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The effect of beaver facilitation on Common Teal: pairs and broods respond differently at the patch and landscape scales

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17 Avian species respond to ecological variability at a range of spatial scales and
18 according to life history stage. Beaver dams create wetland systems for waterbirds
19 that are utilized throughout different stages of the breeding season. We studied
20 how beaver-induced variability affected mobile pairs and more sedentary broods
21 along with the production of Common Teal *Anas crecca* at the patch and landscape
22 scale on their breeding grounds. Beavers *Castor* spp. are ecosystem engineers that
23 enhance waterfowl habitats by impeding water flow and creating temporary
24 flooding. Two landscapes in southern Finland with (Evo) and without (Nuuksio)
25 American Beavers *Castor canadensis* were used in this study. To investigate the
26 patch-scale effect, pair and brood densities along with brood production were first
27 compared at beaver-occupied lakes and non-beaver lakes in the beaver landscape.
28 Annual pair and brood densities/km shoreline and brood production were compared
29 between beaver and non-beaver landscapes. Facilitative effects of beaver activity
30 were manifest on brood density at both patch and landscape scales: these were
31 over 90 and 60 percent higher in beaver patches and landscapes, respectively. An
32 effect of beaver presence on pair density was only seen at the landscape level. Pair
33 density did not strongly affect brood production, as shown earlier for relatively
34 mildly density-dependent Teal populations. Because the extent of beaver flooding
35 was a crucial factor affecting annual Teal production in the study area, we infer
36 beaver activity has consequences for the local Teal population. Ecosystem
37 engineering by the beaver could therefore be considered as a restoration tool in
38 areas where waterfowl are in need of high-quality habitats.

39

40 **Keywords:** *Anas crecca*, brood production, *Castor canadensis*, ecosystem engineer,
41 experienced scale, Teal density, wetland management

42

43

44 Avian habitat selection, population stability and response to disturbance may differ
45 according to the scale at which these are investigated (Wiens 1989a, Denny *et al.*
46 2004). Schneider (2001) identifies three scale-related problems which arise when
47 ecological processes are studied. First, many ecological problems are often large in
48 scale. Second, most variables can only be measured in small areas. Third, patterns or
49 processes at small scales do not necessarily hold or prevail at larger scales (but see
50 Denny *et al.* 2004). Sometimes the mechanisms underlying observed patterns
51 operate at different scales than those at which the patterns are detected. Even
52 investigators addressing the same questions, but at different scales, have been
53 observed to reach differing conclusions (Wiens 1989b). Examples concerning birds
54 include Least Flycatchers *Empidonax minimus* negatively influencing the distribution
55 of American Redstart *Setophaga ruticilla* through interspecific aggression at the
56 scale of four-hectare forest plots. At the regional level, however, the total
57 abundances of the two species correlated positively (Sherry & Holmes 1988).
58 Similarly, variation in habitat use by sedentary Pied-billed Grebe *Podilymbus*
59 *podiceps* was explained solely by within-patch variation whereas area requirements
60 for vagile Black Tern *Chlidonias niger*, which forages up to four km away from the
61 nest wetland, fluctuated in response to landscape structure (Naugle *et al.* 1999).

62 Beavers *Castor* spp. are ecosystem engineers of the boreal forest, creating
63 disruption to riparian areas by their damming of creeks or ponds and forming of
64 inundated areas (Naiman *et al.* 1988, Wright *et al.* 2003, Hyvönen & Nummi 2008).
65 Both American *Castor canadensis* and Eurasian Beaver *C. fiber* are assumed to have
66 a similar effect on the riparian ecosystem (Danilov & Fyodorov 2015) that would
67 otherwise not exist in the landscape (Remillard *et al.* 1987, Johnston & Naiman
68 1990, Nummi & Kuuluvainen 2013). Beaver patches undergo succession from
69 terrestrial to aquatic habitat and back, thereby increasing landscape heterogeneity
70 (Remillard *et al.* 1987). Via ecosystem engineering, beavers may also act as
71 facilitators for various species, such as plants (Wright *et al.* 2002), butterflies (Bartel
72 *et al.* 2010), waterbirds (Nummi & Holopainen 2014), and bats (Nummi *et al.* 2011).
73 Therefore using beaver as a restoration tool for freshwater habitats has been
74 suggested (Törnblom *et al.* 2011, Law *et al.* 2016).

75 Among boreal ducks, patch creation or modification by beavers has been found to
76 especially benefit Common Teal *Anas crecca*, (hereafter Teal), as both Teal pairs and
77 broods rapidly occupy newly formed beaver flowages (Nummi & Pöysä 1997,
78 Nummi & Hahtola 2008). This has been attributed to both habitat modification and
79 resource enhancement (*sensu* Bruno *et al.* 2003): beaver ponds provide more
80 invertebrates that are potential food for Teal and have shallower depths – suitable

81 for foraging – than non-disturbed boreal ponds (Longcore *et al.* 2006, Nummi &
82 Hahtola 2008). Compared to non-flooded lakes, Teal densities overall tend to be
83 higher on beaver ponds due to greater numbers of pairs and broods, as well as
84 elevated Teal duckling survival with ample foods there (Nummi & Hahtola 2008).

85 As is the case for most organisms, ducks may experience their environment
86 differently according to age, i.e. as a mobile flying adult compared to a more
87 sedentary flightless duckling (Levin 1992). In our study we investigate how Teal pairs
88 and unfledged broods (which clearly differ in their mobility) respond to
89 environmental variation at patch (0.1–50 ha) versus landscape scales (40–50 km²).
90 The patches in our study are easily covered by both breeding pairs and broods
91 within tens of minutes or 1–2 hours of swimming. In contrast, shifting between the
92 most distant lakes within each landscape of our study would only take a few
93 minutes for the flying pairs, but at least 15 hours (but most likely 1–3 days) for the
94 non-flying broods (Martin & Forsyth 1983, Duncan 1993). Duck pairs therefore
95 typically have home ranges comprising many small wetlands and they travel a few
96 kilometers between their foraging patches (Gilmer *et al.* 1975, Guillemain & Elmberg
97 2014). We thus predict that the effect of spatial scale will differ between pairs and
98 broods.

99 We hypothesize that Teal broods would be affected by beaver inundation already at
100 the patch scale, whereas the beaver effect would be clearly seen in pairs at the
101 landscape scale.

102

103

104 **METHODS**

105

106 **Study area**

107 Data were gathered in an oligotrophic watershed (area 39 km²) at Evo inhabited by
108 American Beaver (hereafter Beaver) (61°12' N, 25°07' E; 51 lakes) and the Nuuksio
109 lake area (53 km²; 60°19'N, 24°28'E; 54 lakes) in southern Finland not inhabited by
110 Beavers (Arvola *et al.* 2010, Nyberg *et al.* 2010). The study lakes of both areas are
111 oligotrophic, relatively small (Nuuksio 0.2–94.5 ha, Evo 0.1–49.5 ha), have fish
112 populations and are closed or headwater lakes (Väänänen *et al.* 2012). The predator
113 communities of the two areas are similar with Pine Marten *Martes martes* and Red
114 Fox *Vulpes vulpes* as main predators (Natural Resources Institute Finland 2017)

115 along with two alien predators, the American Mink *Neovison vison* and Raccoon Dog
116 *Nyctereutes procyonoides*. Ducks are additionally predated by several birds of prey
117 and the Northern Pike *Esox lucius*.

118 Boreal forest covers most of the two areas, interspersed with lakes and mires.
119 Agriculture and human settlement are very limited and local. Apart from Beaver-
120 created variability in Evo, landscape-level habitat structure of the Evo and Nuuksio
121 lakes has been fairly stable for the last 20 years (Suhonen *et al.* 2011, Thompson *et al.*
122 *et al.* 2016). In Evo, Beavers change their lake of occupancy on average every three
123 years, thus new Beaver habitat patches are created continuously while old ones are
124 abandoned (Hyvönen & Nummi 2008). Lake shores in both study areas are generally
125 steep, with little emergent vegetation (mainly sedges *Carex* spp. and Common Reed
126 *Phragmites australis*), although some lakes have stands of Water Horsetail
127 *Equisetum fluviatile* and cattail *Typha* spp. Emergent vegetation is usually lined with
128 narrow belts of Yellow Water Lilies *Nuphar lutea* and Water Lilies *Nymphaea*
129 *candida*; submerged vegetation is very sparse. Rocky shores are also typical in
130 Nuuksio. In Beaver ponds the shores are significantly shallower than non-Beaver
131 ponds and contain inundated herbaceous vegetation and bushes (Nummi & Hahtola
132 2008). Located in a cool continental climate, all wetlands freeze over from
133 November to April. Each spring, they are thus colonized anew by migrating ducks.
134 Overall, the lakes of our two study areas were very similar and have been previously
135 combined in waterbird studies (Nummi *et al.* 2012; Väänänen *et al.* 2012).

136

137

138 **Teal data**

139 In the Beaver landscape Evo duck data are from 1988–2014 and in non-Beaver
140 landscape Nuuksio data are from 1994–2014. The number of pairs was estimated in
141 both study landscapes once a year between the end of April and the beginning of
142 May. The number of nesting pairs was interpreted using the survey guidelines of the
143 Finnish Museum of Natural History (Koskimies & Pöysä 1991). Brood data from the
144 Beaver landscape were collected from 1988–2008 by conducting five annual brood
145 surveys from June to August, and from 2009–2014 by conducting two annual
146 surveys from June to July. In the non-Beaver landscape, the first brood survey was
147 conducted in June and the second round in July. During each survey, a point count
148 was first made from the shore, after which a round count was performed by circling
149 the lakes by foot or boat (Nummi & Pöysä, 1993); the method was chosen based on
150 lake size and shoreline structure. In the most densely vegetated Beaver ponds all
151 three methods (point count, circling by foot and circling by boat) were combined to
152 attain coverage of the entire pond area. In Beaver ponds the ducks are most difficult

153 to detect (see Holopainen *et al.* 2014), thus the number of birds found there are
154 conservative. In both landscapes, all wetlands inside a certain area were surveyed.

155 Brood surveys included broods, ducklings without a female and also females
156 emitting alarm signals. Duckling number was counted for every observed brood,
157 after which the brood age was determined following the seven age classes of Pirkola
158 and Högmänder (1974). Age class was also estimated for ducklings seen without an
159 adult female.

160 To eliminate the error caused by the irregularity in the number of annual brood
161 counts, brood density was counted per survey in both study landscapes. In the
162 comparison of Beaver and non-Beaver landscapes, we only took into account the
163 two surveys (in June and July) in the Beaver landscape which corresponded to those
164 of the non-Beaver landscape. Brood production was resolved by counting the
165 number of broods per adult pair. The different age classes of the ducklings were not
166 taken into account, but observations of juveniles were excluded. Thus, all sightings
167 of the six age classes were taken into account, but they were not separated from
168 one another.

169 Pairs and brood densities are given per km shoreline, thus information on shoreline
170 length of the lakes and ponds in the study areas were required. Lake shore lengths
171 in the Beaver study area were already measured by Nummi and Pöysä (1993). The
172 shore lengths for the non-Beaver lakes and ponds, excluding a few small ponds,
173 were obtained from the Finnish Environment Institute's open data service
174 (syke.fi/avoindata). Shoreline length was measured for the remaining ponds using
175 the same database's map service "Karpalo". Many lakes and ponds in the non-
176 Beaver study area have a partly rocky shoreline, which is an unsuitable breeding
177 environment for ducks. This amount of rocky shoreline was removed from the total
178 shoreline length during analyses. Lengths of the rocky shorelines were measured
179 using the map service of the Finnish Environment Institute (syke.fi/avoindata).

180

181 **Beaver data**

182 Both European and American Beavers were introduced to Evo during the 1930s and
183 1950s (Lahti & Helminen 1974). Nowadays the Beaver population in Evo is
184 comprised solely of American Beavers (Parker *et al.* 2012).

185 Since 1976, Beaver data have been collected from the lakes and ponds flooded by
186 Beavers. The data indicate the years during which Beavers have flooded a lake or a
187 pond. In Evo, Beaver ponds are most commonly formed by the damming of an

188 existing pond (Nummi & Hahtola 2008). Beavers occupy one site for an average of
189 three years, and often return to the same areas they have flooded before (Hyvönen
190 & Nummi 2008).

191

192 **Patch-scale comparison of teal abundance before and during flooding**

193 On the patch scale we studied whether the Beaver increases pair and brood
194 densities and brood production. The study was conducted in the Beaver area by
195 comparing specific variables before and during a Beaver inundation in a patch. The
196 goal of the comparison was to collect data two years before and two years during
197 the flood. The density of only one year was used if Beaver-induced flooding had
198 occurred for only one year in the patch.

199 Pair density was compared in 19 different lakes before and during Beaver
200 inundation, and brood densities were similarly examined in 18 lakes. Brood
201 production was also examined in 12 different lakes. These different figures result
202 from the fact that in some cases the Beaver flood was only present in a certain lake
203 during the pair time, and in some cases during the brood time, and in 12 cases both
204 parameters were available. In each of these three cases, a control lake was included
205 for each Beaver lake, representing the most similar lake along an environmental
206 gradient of habitat luxuriance (Nummi & Pöysä 1997). In control lakes especially the
207 amount of broods remained extremely low which is the normal pattern in boreal
208 lakes not affected by Beaver (Elmberg *et al.* 2005, Gunnarsson *et al.* 2004). The
209 environmental gradient takes into account the shore's vegetation type, the amount
210 of vegetation, water depth at the shore and lake size (Suhonen *et al.* 2011). The
211 comparison was made using the Wilcoxon signed-rank test, which is a non-
212 parametric version of the pairwise *t*-test (Ranta *et al.* 2012). The examination was
213 made using the IBM SPSS Statistics 21 software (IBM Corp. 2012).

214

215 **Comparison of teal density in Beaver and non-Beaver lakes at Evo**

216 We also studied whether pair and brood densities and brood production differed in
217 lakes with and without Beaver in the Beaver landscape. Lakes where data
218 concerning Beaver floods were available during the study period were included in
219 the data set. Altogether 24 Beaver-flooded lakes and 18 lakes with no Beaver
220 activity during years 1988–2014 were included in the examination. We first tried to
221 perform a glmm analysis using the individual lakes, and after data exploration ended
222 up trying hurdle models (ZAP for broods and ZANB for pairs) with a random lake-

223 effect. Unfortunately the lake level analysis could not be done with the glmm hurdle
224 models, apparently because of so many zeros in both the Beaver occurrence column
225 and teal column. Instead, the comparison was performed using the years when
226 Beaver-induced floods occurred in the Beaver lakes, while all the years of the study
227 period were used in the non-Beaver lakes. Annual average pair density was counted
228 for each lake. Brood density was obtained using the years from 1988 to 2014. The
229 same years were also used in examining pair density and brood production,
230 excluding year 1988, from which no data on pair numbers were available. The
231 comparison was made using the independent samples Mann-Whitney *U*-test by
232 using the IBM SPSS Statistics 21 software (IBM Corp. 2012).

233

234 **Beaver and non-Beaver areas – comparing two landscapes**

235 We compared the annual brood and pair densities and brood production for 1994–
236 2014 between the Beaver and non-Beaver landscapes. All pair and brood sightings
237 of one year were added together, and brood density and broods per pair figures
238 were transformed into figures per one survey. The comparison was made using the
239 Mann-Whitney *U*-test, because the sightings were not normally distributed.
240 Comparisons were performed using the IBM SPSS Statistics 21 software (IBM Corp.
241 2012). In addition to the difference between the study areas, we explored whether
242 annual population variation differs within these two study areas. This annual
243 variation was examined by testing the homogeneity of the variances with Fligner-
244 Killeen's test. Fligner-Killeen's test was chosen, because it also works well with
245 samples that are not normally distributed (Ranta *et al.* 2012). Fligner-Killeen's test
246 was conducted using the variation observed by Conover *et al.* (1981), in which the
247 rank is counted using the median instead of plain values. The test was performed
248 using R 2.3.2 software (R Core Team 2015).

249

250

251 **RESULTS**

252

253 **Patch scale**

254 Teal brood density in the ponds increased significantly with Beaver inundation ($Z = -$
255 2.24 , $P = 0.025$, $n = 18$, Fig. 1a), as did the median number of broods per pair ($Z = -$
256 2.02 , $P = 0.043$, $n = 12$). Pair density, however, did not increase significantly ($Z = -1.6$,

257 $P = 0.110$, $n = 19$). In the non-flooded control lakes no significant change was found
258 in either of the three cases ($P > 0.10$ in all cases, Fig. 1b).

259

260 **Within landscape**

261 Within the Beaver landscape, Teal brood density in Beaver ponds was again
262 significantly higher than that of non-Beaver ponds, as was the number of broods
263 produced per pair (Table 1). The pair density of Beaver and non-Beaver ponds did
264 not differ significantly (Table 1).

265

266 **Between landscapes**

267 Teal pair density ($U = -5.18$, $P < 0.001$, Fig. 2a), brood density ($U = -4.24$, $P = < 0.001$,
268 Fig. 2b), as well as the number of broods per pair ($U = -2.25$, $P = 0.012$, Fig. 2c) were
269 significantly higher in the Beaver landscape (median: 0.34 pairs/ shoreline km, 0.03
270 broods/km, 0.11 broods/pair) than in the non-Beaver landscape (0.15 pairs/km, 0.01
271 broods/km, 0.08 broods per pair). No significant differences were observed in the
272 variability of pair or brood production per pair between the Beaver and non-Beaver
273 landscapes (Fligner-Killeen test, $P > 0.05$ in both cases). Brood density variability was
274 higher in the Beaver landscape ($\chi^2 = 7.24$, $P = 0.007$).

275

276

277 **DISCUSSION**

278

279 We found scale-dependent patterns in the effects of Beaver on breeding Teal. Our
280 study corroborated earlier observations that Beaver ponds increase the number of
281 Teal broods at the patch scale (Nummi & Hahtola 2008), the brood densities being
282 over 90 % higher during Beaver inundation. This finding was coupled with an
283 increase in the number of broods produced per pair. The increase in Teal pairs upon
284 Beaver flooding was not significant, contrasting the earlier study by Nummi & Pöysä
285 (1997). The results from these experimental-like situations of before and during
286 inundation were supported when Beaver ponds and non-Beaver ponds within the
287 Beaver landscape were compared: the densities of pairs and broods along with
288 breeding success were eight to nine times higher in Beaver ponds. These
289 observations fit the conceptual framework created by Levin (1992). He stated that

290 localized disturbances play an important role in the maintenance of species such as
291 the Teal which benefit from disrupted, high-quality habitats; in the case of Teal
292 habitats with abundant invertebrates and shallow vegetated shores suitable for
293 foraging (Nummi *et al.* 2013, Nummi & Hahtola 2008).

294 When the Beaver and non-Beaver landscapes were compared, a similar picture
295 emerged. Both the number of pairs and broods were significantly higher in the
296 Beaver-influenced landscape than in the one which lacked Beavers. In the Beaver
297 landscape the pair density was approximately 50 % and brood density 60 % higher
298 than those found in the non-Beaver landscape. Similarly, the average number of
299 broods per pair was higher in the Beaver landscape. We of course had only one
300 landscape pair to compare, so possible other differences between the landscapes
301 could not be effectively controlled. There appears to be no pronounced difference in
302 general productivity between the two areas, since the densities of two other
303 common ducks, Mallard *Anas platyrhynchos* and Common Goldeneye *Bucephala*
304 *clangula* were similar in Evo (Nummi & Pöysä 1995a) and Nuuksio (Taskinen 1997).

305 We found that the Beaver effect does not appear to emerge as clearly at the patch
306 scale for pairs as it does for broods. However, pair density was also higher with
307 Beaver influence at the landscape level. Once a pattern is detected, it is possible to
308 concentrate on measuring its determinants and the mechanisms behind it (Levin
309 1992). In our case (at least) two mechanisms could bring about the pattern we
310 observed. Firstly, although pairs might use Beaver ponds for foraging, they very
311 likely encompass many small wetlands in their home range, and spend only part of
312 their time in the Beaver flowages. This pattern has been shown for radio-tracked
313 Mallards with home ranges of approximately 230 ha that include e.g. seasonal
314 wetlands (Gilmer *et al.* 1975, see also Dwyer *et al.* 1979); individual breeding Teals
315 have not been followed using radio telemetry but the home ranges of Teal pairs are
316 approximately the same size as those of Mallard (Nudds & Ankney 1982). Less
317 mobile broods, again, may spend all of their time in the optimal Beaver ponds, once
318 they have been discovered (Nummi & Hahtola 2008; the home ranges of
319 comparable Mallard broods were 10–15 ha; Talent *et al.* 1982, Chouinard *et al.*
320 2007). Secondly, and possibly more importantly, other flooded areas in riparian
321 forests, namely seasonal wetlands created by melting snow, have been shown to be
322 suitable for foraging during the pairing season (Paton 2005, see also Holopainen *et al.*
323 2014). This may dilute the Beaver flowage effect during springs when large
324 amounts of flooded shores and vernal pools are available.

325 At the landscape scale Teal broods were concentrated in the few Beaver patches of
326 the Beaver landscape of Evo (Nummi & Pöysä 1995b), while pairs were less so
327 (Elmberg *et al.* 2005). The amount of Beaver flooding was also the most important
328 factor affecting yearly Teal production in the area, among such environmental
329 factors as food abundance (Holopainen *et al.* 2014). This could also be the reason
330 why the brood density varied more in the Beaver landscape. Moreover, our finding
331 that the average number of broods per pair was higher in the higher density Beaver
332 landscape than in the lower density non-Beaver landscape corroborates our earlier
333 study indicating that Teal populations may not show very strong spatial density
334 dependence (Nummi *et al.* 2015). This supports the hypothesis that considering
335 environmental variability, an association is often visible with a species' life history
336 adaptation along a "slow-fast continuum" and temporary vs. permanent habitats
337 (Fowler 1981, Sæther & Engen 2002). "Fast" species typically live in habitats that are
338 either unpredictable in time or short-lived, and those species themselves are often
339 short-lived as well (Sæther & Engen 2002).

340 Considering that 60–90 % of European wetlands were lost during the last century
341 and that similar figures apply to many areas of North America, there is great need
342 for wetland restoration (Junk *et al.* 2013). From geomorphological, hydrological and
343 ecological aspects introducing Beavers has the potential to be a mechanism for
344 wetland restoration (Hey & Philippi 1995, Burchsted 2010, Törnblom *et al.* 2011).
345 Beavers are known to enhance biodiversity by beneficially affecting numerous
346 groups of organisms (Stringer & Gaywood 2016), sometimes facilitating whole
347 species communities (Dalbeck *et al.* 2007, Nummi & Holopainen 2014). Our data
348 support earlier findings which consider Beavers as a feasible and economic way of
349 restoring riparian landscapes (Brown & Parsons 1979, Nummi 1989, Thompson *et al.*
350 2016).

351

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356

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516 Fig. 1. Changes in Teal pair and brood densities as well as broods/pair per census in
517 Beaver flowages (black) and control ponds (grey). Shown are medians and
518 interquartile ranges. For pairs, $n = 19$; for broods, $n = 18$; for broods/pair, $n = 12$.

519 Fig. 2. Teal pair (a) and brood densities (b) as well as broods/pair (c) at Beaver (Evo)
520 and non-Beaver (Nuuksio) landscapes during 1994–2014.

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523 Table 1. Teal pair density, brood density and broods produced per pair at the Beaver lakes and
 524 control, non-Beaver lakes of Evo landscape. Test results indicate the independent Mann-Whitney
 525 U-tests performed between the duck parameters of the Beaver lakes non-Beaver lakes. SD =
 526 standard deviation; Z = test value; significant results are bolded ($P < 0.05$). IQR = interquartile
 527 range.

| | Beaver lakes ($n=24$) | Non-Beaver lakes ($n=18$) | Test results |
|---------------|----------------------------|-----------------------------------|----------------------------------|
| Pair density | | | |
| Median | 0.46 | 0.29 | $Z = -1.707; P = 0.088$ |
| IQR | 1.31 | 0.33 | |
| Brood density | | | |
| Median | 0.06 | 0.00 | $Z = -2.188; P = \mathbf{0.029}$ |
| IQR | 0.46 | 0.04 | |
| Broods/pair | | | |
| Median | 0.03 | 0.01 | $Z = -2.322; P = \mathbf{0.020}$ |
| IQR | 0.15 | 0.02 | |

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