Figure 8. Median departure dates: frequency of occurrence in each moon phase for *L. vulgaris* and *L. helveticus* at Llysindinam pond, Wales, U.K. See Fig. 1 for moon phases.

DISCUSSION

Our hypothesis that breeding phenology in amphibians reflects periodicity in the lunar cycle is strongly supported by our results, including both anurans and urodeles, from a wide range of locations across the temperate northern hemisphere. Lunar periodicity was shown for large arrival and spawning events, the number of animals in amplexus and first sightings. Only first spawning (anurans) and departure dates (*Lissotriton* and *Triturus* newts) showed no evidence of lunar periodicity. The timing of events fell broadly into two categories: events that occurred unimodally, largely around the full moon with very few around the new moon (large arrival, amplexus and spawning events in anurans), and events that occurred bimodally such as first sighting and peak arrival events of *Lissotriton* and *Triturus* newts.

The occurrence of both unimodal and bimodal events suggests that different lunar cues are used for the two categories. Moonlight peaks once per cycle, at full moon, while gravitational pull peaks at both new and full moons (Fig. 1). Large arrival, amplexus and spawning events in anurans may be triggered by moonlight, while large arrival events in newts correspond more closely to the gravitational cycle.

Geomagnetism is modulated by lunar cycles (Markson 1971; Lohmann & Willows 1987), decreasing just before a full moon and peaking at the third quarter (Stolov 1965; Bell & Defouw 1966). The avoidance of the third quarter moon (phase 3) by arriving newts in unrelated studies in Wales and Sussex is striking. It is well known that amphibians, particularly newts, can detect and respond to small geomagnetic changes (Phillips 1986; Sinsch 2006) and they might be using this to regulate reproductive timing.

Lunar cues could form part of the navigational system of amphibians, giving rise to lunar-related reproductive timing as a consequence. Newts are able to make use of small changes in the Earth's magnetic field for 'true' navigation (Phillips et al. 1995). However, departing newts showed no lunar periodicity, suggesting that the phenomenon is related to reproductive timing. The response of newts to the lunar cycle appears more complex than that of anurans. Statistical tests on the newt data gave variable

outcomes. This could be because the tests used were not robust given the apparent bimodality of the data or because the newts are actually showing an avoidance response to the third quarter moon which Rao's test is not adequate to detect. Alternatively, the response of the newts may be complex and require more sophisticated modelling. Further work is underway to clarify this.

The random departure dates of newts suggest that, once breeding is over, other factors may have a greater influence on activity. Sinsch (1988) noticed that migrating *B. bufo* toads followed a direct path to their breeding site but a less direct one on departure. It is possible that different factors influence arrival to and departure from breeding sites in amphibians.

Moonlight may act as a stimulus through either retinal or extraretinal photoreceptors, such as the pineal gland (Takemura et al. 2006). Evidence for such mechanisms has been found in a number of species of fish, such as the rabbitfish in which cues from the moon stimulate the hypothalamus–pituitary–gonadal axis, thus controlling the secretion of gonadotrophin by the pituitary gland (Takemura et al. 2004). Where moonlight is the necessary cue for reproductive events, artificial lighting is likely to hinder synchronization among breeding populations, and may negatively affect reproductive success.

While artificial light undoubtedly affects the behaviour of amphibians (Buchanan 1993, 1998) the torchlight we used is unlikely to have biased the results of this study, as it was shone only briefly to enable animals to be counted. However, levels of ecological light pollution (ELP), which may disrupt normal amphibian breeding activity (Baker & Richardson 2006; Buchanan 2006) differed between sites. ELP is brighter and more focused than moonlight and can have a significant effect on the behaviour of amphibians which have dark-adapted eyes (Cornell & Hailman 1984).

ELP at the sites was not quantified, but all three were in Western Europe, which has high levels of light pollution (Cinzano et al. 2001). If amphibians are responding to lunar light, ELP is likely to disrupt this response; it has been referred to as 'the perpetual full moon' (Longcore & Rich 2004). It may be more difficult to detect the effects of lunar phase at sites with high ELP; previous reports of lunar periodicity in amphibian reproductive activity come from areas with relatively low light pollution, such as Java (Church 1960a, b) and Western Australia (Byrne 2002).

However, observations at San Ruffino Lake suggest that anurans are not responding directly to moonlight, but may have a lunar-entrained endogenous rhythm. On 2 May 2007 (a full moon) there was a large peak in toad arrivals at dusk despite cloud cover and the moon being low on the horizon behind mountains and invisible throughout the survey. It is possible that toads have an endogenous circalunar cycle, entrained at intervals by moonlight. Endogenous cycles of this type can continue for a period of time even when the zeitgeber (entraining factor) is removed, but they need resetting periodically (Franke 1985, 1986).

Climate is likely to modify circalunar rhythms, and Fitzgerald & Bider (1974) found that lunar-related activity in *B. americanus* was masked by weather. While our data are limited to northern temperate regions, evidence for lunar periodicity in amphibian reproduction in tropical and Mediterranean climates has been presented by Church (1960a) and Byrne (2002), respectively. In Java, where humidity and temperature vary little throughout the year, *B. melanostictus* breeds all year round; most females were in reproductive condition around full moon, regardless of temperature or rainfall (Church 1960a). Byrne (2002) observed that the number of mating pairs of the frog *C. georgiana* in Western Australia (with a Mediterranean climate of mild winters and hot summers) was correlated with lunar phase, with more matings occurring around the full moon.

The apparent migration 'response' to full moon in anurans may be a consequence of oocyte development being linked to lunar phase earlier in the year, rather than a direct effect. This has been demonstrated in rabbitfish (where the lunar-entrained ovulation cycle culminates in spawning at a species-specific lunar phase; Park et al. 2006) and in amphibians (female *B. melanostictus* mainly ovulate around the full moon; Church 1960a).

Our results described only events that occur during the amphibian breeding season. Outside the breeding season during new moon phases, Fitzgerald & Bider (1974) have reported increased movements of *B. americanus*, and Church (1960b) found that *Rana cancrivora* come into reproductive condition. This is the reverse of the trend we recorded for movement during the breeding migration, perhaps because different factors operate during different seasons, or because the nature of the lunar response is species specific. Further investigation is needed to clarify such differences.

Breeding in full light under a full moon could be an adaptive antipredator response in *B. bufo*. Animals active in moonlight may be at an advantage if their visual acuity is better than that of their predators. For example, the hylid frog *Smilisca sila* is preyed by bats, which locate frogs by their calls. On clear moonlit nights frogs could more easily see their predators and called more and from less concealed sites (Tuttle & Ryan 1982). Visually oriented diurnal predators such as snakes and birds of prey will be at a disadvantage at low light intensities such as around the new moon (Oseen & Wassersug 2002). However, in the darker moon phases olfactory oriented predators such as foxes and rodents may have an advantage over their more visually oriented amphibian prey. Toads' predators include raptors, crows, owls, snakes, hedgehogs, otters, foxes and rodents (Beebe & Griffiths 2000). The variety of predators on anuran amphibians makes it difficult to speculate on the costs or benefits of breeding under a full moon in relation to predation. Anurans in large breeding aggregations may also gain protection from predators by predator satiation (Ims 1990) leading to continued selection for synchronous reproduction. Synchronous breeding could also lead to synchronous metamorphosis, thought to be an antipredator strategy in *B. americanus* (DeVito 2003). Anurans could be responding to increases in the number of insect prey; however, this seems unlikely as common toads, at least, do not eat while breeding (Beebe & Griffiths 2000). Alternatively, light may be important for visual mate choice (Byrne 2002). More work is needed to clarify the adaptive function of lunar-related reproductive synchronization in amphibians.

It is evident from the literature that temperature and rainfall influence reproductive timing (Hurlbert 1969; Semlitsch 1985; Reading 1998; Todd & Winne 2006). Amphibians have a temperature threshold for activity (Reading 1998), regardless of moon phase, and events occurring early in the year, such as first spawn, may be more influenced by minimum temperature than moon phase. This may explain why first spawn dates were not influenced by lunar phase in this study.

First spawn dates used in this study were all from species located at temperate latitudes 44°N–54°N. It is likely that at other latitudes, the interaction of climatic variables with moon phase is different. Animals may be responding to weather rather than lunar cues per se, but the case for a lunar effect on weather and how it affects amphibians is not clear and merits further investigation. Some studies report that climate varies according to the semilunar cycle (Brier & Bradley 1964; Carpenter et al. 1972), while other studies report no correlation (O'Mahoney 1965; Premachandra et al. 2005).

In this study we considered only the 29.5-day synodic lunar cycle, that is, the time it takes for the Moon to return to the same phase. Other potentially important lunar cycles such as the

18.6-year nodal cycle, caused by variations in the inclination of the orbit of the Moon with respect to the Earth's equator, were not addressed. The nodal cycle can modulate lunar-synchronized breeding in some mammals (Kollerstrom 2004) and marine invertebrates (Dan & Kubota 1960) and might also affect amphibian migrations.

As a consequence of retrospective use of data collected for other purposes, there are some limitations to our study including inconsistencies of methods between sites, and a lack of data on light levels, moon rise and set times, or cloud cover. Data collected using pitfall traps might have given more reliable data on arrival totals. Our analysis is further limited by the lack of statistical methods to control for multiple factors when analysing circular data. This means that where otherwise we might have pooled data sets and controlled for categorical variables such as site or species, it was instead necessary to analyse each data set separately, giving smaller sample sizes and potential issues with multiple testing. However, we consider that multiple testing was not a serious issue in this study as significant outcomes were clustered around particular reproductive events (large anuran arrival and spawning events), whereas nonsignificant results were clustered around first spawn, newt departures and some newt arrivals, indicating the results have biological relevance, and are not statistical artefacts. Data were still in some cases pooled by sex; this was unavoidable where sex was not recorded (i.e. first newt arrivals, arrivals at San Ruffino in 2006, arrivals of *R. kl. hispanica*).

The response of amphibians to the moon is likely to be more complex than the analysis here suggests, and further work is underway to unravel some of these more complex responses. Despite current limitations, our results point to a clear lunar effect in amphibian breeding phenology and provide a useful starting point for further research in this area.

Few studies of breeding phenology consider lunar phase as a variable, and to our knowledge this is the first study that has investigated the effect of lunar phase on urodele reproductive timing. Population censuses and long-term monitoring should take lunar phase into account, as the number of amphibians active varies with the lunar cycle and may give inconsistent results from year to year. For example, programmes designed to avoid mass road deaths could be coordinated with the appropriate parts of the lunar cycle for a particular species. The findings of this study therefore have important implications for the conservation of amphibians, which are declining globally (Halliday 1998; Stuart et al. 2004).

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