Article

Relationship of calling intensity to micrometeorology in pond breeding frogs from central eastern New South Wales

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Received 30 December 2011; Accepted 2 February 2012; Published online 1 June 2013

Abstract

Micrometeorological factors can strongly influence calling activity in frogs, but relatively little empirical evidence has examined possible relationships in Australian species. Such information is important when using surveys to detect species for management and research. We recorded the calling activity of frogs breeding at 93 ponds through coastal northern New South Wales and used linear mixed effects models to compare the number of calling males with temperature, humidity and cumulative rainfall at 24 hours and 72 hours prior to calling surveys. We obtained sufficient data to analyze the relationships for nine species, obtaining a positive response to 72-hour rainfall in eight of the nine species. Twenty-four hour rainfall provided a positive response for six species and a negative response for two species. Similarly, temperature and humidity provided positive responses for three and five species and negative effects for three and three species respectively. Calling of all species was related to multiple micrometeorological factors and these varied between species.

Keywords anurans; communication; weather; activity; detection.

Proceedings of the International Academy of Ecology and Environmental Sciences
ISSN 2220-8860
URL: http://www.iaees.org/publications/journals/piaees/online-version.asp
RSS: http://www.iaees.org/publications/journals/piaees/rss.xml
E-mail: piaees@iaees.org
Editor-in-Chief: WenJun Zhang
Publisher: International Academy of Ecology and Environmental Sciences

1 Introduction

Male anurans often use acoustic signals, the calls of males, to communicate with conspecifics and, most notably to attract females for reproduction. Calling is energetically expensive (Mac Nally, 1981, Taigen and Wells, 1985; Prestwich, 1994) and may attract predators (Ryan et al., 1981; Lode et al., 2004), hence males are both more inclined to call and to call more intensely when conditions are likely to lead to mating opportunities. Micrometeorological variables have been implicated in controlling or influencing the calling activity of anurans. Rainfall (Balinsky, 1969; Telford and Dyson, 1990; Krupa, 1994; Lemckert, 2001) and temperature (Jackson, 1952; Einem and Ober, 1956; Storm, 1960; Almeida-Gomes et al., 2007) or both (Storm, 1960;

Humphries, 1979; Okuno, 1985; Radwan and Schneider, 1988) have most consistently been found to correlate with the number of males calling at a given time and/or the intensity of their calling activity, usually showing a positive relationship. Humidity also often correlates with calling activity (Almeida-Gomes et al., 2007; Hauselberger and Alford, 2005). These variables are most strongly related to calling, presumably because anurans dehydrate when conditions are dry and, being ectothermic, are able to call most effectively when conditions are warm. However, species will respond to these variables differently based on the breeding environments and seasons in which breeding occurs (Saenz et al., 2006).

The relationship between calling and micrometeorology for Australian anurans has received little attention in the published literature. However, these factors have been examined for some species. Intensity of calling by *Crinia signifera* correlates weakly with rainfall from the previous 72 hours (Lemckert, 2001). Calling by *Austrochaperina robusta* is significantly related to rainfall and humidity (Hauselberger and Alford, 2005) and calling by *Cophixalus ornatus* is most affected by humidity (Hauselberger and Alford, 2005). The presumption is that Australian anurans have a similar response to those reported in North America and Europe, however the limited published work does not allow us to establish this relationship. Australian anurans evolved from somewhat distinct lineages and in very different environments (Slatyer et al., 2007), so frogs may exhibit different relationships between calling activity and micrometeorology.

The relationship between micrometeorological conditions and calling in anurans is of particular importance to wildlife managers. Surveys for anurans generally rely on detecting the calls of male frogs to determine the presence or absence of species and are undertaken for a variety of reasons including to assess habitat relationships of species (Hazell et al., 2001; Afonso and Eterovick, 2007; Pillsbury and Miller, 2008; Brand and Snodgrass, 2009), monitor the status of populations (Crouch and Paton, 2002; De Solla et al., 2006; Brodman, 2008; Lemckert et al., 2011), and to locate individuals for conservation actions (Lemckert and Morse, 1999). Surveys conducted when calling is at its most intense and/or consistent will have the greatest success in detecting species. Hence developing an understanding of the relationship between micrometeorological conditions and calling activity is of considerable importance in order to optimize survey outcomes.

In this paper we examine the relationship between the number of calling male frogs detected at ponds in eastern New South Wales (NSW) with three micrometeorological factors; rainfall, air temperature and humidity. If surveys can be undertaken when more males are calling, the sound volumes will be greater and so frogs more detectable. Counts at optimum times will also provide better estimates of total frog abundance for use in monitoring studies. We predict that:

a) species that call from aquatic positions are unlikely to have significant positive relationship between calling and humidity and as the males are not subject to desiccation.

b) species with very extended calling seasons ($\geq$ nine months) will not show relationships between calling and temperature as males will be exposed to widely varying temperatures over time and so will be adapted to call at a wide range of temperatures.

c) species known to also breed in temporary water bodies are likely to demonstrate positive correlations with rainfall as they rely on rainfall to inundate breeding sites.

2 Methods

We undertook searches of frogs at 93 pond sites located between the Hawkesbury River in central NSW and the Coffs Harbour area of mid-northern NSW, a transect of approximately 500 km (between latitudes 30^{o} and 34^{o} south). Data was collected at various times between the 27^{th} of September 1993 and the 18^{th} of December 2007, with surveys being undertaken in a variety of conditions as time allowed. The ponds were in forested

areas, although some were on the border with cleared private lands. The ponds varied in size from a minimum of 25 m^2 to a maximum 2250 m^2 (mean 435 m^2, SD = 411), but 80% of the ponds were between 300 m^2 and 700 m^2 in area and approximately round in shape (20-30 m diameter). All but the two smallest ponds visited in the study are essentially permanent and retain water throughout the year except in times of heavy drought. Calling surveys were usually carried out over the first three hours after sunset (80% of searches were completed before 23:00 hours) and usually between September and March (spring to early autumn in NSW), which is the primary calling period for the majority of frogs in this region (Lemckert and Mahony, 2008). However, some were carried out in other months of the year to target autumn and winter breeding species (see Table 1). The surveys at these sites follow those described in Lemckert et al (2006) and consisted of a 2-5 minute period of listening for calling frogs in dark and quiet conditions to encourage frogs to commence calling. This was followed by a headlamp search of the water body and surrounding habitat during which male frogs would sometimes commence calling as they became accustomed to the presence of the surveyors. Any frogs heard calling were identified to species (based on Cogger, 2000) and their numbers recorded. Estimates of calling frogs (to the nearest multiple of 10) were made where numbers of calling males exceeded 30, with a maximum recognised number of calling males being 100+ animals. Searches of sites generally covered between 10 and 30 minutes, depending on pond size and number of frogs calling. We included the data from a site only if it was searched on at least three separate occasions.

Air temperature and humidity readings were taken using either a Brannan Compact Whirling Hygrometer or Silva Alba Windwatch, either at the start or the end of a site search. Readings were not always taken at each site. If readings were not taken at a particular pond, they were assigned the mean value of the first available readings taken before and after that survey point. In practice readings were taken at more than 75% of the sites visited on a night and the micrometeorological readings rarely differed by more than 5% between any sequential set of readings. Hence, the assumed readings would be relatively accurate for the purposes of the analysis.

Table 1 Number of survey nights with data available in each month of the year

Month	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Records	224	69	91	3	0	0	0	10	111	135	194	123

We obtained rainfall records from the closest available Bureau of Meteorology station (between 1 km and 40 km distant) and compared calling with the rainfall recorded at 21:00 on the day of the record and with the combined rainfall total for the day of the record and the previous two days (24 and 72 hour rain respectively). We recognise that the rain that fell at the search sites may not correspond exactly with that recorded at the weather station, but should be similar in most circumstances. The relatively large number of readings available should also compensate for any variations that may have occurred through this method. There could also have been instances when rain did not fall until after the search and so the search conditions may have been dry when significant rainfall was recorded for that day. Such occasions would have been rare and again we consider that the large number of available records should provide buffering against such measurement "errors" in the data.

Four explanatory variables of interest were selected for inclusion in the models: air temperature, humidity, 24-hour rainfall and 72-hour rainfall. These variables have been found most commonly to correlate with anuran calling activity and appeared most likely to be important through personal observations. 72-hour rainfall was transformed using ln (x+1) to normalize its distribution and all variables were standardized to have a mean of zero and a standard deviation of one. A correlation matrix comparing the four micrometeorological variables indicated that none were highly correlated ($r > 0.60$) and so all were available for the analysis with

calling activity. When comparing calling activity with the four variables we only included records where males of the species were recorded calling as the large number of non-calling records leads to zero-inflation that confounds the analysis process. Hence, the study examines the relationship between micrometeorology and the intensity of calling and not the occurrence of calling. This process leads to variable numbers of records being available for the different species recorded in the study and we only analyzed the data when there were a minimum 40 calling records available with the commensurate micrometeorological data.

Data were analyzed using a linear mixed effects model to account for the serial correlation associated with repeated measures (Gelman and Hill, 2007). The model was implemented with random intercepts for each pond and a common slope across all ponds for each of the climatic variables. A random intercept for each pond allows each model to account for the variation between ponds that may be caused by environmental variables (e.g. pond size, presence of macrophytes), and allows the modeling to focus on the direct effects of climate. Models were calculated in the R-statistical package v.2.8.1 (R-core Development Team, 2008) using the *lmer* statement in the lme4 package (Bates et al., 2008) which is based on the formulation of Laird and Ware (1982). These models optimize for the REML criterion. For all models we used a Poisson error distribution with a log link. The response variable was the number of calling males and the variables of interest were the various combinations of the four climatic variables. The list of models calculated for each species is presented in Table 2.

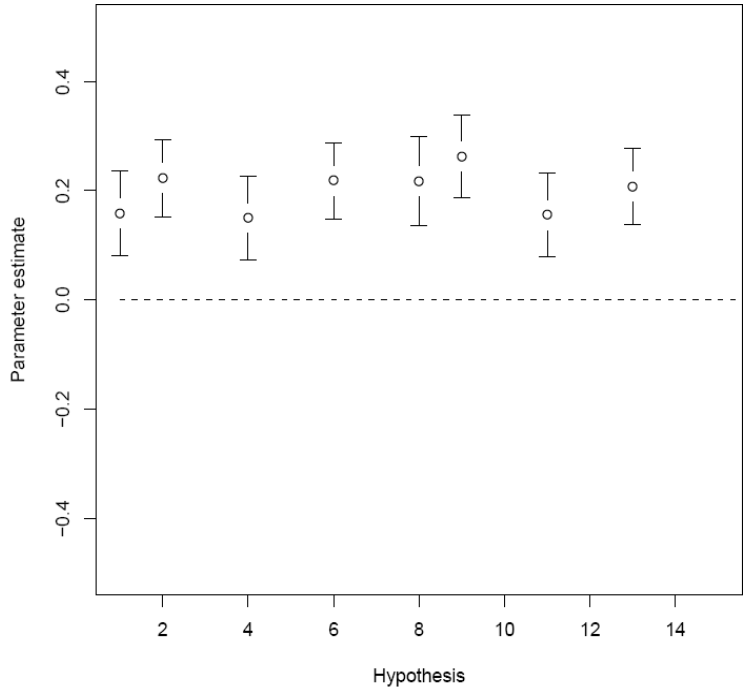
Table 2 Models considered in the analysis of calling intensity versus micrometeorological variables. # calls = number of calling males, 24-hour rain = rainfall during the previous 24 hours, 72-hour rain = rain within the previous 72 hours, temp = dry bulb temperature, RH = relative humidity. Models were run using a Poisson error structure and a log link with a random intercept for each site.

Model #	Model form
1	# calls ~ 24-hour rain + temp + RH
2	# calls ~ 24-hour rain + temp
3	# calls ~ 24-hour rain + RH
4	# calls ~ 24-hour temp + RH
5	# calls ~ 24-hour rain
6	# calls ~ temp
7	# calls ~ RH
8	# calls ~ rain + temp + RH + 72-hour rain
9	# calls ~ rain + temp + 72-hour rain
10	# calls ~ rain + RH + 72-hour rain
11	# calls ~ temp + RH + 72-hour rain
12	# calls ~ rain + 72-hour rain
13	# calls ~ temp + 72-hour rain
14	# calls ~ RH + 72-hour rain
15	# calls ~ 72-hour rain

We obtained and graphed the regression coefficient and 95% confidence intervals for each of the models produced for each species and used these to estimate the significance of each variable in relation to calling activity (following the methods of Parris, 2006 and Penman et al., 2009; Fig. 1). A positive response was recognized where all model 95% confidence intervals were above the zero parameter estimate and a negative response where they were all below the zero parameter estimate (see Fig. 1). Modeling that produced 95% confidence intervals for response size that overlapped zero was considered to represent an uncertain relationship. This method allowed for consideration of the magnitude and direction of the relationship between

calling and the climatic variables in all models. Consistency in the magnitude of the response indicates a true relationship, whereas variable response while significant suggests a less meaningful and potentially statistically unstable relationship. Model averaging (after Burnham and Anderson, 2002) was not undertaken as we were not attempting to make a prescriptive model to determine the intensity of calling. Rather, we were primarily concerned with the direction of the response as the magnitude of the variation may simply be the result of natural variation in calling behavior independent of climatic conditions.

a)



b)

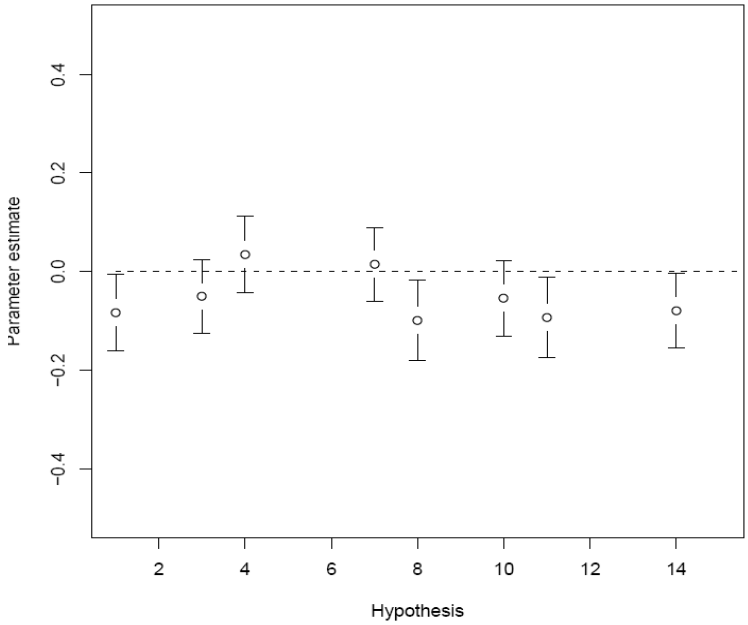


Fig. 1 Graphs of two modelled regression coefficients and 95% confidence intervals representing samples of the types of responses recorded in the study: a) Certain positive response to temperature for *Litoria latopalmata* with no overlap of zero by the 95% confidence intervals; b) Uncertain response to relative humidity for *Crinia signifera* with confidence intervals overlapping zero extensively. The x-axis represents different models tested for the species.

3 Results

The minimum and maximum values recorded for each variable were: 9.0^{o}C and 31.5^{o}C for temperature, 27% and 100% for humidity, 0 mm and 112 mm for 24-hour rainfall and 0 mm and 120 mm for 72-hour rainfall. Thirty-two species were recorded amongst the sites searched, but we were ultimately able to obtain enough data to analyze the calling activity of five hylid and four myobatrachid species (Table 3). The most widespread species, *Litoria peronii*, was recorded at 83 sites and 302 separate calling records were available for this species.

The relationship for 24-hour rainfall and calling activity varied among the nine species modeled (Table 4). There was a positive relationship for six species, a negative relationship for one, and an uncertain relationship for two species. The variable 72-hour rainfall provided the most consistent response, being positive for seven of the nine species and uncertain for the other two. Air temperature provided mixed responses with two species each showing a positive and negative response, and five species uncertain responses. The relationship between calling and humidity was similarly mixed with four positive, three negative, and two uncertain responses.

Table 3 List of species analyzed in this study including the number of sites occupied (out of 93), number of available calling records, preferred calling position (in or out of water), length of core calling season (based on Lemckert and Mahony 2008) and willingness to use temporary pools as breeding sites.

Species	Sites	Records	Call Position	Call Season	Temporary
Adelotus brevis	35	55	Aquatic	Oct-Feb	No
Crinia signifera	63	137	Terrestrial	All year	Yes
Limnodynastes peronii	72	180	Aquatic	Sept-Apr	Yes
Litoria fallax	58	170	Aquatic	Sept-March	No
Litoria latopalmata	39	72	Terrestrial	Sept-Feb	No
Litoria peronii	83	302	Terrestrial	Sept-Mar	No
Litoria tyleri	39	48	Terrestrial	Oct-Mar	No
Mixophyes fasciolatus	39	136	Terrestrial	Oct-Mar	No
Uperoleia fusca	57	274	Terrestrial	Sept-Mar	No

Table 4 Species responses to the four modeled climatic variables.

Species	**24-hour Rainfall**	**72-hour Rainfall**	**Air Temp.**	**Humidity**
Adelotus brevis	Uncertain	Uncertain	Uncertain	Negative
Crinia signifera	Positive	Positive	Uncertain	Uncertain
Limnodynastes peronii	Positive	Positive	Positive	Positive
Litoria fallax	Negative	Positive	Negative	Negative
Litoria latopalmata	Uncertain	Positive	Positive	Negative
Litoria peronii	Positive	Positive	Uncertain	Positive
Litoria tyleri	Positive	Uncertain	Uncertain	Uncertain
Mixophyes fasciolatus	Positive	Positive	Uncertain	Positive
Uperoleia fusca	Positive	Positive	Negative	Positive

4 Discussion

Relationships were found between calling activity of frogs and all four of the variables measured. However, the relationships were species specific with the size and direction of the relationships differing between each species and not all variables being significant for all species. Such variability in responses can be expected

between species, when species have differing life histories, as is the case in this study (e.g. Saenz et al., 2006; Brooke et al., 2000).

Rainfall provided the most consistent significant relationship with calling activity. 72-hour rainfall was positively related to calling in seven species modeled, but showed an uncertain relationship for two species. This was predicted to occur as rainfall is believed to strongly and positively influence reproductive activity in anurans (Duellman and Trueb, 1986). 24-hour rainfall showed a significant positive response in six species, including the two species that often breed in temporary pools. In one species however, we found a negative response to 24-hour rainfall. Given the permeable skins of anurans it would be expected that periods after rainfall would be highly suitable for breeding as the moist conditions would reduce the effects of desiccation, both for calling males and females migrating to the pond to reproduce. The 24-hour rainfall reading may not be expected to provide such a strong correlation, because the majority of rain may have fallen during or just after the call survey and so not have had time to effectively influence calling activity.

Air temperature provided a less obvious and consistent relationship with calling activity. Two species showed a certain positive relationship and two a negative relationship, even though temperature has generally been found to correlate positively with calling activity for other species in other continents (Jackson, 1952; Einem and Ober, 1956; Storm, 1960; Almeida-Gomes et al., 2007) and is widely regarded as being a strong positive influence on calling in frogs (Duelmann and Trueb, 1986). In the case of *U. fusca*, the evident negative relationship might be a result of the strong early season calling of this species. Its calling season is listed as September to March (Lemckert and Mahony, 2008), but personal observations indicate that calling is very strong early in this season when the frogs have moved to the pond. The activity appears to reduce later in summer when temperatures are higher. They also appear to have a burst of calling activity if rains fall in February or March, which again is when temperatures in the region are falling. So, a relationship may reasonably be present with cooler temperatures. We cannot explain the negative relationship between *Litoria fallax* calling and temperature. Personal observations would suggest that this species calls strongly on very warm nights and is very active in the middle of summer.

The possible effect of humidity on calling activity is rarely investigated compared to temperature and rainfall, but appeared to be just as important as temperature for the species in this study. We would expect humidity to show a positive relationship with calling as males calling in more humid conditions would dehydrate less rapidly. However, we found three species to show a negative relationship. Two of the species, *Adelotus brevis* and *Litoria fallax*, call from within water on directly over it (Cogger, 2000) where desiccation is not likely an issue. Hence we are not surprised by a lack of a positive relationship, but a negative relationship is more difficult to understand. We did feel that these two species reduced calling activity when it was actually raining, perhaps because of noise interference as the rain struck the pond. We have no explanation for the negative result for *Litoria latopalmata*. Males call from terrestrial positions adjacent to water, often some meters from the edge of the water (Cogger, 2000) and higher humidity would seem to be advantageous.

Our three predictions made in regards to calling and climate were relatively accurate. None of the three species that call from aquatic positions showed a positive relationship with humidity and two showed a negative relationship. The one species that calls year-round, *Crinia signifera*, did not show any response to temperature, also meeting our prediction. In the case of the third prediction, the two species that are well known for calling around and breeding in temporary pools (*C. signifera* and *Limnodynastes peronii*) showed a positive relationship between calling and both 24-hour and 72-hour rainfall. Thus we have some ability to predict the responses of species based on their ecology, even though we have not made specific studies on the relationships between calling and micrometeorlogy.

The occasions where we obtained unpredicted negative or no relationships may be a result of other factors overriding or interacting with micrometeorology. Canavero et al. (2008) found that a circannual rhythm of activity was more important in explaining the variation in calling activity of a number of anuran species than the weather variables considered. That is, calling activity was more strongly related to the time of season than the weather itself, although weather did still appear to have some influence on calling. In our study region, temperatures are relatively mild throughout the year and rainfall does not show strong seasonal variation. Hence, we do not believe that the frogs from this region would develop a strong circannual rhythm because there are no extreme variations in temperature and rainfall.

The influence of rainfall may also be dependent on the relative dryness of the year. For example, the tungara frog of the tropics has been recorded to call more on wet nights in dry years, but not during years when the soil remained relatively moist (Marsh, 2000). The rainfall levels during much of this study were considerably lower than average as south-eastern Australia went through a severe drought. Hence, when rainfall is a relatively rare event we should see strong positive relationships for rainfall and humidity on calling intensity in any in which rainfall is important for maximizing reproductive success. 72-hour rainfall may be a better predictor of calling intensity than 24-hour rainfall because shorter rainfall events may not be sufficient to saturate the ground and so allow migration to ponds from longer distances and especially so in drought years.

One factor that may be of importance is social environment, including intraspecific and interspecific interactions (Damgaard, 2011; Zhang, 2011). The calling intensity of male *Crinia signifera* increases with increasing temperature, but only for individuals calling continuously on their own (Wong et al., 2004). The relationship with temperature was lost when frogs either called in groups or individuals did not continuously. The species in question is present at our study sites, but we still managed to obtain certain responses, which may result from the relatively large number of observations available that can overcome this effect. Interspecific and intraspecific competition among calling male anurans, including calling interference, is possibly widespread (Duellman and Trueb, 1986) as complex choruses with multiple species are common. The suppression of calling by one species due to the presence of calling males of another species appears likely, although it has been rarely demonstrated (but see Littlejohn and Martin, 1969; Schwartz and Wells, 1984 and Wong et al., 2009). Analysis of community structure at some of the ponds in our study did not suggest correlations between the presence and absence of any species (Lemckert et al., 2006), but call interference may still be occurring, at least under some circumstances. If “suppressing” species are present at some, but not all sites, then the changes in calling patterns would probably confound our ability to detect relationships with micrometeorological conditions and possibly explain at least some of the “no response” results. We do not know if any species at our study sites are able to suppress the calling activity of others and so we cannot comment on such a situation occurring and it is an area worthy of further study.

Our results indicate that micrometeorological variables appear to have some, albeit limited importance, in relation to the intensity of calling activity of pond breeding frogs in southeastern Australia. However, the relationships appear to be more complex than has generally been found in these other studies, with these Australian frogs showing a number of negative relationships with rainfall and temperature and so present a contrasting picture to that found in other areas of the world. The reasons for these unpredicted negative relationships need more study to determine their cause and so provide more certainty in understanding specifically how climate influences calling.

Acknowledgements

We thank Traecey Brassil for her assistance in various aspects of the study. We thank Alison Towerton, Mark Chidel, Yvette Lieschke-Mercer, Maria Adams, The Peacocks and Cameron Slatyer for assistance in the field and to Will Osborne, Michelle Christy, Jim Shields and Jean-Marc Hero for reviews of this manuscript. This work has received the ongoing financial support of the University of Newcastle and Forests NSW (NSW Department of Primary Industries) and was carried out with permits from the NSW Department of Environment and Climate Change, the Forests NSW ACEC and the Newcastle University ACEC.

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