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NESTING BIOLOGY OF GRASSLAND BIRDS AT FORT CAMPBELL, KENTUCKY AND TENNESSEE

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ABSTRACT.—Grassland birds have experienced greater population declines than any other group of birds monitored by the North American Breeding Bird Survey. Our goal was to compare demographic rates among years within species and among species of grassland birds. Eight-hundred and eleven nests of Henslow's Sparrows (*Ammodramus henslowii*), Grasshopper Sparrows (*A. savannarum*), Field Sparrows (*Spizella pusilla*), Dickcissels (*Spiza americana*), and Eastern Meadowlarks (*Sturnella magna*) were monitored between 1999 and 2003. Mayfield nest success including the egg-laying stage, as well as the incubation and nestling periods, was 20, 34, 15, 20, and 18%, respectively. Most nest failures were attributed to predation. Nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) was infrequent (<2% of all nests parasitized). Clutch size decreased during the nesting season for Dickcissels, Grasshopper Sparrows, and Field Sparrows. Nesting phenology suggests the possibility of multiple-brooding for all five species in this study. *Received 21 February 2006. Accepted 14 April 2007.*

Grassland bird population declines have been attributed to the dramatic decrease of native grasslands during the 20th century because of clearing of non-forested land for agriculture or development, and discontinued use of prescribed fire (Askins 1993, Herkert et al. 1996, Peterjohn and Sauer 1999). Military lands in the eastern United States are an exception to the trend in loss of native grasslands. Some installations have maintained large areas of grasslands through use of prescribed burning and mowing to facilitate military training. For example, Fort Campbell Military Reservation in Kentucky and Tennessee, a 42,000-ha U.S. Army Base, has ~10,000 ha of grassland habitat including remnant patches of native grassland (Moss 2001). Several other military installations in the eastern United States including Fort Knox, Kentucky, Fort Bragg, North Carolina, and Fort Drum, New York, also have large areas of early-successional habitats (Eberly 2002).

It is important to understand not only the distribution of grassland bird species in the eastern United States, but also their productivity. Many studies report densities and diversity of bird species, but these measures may be misleading indicators of habitat quality or breeding success (Van Horne 1983, Vickery et al. 1992). Few studies have collected detailed demographic information needed to understand productivity (i.e., nesting success, clutch size) (Marzluff and Sallabanks 1998). Many grassland bird nests are difficult to find and monitor, and relatively few studies have attempted to monitor more than one to two species for more than a few years (Winter 1998). Managers of military installations need demographic information to understand if and how their management actions and military training may impact bird populations.

We monitored Henslow's Sparrow (*Ammodramus henslowii*), Grasshopper Sparrow (*A. savannarum*), Field Sparrow (*Spizella pusilla*), Dickcissel (*Spiza americana*) and Eastern Meadowlark (*Sturnella magna*) nests at Fort Campbell from 1999 through 2003. Our objectives were to obtain annual, species-specific demographic information including nest success, clutch size, young produced per successful nest, causes for nest failure, nest parasitism rates, timing of nest initiation, and seasonal clutch size variation, and to compare these demographic rates among years within species and among species.

METHODS

Study Area.—The study was conducted on Fort Campbell on the Kentucky-Tennessee

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border. Fort Campbell contains some of the largest remaining blocks of native prairie ''barrens'' east of the Mississippi River. Barrens are grass-dominated, treeless areas occurring on the hilly, karst topography of west-central Kentucky and northwestern Tennessee (Chester et al. 1997). Historically, these grasslands were maintained primarily through burning by native Americans (Delcourt et al. 1993). Many grasslands on Fort Campbell contain at least some native warm-season grasses including little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), Indian grass (*Sorghastrum nutans*), and broomsedge (*Andropogon virginicus*). Approximately 60% of the area is in oak (*Quercus* sp.)-hickory (*Carya* sp.) forests with many leased agricultural fields (cool-season grasses, corn, millet, and soybeans) interspersed among the grasslands. Most of the grassland areas monitored in this study were managed mainly for military training and not specifically for hay production.

Nest Searching.—We concentrated primarily on finding an adequate sample (~20) of nests each year for our five target species including Henslow's Sparrow, Grasshopper Sparrow, Dickcissel, Eastern Meadowlark, and Field Sparrow. Fields with appropriate grassland habitat, such as dead standing clumps of grass, were systematically searched by one crew leader and four field assistants for males of target species defending territories or exhibiting nesting behavior between 1 May and 31 July, 1999–2003. Fields were selected to provide the maximum opportunity to find a representative sample of nests for the more difficult species to monitor, especially Henslow's Sparrows. Most fields on Fort Campbell are burned every 1–3 years; thus, a different set of fields was searched each year allowing us to search in areas with dead standing vegetation that is not present the first year after a field is burned. Up to 20 fields were searched each year, but most nest searching was concentrated in a few larger fields (>150 ha) that provided habitat for all five species in all years. Field sizes ranged from 4 to 600 ha. Behavioral cues, such as birds flushing close to an observer, chipping, carrying nesting material, or carrying food or fecal sacs, were used to locate nest sites.

Once nests were located, a flag was placed at least 5 m from the nest and detailed maps of the nest locations were drawn. Nests were monitored every 2–4 days to ascertain nest fate. We calculated apparent yearly nest success (successful nests/total nests), Mayfield (1961, 1975) nest success, and standard error for individual species where sample sizes were sufficient (~9 nests, Johnson 1979).

Demographic Rate Estimates.—Average clutch size was calculated using the highest number of eggs or young for nests with a stable clutch size for two consecutive visits. Successful nests were defined as any nest fledging at least one host young. Nests with no exposure time (e.g., induced fledging when the nest was found) were not included in nest success calculations. We calculated daily survival rates and the probability of nesting success for five periods: egg laying, incubation, nestling, incubation and nestling combined, and all periods. The combined probability of nesting success during the incubation and nestling stages was calculated to facilitate comparison with studies that did not explicitly include the egg laying stage.

We used mean period lengths as exponents to calculate the probability of nest success from daily survival probabilities for each species. We rounded mean clutch size to the nearest half-egg for the mean number of days during the egg laying stage for each species. Generally, one egg is laid per day for the five target species until the clutch is completed with incubation starting with laying of the last egg. We used published values for mean number of days for the incubation and nestling stage (Ehrlich et al. 1988). The number of days in the incubation and nestling stages combined, and all stages combined was the sum of the appropriate number of days in the respective component stages. Mean and standard errors for daily survival probabilities, and mean nest success were calculated by nesting period and year for each species (Johnson 1979).

Statistical Analysis.—Yearly means of young per successful nest were compared within species using one-way ANOVA. Nest initiation dates were estimated to the day laying started by back dating from the day the nest was found. Average start and end dates of nest initiation were calculated by averaging the first and last 10% of all nests combined

TABLE 1. Demographic data for Henslow's Sparrow, Grasshopper Sparrow, Dickcissel, Eastern Meadowlark, and Field Sparrow at Fort Campbell, Kentucky, 1999–2003.

	Henslow's Sparrow (n = 113)[a]	Grasshopper Sparrow (n = 131)[a]	Dickcissel (n = 204)[a]	Eastern Meadowlark (n = 87)[a]	Field Sparrow (n = 276)[a]
Successful nests	65	85	87	36	126
Unknown fate	1	0	0	1	0
Failed nests	47	46	117	50	150
Depredated	44	38	97	45	139
Abandoned	3	3	9	2	7
Abandoned-parasitized	0	0	0	0	1
Mowing for hay	0	4	4	1	2
Military activity	0	1	3	0	0
Weather	0	0	4	2	1
Apparent nest success, %	58	65	43	41	46
Clutch size average (n)	4.1(108)	4.4(131)	4.3(191)	4.6(87)	3.6(264)
Hatching success, % (n)	90.4(80)	93.2(104)	90.3(116)	94.1(53)	95.9(171)
Young fledged/nest	2.2	2.6	1.7	1.7	1.6
Young fledged/successful nest	3.9	4.1	3.9	4.0	3.6
Parasitized nests	1	0	0	0	3

[a] n = number of nests.

for each species. We used the difference between start and end dates as a measure of the minimum window of time available for each species to initiate nesting (nest initiation window). We used linear regression to examine the relationship between clutch size and nest initiation dates. We used program CONTRAST (Sauer and Hines 1989) to test for differences among daily survival rates within species, comparing different nesting intervals, and among species. The level of significance was set at $\alpha = 0.05$ and we used a Bonferroni correction to adjust our level of significance for multiple tests (Zar 1998).

RESULTS

Eight-hundred and eleven nests were monitored between 1999 and 2003; apparent nest success ranged between 41 and 65% for each species (Table 1). Most nest failures were attributed to predation. The primary predators of nests appeared to be snakes based on numerous observations of snakes in nests. Other causes of nest failures included abandonment, hay mowing and harvesting, military training activities, and Brown-headed Cowbird (*Molothrus ater*) parasitism (Henslow's Sparrow = 1, Field Sparrow = 3; Table 1). Average clutch size ranged from 3.6 for Field Sparrows to 4.6 eggs for Eastern Meadowlarks. Hatching success ranged from 90% for Dickcissels and Henslow's Sparrows to 96% for Field Sparrows (Table 1). Average young fledged per nest ranged from 1.6 to 2.6, and the average number of young per successful nest ranged from 3.6 for Field Sparrows to 4.1 for Grasshopper Sparrows (Table 1).

Eastern Meadowlarks initiated nests earliest with average nest incubation starting on 16 April. Field Sparrow nest initiation started on 25 April followed by Henslow's Sparrows (27 Apr) and Grasshopper Sparrows (1 May). Dickcissels consistently were the last species to arrive and began incubation on 10 May. The average end of the nest initiation window was between 28 June and 4 July for all five species, but active nests were found through August for all species. The length of the nest initiation window was longest for Eastern Meadowlarks (75 days), intermediate for Henslow's Sparrows (63 days), Grasshopper Sparrows (64 days), and Field Sparrows (64 days) and shortest for Dickcissels (51 days).

Clutch size decreased during the nesting season for Dickcissels ($t = -6.19$, df = 190, $P < 0.001$), Grasshopper Sparrows ($t = -2.23$, df = 130, $P = 0.03$), and Field Sparrows ($t = -5.52$, df = 259, $P < 0.001$). On average, Dickcissel clutch size was reduced by one egg every 50 days, and Grasshopper Sparrow and Field Sparrow clutch sizes were reduced by 0.5 eggs every 62 and 52 days, respectively. We did not detect a linear decrease in clutch size during the nesting season

for Henslow's Sparrow ($t = -0.37$, df = 104, $P = 0.71$) and Eastern Meadowlark ($t = -0.94$, df = 85, $P = 0.35$). The clutch size for both Henslow's Sparrows and Eastern Meadowlarks initially increased, peaked in the middle of the season, and then gradually decreased.

Nesting success was generally greatest for nests found during the laying stage and least during the incubation stage. Combining nests found in all years, nesting success for Field Sparrows was lower than for Grasshopper Sparrows because of the difference in nest success during the incubation stage (Table 2). Nesting success varied among years, but we were unable to detect differences after Bonferroni correction (Table 3).

DISCUSSION

Overall mean nesting success rates (Mayfield 1975) were within the range of values previously reported for Henslow's Sparrows (27% [incubation and nestling stages only]; Table 4), and Dickcissels (26%). Eastern Meadowlark (22%) and Grasshopper Sparrow (41%) nesting success was near the high end of previously reported values (Table 4). Almost all nests of these four species were found in the largest fields (>150 ha). A few Henslow's Sparrow nests were found in fields as small as 4 ha, but these small fields were within 10 km of larger fields. Henslow's Sparrow densities were too low in small fields to allow for an adequate sample of nests each year. Field Sparrow nesting success was lower at Fort Campbell (20%) than previously reported (Table 4). Low nesting success may be related to the ubiquitous distribution of Field Sparrow nests in grassland fields, including some fields as small as 2 ha. Smaller fields had more habitat features that might attract potential predators (e.g., small trees for perch sites), possibly accounting for reduced nesting success rates (Herkert 1994).

Published nesting success rates usually do not include the egg laying stage. Between 6 and 36% of our nests, depending upon species and year, were found during the egg laying stage. This study is one of only a few that explicitly reports a daily survival rate of nests during the laying stage. We detected nest failures for three of the five species monitored during this short but critical part of the nesting cycle, resulting in estimates of nest success during the egg-laying stage of 65–79%. The egg laying stage should be treated separately from the incubation stage because incubation usually starts between laying the penultimate egg and up to a few days thereafter. Eggs usually are less conspicuous when the female is on the nest during incubation, reducing the probability predators will find the nest through visual cues. Exposed eggs during the laying stage may be more vulnerable to predators such as common raccoons (*Procyon lotor*) or Blue Jays (*Cyanocitta cristata*). The laying stage tended to have the greatest nest success rates followed by the nestling stage and the incubation stage (Table 2).

Brown-headed Cowbird parasitism rates were low at Fort Campbell for these grassland species, but were within the range of reported parasitism rates for each species (Table 4). The lack of Dickcissel nest parasitism was particularly noteworthy when compared with other areas, but was consistent with records from Tennessee (Nicholson 1997). Our nest parasitism rates probably were low because most nests were in large grassland fields (>100 ha) far from forest edges or other tall woody perch sites (Hauber and Russo 2000, Jensen and Cully 2005), except those of Field Sparrows, which were found in the full range of field sizes (4–600 ha). Nest parasitism rates may be related to the proximity of songbird populations to the greatest densities of Brown-headed Cowbirds (Basili 1997, Winter et al. 2004). Fort Campbell is outside the greatest density areas for Brown-headed Cowbird populations (Sauer et al. 2004). Morris and Thompson (1998) found Brown-headed Cowbirds were most associated with grazed pastures, regardless of grass height. There is no livestock grazing activity at Fort Campbell.

Clutch sizes of Henslow's Sparrows, Grasshopper Sparrows, Dickcissels, and Eastern Meadowlarks were slightly greater at Fort Campbell than average but were within the range of published rates (Table 4). Field Sparrow clutch size was less than average, but within the range of published rates. Average clutch sizes included two nests with more than twice the average number of eggs, one Dickcissel with nine eggs and one Eastern Meadowlark with 10 eggs. These individual nests may represent egg laying efforts of more than

TABLE 2. Mayfield nesting success of grassland birds at Fort Campbell, Kentucky, 1999–2003, by nest cycle interval.

Species	Nest cycle interval[a]	Mean days in period[b]	*n*[c]	Failures (*n*)[d]	Exposure days[e]	Daily survival[f]	SE	Success (%)[g]
HESP[h]	Laying	4.0	8	2	19.5	0.897	0.069	64.9
GRSP	Laying	4.5	8	0	17.0	1.000	0.000	100.0
DICK	Laying	4.0	75	13	229.0	0.943	0.015	79.2
EAME	Laying	4.0	13	0	26.0	1.000	0.000	100.0
FISP	Laying	3.5	47	11	124.0	0.911	0.026	71.6
HESP	Incubating	11.0	54	21	297.5	0.929	0.015	44.7
GRSP	Incubating	11.5	73	23	445.0	0.948	0.010	54.3
DICK	Incubating	12.5	145	67	997.0	0.933	0.008	41.9
EAME	Incubating	12.5	54	25	354.5	0.929	0.014	40.1
FISP	Incubating	12.0	176	83	912.5	0.909	0.010	31.8
HESP	Nestling	9.5	88	23	412.5	0.944	0.011	58.0
GRSP	Nestling	9.0	108	23	621.0	0.963	0.008	71.2
DICK	Nestling	9.0	124	37	694.5	0.947	0.009	61.1
EAME	Nestling	9.0	61	25	387.0	0.935	0.012	54.8
FISP	Nestling	7.5	183	56	849.5	0.934	0.009	60.0
HESP	Inc. and nestling	20.5	111	44	710.0	0.938	0.009	26.9
GRSP	Inc. and nestling	20.5	129	46	1,066.0	0.957	0.006	40.5
DICK	Inc. and nestling	21.5	191	104	1,691.5	0.939	0.006	25.6
EAME	Inc. and nestling	21.5	86	50	741.5	0.933	0.009	22.3
FISP	Inc. and nestling	19.5	266	139	1,762.0	0.921	0.006	20.1
HESP	All stages	24.5	113	46	729.5	0.937	0.009	20.3
GRSP	All stages	25.0	129	46	1,083.0	0.958	0.006	33.8
DICK	All stages	25.5	204	117	1,920.5	0.939	0.005	20.1
EAME	All stages	25.5	86	50	767.5	0.935	0.009	17.9
FISP	All stages	23.0	276	150	1,886.0	0.920	0.006	14.7

[a] Nesting cycle intervals include laying, incubating, nestling, incubation and nestling combined, and all stages combined.
[b] Expected length (days) of each stage from Ehrlich et al. (1988).
[c] Number of nests monitored in each nest cycle interval.
[d] Total number of failed nests.
[e] Total number of exposure days (Mayfield 1975).
[f] Probability of daily nest success (Mayfield 1975).
[g] Probability of nest success (Mayfield) through the nesting cycle interval.
[h] HESP = Henslow's Sparrow, GRSP = Grasshopper Sparrow, DICK = Dickcissel, EAME = Eastern Meadowlark, FISP = Field Sparrow.

TABLE 3. Annual daily survival and nest success rates for grassland birds at Fort Campbell, Kentucky, 1999–2003.

Year	Rate	Henslow's Sparrow	Grasshopper Sparrow	Dickcissel	Eastern Meadowlark	Field Sparrow
1999	Days(*n*)[a]	25.5(6)	96.0(19)	111.0(14)	125.5(12)	150.5(23)
	DSR(SE)[b]		0.948(0.023)	0.910(0.027)	0.920(0.024)	0.907(0.024)
	Success		26.3	9.0	12.0	10.5
2000	Days(*n*)	276.5(40)	257.5(30)	324.0(40)	149.0(17)	522.5(84)
	DSR(SE)	0.920(0.016)	0.973(0.010)	0.935(0.014)	0.913(0.023)	0.912(0.012)
	Success	13.1	50.2	18.1	9.7	11.9
2001	Days(*n*)	235.5(26)	215.0(26)	755.5(74)	201.5(23)	536.0(71)
	DSR(SE)	0.958(0.013)	0.944(0.016)	0.943(0.008)	0.945(0.016)	0.920(0.012)
	Success	34.5	23.8	22.4	23.9	14.5
2002	Days(*n*)	116.0(20)	231.0(24)	311.0(30)	142.5(15)	298.0(47)
	DSR(SE)	0.940(0.022)	0.952(0.014)	0.949(0.013)	0.951(0.018)	0.906(0.017)
	Success	21.8	29.5	26.0	27.7	10.2
2003	Days(*n*)	77.5(20)	283.5(30)	419.0(46)	149.0(19)	379.0(51)
	DSR(SE)	0.948(0.025)	0.961(0.011)	0.936(0.012)	0.940(0.020)	0.950(0.011)
	Success	27.3	37.2	18.3	20.4	30.5

[a] Days = total exposure days, *n* = number of nests. Nest exposure includes laying, incubation, and nestling stages.
[b] DSR = Daily survival rate (Mayfield 1975).

TABLE 4. Weighted average and range of published demographic rates for Henslow's Sparrow, Grasshopper Sparrow, Field Sparrow, Eastern Meadowlark, and Dickcissel.

Species		Clutch size	Parasitized	Apparent success	Mayfield success[a]
Henslow's Sparrow[b]	Average[c]	3.8	0.03	0.51	0.29
	Range[d]	3.3–4.4	0.00–0.08	0.19–0.74	0.07–0.46
Grasshopper Sparrow[e]	Average	4.2	0.09	0.44	0.32
	Range	3.7–4.6	0.00–0.50	0.15–0.80	0.07–0.52
Dickcissel[f]	Average	4.0	0.40	0.48	0.26
	Range	3.7–4.7	0.03–0.95	0.46–0.67	0.12–0.50
Eastern Meadowlark[g]	Average	4.4	0.08	0.32	0.10
	Range	4.1–5.2	0.00–0.70	0.30–0.70	0.10–0.25
Field Sparrow[h]	Average	3.7	0.12	0.36	0.27
	Range	3.4–4.0	0.00–0.80	0.10–0.72	0.21–0.47

[a] Probability of nest success corrected for exposure time (Mayfield 1975).
[b] Robins 1971, Peck and James 1987, Winter 1998, Reinking et al. 2000, Monroe 2001, Burhans 2002.
[c] Average for published values weighted by sample size.
[d] Range of published average values.
[e] Price 1934, Elliot 1978, Wray et al. 1982, McNair 1987, Vickery et al. 1992, Winter 1998, Reinking et al. 2000, Balent and Norment 2003, Vos 2003, Giocomo 2005, Sutter and Ritchison 2005.
[f] Long 1963; Gross 1968; Elliot 1978; Zimmerman 1982, 1983; Basili 1997; Winter 1998; Vos 2003; Jensen and Finck 2004; Fletcher et al. 2006.
[g] Saunders 1932, Johnston 1964, Roseberry and Klimstra 1970, Elliot 1978, Peck and James 1987, Knapton 1988, Lanyon 1995, Granfors et al. 1996, Winter 1998.
[h] Hicks 1934, Walkinshaw 1939, Crooks 1948, Best 1978, Wray et al. 1982, Carey et al. 1994, Barber et al. 2001, Vos 2003.

one female each. Both nests were lost to predation before the eggs hatched, and we were not able to confirm the number of parents visiting the nest.

Grassland birds have relatively low nesting success, compensated by several nesting attempts within a single season (Wiens 1969, Martin 1995, Winter 1999). The length of the nest initiation window (51–75 days) suggests the possibility of multiple breeding attempts or multiple successful broods within a single breeding season for all five species. Henslow's Sparrows and Grasshopper Sparrows are generally considered at least double brooded; two pairs from a color-banded Henslow's Sparrow population in Kentucky had three successful broods in one season (Monroe 2001). Some nests initiated in July could represent third attempts or successful broods for some nesting pairs. The amount of time from the start of the nesting season (late Apr) and the last nests (early Aug) allows for the possibility of three broods if the time to finish a complete nesting cycle is less than 32 days including nest building (Ehrlich et al. 1988). Dickcissels are considered single brooded, or may move to a different location to re-nest (Winter 1998), but the nest initiation window for Dickcissels at Fort Campbell was sufficiently long to allow for the possibility of double brooding (51 days). Field Sparrows are considered double brooded, but their nesting success was so low at Fort Campbell that few pairs could produce two successful nests within the nesting season without many unsuccessful nesting attempts. Field Sparrows had sufficient time to complete at least two successful nests with several unsuccessful attempts (64 days).

The length of the nest initiation window for Eastern Meadowlarks at Fort Campbell was sufficiently long for three successful nesting attempts, but Eastern Meadowlarks may delay for a longer period between successive nests than expected. Kershner et al. (2004) radiotracked female Eastern Meadowlarks in Illinois and reported although they had time in the season to nest more than once, many birds did not re-nest in the same territory. This behavior would spread the distribution of nesting attempts across the season, and could account for the long nesting season for Eastern Meadowlark (75 days) in our study.

Clutch size decreased during the nesting season for Dickcissels, Grasshopper Sparrows, and Field Sparrows. The second brood would be reduced by about one for Dickcissels, and about 0.5 for Grasshopper Sparrows and Field Sparrows if these species were double brooded. Clutch size did not show a linear relationship with time of egg laying during the nesting season for Henslow's Sparrows and Eastern Meadowlarks. Winter (1998) also re-

ported a lack of relationship between clutch size and time in nesting season for Henslow's Sparrow. Eastern Meadowlarks and Henslow's Sparrows tended to have smaller clutch sizes at the beginning and end of the nesting season.

The fields monitored at Fort Campbell were used extensively for army training exercises, such as airborne-troop parachute drops and associated vehicle activity, throughout the breeding season for grassland birds. However, most (88%) recorded nest losses were attributed to predation and few (<1%) nests were affected directly by military activities. Vehicle or troop movements crushed a few nests. Mowing for hay and weather accounted for more recorded nest losses (3 and 1.7%, respectively) than military activities. Nest searching activities were concentrated in grasslands not managed specifically for hay production, and land management effects observed were not representative of all grasslands in the area. Undoubtedly, a much larger proportion of nests failed because of mowing in grassland fields managed for hay production. However, nest searching was concentrated in areas used extensively for military training, and nest failure rates may be considered representative of direct military training impacts at Fort Campbell.

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