**TITLE**: Lunar phase as a cue for breeding migrations in common toads (*Bufo bufo*) and common frogs (*Rana temporaria*) - implications for conservation

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**Abstract**

In species with explosive breeding strategies large numbers of individuals may congregate at a defined location for a very short period of time. Effective synchronisation in arrival at breeding sites is crucial to ensure mating success. Amphibians with explosive breeding strategies often congregate at ponds for only a few days or weeks a year. Previous research has shown that frogs and toads may use a variety of exogenous cues to initiate breeding migrations which include temperature, rainfall, and lunar cues. Although the effects of temperature and rainfall on amphibians are widely studied and understood, the impacts of lunar phase is poorly known and varies by species and location. In this study we examined the effects of lunar phase on the numbers of common toads (*Bufo bufo*) and common frogs (*Rana temporaria*) migrating to breeding ponds at 43 sites across the UK over four years. Our findings show that peak migration of both common toads and common frogs coincides with the waxing phase of the moon, peaking around the full moon. Temperature and rainfall also had an effect on peak migrations with the highest numbers of common toads and common frogs occurring on warm and damp evenings close to a full moon. Our results have implications for amphibian conservation initiatives such as ‘Toads on Roads’ as it will help inform conservationists on the most effective timing to help toads and frogs across roads.

Keywords: amphibian, reproduction, movements*,* moon, circular regression, circular statistics

**Introduction**

Many amphibians exhibit explosive breeding strategies with often large numbers of both sexes congregating at breeding sites within a very short period of time (reviewed in Wells 2007). Several species within the genus *Bufo* are well documented in having short and often explosive breeding seasons with individuals attending ponds for only a few days or weeks. In the Neotropical hylid frog, *Scinax ruber*, individuals emerge and attend breeding aggregations on just a single night (Bevier 1997). Another example is the Australian myobatrachid frog, *Crinia georgiana*, in which males emerge and defend small depressions in the ground for just a few days before returning to their terrestrial habitats (Byrne and Roberts 2004). Finally, the European spadefoot toad, *Pelobates* *syriacus,* is well known for its explosive breeding strategy with individuals spending the majority of the year in a fossorial state before emerging extremely rapidly and breeding over a period of a few days (Cogăniceanu *et al*. 2013; Degani 2015).

Synchronisation of emergence for such breeding aggregations is extremely important for reproductive success and amphibian species have evolved a range of strategies to ensure they arrive simultaneously at breeding sites (Wells 2007). Rising temperature has been reported as a cue to initiate emergence from winter hibernation in many temperate species including Bufo boreas and Rana cascadae in North America (Blaustein et al. 2001), Rana temporaria in the UK (Beebee 1995) and *Hynobius tokyoensis*, *Rana ornativentris*, and *Rhacophorus arboreus* from Japan (Kusano and Inoue 2008). Rainfall is a major trigger for amphibian migration and breeding in a range of species (Duellman and Trueb 1994; Padro et al. 2005). Sudden rainfall events often trigger mass emergence, particularly in Neotropical species (Gottsberger and Gruber 2004) such as the Túngara Frog, Physalaemus pustulosus (Marsh et al. 2000), and P. nattereri (Rodrigues et al. 2004). Species living in arid climates often emerge rapidly in response to rainfall including the South American Andean toad Melanophryniscus rubriventris (Vaira 2005) and the spadefoot toad Scaphiopus holbrooki (Greenberg and Tanner 2004). Other cues which have been reported to trigger emergence and attendance at breeding sites are changes in barometric pressures (FitzGerald and Bider 1974; Greenberg and Tanner 2004), photoperiod (Narayan et al. 2010), light intensity (Baker and Richardson 2006; Heinzmann 1970), humidity (Bellis 1962; Walther et al. 2002) and wind (Henzi et al. 1995).

The effects of the lunar phase on emergence and aggregations of amphibians at breeding ponds are only recently being understood (reviewed by Grant et al. 2012). An increasing number of amphibian species are being recognised as being affected by lunar phase with apparent differences in species’ response to the moon which often relates to their specific ecology. Some species appear to become more active during the brighter phases of the moon (e.g. Grant et al. 2009; Green et al. 2016), whilst others become more active during the new moon phase (Hiert and Moura 2010; Johnson and Batie 2001; Kusano et al. 2015). The adaptive response of amphibians appears to depend on species ecology and predation risk (Byrne and Roberts 2004; Grant et al. 2012).

Both the common toad *Bufo bufo* and common frog *Rana temporaria* are described as having an explosive breeding strategy with males only remaining at ponds for a few weeks during the breeding season (Beebee and Griffiths 2001). In addition, individuals within both species exhibit scramble competition and the first males often obtain the first mates. The operational sex ratio may often be highly skewed with a male bias as females do not breed or migrate every year (Loman and Madsen 2010). Common toads overwinter in habitats which may be several hundred metres from breeding ponds, often with inhospitable terrain between them. It may therefore take individuals several days or weeks to finally reach their breeding site (Sinsch 1987; 1988). Effective synchronisation of arrival at breeding ponds is therefore crucial to ensure effective reproductive success (Akçakaya 2000; Sinsch 1988; Trenham et al. 2003) and enhance survival of metamorphs through predator dilution or selfish herd geometry (Grant et al. 2012). Previous research has identified weather as a key factor, especially night time temperatures, in triggering migration to breeding ponds in common toads (Sinsch 1988; Gittins et al. 1980; Reading 1998). In particular, when night time temperatures approach 6°C, common toads are known to appear in large numbers (Gittins et al. 1980; Reading 1998; Reading and Clarke 1983). However, weather conditions in the UK, especially during March and April can fluctuate widely in a very short time period, which makes using weather cues to initiate breeding unpredictable. The impacts of lunar phase on amphibians are poorly understood and relatively few studies have investigated the possible effects of lunar phase on amphibian migration (Arnfield et al. 2012). Most studies which have examined the effects of lunar phase on breeding migrations have done so at a small number of sites or over a relatively short time period. Moon phase studies need to be conducted over a (removed as we only did 4 years which is not considerable!) number of years to have any validity (Grant et al. 2012).

In recent decades that has been a rapid increase in transport infrastructure across the UK with associated increases in traffic density which has had major impacts on amphibian populations worldwide (Fahrig et al. 1995; Glista et al. 2008; Beebee, 2013), causing habitat loss, pollution and fragmentation, as well as substantial rates of road traffic mortality (Hels and Buchwald 2001; Mazerolle 2004; Petrovan and Schmidt 2016). Amphibians that exhibit large migration events, such as common toads, are particularly vulnerable to road mortality since they emerge in large numbers, often at dusk which coincides with highest commuter traffic density (Fahrig et al. 1995). They are therefore at risk of very high road mortality due to the combination of large numbers of migrating toads along with busiest traffic density. In 2019, volunteer toad patrollers from 218 sites across the UK helped 107,401 common toads across roads (Froglife, 2019). Volunteer toad patrollers are therefore crucial in helping to transport common toads, and other amphibian species, across roads during these mass migration events. Understanding the cues which trigger peaks in numbers of migrating amphibians are essential in enabling volunteers to coordinate their efforts and save the greatest numbers of amphibians from traffic mortality.

In this study we examine the timing of breeding migrations of both common toads and common frogs at 43 sites across the UK over a four-year period, providing a large-scale investigation into the effects of lunar phase on two amphibian species. Understanding the cues involved in migration to breeding sites is important to assist in the timing of conservation interventions such as moving amphibians across roads, which is a common and inexpensive strategy. Furthermore, the role of the lunar cycle is a key factor which must be taken into account when monitoring amphibian populations across multiple years as the lunar cycle is out of phase with Julian calendar date.

**MATERIALS AND METHODS**

*General methods*

Volunteers collected data as part of a citizen science project which helps to move toads across roads. A national conservation charity in the UK has been coordinating this project since the early 1980s and involves volunteers (toad patrollers) visiting roads where common frogs and common toads are known to cross during breeding migrations to ponds in early spring. The aim of each toad patrol is to transport adult migrating common toads from one side of the road to another to avoid mortality due to traffic collisions. In 2019, across the UK, over 107,401 common toads were transported across roads by toad patrollers (Froglife, 2019). In addition to common toads, common frogs often also cross roads to reach breeding ponds at the same time of year. Volunteers also help this species across roads where they occur. However, the number of common frogs crossing roads is generally much lower so the focus of toad patrols is on helping common toads.

Each group of toad patrollers is coordinated by a toad patrol manager, who is responsible for the organisation of volunteers, collection and collation of data. The patrol manager is responsible for ensuring the health and safety of the volunteers, as they are often collecting data on busy roads in the dark. They also ensure common toads are handled ethically and transported across roads in the correct manner. In addition, patrol managers are responsible for ensuring the number of toads saved is counted accurately and collated at the end of each night survey.

*Specific methods*

The detailed methodology employed by each toad patrol varied slightly, but all adhered to the same general methods. Toad patrollers worked in pairs or small groups and visited toad crossing sites between 14th February and 15th April from 2014 to 2017. Toad patrollers generally initiated surveys after observing the first toad crossings and continued until the last toads were observed. Since the peak number of toads was of interest in this study, it does not matter if a few outlier individuals were missed at the start or end of the breeding season. During each survey period, toad patrollers visited their local toad crossing site between the hours of 17:00 and 00:00 hrs every night. To survey for toads, each toad patroller walked up and down the stretch of road where common toads and common frogs were known to cross at their site. The exact distance covered varied from 100 m to 300 m (see Supplementary Data, Table 1) depending on where the amphibians were crossing roads at each particular site. This depended on the position of the breeding pond in relation to terrestrial habitat on the opposite side of the road. Toad patrollers used torches to search for common toads and common frogs and they picked up any encountered on the road, placed them into a bucket and transported them to the opposite site of the road, where they were released. Individual toad patrollers counted the number of frogs and toads collected and data for each site was collated at the end of each evening of surveying by the toad patrol manager for that site. The brand and strength of torch varied between toad patrollers but was deemed bright enough by toad patrol managers to enable the toad patrollers to find and identify toads. Common toads and common frogs on roads are very obvious during migration, as they hop or crawl and are easily observed. Therefore, it is unlikely that toad patrollers would have failed to spot a migrating frog or toad during night time surveys.

*Study sites*

There are currently 182 active toad patrols registered with the UK national charity and each collects data from their own dedicated site. To analyse the possible effects of lunar phase on the numbers of toads and frogs migrating, we required that toad patrols had recorded the number of toads and frogs on each given night of the survey period. However, 139 of the toad patrols only submitted annual totals for each year, which was not suitable for this study. Therefore, we did not include data from these patrols in the current analysis. Data presented in this study comes from 43 sites across the UK between 2014 and 2017. Not all of the toad patrols used in this study submitted daily records for all years, so data is only available from a subset of the sites in each given year (26 in 2014; 17 in 2015; 20 in 2016; and 10 in 2017). Figure 1 shows the location of sites across the country. Details of site location coordinates, the years in which data was collected and a brief description of each site is available in the Supplementary Data.

*Moon phase data*

We obtained data on the fraction of moon illuminated from the US Naval Observatory Astronomical Applications Department (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>) for midnight at Universal Time (GMT). Each day of the year had a luminosity value attached to it, based on the fraction of the moon’s visible disc illuminated, with the full moon being 1 and the new moon 0. We used the same values for each site since moon phase is not dependent on geographical position. Since we applied the hypothesis retrospectively after data collection, we were unable to obtain data on light levels at the breeding sites and whether the moon was visible. Furthermore, we did not measure the moon’s angle of declination, the presence of lunar cycles other than the 29.53 day synodic cycle and moon rise and set times. We carried out rank correlation tests between luminosity (fraction of the moon illuminated) and weather variables (rainfall, temperature) to rule out confounding correlations.

*Weather data*

Toad patrollers did not collect temperature or rainfall data since this was outside of the scope their volunteer remit and before the current study hypothesis was proposed. We obtained minimum daily temperature from the nearest UK weather recording station to each study site obtained from Weather Underground (<https://www.wunderground.com>). Weather stations varied from between 3 km and 18 km from each study site. Daily rainfall on this website was only available for eight of the study sites over the four year period and was not available elsewhere. The Met Office provided monthly rainfall values (<http://www.metoffice.gov.uk/public/weather/climate-historic/#?tab=climateHistoric>) but these weather stations were often too distant from study sites (typically 20 km to 50 km) and monthly totals would have been too general to generate meaningful results. Preliminary analysis on the rainfall values from the sites that did have data revealed no significant relationship between amount of rainfall and numbers of frogs / toads arriving (n = 9, z= -0.8, *p* = 0.425). This is likely to be because the effects of rainfall will have a lag-time, with common toads often moving several days after rainfall events (Verrell and Halliday 1985; Andreone and Giacoma 1989; Reading 1998). Rainfall may be a trigger for initial migration, but become less important once migration has started. Common toads may migrate several hundred metres to breeding ponds so by the time they are encountered attempting to cross roads, the migration had already been initiated and rainfall may be less important in synchronising movements. Also, the soil and leaf litter moisture levels, rather than the rainfall amount, may be more important in migration in the common toad. Therefore, we did not include rainfall values in weather analysis.

*Statistical analysis*

Due to several constraints balanced data could not be collected, e.g. number of days observed at different sites was different over different years. Therefore, site was considered as a categorical variable and labelled from 1 to 43. Luminosity is a periodic variable so to study its effect on the migration rate, it was transformed to a circular variable by mapping the fraction ε (0, 1] of moon illuminated to the angle θ ε (0o, 360o]. It is necessary to transform circular variables such as moon phase as there is an arbitrary or undefined origin and wrapping of the scale, which non circular statistics would view as outliers (SenGupta & Ugwuowo 2006; Hussin 2007). Finally, the days in the observational time period within eachyear was taken in continuum as t = 1, 2, 3, etc.

There were a large number of days on which no toads migrated. The migration frequency was generally unimodal with mode at 0 (full moon) and rapid decay. The high number of zero records resulted in a zero-inflated Poisson distribution for modelling. To understand how lunar phase affects the arrival rate per lunar day, a zero-inflated Poisson regression model was carried out. The frequencies of toads were low at the start of the lunar cycle, increased as full moon was approached and then declined and fell back to low values at the ending day with a new moon. Throughout the entire observational period there were several full and new moons. Therefore, we adopted a time series regression model with the covariate time modelled as a quadratic function. The smaller periods, arising out of the periodicity of luminosity for each month within each year, were intended to be captured by circular statistics, e.g. the sine and cosine of the luminosities. Dummy variables (42 in number, to avoid the “dummy variable trap”) were used to represent sites. Thus, in general we adopted a generalized cylindrical regression model, where the response migration rate per lunar day was linear – a zero-inflated Poisson random variable, and the explanatory variables were linear (temperature, year, day), categorical (site) and circular (luminosity).

*Regression formula [Count model coefficients (Poisson with log link)](in R parlour):*

zeroinfl (formula = toad$Number.of.toads ~ air + as.factor (site) + poly (day, 2) + year

+ sin\_lu + cos\_lu.

Pearson residuals: Min = -3.0403, 1Q = 0.6617 , Median = -0.3973, 3Q = -0.1664, Max = 30.5390.  
Number of iterations in BFGS optimization: 93; log-likelihood: -2.686e+04 on 102 df.

Table 1 presents the results of the regression analysis with p values shown.

The major factor affecting toad numbers was site, due to variation in population sizes between sites. The year of data collection was also a significant predictor of the number of animal crossings. There was clear autocorrelation in the data, meaning the likelihood of arrivals was correlated to the arrivals the day before, these terms were included in the time-series model. The coefficient of the squared term “poly(day, 2)2” is negative (- 16.99), establishing the concavity of the quadratic function in day.

For frogs, the data did not conform to normal, Poisson or negative binomial distributions. They also did not conform to von Mises (circular) distributions. The data were patchy and sparse (over-dispersed) making analysis difficult. For this reason we did not carry out a time series regression but analysed the frog migrations with a circular goodness of fit test which was more suitable for the data. We used Oriana 4 (Kovak Computing) to test for non-uniformity of the frog arrivals with respect to lunar day. These were plotted on a circular histogram (where 0 degrees represents the full moon and 180 degrees represents the new moon) and tested using the Rayleigh test, where the null hypothesis states that values are distributed uniformly around the circular space.

**RESULTS**

The total number of migrating toads and frogs across all sites is shown below, broken down by year.

|  |  |  |
| --- | --- | --- |
| **Year** | **Number of migrating toads** | **Number of migrating frogs** |
| **2014** | 16,416 | 609 |
| **2015** | 7014 | 62 |
| **2016** | 7916 | 418 |
| **2017** | 6535 | 178 |

*Toads*

Results from our study show that at 43 toad migration sites across the UK spanning four years, the mean number of common toads observed migrating to breeding ponds coincided with the waxing phase of the moon, specifically days 28, 29 and 0 (which all correspond to the full moon) (Table 1) (Figure 2). There were minor peaks in abundance at other phases of the moon, notably days 5-7, 10-12 and 18-20 but these were smaller in magnitude and likely to be due to synergistic effects of temperature or other factors. Peak movements of common toads were therefore more likely to occur on warmer nights closer to a full moon, with differences in the timing between sites. The effect of site is likely to be due to the large variations in population size between sites, as well as differences in the temperatures experienced. The statistical analysis lends support to, and clearly establishes, that the migration rate per lunar day for the common toad *Bufo bufo* increases with the luminosity as full moon is approached.

*Frogs*

The null hypothesis that frog arrivals were uniform or randomly spaced across the lunar cycle was rejected, i.e. the distribution of arrival times (lunar days) was anisotropic (Batschelet 1981; Jammalamadaka and SenGupta 2001; SenGupta and Ugwuowo 2006; Landler et al. 2018). The mean number of common frogs observed migrating per lunar day followed a similar pattern to that of common toads with the highest numbers of frogs migrating in the waxing phase of the moon, days 27 to 0. The modal frequency was 0 degrees, full moon (Rayleigh test: n = 30, Z = 29.9, P < 0.00001) (Figure 3). There was also a high abundance on day 19, but this only occurred at a small number of sites and in one year (2014). This anomaly is not well understood and could be due to site-specific factors possibly interacting with local microclimatic variations. Therefore, the movement patterns of common frogs were very similar to those observed for common toads, with peaks in the numbers migrating occurring on warmer nights closer to a full moon, with differences in timing between sites.

*Moon phase -weather correlations*

There was no meaningful correlation between minimum daily temperature and lunar phase (n = 3553; r = 0.066), or between rainfall and lunar phase (n = 655; r = -0.12).

**DISCUSSION**

Data collected from 43 common toad and common frog migration sites from across the UK over a four-year period show a peak in migratory activity in days 28 to 0 of the lunar cycle, just before, and on the day of, the full moon. In both species, migratory activity was also significantly affected by minimum daily temperature and location of site with peak abundances more likely to occur on mild nights just preceding full moon. Peaks in migratory activity in common toads under milder conditions, which also coincide with lunar phases close to the full moon, have also been recorded in common toads at other breeding sites around the UK. Arnfield et al. (2012) noted that at 25 sites in Derbyshire peak common toad abundance at toad migration crossings occurred on milder nights in the 10 days preceding full moon (waxing part of the cycle). Our preliminary analysis revealed no significant impact of rainfall on peak abundance of common toads, which was the same pattern observed by Arnfield et al. (2012). In an earlier study by Grant et al. (2009) at two ponds in the UK (Oxford and Wales), the largest migration peaks coincided with the days just before or on the full moon. Our study adds to this evidence showing that at UK sites encompassing a wide latitudinal range, common toads synchronise their peak breeding migrations with dates close to the full moon. In addition, our study is the first to demonstrate a link between lunar phase and migratory activity in the common frog, although Grant et al. (2009) showed that spawning in the common frog was highly non-random with respect to lunar phase; most spawning took place just before and after the full moon.

Both common toads and common frogs exhibit an explosive breeding strategy so synchronisation of individuals at breeding ponds is crucial to ensure highest reproductive success. Previous research has shown that increasing night time minimum temperatures are the initial cue to triggering the first movements of common toads (Gittins et al. 1980; Reading 1998; Reading and Clarke 1983). Amphibians are ectothermic so an increase in ambient temperature is likely to result in increased metabolic activity and thus increase the likelihood of triggering breeding migration (Duel and Trueb 1994). However, we suggest that this alone is not enough to cause the high synchronisation of breeding events, especially in explosively breeding anurans such as the common toad and common frog. We propose that minimum night time temperatures are a trigger to initiate activity in both species and they synchronise their peak movements with the next full moon. Weather conditions in the early spring are highly variable with periods of cold and mild weather occurring sporadically and often unpredictably. A period of mild weather in early spring may be followed by a sudden and unexpected cold spell. To rely on weather conditions alone is unlikely to result in the high synchronisation in peak movements of common toads and frogs at breeding sites. Therefore, to ensure a synchronous arrival at breeding ponds, the use of lunar phase may be more reliable for common toads and common frogs in timing peak migration to ponds, as long as certain day length and temperature thresholds have been reached.

Studies have shown that common frog spawning dates are affected by climate change with an advance in congregation at breeding ponds over recent decades (Scott et al. 2007). Carroll et al. (2009) found that a 1 °C increase in Central England Temperature advanced national mean spawning by 5.1 days. However, common toad breeding times seem less affected by climate change with no observed effect of increasing winter temperatures on breeding times (Reading 1998). Although common toads appear to spawn earlier in years with milder winters (Reading 2007), there does not appear to be a trend towards common toads breeding earlier with climate change (Reading 2007). Although increasing temperatures and climate change may play an important role in overall initial migratory activity and spawning dates in these species, the role of lunar phase may still be important in modulating and synchronising peak migratory activity. Results from our study and previous studies by Arnfield et al*.* (2012) and Grant et al. (2009) indicate there is a degree of flexibility in the peak movements of common toads in relation to lunar phase such that climatic variables along with lunar phase are likely to work synergistically to synchronise peak migratory movements.

Common frogs breed earlier in the season than common toads and are the first UK anurans to initiate breeding activity (Beebee and Griffiths 2000). Our results suggest that in the common frog a combination of increasing day length and rising temperatures initiate migratory activity and subsequently synchronise peak movements with the full moon.

The impact of lunar phase on amphibian activity from a range of families has been systematically reviewed by Grant et al. (2012) who revealed 79 examples of amphibian behaviour where moon phase was recorded. 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. For example, Green et al. (2016) reported that in Fowler’s Toads, *Anaxyrus fowleri,* emergence from winter dormancy correlated strongly with increased moon light, specifically with peak numbers of toads emerging on the waxing or waning gibbous moon, averaging 4.6 days away from the full moon in either direction, especially under milder conditions. In the Australian myobatrachid frog *Crinia* *georgiana*, the density of males and the number of females detected in a chorus varied greatly over the course of a breeding season (Byrne and Roberts 2004). A significant amount of this variation was explained by rainfall and lunar phase, with the highest numbers of individuals occurring close to the full moon (Byrne and Roberts 2004). The Asian toad *Duttaphrynus melanostictus* (formerly *Bufo melanostictus)* has been shown to synchronise ovulation with the full moon. As the moon is not guaranteed to always be visible, this synchronisation likely occurs at an earlier stage of oogenesis and is entrained periodically by lunar light (Grant et al. 2009, 2012).

In contrast, some studies have shown increased movement of anurans under new moon conditions. For example, in the Japanese common toad, *Bufo japonicus formosus* a greater number of reproductive events occurred around the new moon and very few events occurred around the full moon (Kusano et al. 2015). Also, in the American toad, *Bufo americanus*, toads were less active at full moon than at new moon (Fitzgerald and Bider 1972), although this was looking at locomotory activity outside the breeding season, and in the fine-lined tree frog, *Hypsiboas leptolineatus*, from southeast Brazil greatest mean abundance was around the new moon (Hiert and Moura 2010).

Since the response of difference amphibian species to lunar phase appears to be variable, this implies that there are different ecological pressures acting on different species, which determine their response to lunar phase (Byrne and Roberts 2004; Grant et al. 2012). Some amphibian species may rely on sight to find conspecifics or detect predators (Byrne and Roberts 2004), locate suitable calling sites (Backwell and Passmore 1990) and orientate using landmarks (Green et al. 2016). In these species, the bright light conditions experienced under a full moon may be used to synchronise movements. However, in species which are more vulnerable and prone to predation at night, synchronising movements in the darkest new moon phase may be more ecologically adaptive (Fitzgerald and Bider 1972; Hiert and Moura 2010; Kusano et al. 2015; Grant et al. 2012). Migrating in a full moon is liable to make an individual more vulnerable to visual predators; however, the emergent behaviour depends on the balance between the costs and benefits for the particular species. For species migrating under a full moon the advantages of synchronisation, and the advantages of using lunar light to entrain a biorhythm, must outweigh any disadvantages caused by vulnerabilities to predation. In addition, full moon migrators will be at an advantage in detecting olfactory and auditory predators in higher light conditions. Other frogs (e.g. *Fejervarya cancrivora*) primarily breed on a new moon (Church, 1961), so the response to lunar cycles appears to be highly species specific and depends on the cost - benefit of the particular species' ecology. Both common frogs and common toads are vulnerable during migration and are prey items to a range of nocturnal predators including owls, foxes and rats (Beebee and Griffiths 2000). However, common toads do possess toxic glands in their skin, which may help prevent some predation. Common frogs are highly mobile and may evade many land-dwelling predators e.g. foxes and rats. Despite this, both species are still vulnerable to predation when moving under a full moon. Barn owls hunt primarily using auditory cues and avoid hunting in bright light intensities (Lovari et al. 1976). By migrating in large numbers, common toads and common frogs may convey anti-predator advantages by selfish herd geometry (Olson 1989; Ryan et al. 1981). Any predation risk on an individual will be diluted by the number of individuals present at breeding aggregations. Both common toads and common frogs have been found to use a combination of cues to orient to breeding ponds including celestial, gravitational, visual and olfactory cues (Sincsh 1988). Moving under full moon conditions may allow these species to fully utilise celestial cues as well as use visual landmarks to help them orientate towards ponds.

*Conservation implications*

Common toad populations are in decline (Petrovan and Schmidt, 2016) due to a combination of factors including habitat loss and fragmentation, climate change and pollution (Beebee 1996; 2013; Carrier and Beebee 2006; Tomašević et al. 2007). One conservation strategy employed across the UK is a ‘Toads on Roads’ campaign with hundreds of volunteer ‘toad patrollers’ helping to assist toads across roads which fragment breeding and terrestrial habitats in the spring. Volunteers are not always able to patrol roads on every single day in the breeding season due to variations in commitments (C. Monk pers. comm.) and often use environmental cues to determine the most effective nights to go out on toad patrols. Currently, toad patrollers tend to become most active on mild and damp nights in early spring as these are often when toad numbers crossing roads are high. Results from our research indicates that to ensure that the peak migration period is covered, toad patrollers should aim to patrol roads in mild and damp conditions closest to the full moon through the migration period (March and April). The date of the full moon with respect to the Julian Calendar varies each year which may result in peak toad migrations occurring on different calendar dates. If toad patrollers have limited time and resources, identifying the few days in each season when common toad and frog migrations are at their peak is crucial in enabling them to help the greatest numbers of individuals across roads.

*Conclusions*

Our study of common toads and common frogs at 43 sites over four years across the UK demonstrates a link between lunar phase and peak migratory activity with both species exhibiting peak abundance in days 28 to 0 which corresponds to just before, and the day of, the full moon. In addition, there was a significant effect of minimum daily temperature with individuals of both species showing peak migratory movement on mild nights close to a full moon. Our findings have conservation importance, as it will enable toad patrollers to more effectively identify peak migration dates in common frogs and common toads and enhance volunteer effort on these days. Overall, this study highlights the importance of lunar phase in modulating and synchronising breeding in two UK anuran species and has implications for conservation of both species.

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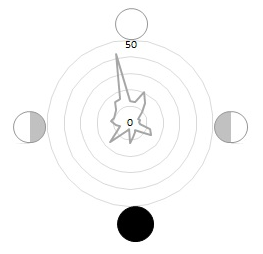
**Table 1**. Time series regression model of toad arrival rate with zero inflated Poisson distribution. P values are shown as well as asterisks denoting the significance level for each parameter (\*<0.05; \*\*<0.01; \*\*\*<0.001). The sin\_lu and cos\_lu significance rejects the null hypothesis that toad arrivals are random with respect to moon phase and there are also significant year and site effects.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Factor** | **Estimate** | **Std. Error** | **Z value** | **Outcome** |
| Intercept | 1.517553 | 0.069777 | 21.749 | \*\*\* |
| poly(day, 2)1 | 8.154352 | 0.524720 | 15.540 | \*\*\* |
| poly(day, 2)2 | -16.992627 | 0.502377 | -33.824 | \*\*\* |
| year2015 | 0.369620 | 0.023338 | 15.838 | \*\*\* |
| year2016 | 0.842937 | 0.034458 | 24.463 | \*\*\* |
| year2017 | 0.716342 | 0.037046 | 19.337 | \*\*\* |
| sin\_lu | 0.187557 | 0.009466 | 19.814 | \*\*\* |
| cos\_lu | 0.070698 | 0.007568 | 9.342 | \*\*\* |
| air | 0.129857 | 0.002251 | 57.686 | \*\* |
| Site 2 | -0.343310 | 0.121626 | -2.823 | \*\* |
| Site 3 | -0.882266 | 0.089850 | -9.819 | \*\*\* |
| Site 4 | 0.605325 | 0.074458 | 8.130 | \*\*\* |
| Site 5 | 1.219707 | 0.071379 | 17.088 | \*\*\* |
| Site 6 | 2.031570 | 0.072564 | 27.997 | \*\*\* |
| Site 7 | 0.010591 | 0.093533 | 0.113 |  |
| Site 8 | -0.598494 | 0.079384 | -7.539 | \*\*\* |
| Site 9 | 2.161621 | 0.071445 | 30.256 | \*\*\* |
| Site 10 | -0.046745 | 0.095869 | -0.488 |  |
| Site 11 | 0.448165 | 0.085889 | 5.218 | \*\*\* |
| Site 12 | 2.277863 | 0.071563 | 31.830 | \*\*\* |
| Site 13 | 1.644121 | 0.071692 | 22.933 | \*\*\* |
| Site 14 | 0.740392 | 0.077607 | 9.540 | \*\*\* |
| Site 15 | 1.719504 | 0.072716 | 23.647 | \*\*\* |
| Site 16 | 0.434966 | 0.101825 | 4.272 | \*\*\* |
| Site 17 | -0.152415 | 0.092864 | -1.641 |  |
| Site 18 | 1.603092 | 0.073306 | 21.869 | \*\*\* |
| Site 19 | 0.423581 | 0.092512 | 4.579 | \*\*\* |
| Site 20 | 0.606388 | 0.082076 | 7.388 | \*\*\* |
| Site 21 | 0.860960 | 0.078683 | 10.942 | \*\*\* |
| Site 22 | 1.510190 | 0.076768 | 19.672 | \*\*\* |
| Site 23 | 0.287575 | 0.103602 | 2.776 | \*\* |
| Site 24 | 0.123409 | 0.078285 | 1.576 |  |
| Site 25 | 1.065140 | 0.075578 | 14.093 | \*\*\* |
| Site 26 | 0.609502 | 0.095996 | 6.349 | \*\*\* |
| Site 27 | 0.603248 | 0.079817 | 7.558 | \*\*\* |
| Site 28 | -0.347709 | 0.103680 | -3.354 | \*\*\* |
| Site 29 | -0.000723 | 0.097977 | -0.007 |  |
| Site 30 | -1.420313 | 0.156771 | -9.060 | \*\*\* |
| Site 31 | 0.504036 | 0.081631 | 6.175 | \*\*\* |
| Site 32 | 0.100857 | 0.088931 | 1.134 |  |
| Site 33 | -0.626553 | 0.114237 | -5.485 | \*\*\* |
| Site 34 | -1.876597 | 0.268150 | -6.998 | \*\*\* |
| Site 35 | 0.249719 | 0.084821 | 2.944 | \*\* |
| Site 36 | 0.639027 | 0.082096 | 7.784 | \*\*\* |
| Site 37 | 0.788577 | 0.081517 | 9.674 | \*\*\* |
| Site 38 | -1.143593 | 0.121397 | -9.420 | \*\*\* |
| Site 39 | -0.221538 | 0.094803 | -2.337 | \* |
| Site 40 | -0.885510 | 0.135993 | -6.511 | \*\*\* |
| Site 41 | -0.355363 | 0.092584 | -3.838 | \*\* |
| Site 42 | 0.451147 | 0.084109 | 5.364 | \*\*\* |
| Site 43 | 0.653908 | 0.084811 | 7.710 | \*\*\* |
|  |  |  |  |  |

**Fig. 1.** Locations of the 43 toad and frog breeding sites across the UK where data were collected by toad patrols. Black circles denote toad patrol and the number relates to site details as shown in Table 1 in Supplementary Data.



**Fig. 2**. A circular histogram showing the mean number of common toads migrating with respect to the lunar cycle. The mean number of toads migrating was plotted for each day of the lunar cycle from 0 to 29, with 0 being the full moon (all years and sites amalgamated). This figure is for ease of visual interpretation and further statistical tests were not carried out on toads.



**Fig. 3.** A circular histogram showing the mean number of common frogs migrating with respect to the lunar cycle. The mean number of frogs migrating was plotted for each day of the lunar cycle from 0 to 29, with 0 being the full moon (all years and sites amalgamated). Rayleigh test: n = 30, Z = 29.9, P < 0.00001. The secondary peak of migrations was seen at day 19 of the lunar cycle but only occurred at 4 sites in one year.

