Prey preparation as a way that grasshopper sparrows (*Ammodramus savannarum*) increase the nutrient concentration of their prey

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Grasshopper sparrows (*Ammodramus savannarum*) facultatively prepare their grasshopper prey. A variable number of prey parts are removed before the remainder is swallowed whole. Previous work demonstrated that the sparrows optimally adjust preparation times to maximize the rate of nutrient intake. Here I explore what the sparrows do during these variable bouts of preparation time; i.e., by what criteria are some parts removed and others left behind? I compare two hypotheses. The width-reduction hypothesis posits that prey preparation increases the ability to swallow prey. The nutrient concentration hypothesis posits that prey part removal maximizes the rate at which nutrients are concentrated in the remaining prey. Prey parts differ widely in quality as determined by these hypotheses. Three grasshopper types across a range of sizes showed qualitatively the same pattern: highest removal rates for hind tibiae and wings, intermediate removal rates for legs, and low removal rates for head, thorax, and femora. Preparation tactics of insectivores and frugivores suggest that nutrient concentration is a common function of prey preparation. *[Behav Ecol 1991;2:234–241]*

Foraging decisions are typically considered as parts of a hierarchy (Tinbergen, 1981). Foragers must choose among habitats (Fretwell and Lucas, 1970; Rosenzweig, 1981), patches within habitats (Charnov, 1976), and prey within patches (Pulliam, 1974; also see Stephens and Krebs, 1986). Yet, once prey are captured, the forager often still has decisions to make.

First, the consumer must decide how much time to spend handling prey. Time spent handling prey is typically unavailable to search for more prey (Kaspari, 1990; Sih, 1980). However, decreased encounter rates may be offset by increased tissue recovery from the prey (Cook and Cockrell, 1978; Sih, 1980) or the removal of low-quality or deleterious prey parts (Davies, 1977; Sherry and McDade, 1982). For example, grasshopper sparrows (*Ammodramus savannarum*) facing decreased gut volumes and/or increased encounter rates optimally increase preparation time, removing more prey parts in the process (Kaspari, 1990).

A second decision is less explored: Which parts should be consumed and which should be left behind? Continuous ingesters (e.g., browsers: Harvel, 1984; sucking predators: Haynes and Sisojevic, 1966; and large carnivores: Kruuk, 1972; Schaller, 1972) are characterized by protracted, piecemeal ingestion of prey and often serially consume prey parts in a stereotyped fashion. Discontinuous ingesters, in contrast, swallow prey whole after varying amounts of preparation. This preparation, best documented in insectivorous birds (Kaspari, 1990; Krebs, 1980; Zach and Falls, 1978), typically involves removal of a varying number of prey parts.

In this paper, I explore the criteria by which some portions of a prey are removed (henceforth "the parts") and others left behind and swallowed (collectively, "the carcass"). I generate and test two hypotheses of prey-part ranking for a discontinuous ingester, the grasshopper sparrow (sF. Emberizinae) feeding on grasshoppers (O. Orthoptera, F. Acrididae). Grasshopper sparrows are small (approximately 17 g) emberizine finches that forage on the ground and include a large portion of grasshoppers in their diet (Kaspari, in press).

Grasshopper sparrows typically dismember grasshoppers in the field before consumption or feeding nestlings (Kaspari M, unpublished data). Upon capture, the sparrows first pinch the grasshopper's thorax, stunning the grasshopper, which then falls on its side. Individual parts are then grasped and vigorously shaken until detached. The part is dropped, and either a new part is selected or the remaining carcass is swallowed, head first. Parts are typ-

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Received 17 September 1990
Revised 5 March 1991
Second revision 23 April 1991
Accepted 25 April 1991
1045-2249/91/$4.00

ically removed in homologous pairs (e.g., both midlegs followed by both forelegs).

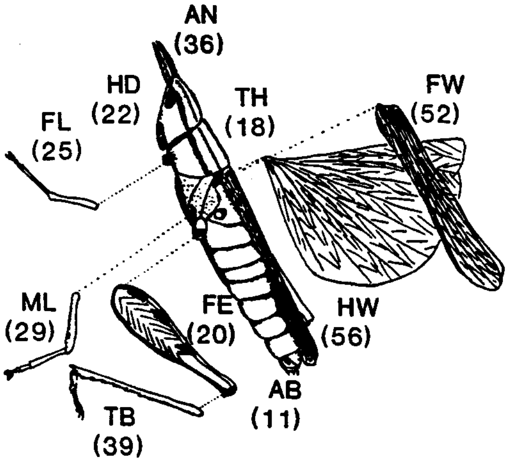

Figure 1
An "exploded" view of a female *Amphitornus coloradus.* Numbers in parentheses are the percentage chitin found in each part. Two-letter abbreviations for each part are as follows: AN = antenna, HD = head, TH = thorax, AB = abdomen, FE = femur, TB = tibiae, ML = midleg, FL = foreleg, FW = forewing, HW = hind wing. The grasshopper is approximately 2 cm in length.

The sparrows remove a variety of grasshopper parts: antennae, head, thorax, forelegs, midlegs, hind femora, and hind tibiae (Figure 1). The abdomen, which is lowest in chitin concentration and often contains fatty varioles, is invariably consumed. Some parts can be removed in groups. The antennae can be removed separately or by removing the head; the tibiae can be removed separately or with the femur. The thorax is rarely removed and then only after the head has first been detached.

Prey preparation can be costly to grasshopper sparrows beyond the time taken away from searching for more prey. When vigorously shaken, the carcass often flies off some distance into the grass, and must be relocated. Sparrows close their eyes when shaking off parts, potentially increasing risk of predation by northern harriers (*Circus cyaneus*). Finally, preparing rather than immediately swallowing prey increases the risk that the prey might be stolen by other foraging birds (Kaspari M, personal observation; see also Barnard and Stephens, 1981). Thus, without some accompanying benefit to prey-part removal; one would expect sparrows to swallow prey whole, a behavior observed only at low encounter rates or in very hungry birds (Kaspari, 1990).

The width reduction hypothesis

Many discontinuous ingesters are gape limited (Hespenheide, 1973). Spines and other structures increase a prey's absolute size along one axis, decreasing its ingestibility (Brooks and Dodson, 1965; Kerfoot, 1977; Vermeij, 1987). A predator can counter this defense via preparation, removing or breaking parts and decreasing the prey's width (by width I refer to the maximum cross-sectional diameter orthogonal to the long axis of the prey). For example, roadrunners (*Geococcyx californianus*) beat large mice (*Mus musculus*) before consumption, fracturing the pelvic and pectoral girdles (Beal and Gillam, 1979). Neotropical hover-gleaning birds beat a variety of insects, fracturing the spines and exoskeletons of the prey (Sherry and McDade, 1982).

Even when prey are small enough to swallow whole, part removal may reduce ingestion time or make swallowing large prey less risky. Choking among discontinuous ingesters (e.g., fish: Hobson and Chess, 1978; little grebes, *Podiceps ruficollis*: Bell, 1968) is a risk when consuming large prey. In the grasshopper sparrow, preparation decreases the ingestion time for larger, but not for smaller, grasshoppers (Kaspari, 1990).

The width reduction hypothesis assumes that parts differ in the width contributed to the prey and that decreasing the width of large prey is beneficial in at least one of the above ways. The width reduction hypothesis predicts that parts contributing most to prey width should be more frequently removed. Because larger prey are more likely to occlude the throat, part removal according to width should be more likely as prey size increases.

The nutrient concentration hypothesis

The gut-energy maximization model (Kaspari, 1990) posits that prey preparation is a compromise between maintaining encounter rates with future prey and maximizing the amount of prey that can be consumed within a foraging bout. The nutrient concentration hypothesis follows from the model's assumption that preparation, by removing parts high in indigestible bulk, concentrates the prey's nutrients while freeing up room in the gut for more prey. Some frugivores, for example, mash out seeds of fruits before ingesting the pulp (Foster, 1987; Levey, 1987). Ovenbirds remove chitinous legs and elytra before swallowing beetles (Zach and Falls, 1978).

The nutrient concentration hypothesis assumes that the forager monitors three parameters for each part: nutritive mass, bulk mass, and removal time. It assumes a strategy of maximizing the rate of nutrient concentration in the carcass, and it predicts that parts which concentrate nutrients in the carcass most quickly will be removed more frequently.

METHODS

Ranking parts according to width

I used grasshoppers of three sizes, all from the subfamily Gomphocerinae and representing a size gradient within one general body shape (see Otte, 1981). These grasshoppers were *Amphitornus coloradus* males (0.047 g) and

Table 1
Mean chitin weight (mg) and percent chitin for parts of three grasshopper sizes

	Grasshopper size											
	Small				Intermediate				Large			
Part	*n*	Mean chitin	SD	%	*n*	Mean chitin	SD	%	*n*	Mean chitin	SD	%
Abdomen	7	3.17	0.72	14.1	8	5.38	1.54	10.9	8	9.40	1.21	10.1
Antenna	3	0.10	0.05	30.9	8	0.08	0.03	35.8	8	0.37	0.12	42.0
Femur	7	2.20	0.18	20.6	8	2.84	0.69	19.6	8	6.36	0.77	22.4
Foreleg	8	0.33	0.17	41.3	8	0.29	0.09	25.2	8	0.72	0.19	33.0
Forewing	8	0.60	0.22	46.9	7	1.01	0.39	52.4	8	1.25	0.51	36.0
Head	8	2.71	0.57	24.1	8	4.60	1.30	22.0	8	8.62	3.00	24.3
Hind wing	7	0.64	0.16	61.6	7	0.87	0.17	56.1	8	1.75	0.51	51.5
Midleg	8	0.31	0.10	26.7	8	0.40	0.22	28.9	7	0.87	0.24	28.5
Thorax	8	0.55	0.37	25.1	8	0.80	0.24	17.9	8	1.48	0.32	21.7
Tibiae	7	0.76	0.36	53.3	8	1.01	0.24	38.8	8	3.26	1.17	57.6

females (0.087 g) and *Mermiria bivitatta* females (0.14 g). *Mermiria* is the largest grasshopper species commonly swallowed whole by the grasshopper sparrow on Arapaho Prairie (Kaspari, 1990). This range of prey sizes corresponds to that commonly consumed by the sparrow. It also allowed me to test the prediction that contribution to width is a more important ranking criterion with increasing prey size.

I measured each part's contribution to prey width by observing eight individuals of each grasshopper size head-on under a dissecting microscope equipped with a micrometer. Appendages were gently laid backward with a probe until the part resisted. I then measured the perpendicular distance of the most distal portion of the part from the maximum abdomen width.

Ranking parts by rate of nutrient concentration

Chitin weight for eight samples of each part (Figure 1) was calculated by freeze drying, weighing, immersing the parts in 2 M KOH for 2 days, rinsing in tap water, freeze drying, and reweighing on the same balance. KOH dissolves all tissue except chitin (Zach and Falls, 1978), which in birds is indigestible or poorly digested (Karasov, in press; Scott et al., 1976). I assume that whatever is left behind is indigestible bulk and what was dissolved had some nutritional value.

I recorded removal times (seconds, measured from the time a part is grasped until it detaches from the rest of the grasshopper) from audio tapes of feeding trials (see below). I used five grasshopper sparrows to generate removal times. This was judged an adequate sample size because a previous study (Kaspari, 1990) found no between-bird differences in grasshopper handling times. I measured removal times for up to 10 parts per individual sparrow, although some parts are less frequently removed (e.g., thorax or head, see Results), and sample sizes for these parts are correspondingly smaller.

For the nutrient concentration hypothesis, I first calculated the difference in nutrient concentration when a class of parts (e.g., two hind tibiae) was removed from the grasshopper, using values from Table 1. The parts were then ranked by the quotient of this value and the mean removal time of that part for each sparrow measured. Thus, this protocol resulted in five estimates (one per sparrow) of nutrient concentration rates for each class of part.

How grasshopper sparrows rank parts

This study used sparrows from Arapaho Prairie, 2 ha of Sand Hills prairie in west central Nebraska, USA (41.5° N, 102° W) in the summers of 1983 and 1984. Sparrows were mist netted on Arapaho Prairie, 56 km north of Cedar Point Biology Station, transported back to the station, and kept in 1 × 1 × 0.3-m cages, where they were fed grasshoppers and watered ad libitum. The sparrows were allowed 2–3 days to acclimate to the cages, but were typically eating within 2 h.

Before a feeding trial, sparrows were deprived of food for 2 h. Individual grasshoppers were then dropped into the cage with the sparrow either one after the other until the bird was sated or at periodic intervals of one grasshopper per 10, 20, or 30 min for 2 h (Kaspari, 1990). Both procedures assured that the sparrows were exposed to widely varying degrees of gut fullness and perceived presentation rates, which in turn caused them to prepare some grasshoppers little and some grasshoppers a lot. I observed the sparrows from behind a one-way mirror, recorded the parts removed on audio tape, and later transcribed the tapes. After approximately 7 days,

Table 2
Maximum width (mm) contributed by parts compared with width of the abdomen

	Grasshopper size[a]		
	Small	Intermediate	Large
Part[b]	Mean (SD)	Mean (SD)	Mean (SD)
Abdomen	4.98 (0.27)	5.48 (0.09)	7.12 (0.44)
Antenna	0.18 (0.01)†‡	0.16 (0.02)†	0.27 (0.07)*†
Femur	0.29 (0.25)*†‡	0.46 (0.19)*	0.62 (0.44)*†
Foreleg	0.78 (0.62)*†	0.03 (0.06)†	0.67 (0.53)*†
Head	0.07 (0.15)‡	0.13 (0.14)†	0.09 (0.24)†
Midleg	0.90 (0.67)*	0.47 (0.35)*	0.87 (0.44)*

[a] Sample size is eight per grasshopper size. Means of paired homologous parts (e.g., midlegs, forelegs) are the sum of both parts. Values in a column with the same symbols (*, †, ‡) indicate that the corresponding parts do not differ significantly (Tukey's test) for that grasshopper size.

[b] Tibiae, forewing, hind wing, and thorax do not measurably contribute to the width of the grasshopper.

sparrows were released back on Arapaho Prairie.

In this study, I compare the sparrow's consumption frequencies for each part with those predicted by the two hypotheses. I calculated mean consumption frequencies from a minimum sample size of 10 grasshoppers per individual sparrow (for the two smaller sizes) and three grasshoppers per sparrow (for the larger *Mermiria*, which sated birds more quickly in a feeding trial). Five sparrows met this sample-size criterion for each grasshopper size. Eight of the 11 individual sparrows used had the requisite sample sizes for only 1 grasshopper size.

Statistics

Prey-part rankings were generated using Tukey's multiple comparison test, producing statistical clusters of parts. These clusters constitute the predicted performances of the sparrows under each hypothesis–grasshopper-size combination. I evaluated between-bird and between-grasshopper size similarity in consumption frequencies using Kendall's measure of concordance.

For each sparrow I calculated each part's mean consumption frequency to estimate the sparrow's prey part preferences. A Tukey's multiple comparison test clustered parts by similar consumption frequencies. These clusters were compared to the ranking cluster generated by each hypothesis. All tests were two-tailed, and p-values were set at .05.

RESULTS

Ranking by width

In all three grasshopper sizes, the midlegs contributed most to prey width. In two of three sizes, the head contributed least to width (Table 2). The grasshopper sizes differed in the relative contribution of forelegs to prey width: the foreleg ranked last in the intermediate-size grasshopper, and second in the smallest and largest. In all cases, the tibiae, thorax, forewings, and hindwings did not measurably exceed the width of the abdomen.

The width model thus predicts that the midleg should be removed before the head for all three grasshopper sizes. It also predicts that the hind tibiae, wings, and thorax should not be removed.

Ranking by nutrient concentration

Part removal times were typically small across all grasshopper sizes, averaging less than 2 s for all parts but the head. Removal times for each part were log-transformed and analyzed with a two-way ANOVA, examining between-bird variance across the three sizes of grasshoppers (Table 3). Only forewing removal times showed differences between birds ($p <$ .0001). Despite a difference in dry weights from 0.047 to 0.14 g, only hind tibia removal times varied between three grasshopper sizes ($p <$ .0275) and were highest for the intermediate-size grasshopper. Values for chitin weight and chitin percentage are reported in Table 1.

Nutrients are most quickly concentrated in all three grasshopper sizes by the removal of the hind tibiae and least quickly concentrated by the removal of the femora and head. Concentration rates varied over an order of magnitude (Table 4). For the small and intermediate grasshopper size, the femora have a sufficiently high nutrient concentration that their removal actually decreases the nutrient concentration of the residual prey. This is not true for the largest grasshopper. Across all grasshopper sizes, the nutrient concentration hypothesis predicts that hind tibiae should be removed before the midlegs and forelegs, head, and femora.

Table 3

Removal times (s) of parts for three grasshopper sizes

	Grasshopper size					
	Small		Intermediate		Large	
Part	*n*	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Antenna	12	0.89 (0.33)	20	0.74 (0.33)	8	1.86 (2.57)
Femur	40	1.07 (1.62)	42	1.25 (1.11)	27	1.07 (0.62)
Foreleg	27	1.37 (1.01)	42	1.13 (0.75)	25	1.07 (0.67)
Forewing**	36	1.89 (1.10)	41	1.82 (1.01)	27	1.89 (1.58)
Head	2	3.37 (0.30)	13	5.94 (3.80)	12	7.26 (7.62)
Hind wing	30	1.56 (0.90)	39	1.45 (1.18)	27	1.40 (0.96)
Midleg	34	1.23 (1.13)	42	1.11 (0.83)	31	1.25 (0.87)
Tibiae*	45	0.82 (0.45)	48	1.23 (0.90)	30	0.81 (0.31)

* Significant between-bird differences ($p < .0001$).

** Significant between-grasshopper size differences ($p < .0275$).

How the sparrows ranked parts

The five sparrows consuming each grasshopper size consumed parts in similar frequencies (Kendall's $W = 0.34$, $p < .1$ for the smallest grasshopper size; $W = 0.79$, $p < .005$ for the intermediate size; $W = 0.52$, $p < .01$ for the largest). Much of the residual variance appears due to the variable magnitude of preparation (i.e., some sparrows tended to remove more parts on average, others less) rather than differences in ranking per se.

For each grasshopper size, some parts were consumed more than others (all three ANOVA's $p < .0001$). Tukey comparisons yielded two or three clusters of consumption frequencies (Table 5). For the small grasshopper, tibiae and forewings were removed >25% of the time compared to the thorax, midlegs, femora, and head, which were rarely removed. The intermediate grasshopper showed 50% removal frequencies for tibiae and hindwing compared to <15% removal of the remaining legs, head, and thorax. The large grasshopper showed the least distinct clusters (likely due to the smaller sample sizes) and highest overall level of preparation. The tibiae were removed in 80% of the foraging bouts compared to the head and femora, which were removed <30% of the time.

Table 4

Rate of percentage increase (%/s) in nutrient concentration resulting from part removal

	Grasshopper size[a]					
	Small		Intermediate		Large	
Part	*n*[b]	Mean (SD)	*n*	Mean (SD)	*n*	Mean (SD)
Antenna	2	0.0005†‡ (0.0001)		—		—
Femur	4	−0.0066 (0.0024)	5	−0.0001† (0.0000)	4	0.0004†‡ (0.0023)
Foreleg	4	0.0022†‡ (0.0013)	5	0.0005† (0.0002)	5	0.0008‡§ (0.0001)
Forewing	4	0.0026†‡ (0.0006)	5	0.0034* (0.0007)	5	0.0015†‡§ (0.0008)
Head	1	−0.0001‡ (—)		—		—
Head + antenna		—	3	0.0009† (0.0002)	4	0.0020†‡ (0.0010)
Hind wing	4	0.0040† (0.0007)	5	0.0040* (0.0012)	5	0.0033† (0.0007)
Midleg	5	0.0006†‡ (0.0002)	5	0.0011† (0.0004)	5	0.0008‡§ (0.0001)
Thorax		—	1	0.0000† (—)	2	0.0000§ (0.0000)
Tibiae	5	0.0082 (0.0012)	5	0.0041* (0.0014)	5	0.0121 (0.0010)

[a] Means of paired homologous parts (e.g., midlegs, forelegs) are the sum of both parts. For intermediate and large grasshoppers, removing the head with the antennae attached yields higher rates of nutrient concentration than removing the antennae, then the head. Values in a column with the same symbols (*, †, ‡, §) indicate that the corresponding parts are not significantly different (Tukey's test) for that grasshopper size.

[b] Sample sizes represent the numbers of sparrows for which there are removal time values.

Table 5

Contrasting the predictions of three models of part ranking with the consumption frequencies of grasshopper sparrows[a]

	Grasshopper size		
	Small	Intermediate	Large
Width reduction	ML < AN,HD < TB,FW,HW,TH	ML,FE+TB < AN,HD,FL < TB,FW,HW,TH	ML < HD < TB,FW,HW,TH
Nutrient concentration	TB < HW < HD < FE	TB,HW,FW < ML,HD+AN,FL,TH,FE	TB < HW < ML,FL < TH
Observed	TB FW HW ML,TH,FL HD,AN FE	TB HW FW ML FL FE HD,AN TH	TB FW HW FL ML HD,AN FE TH
Frequency[b]	0.39 0.53 0.75 0.98 0.99 1.00	0.54 0.58 0.60 0.88 0.92 0.95 0.98 1.00	0.13 0.38 0.43 0.51 0.62 0.75 0.82 0.86

[a] Prey parts: AN = antenna, HD = head, TH = thorax, AB = abdomen, FE = femur, TB = tibiae, ML = midleg, FL = foreleg, HW = hindwing, FW = forewing.

[b] Lines group consumption frequencies that are not significantly different by Tukey's test.

Using the mean consumption frequencies of parts from each grasshopper size, Kendall's concordance was significant ($W = 0.837$, $p < .01$; Table 5). This suggests the same criteria were used to remove the prey parts of small and large grasshoppers.

Evaluating the hypotheses

The width reduction hypothesis posits that parts differ in their contribution to maximum prey width and that the widest parts are consumed least. A number of lines of evidence argue against this hypothesis (Table 5). First, all three sizes of grasshopper shared the prediction that the midleg should be consumed least frequently. However, the midleg is consumed significantly more frequently than three parts (tibiae, hindwings, forewings) in the two smaller grasshoppers and three times more frequently than the tibiae (.62 versus .13, nonsignificant) in the largest. Second, the forewings and hindwings were consistently removed from all three grasshopper sizes, yet do not measurably contribute to prey width. Third, the tibiae are removed distinct from the femur in the intermediate-size grasshopper, contrary to prediction. Finally, the width reduction hypothesis is no more supported for large prey than it is for smaller, more easily swallowed prey.

In contrast, the nutrient concentration hypothesis fared better (Table 5). This hypothesis predicts the preferential removal of parts that maximize the rate of nutrient concentration in the carcass. It successfully predicts that tibiae would be least consumed in all three grasshopper sizes. For the smaller grasshopper, it predicts the ranking of consumption frequencies (tibiae, hindwing, head, femur). In the intermediate-size grasshopper, it predicts the grouping of tibiae, hindwing, and forewing as less consumed than the other parts. Finally, in the larger grasshopper, the nutrient concentration hypothesis predicts the order of consumption frequencies (tibiae, hindwing, midleg, foreleg, thorax). In both the smaller grasshoppers, statistical resolution breaks down at higher consumption frequencies (e.g., >0.9).

DISCUSSION

Prey preparation is a conspicuous, stereotyped behavior in this and other studies (Kaspari, 1990; Krebs, 1980; Sherry and McDade, 1982; Zach and Falls, 1978). In each case, predators treat prey not as homogenous entities but as collections of parts of varying profitability. Furthermore, in all but the Sherry and McDade study (1982), prey preparation is facultative, with more parts removed as satiation and/or presentation rate increase. The present study is the first to explore in detail the criteria used to drop prey parts from the diet.

Grasshopper sparrows do not appear to selectively remove prey parts on the basis of their contribution to width. This is not to downplay width reduction as a benefit because grasshopper sparrows are able to consume some large prey only after preparation (Kaspari, 1990). However, the stereotyped prey-part removal shown here does not serve that function particularly well, and prey parts are removed from grasshoppers that could nonetheless be swallowed whole.

Instead, prey parts are more likely to be removed if, by their removal, they maximize the rate at which nutrients are concentrated in the remaining carcass. Such preparation is capable of increasing the nutrient concentration from a baseline of 77% for a small, whole grasshopper to 86% for the abdomen alone (and 79% to 90% for the largest grasshopper).

The nutrient concentration hypothesis is strengthened by two additional observations. When a femur—a relatively nutrient-rich

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