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Research Papers

Predator Exclosures Enhance Reproductive Success but Increase Adult Mortality of Piping Plovers (*Charadrius melodus*)

Utilisation d'exclos chez le Pluvier siffleur (*Charadrius melodus*): succès de reproduction plus élevé, mais mortalité accrue chez les adultes

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ABSTRACT. Piping Plovers (*Charadrius melodus*) are listed as endangered throughout Canada and the United States Great Lakes region. Most attempts to increase their numbers have focused on enhancing reproductive success. Using 22 years of data collected by Parks Canada in Prince Edward Island National Park of Canada, we examined whether predator exclosures installed around Piping Plover nests increased nest success and hatching and fledging success when compared to nests without exclosures. Nests with exclosures were significantly more likely to hatch at least one egg than nests without exclosures, and they hatched a significantly greater number of young. The greater reproductive success observed in exclosed nests is likely due to the increased protection from predators that the exclosures conferred; significantly fewer exclosed nests were depredated than nonexclosed nests. However, significantly more exclosed than nonexclosed nests were abandoned by adults, and they had significantly greater adult mortality. Whether benefits of increased reproductive success from exclosures outweigh costs of increased abandonment and adult mortality remains unknown, but must be considered.

RÉSUMÉ. Le Pluvier siffleur (*Charadrius melodus*) est désigné comme « en voie de disparition » dans l'ensemble du Canada et dans la partie états-unienne des Grands Lacs. La plupart des actions visant à augmenter ses effectifs se sont concentrées sur l'augmentation de son succès de reproduction. À partir des données récoltées par Parcs Canada au Parc national du Canada de l'Île-du-Prince-Édouard durant 22 ans, nous avons examiné si l'utilisation d'exclos installés autour des nids de Pluviers siffleurs augmentait les succès de nidification, d'éclosion et d'envol comparativement aux nids sans exclos. Les nids protégés par un exclos avaient significativement plus de chance qu'au moins un œuf éclose par rapport aux nids sans exclos, et ils ont produit significativement plus de jeunes. Le succès de reproduction plus élevé des nids avec exclos est vraisemblablement attribuable à la protection accrue contre les prédateurs que confère l'exclos; ainsi, beaucoup moins de nids protégés par un exclos ont été prédatés comparativement aux nids sans exclos, et ce, de façon significative. Toutefois, les nids avec exclos ont été abandonnés significativement plus souvent par les adultes que les nids sans exclos, et la mortalité adulte y était également plus élevée. Nous ne savons pas si l'amélioration du succès de reproduction des nids munis d'un exclos l'emporte sur le fait que ces nids sont plus souvent abandonnés et que la mortalité adulte y est plus élevée; nous recommandons donc que ces facteurs soient évalués.

Key Words: *adult mortality; Charadrius melodus; endangered species; exclosure; Piping Plover; reproductive success*

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INTRODUCTION

Predator exclosures were designed to prevent potential predators from accessing the eggs of ground-nesters and are considered to be an important management tool for increasing population sizes of endangered and threatened species. They have been effective in increasing reproductive success in several shorebird species, e.g., Pectoral Sandpipers (*Calidris melanotos*; Estelle et al. 1996), Killdeer (*Charadrius vociferous*; Johnson and Oring 2002), Northern Lapwings (*Vanellus vanellus*) and Redshanks (*Tringa totanus*; Isaksson et al. 2007), Southern Dunlins (*Calidris alpina schinzii*; Pauliny et al. 2008), and in Piping Plovers (*Charadrius melodus*; Rimmer and Deblinger 1990, Melvin et al. 1992, Larson et al. 2002, Maslo and Lockwood 2009).

In fact, nest exclosures have been used extensively on breeding Piping Plovers, an endangered shorebird throughout Canada and the United States Great Lakes region, and threatened elsewhere in North America (Haig et al. 2005). In 2001, there were fewer than 3000 breeding pairs documented within North America (Haig et al. 2005). In eastern Canada, 1991 census reports documented 509 adults, while in 2001 there were reports of 481 individuals (Haig et al. 2005). From breeding surveys, Atlantic Canada accounted for 8.1% of this species, while Prince Edward Island (PEI) accounted for 1.9% of the global population (Haig et al. 2005). Piping Plover populations are heavily managed in attempts to increase reproductive success and recruitment of young into the population. Critical threats faced by Piping Plovers are predation on breeding adults and their nests (e.g., Melvin et al. 1992, Ivan and Murphy 2005), loss of habitat (Haig and Oring 1985), and human disturbance on the breeding grounds (Flemming et al. 1988, Burger 1994).

Many studies have documented that exclosed Piping Plover nests have increased hatching success (e.g., Rimmer and Deblinger 1990, Murphy et al. 2003*a*). However, several studies have also documented increased rates of abandonment and/or adult mortality at exclosed Piping Plover nests (Vaske et al. 1994, Murphy et al. 2003*b*, Isaksson et al. 2007, Roche et al. 2010), and those of other shorebirds (e.g., Neuman et al. 2004). Greater hatching success may not be enough to increase population sizes (Pauliny et al. 2008), especially if young are not being recruited into the population, or adults with exclosures are dying disproportionately more often than those without exclosures.

Our main objective was to determine whether predator exclosures increased the reproductive success of Piping Plovers by examining nest success, hatching success, and fledging success as well as the frequency of predation, nest abandonment, and adult mortality between nests with and without exclosures. Based on findings from prior studies, we predicted that exclosures would enhance Piping Plover reproductive success. We also wanted to determine whether exclosures were associated with increased nest abandonment and adult mortality in our study population. Parks Canada collected 22 years of such data, for 1984-1992 and 1994-2006, with exclosures installed since 1988, on Piping Plovers breeding within Prince Edward Island National Park of Canada (PEINP). Our second objective was to determine whether the timing of exclosure installation around a nest, i.e., with one to two eggs vs three to four eggs present, affected the probability of nest predation, abandonment, or adult mortality. Typically, exclosures were installed once a clutch was complete and incubation had been initiated, at the four-egg stage, but erecting them earlier in the laying period may have increased Piping Plover reproductive success. Such information would be invaluable to managers responsible for the recovery of this species.

METHODS

Study species

Male Piping Plovers build nests which are small depressions in the sand (Elliott-Smith and Haig 2004) and often line them with shells, pebbles, or driftwood. Females lay an average clutch size of four eggs and lay one egg every second day (Wilcox 1959). Pairs usually raise only one brood per year, but if the first nest attempt fails, they will renest; three-egg clutches are common in these replacement clutches (Wilcox 1959). Both males and females incubate the eggs over 27 to 31 days (Elliott-Smith and Haig 2004). The chicks leave the nest several hours after hatching when their down is dry, and remain in the area but do not return to the nest (Wilcox 1959). They are able to fly between 25 days of age (Cairns 1982) and 35 days of age (Wilcox 1959). However, for this study, we defined fledging as surviving until 20 days of age posthatch (Larson et al. 2002, Murphy et al. 2003*a*). None of the Piping Plovers in this population were banded.

Study area and field research

Data were collected over 22 years (1984-2006 except for 1993; exclosures were used starting in 1988; Table 1) from 11 sites within PEINP (46° 30' 43" N to 46° 23' 53", 63° 28' 45" W to 62° 58' 18" W). PEINP represents the Maritime Plain Natural Region within the National Parks System. This region is characterized by an undulating landscape of low elevation, underlain by relatively soft sandstone, conglomerate, and shale. Sandy beaches, sandspits, barrier islands, and shifting sand dunes are common along the coastal margins. Combined, these areas cover 48 km of beach and consist of habitats such as dune, open sand, cobble, marram grass, and foredune. Beaches were surveyed starting in mid-April when Piping Plovers arrived until the end of breeding. Students were trained by Parks Canada staff and monitored adult Piping Plovers as soon as they settled on their territory.

Every year, nests were assessed as to whether they would benefit from having a predator exclosure around them. Considerations included: nest history, i.e., nest attempt and reason for previous nest loss; proximity to other Piping Plover nests; frequency and type/evidence of nest predation in the area; visibility and access of nest to the public; proximity of nest to high tide line; physical characteristics of the site; and how tolerant the nest pair was to disturbance, e.g., nontolerant birds would repeatedly react with stressful behavior such as feigning a broken wing, or making guttural sounds prior to 100 m approach of the nest. Ideally, in a study such as this, predator exclosures would be randomly assigned to Piping Plover nests (e.g., Mabee and Estelle 2000). This was not the case in our study; exclosures were erected around nests that were deemed to need them most. Still, we believe that when working with endangered species such as Piping Plovers, retrospective studies using nonrandom assignment of exclosures are valuable.

Circular exclosures had a circumference of 7.6 m and a diameter of 2.4 m and were made of wire mesh gauged 5.1 x 10.2 cm (Deblinger et al. 1992), which was large enough for adult Piping Plovers to fit through, but small enough to keep out many predators. Metal rods were woven through the mesh for support. The top of the exclosure wire was higher than the top of the support rod to discourage avian predators from perching. Bird-X netting with a mesh size of 2 x 2 cm was used to cover the top of the exclosure. The exclosure was first placed over the nest so that a line could be traced lightly around it in the ground. It was then removed, and a 20 cm deep trench was dug around the line to support the exclosure. The bottom rung of the exclosure was buried for stability and to allow for easy passage of the adults. Installation took between 9 and 15 minutes, depending on the substrate, and was done either during the laying period, i.e., one, two, or three eggs present (n=94 nests), or during incubation, i.e., four eggs present (n=89 nests). The nest was then observed for 30 minutes; if one of the adults did not return within this time, the exclosure was removed (n=6). Nests that were exclosed during the laying period were checked within 24 h for signs of nest activity by adults, to monitor potential nest abandonment. If no adult activity was seen around the nest after 48 h, the exclosure was removed and eggs were left in the nest until monitors were certain that the nest was abandoned. Nests with and without exclosures were monitored daily.

Data collection and analysis

Data from the 11 sites in PEINP were pooled across sites and across years. Data from the earliest known nesting attempt per pair were used each year. If this nest failed because of flooding (n=59) or burial by sand from high winds (n=8), the second nest attempt was instead used in the analysis (Melvin et al. 1992). Exclosed nests were no more likely to be flooded (22/209 vs 37/342, $\chi^2 = 0.012$, df = 1, P = 0.91) or buried by sand than nonexclosed nests (4/209 vs 4/342, $\chi^2 = 0.117$, df = 1, P = 0.73). Nests were considered successful when at least one egg hatched from the clutch. Hatch failures were recorded and investigated. Causes for hatch/nest failures included nest abandonment, and predation on adults or eggs. Clutches were classified as abandoned when the clutch was unattended for more than 48 h. Eggs were collected and candled for viability and if fostering opportunities existed, eggs were incubated. Nests were considered as depredated if eggshells or animal footprints were observed around the nest. Adults were considered depredated when their body parts were found on or within 2 m of the exclosure. If there was no evidence of body parts, missing adults were deemed to have abandoned. Nests with missing information on both number of eggs hatched and chicks fledged were omitted from the

Table 1. Total number of nests analyzed and number of exclosed nests in each year over a 22 year period.

Year of Study	Total Nests Analyzed	Nests with Exclosures
2006	15	4
2005	17	5
2004	22	13
2003	24	10
2002	21	12
2001	29	6
2000	24	10
1999	42	18
1998	29	14
1997	22	9
1996	17	5
1995	14	4
1994	11	10
1992	23	15
1991	17	15
1990	19	19
1989	8	7
1988	27	7
1987	39	0
1986	22	0
1985	22	0
1984	20	0
Total:	484	183

analysis. A total of 484 nests were used in the hatching analysis, 183 of those were exclosed and 301 nonexclosed. When examining fledging success from only the successful nests, i.e., with at least one egg hatched, 202 nests were used, 114 of those exclosed and 88 nonexclosed.

Data were analyzed with GraphPad Prism 5 (version 5.02) for Windows, GraphPad Software, San Diego, California, USA. For the count data, Chi-square tests with Yates' correction were done, while Fisher's Exact tests were done when sample sizes were small. All continuous data were analyzed for normality using a d'Agostino and Pearson omnibus normality test. The data were not normally distributed, and so Mann-Whitney tests were done. All tests are two-tailed. Mean ± SE are presented. Results were considered significant when $P \leq 0.05$.

RESULTS

Significantly more exclosed nests (118/183) had at least one egg hatch than nonexclosed nests (102/301; 64.5% vs 33.9%; $\chi^2 = 41.739$, df = 1, $P < 0.0001$). Many nests (104/484 = 21.5%) failed during the laying period, typically before exclosures were erected around designated nests. Mean number of hatchlings/nest ± SE was significantly higher in exclosed nests (2.3 ± 0.13) than in nonexclosed nests (1.2 ± 0.10; Mann-Whitney U = 19354, $n_1 = 183$, $n_2 = 301$, $P < 0.0001$). The mean number ± SE of fledglings from successful nests, where at least one egg hatched, was not significantly different between exclosed and nonexclosed nests (2.5 ± 0.14 vs 2.8 ± 0.13, respectively; Mann-Whitney U = 4343, $n_1 = 114$, $n_2 = 88$, $P = 0.10$). However, when including failed nests, there were significantly more 20-day old chicks, i.e., fledglings, that hatched from exclosed than nonexclosed nests (2.0 ± 0.14 vs 1.4 ± 0.13, respectively; Mann-Whitney U = 9951, $n_1 = 141$, $n_2 = 178$, $P = 0.0009$).

Nests failed for various reasons (Table 2). Flooding caused nest failure in 11% (59/551) of nests while burial by sand occurred in 1.5% (8/551) of nests; these data were omitted from our analyses in comparing reproductive success of exclosed vs nonexclosed nests. Significantly fewer exclosed nests (4/183) were depredated as compared to nonexclosed nests (126/301; 2.2% vs 41.9%, respectively; $\chi^2 = 89.181$, df = 1, $P < 0.0001$). Known predators on the nonexclosed nests included American Crows (*Corvus brachyrhynchos*; 23 nests), red foxes (*Vulpes vulpes*; 11 nests), striped skunks (*Mephitis mephitis*; 7 nests), gulls (*Larus* spp.; 6 nests), Common Ravens (*Corvus corax*; 5 nests), and American mink (*Neovison vison;* 1 nest). Known predators on the exclosed nests included American Crows (2 nests) and red foxes (2 nests; the fox dug under the exclosure at one of the nests).

Significantly more exclosed (36/183) than nonexclosed nests (19/301) were abandoned (19.7% vs 6.3%, respectively; $\chi^2 = 18.863$, df = 1, $P < 0.0001$) and they had significantly more adult mortality, including predation on adults, associated with them (16/183 vs 2/301; 8.7% vs 0.7% respectively, Fisher's Exact Test: $P < 0.0001$).

For exclosed nests, 11/16 cases of adult mortality were confirmed to be due to predation, whereas only one of the adults on nonexclosed nests was confirmed as being depredated. However, 7/183 exclosed nests and 46/301 nonexclosed nests failed because of unknown causes. Two known predators on adults at exclosed nests were an American mink and a red fox. Merlins (*Falco columbarius*) were suspected predators on adults, but this suspicion could not be confirmed as Merlins did not leave prints in the sand.

Exclosed nests had a 64.5% success rate and produced a mean of 2.5 ± 0.14 fledglings/nest, resulting in 1.6 ± 0.09 fledglings produced per exclosed nest. Nonexclosed nests had a 33.9% success rate and produced a mean of 2.8 ± 0.13 fledglings/nest resulting in production of 0.9 ± 0.04 fledglings per nonexclosed nest in our population.

The stage at which exclosures were installed around the nests, i.e., one to two vs three to four eggs, had no effect on the probability of predation (Fisher's Exact Test: $P = 1.0$), but had a significant effect on the probability of parents abandoning the clutch ($\chi^2 = 8.410$, df = 1, $P = 0.004$), with parents more likely to abandon at the one to two egg stage than at the three to four egg stage (Table 2). Stage of installation had no effect on adult mortality (Fisher's Exact Test: $P = 1.0$) or on the likelihood that adults would be depredated (Fisher's Exact Test: $P = 1.0$).

Table 2. A summary of nesting failure causes for exclosed and nonexclosed nests.

	Number of eggs when exclosed				Total Exclosures	No Exclosure
	1	2	3	4		
Total number of nests	17	36	41	89	183	301
No. nest failures (no hatch)	9	15	13	28	65	199
No. nest failures with known cause	8	15	12	23	58	154
No. depredated nests	0	1	1	2	4	126
No. abandoned nests	6	12	8	10	36	19
Total nests with adult mortality	2	2	2	10	16	2
No. nests with adult mortality due to confirmed depredation	2	1	2	6	11	1
No. nests destroyed by humans	0	0	0	1	1	5
No. nests with inviable eggs	0	0	1	0	1	1
No. nests with unknown cause of loss	1	0	1	5	7	46

DISCUSSION

Nests with exclosures were significantly more likely to hatch at least one egg than were nests without exclosures (65% vs 34%), and they hatched a significantly greater mean number of hatchlings/nest than did nonexclosed nests (2.3 ± 0.13 vs 1.2 ± 0.10 hatchlings/nest). These findings of increased reproductive success for Piping Plovers from exclosed nests have also been documented by others. Rimmer and Deblinger (1990), Melvin et al. (1992), and Murphy et al. (2003*a*), respectively, found that 92%, 90%, and 84% of exclosed nests hatched at least one egg, while only 25%, 17%, and 45% of nonexclosed nests did so.

Our findings of a mean of 2.3 hatchlings/exclosed nest and 1.2 hatchlings/nonexclosed nest was similar to that found by Rimmer and Deblinger (1990), at 3.5 and 1.0 hatchlings/nest, respectively. Piping Plover chicks leave the nest within a few hours of hatch and do not return to it, but remain in the area (Wilcox 1959). Therefore, it is not surprising that when examining successful nests, exclosures had not affected the mean number of chicks surviving to 20 days of age posthatch, i.e., fledglings, compared to nonexclosed nests in our population (2.5 ± 0.14 vs 2.8 ± 0.13 chicks/nest). Melvin et al. (1992), Larson et al. (2002) and Murphy et al. (2003*a*), however documented higher mean fledging success from exclosed nests (1.96, 1.28, and 1.73, fledglings, respectively) than from nonexclosed nests (0.12, 0.72, and 0.73-0.84 fledglings, respectively); they likely estimated fledging success from both successful and failed nests. If we do the same, our result of a mean of 2.0

± 0.14 fledglings/nest from exclosed nests is comparable to that of Melvin et al. (1992), but our mean fledging success from nonexclosed nests is substantially higher (1.4 ± 0.13 fledglings/nest).

The timing of exclosure installation, i.e., one to two eggs vs three to four eggs, did not appear to statistically affect the probability of nests or adults being depredated, but it had a significant effect on the likelihood that the nest would be abandoned. Exclosures set up during the early laying stage, i.e., one to two eggs, were abandoned significantly more frequently than were nests with exclosures erected during the three to four egg stage. Although our finding of 20% of nest failures occurring during the laying stage would suggest a benefit of erecting exclosures early in the laying stage, the increased frequency of abandonment does not. PEINP now only installs exclosures on nests when three or more eggs are present.

The enhanced reproductive success observed from exclosed nests can likely be attributed to the increased protection from predators that the exclosures conferred; significantly fewer exclosed nests (2.2%) were depredated than nonexclosed nests (42%), as was also found by Rimmer and Deblinger (1990), and Melvin et al. (1992). In our population, nests receiving an exclosure were not randomly chosen, but were selected on the basis of apparent risk. A random design might have shown an even greater benefit of the exclosures.

Confirmed nest predators included American Crows and foxes on both exclosed and nonexclosed nests, as well as striped skunks, Common ravens, gulls, and American mink on the nonexclosed nests. Ivan and Murphy (2005) determined that nest predators were typically mammals while predators of chicks consisted mainly of avian species. Although we cannot comment on chick predation, we found birds to be important nest predators as well as mammals.

Although exclosed nests benefited from decreased predation on the eggs, they were significantly more likely to be abandoned by the parents (20%) than were nonexclosed nests (6.3%). In their study, Vaske et al. (1994) found that 10% (22/211) of Piping Plover nests were abandoned after different types of exclosures were erected, less than what we observed. Exclosure size, among other variables, can affect both the probability of abandonment (Vaske et al. 1994) and nest predation (Deblinger et al. 1992). Medium-sized exclosures, such as the ones used in our study (4.5 m^2) were found to have a lower probability of abandonment than smaller exclosures, i.e., those less than 3 m^2 (Vaske et al. 1994), but a higher probability of nest predation than smaller or larger (> 6 m^2) exclosures (Deblinger et al. 1992).

Often when adults disappear, the nests are deemed abandoned, although the true cause may be depredation of one of the adults, and not desertion (Neuman et al. 2004, Roche et al. 2010). Murphy et al. (2003*a*) noted predation on incubating adults to be 5% for exclosed nesters and 0% for nonexclosed nesters, which is similar to our confirmed findings of 6.0% adult predation at exclosed nests and 0.3% at nonexclosed nests. Isaksson et al. (2007) found that adult Redshanks incubating in exclosed nests suffered significantly greater predation than adults that incubated in nonexclosed nests, as did we with Piping Plovers. However, as noted by Isaksson et al. (2007), adult susceptibility to predation on the nest may depend on whether birds flush early or late when a predator approaches; no adult Northern Lapwings were depredated on exclosed or nonexclosed nests in their study. Similarly, adult Southern Dunlins on exclosed nests were no more likely to be depredated than those on nonexclosed nests (Pauliny et al. 2008). Both Northern Lapwings and Southern Dunlins flush off their nest early upon detection of a predator while Redshanks do not. Piping Plovers are more variable in their response times to potential predators with some flushing early and others flushing later (Flemming et al. 1988; L. Thomas *personal communication*).

Roche et al. (2010) had erected exclosures on all Piping Plover nests, and found abandonment rates accounted for 50% of all the nest failures with known cause in their study population; they included flooded nests. They discovered that as many as 70% (34/49) of those abandoned nests were likely attributable to adult mortality. We documented abandonment rates of 43% (36/84) in exclosed nests with known cause of failure, including nests that failed because of flooding or burial. Adult mortality was confirmed at another 19% (16/84) of exclosed nest failures. Roche et al. (2010) suggested that much of the previous findings on adults abandoning exclosed nests are in fact not due to adult desertion, but instead to adult mortality. If so, then up to 62% (52/84) of nest failures may be due to adult mortality, most likely through depredation. Exclosures can potentially attract predators (Nol and Brooks 1982), and/or make it more difficult for incubating adults to escape (Isaksson et al. 2007).

Given that, on average, 1.6 young fledged from each exclosed nest and 0.9 fledged from each nonexclosed nest, 100 nests (200 adults) would produce 160 and 90 young respectively. As the known mortality for adults was 8.7% at exclosed nests and 0.7% at nonexclosed nests of the 200 adults (100 nests; includes confirmed depredation), approximately 183 and 199 adults would survive at exclosed and nonexclosed nests, respectively. The cost of greater fledging from exclosed nests is that of 16 more adults dying than at nonexclosed nests. However, these exclosed nests would produce 70 more fledglings than the nonexclosed nests. Therefore, a minimum of 23% (16/70) of the juveniles would need to survive to replace these dead adults. Piping Plovers in the Great Plains have a juvenile survival rate of 31.8% (Larson et al. 2000), suggesting that there would be an overall benefit to using exclosures, if the juvenile survival rate in the Atlantic population was greater than 23%. However, caution must be used. Adult mortality may be underestimated, as indicated by Roche et al. (2010); adults who were categorized as abandoning may actually have died. There are also regional differences in reproductive success and survival among Piping Plover populations, and the results for this Atlantic population may not be generally applicable, but must be considered.

CONCLUSION

Although exclosed nests produced on average a greater number of fledglings than nonexclosed nests in our population (1.6 ± 0.09 vs 0.9 ± 0.04), it came at a cost of increased adult mortality. Piping Plovers can live up to 11 years (Wilcox 1959), and so loss of an adult, especially in an endangered species, is critical. Results from our study indicate a net benefit to using exclosures, if adult mortality has not been underestimated. Benefits would be increased if exclosure design could be revisited to minimize the probability of adult mortality. Our results underscore the necessity of examining both the potential costs as well as benefits of exclosures to shorebird populations. As noted by Murphy et al. (2003*b*), Isaksson et al. (2007) and Roche et al. (2010), caution must be used in deciding whether exclosures, although successful in increasing reproductive success, are the best tool to increase population sizes of endangered shorebirds.

Responses to this article can be read online at:
http://www.ace-eco.org/vol5/iss2/art6/responses/

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