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A combination of body condition measurements is more informative than conventional condition indices: Temporal variation in body condition and corticosterone in brown tree snakes (*Boiga irregularis*)

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Abstract

The body condition index is a common method for quantifying the energy reserves of individual animals. Because good body condition is necessary for reproduction in many species, body condition indices can indicate the potential reproductive output of a population. Body condition is related to glucocorticoid production, in that low body condition is correlated to high concentrations of corticosterone in reptiles. We compared the body condition index and plasma corticosterone levels of brown tree snakes on Guam in 2003 to those collected in 1992/1993 to determine whether that population still showed the chronic stress and poor condition apparent in the earlier study. We also examined the relationship between fat mass, body condition and plasma corticosterone concentrations as indicators of physiological condition of individuals in the population. Body condition was significantly higher in 2003 than in the earlier sample for mature male and female snakes, but not for juveniles. The significantly lower levels of corticosterone in all three groups in 2003 suggests that although juveniles did not have significantly improved energy stores they, along with the mature males and females, were no longer under chronic levels of stress. Although the wet season of 2002 was unusually rainy, low baseline levels of corticosterone measured in 2000 indicate that the improved body condition of snakes in 2003 is likely the result of long-term changes in prey populations rather than annual variation in response to environmental conditions.

Keywords: Body condition; Corticosterone; Brown tree snake

1. Introduction

The study and management of animal populations requires information about the factors affecting population dynamics. Information on the relative condition of individuals in a population over time is necessary to predict potential reproductive output or an impending increase or decline in numbers. Body condition, an important measure of the fitness of an animal, usually refers to the relative amount of energy stores compared to some measure of body size (Green, 2001). Energy stores can be allocated to maintenance, growth or to reproduction (Perrin and Sibly, 1993; Heino and Kaitala, 1999; Madsen and Shine, 2002), so a population with many animals in poor condition could indicate that individuals of reproductive size are not reproductively active and the population might be declining.

Male snakes generally invest little energy in their offspring, but the activities necessary to obtain matings (e.g. searching for mates, male–male combat) can be energetically expensive (e.g. Devine, 1984; Duvall et al., 1993; Bonnet and Naulleau, 1996; Shine and Mason, 2005). Although males in poor condition may be able to mate, they may be less able to search or compete for females (Aubret et al., 2002). Females of some species need an initial investment of energy for reproduction and may require several years to accumulate the necessary stores before they can reproduce (Aubret et al., 2002) while other species forage while

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they are reproducing (Naulleau and Bonnet, 1995). In all species, an adequate supply of food is crucial to provide the energy needed for reproduction.

The fat reserves, or condition, of an individual snake is usually estimated using the residuals from a regression of body mass on body length (e.g. Bonnet and Naulleau, 1996; Shine and Madsen, 1997; Moore et al., 2001; Aubret et al., 2002; Brown et al., 2002). However, because condition may vary heteroskedastically with body size, direct measurements of body fat are considered to be a more accurate measure of condition (Weatherhead and Brown, 1996). Even so, several studies have shown that only half of the variation in condition scores is due to variation in fat mass (Weatherhead and Brown, 1996; Madsen and Shine, 2002); much of the remaining variance may be due to energy storage in liver or muscle (Madsen and Shine, 2002).

Plasma concentrations of the steroid hormone corticosterone, the primary glucocorticoid in snakes, are also related to body condition. The elevated levels of corticosterone that are observed during times of stress produce physiological and behavioral changes, such as suppression of digestion and reproduction and mobilization of fat stores for energy (reviews by Greenberg and Wingfield, 1987; Guillette et al., 1995; Buchanan, 2000). High baseline levels of plasma glucocorticoids are often used as an indicator of chronic stress in a population and have been correlated with body condition (Romero and Wikelski, 2001); individuals with low body condition tend to have high levels of plasma corticosterone (Moore et al., 2000).

The brown tree snake (*Boiga irregularis*), a large arboreal member of the family Colubridae, is native to northern Australia and Papua New Guinea (Cogger, 1994). This species was accidentally brought to the island of Guam near the end of World War II and quickly spread throughout the island (Savidge, 1987). Ten species of forest birds and six species of lizards have been extirpated from the island mainly due to predation by this invasive snake (Rodda et al., 1999b). A survey of this population in 1992 and 1993 found that these snakes had highly elevated baseline concentrations of corticosterone and low body condition compared to captive snakes and brown tree snakes from the native range in eastern Australia (Moore et al., 2005). The conclusion of that study was that the snakes, having drastically reduced the larger-bodied bird and mammal prey on Guam, were food-stressed and possibly near starvation. In addition, very few snakes of reproductive size were reproductively active, another indication that this population was under chronic stress. We compared the body condition index and plasma corticosterone levels of brown tree snakes on Guam in 2003 to those collected in 1992/1993 to determine the relationship between fat mass, body condition and plasma corticosterone concentrations as indicators of physiological condition of individuals in the population, and to determine whether the poor body condition and chronic stress in 1992/1993 were present in 2003.

2. Methods

Free-living snakes on Guam were caught by hand at night from April to September 2003, and blood samples (300 μl) were collected within 3 min of capture from the caudal vein using a heparinized 1-cm^3 syringe and 25-g needle. All blood samples were placed in a cooler with an ice pack until return to the field laboratory, centrifuged and the plasma removed. Plasma was stored at −20 °C until the samples could be shipped to Oregon State University and once there, stored at −70 °C until assayed. Mass (g) and snout-vent length (SVL) (cm) were recorded, and after the snakes were sacrificed the fat bodies were weighed to the nearest 0.01 g. The amount of fat in each snake was converted to a percentage of the total body weight.

Plasma corticosterone levels for snakes collected between 1991 and 1993 were collected using similar methods (Moore et al., 2005). The SVL and mass for snakes measured from April to September 1992 and 1993 were added to the 2003 data to generate the body condition index (BCI) of each individual as an estimate of the energy stores or fat reserves.

The BCI of each individual was calculated as the residual score from the general linear regression of ln-transformed mass against ln-transformed SVL. In other words, a snake that weighs more than predicted for its length will have a positive residual and be regarded as being in relatively good condition (Weatherhead and Brown, 1996). The data set was then divided into three groups; snakes 90 cm SVL and greater (males and females), and those less than 90 cm SVL (juveniles) as the approximate size where brown tree snakes undergo an ontogenetic shift in diet from small ectothermic to larger endothermic prey (Greene, 1989). The combined data set consisted of a total of 129 juveniles, 154 females and 105 males (Table 1).

The measurements for the snakes from the 2003 Guam sample were combined with those of brown tree snakes from a variety of locations in Australia (data from Moore et al., 2005). A second set of BCI were calculated for the individuals in this data set to directly compare the body condition of the snakes captured in 2003 on Guam to that of snakes from the native range. Only males with 100–142 cm SVL and females with 100–120 cm SVL were used for this calculation, in order to match the range of SVL from both data sets.

2.1. Radioimmunoassay

Plasma levels of corticosterone were determined using radioimmunoassay following the procedure described by Moore et al. (2000). Briefly, plasma volumes of 4–200 μl were equilibrated overnight with tritiated corticosterone (Amersham). Each sample was extracted twice in 2 ml diethyl ether, and dried in a warm water bath under a stream of nitrogen gas. The

Table 1
Mean snout-vent length and mass (and ranges) of brown tree snakes measured during three sampling years on Guam, and a sample from Australia

	N	SVL (cm)	Mass (g)
1992			
Juvenile	37	76.9 (46.0–89.0)	38.4 (12.0–73.0)
Male	36	106.5 (90.0–130.0)	109.5 (30.0–280.0)
Female	74	104.4 (90.0–120.0)	95.9 (30.0–185.0)
1993			
Juvenile	18	72.4 (60.0–81.0)	28.7 (16.0–46.0)
Male	31	104.5 (90.0–162.0)	124.9 (45.0–1101.5)
Female	45	103.9 (90.0–120.0)	104.4 (45.0–283.0)
2003			
Juvenile	74	73.9 (57.0–89.5)	36.7 (17.5–68.4)
Male	38	104.9 (91.0–142.0)	124.9 (55.4–510.0)
Female	35	99.5 (90.0–119.0)	102.5 (52.0–213.9)
Australia			
Male	25	123.4 (101.0–161.0)	321.9 (127.0–925.0)
Female	22	117.6 (99.5–144)	223.7 (129.0–487.0)

extracts were resuspended in 10% ethyl acetate in isooctane, and were chromatographed through individual Celite columns to separate the steroid fractions and neutral lipids. The purified elutes were dried and resuspended in buffer. For the assay, all samples, including serial dilutions and 100% bounds, were incubated overnight with 100 μl of corticosterone antibody (B3-163 from Esoterix Endocrinology) and 100 μl of tritiated steroid. Unbound steroid was separated using dextran-coated charcoal and the bound steroid decanted into scintillation vials, resuspended in 3.5 ml scintillation fluid, incubated for 12 h and counted on a Beckman LS1800 scintillation counter. Intraassay variation was 15% and interassay variation was 18%. The limit of detection for corticosterone was ~0.04 ng/ml. Although the 1992/1993 samples and the 2003 samples were not assayed together, they were assayed in the same laboratory using similar methods and protocols.

2.2. Statistics

Two-way ANOVAs, with group and year as the factors, were used to examine BCI between years and groups, and pairwise multiple comparisons using the Tukey test were used to find the sources of variation. A two-way ANOVA, with year and group as the factors, was used to compare corticosterone levels. Spearman Rank Order correlation was used to test for correlations between BCI, corticosterone levels, percent fat and date of sample. All statistical analyses were performed using Jandel SigmaStat version 3.1 software package (Jandel Corporation). Analyses were considered statistically significant when $p < 0.05$.

3. Results

Body condition of brown tree snakes on Guam varied significantly among years ($F = 18.346$, $p < 0.001$) and among groups ($F = 3.168$, $p = 0.043$). There was no statistically significant interaction between years and groups ($F = 2.092$, $p = 0.081$).

Adult female BCI differed from all juveniles in 1992 ($p = 0.003$), 1993 ($p < 0.001$) and 2003 ($p < 0.001$), while adult male BCI differed from all juveniles in 1993 ($p = 0.002$) and 2003 ($p < 0.001$), but not in 1992 ($p = 0.178$). Male and female BCI did not differ ($p = 0.223$). Males had significantly different BCI between 2003 and 1992 ($p < 0.001$) and 2003 and 1993 ($p = 0.006$), but not between 1993 and 1992 ($p = 0.405$). Female BCI was significantly different between 2003 and 1992 ($p = 0.016$), but not between 2003 and 1993 ($p = 0.188$) or 1992 and 1993 ($p = 0.3$). Juvenile BCI was not significantly different between any of the three years (Fig. 1).

Corticosterone concentrations were significantly different among years ($F = 73.319$, $p < 0.001$) but not between groups ($F = 2.412$, $p = 0.092$). Corticosterone levels were significantly different between 2003 and 1993 ($p < 0.001$) and between 2003 and 1992 ($p < 0.001$), but not between 1992 and 1993 ($p = 0.999$) (Fig. 2).

Body condition was significantly correlated to corticosterone ($r = -0.447$, $p < 0.0001$). Body condition in 2003 was also significantly correlated to percent fat in females ($r = 0.481$, $p < 0.0001$) and males ($r = 0.419$, $p < 0.0001$), and had a significant negative correlation with date for both females ($r = -0.342$, $p = 0.0069$) and males ($r = -0.450$, $p < 0.0001$).

Body condition differed significantly between the 2003 Guam sample and the sample from Australia, for snakes 100 cm SVL and greater ($F = 20.337$, $p < 0.001$) (Fig. 3). There was no significant difference between male and female BCI ($F = 0.151$, $p = 0.699$).

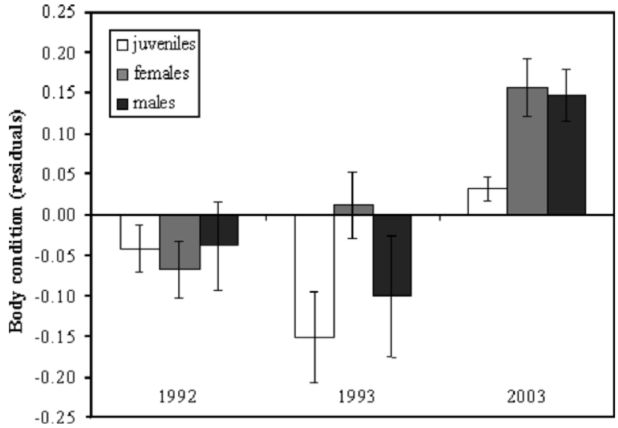

Fig. 1. Body condition of free-living male, female and juvenile brown tree snakes on Guam in 1992, 1993 and 2003. Bars represent means and standard errors.

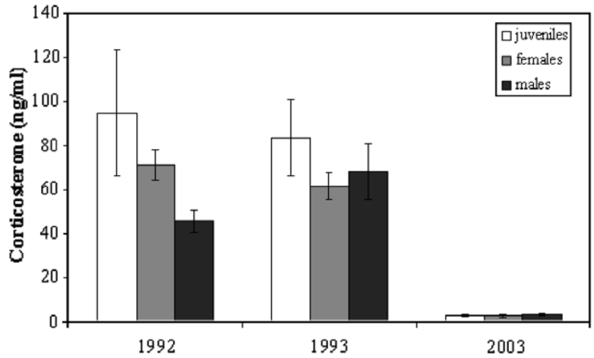

Fig. 2. Plasma levels of corticosterone for juvenile, female and male brown tree snakes sampled in different years on Guam. Bars represent means and standard errors.

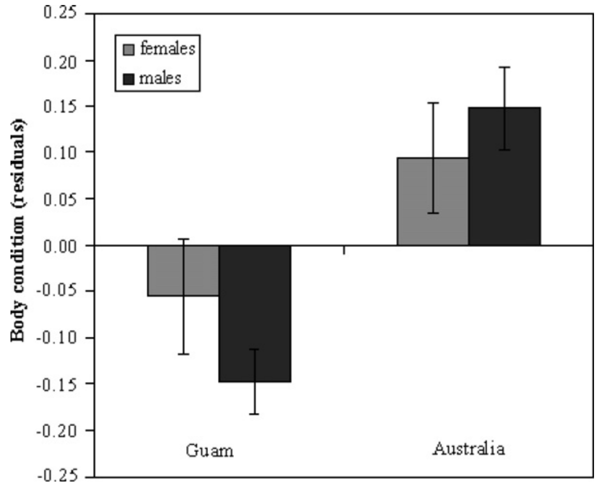

Fig. 3. Body condition of free-living male and female brown tree snakes at least 100 cm SVL, from Guam in 2003 and from Australia. Bars represent means and standard errors.

4. Discussion

Body condition of mature brown tree snakes on Guam was significantly greater in 2003 than in 1992 and 1993; juvenile body condition also improved, but not significantly. Brown tree snakes in Australia show a shift in prey preference at around 80–90 cm SVL, where larger snakes eat more endothermic prey (birds and mammals) and fewer ectothermic prey (lizards and frogs) than smaller snakes (Greene, 1989). On Guam, medium to large snakes originally preyed on birds and small mammals, while small to medium snakes ate small lizards (Savidge, 1988). Much of the larger, endothermic prey species became scarce or have completely disappeared, so adult snakes now subsist on small lizards (Rodda et al., 1999a) and some of the introduced species of birds and small mammals (Rodda et al., 1999b). The change in BCI between years suggests a change in prey availability, although it is uncertain whether the increase was in endothermic prey species or lizards. The slight increase in juvenile BCI could indicate that their access to food species did not improve as greatly as it did for adults. Adult snakes with their larger gape would be able to manage a wider range of prey types than small snakes and would be better able to take advantage of an increase or change in prey type. Alternatively, juveniles could have benefited from the increase in prey as much as the adults, but allocated much of that extra energy to growth (i.e. length) instead of to accumulating fat stores or for reproductive effort (Madsen and Shine, 2002).

The body condition index, while a good estimator of relative condition, is more informative when paired with additive indicators (Weatherhead and Brown, 1996), such as corticosterone concentrations or fat body measurements. Baseline levels of plasma corticosterone were significantly lower in 2003 than in 1992/1993 for all three groups of snakes, and there was a significant negative correlation between body condition and corticosterone. This decrease in corticosterone and increase in body condition indicates that food was more available in 2003 and that the snakes were not food-stressed. Although the increase in juvenile body condition from the earlier sample was not significant, corticosterone levels of juveniles were very low in 2003. This observation lends credence to the idea that the slight increase in juvenile body condition, while mature snakes showed a significant improvement, was due to differences in energy allocation between juveniles and adults rather than a disparity in prey availability.

Brown tree snakes might not achieve high body condition scores relative to other species, as they are arboreal snakes that benefit from having long, slender bodies and probably do not ever accumulate large reserves of fat (Lillywhite and Henderson, 1993; Naulleau and Bonnet, 1995). Females of another species of semi-arboreal snake regularly initiated vitellogenesis with few body reserves, and instead relied on active foraging to provide energy for reproduction (Naulleau and Bonnet, 1995). The maximum amount of fat found in those snakes was no more than 4% of the total body mass (Naulleau and Bonnet, 1995); brown tree snakes in 2003 had fat bodies weighing up to 10% of the total body mass, although most were in the 4–6% range. It might not take much extra food to increase the body condition of a brown tree snake from the near-starvation conditions in 1993 to the more robust snakes in 2003. However, the 2003 snakes, although relatively robust and with low levels of corticosterone, had significantly lower body condition scores than a sample of brown tree snakes from the native range in Australia. The Australian snakes were collected from a variety of locations over several decades (1950–1993) (Bull et al., 1997), but it appears that brown tree snakes in the wild are capable of even greater masses than those recorded for snakes in 2003 on Guam. To fully understand this difference in body condition between the native and the introduced snakes, we must compare relative fat mass and corticosterone concentrations of brown tree snakes from Guam and tropical Australia collected during the same period of time.

The condition of snakes captured in 2003 declined from April to September, indicating a relationship between food availability or energy expenditure and seasonally variable environmental conditions. Weather on Guam is affected by the El Niño/Southern Oscillation (ENSO), which causes an exceptionally arid and extended dry season around once every four years on Guam (Lander, 1994). The dry seasons preceding the three sampling years were all moderate El Niño years, but 1992 was the second El Niño year in a row and had lower than average rainfall in the dry season (Fig. 4); the following year had the lowest BCI for juveniles and males. Habitats in northern Australia have high temporal variation in prey availability due to the ENSO (Madsen and Shine, 2002), and filesnakes in these habitats show significant annual variation in body condition that is correlated to prey availability and rainfall (Madsen and Shine, 2000). When the amount of precipitation in the wet season prior to each year of sampling is compared to the average monthly rainfall over the last half-century, it is apparent that 2002 had a very rainy, extended wet season (due to Typhoon Chata'an in July and Supertyphoon Pongsona in December) (Fig. 4). Environmental conditions can vary dramatically from year to year, and it appears that the condition of the snakes varies widely as well. It could be that the increase in condition of brown tree snakes on Guam in 2003 was a result of the unusually extended wet season the previous year, and not an indication of a long-term shift in prey populations.

On the other hand, it seems likely that the environment on Guam has changed over the last decade. There was a sharp decline in body condition of brown tree snakes on Guam from 1985 to the late 1990s (Wiles et al., 2003), but free-ranging snakes sampled in July of 2000 had low baseline plasma corticosterone levels (5–10 ng/ml) (Mathies et al., 2001) compared to those in 1992/1993 (average $\sim$ 60 ng/ml). The wet season prior to the 2000 sample was drier than average, in contrast to the wet season preceding the 2003 sample (Fig. 4). It is possible that

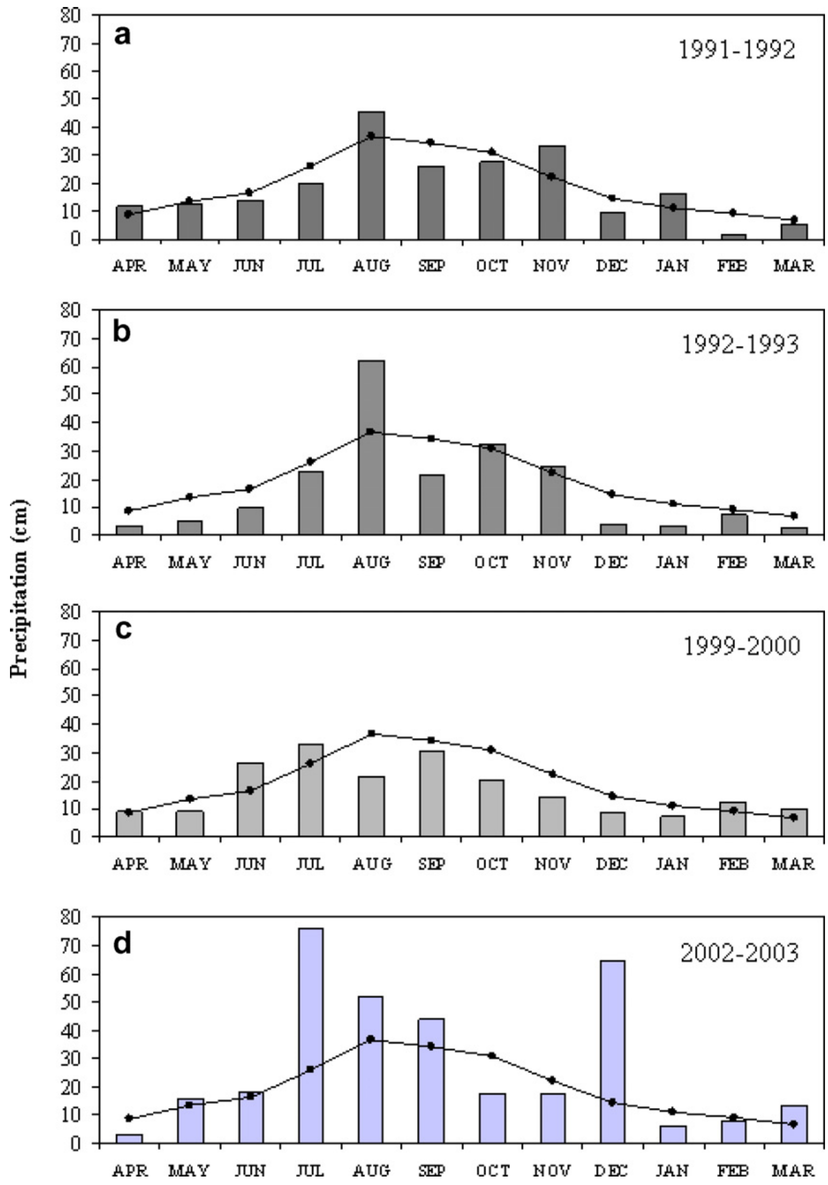

Fig. 4. Rainfall totals for each month in the years immediately preceding the three sampling years analyzed in this study, (a) 1992, (b) 1993 and (d) 2003 and (c) the sample taken in 2000 (Mathies et al., 2001). The line in each graph is the average total rainfall on Guam for each month between 1948 and 2004. The graph starts with the end of the dry season preceding the sample year (e.g. April 1991–March 1992).

either the population has now reached a point where it is better able to exploit the resources at hand (fewer large snakes competing for preferred prey), or a new food source is available on Guam and the snakes are taking advantage of an expanded prey base. For example, only two amphibian species were known to be breeding on Guam in the early 1990s, the poisonous Cane Toad (*Bufo marinus*) and the Dwarf Treefrog (*Litoria fallax*). The recent introduction of several additional frog species (including *Eleutherodactylus planirostris* and *Rana guentheri*) will likely provide the snakes with a new food source available to both juveniles and adults (Christy et al., 2007).

Weatherhead and Brown (1996) concluded that direct measurement of the condition of an individual is more accurate than an estimation using a body condition index. We found that the combination of corticosterone concentrations and fat mass as measures of condition with residuals from a regression of body mass on body length was much more informative than any one measure alone. The question of whether or not there has been a long-term improvement in body condition of brown tree snakes has important implications for management of this species on Guam. If the prey population has indeed changed to provide sufficient energy resources for the snakes to reproduce, brown tree snakes will become more numerous. Growth of the brown tree snake population will compromise efforts to reintroduce extirpated species on Guam, and will increase the potential for snake dispersal to other locations through airlines and cargo ships. Snakes that are in better condition may not be as likely to enter food-based traps, so monitoring and eradication programs will be somewhat less effective. The effect of annual variation in rainfall on the population dynamics of prey species should be monitored, as well as the relative condition of brown tree snakes from year to year, to predict changes in the snake population.

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