EFFECTS OF AGE, SEX, AND FAT LEVEL ON WING LOADING IN DARK-EYED JUNCOS

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Abstract.—Age- and sex-related variation in aerodynamically important traits such as wing loading may contribute to behavioral variation within a population. Increased wing loading also may be an important cost of carrying extra body fat, placing constraints on viable strategies of migratory and winter fattening. Therefore, we quantified the effects of age, sex, and fat level on wing loading in Dark-eyed Juncos (*Junco hyemalis*). Female juncos had significantly greater wing loading than males; wing loading did not differ among age classes. Increased fat levels (as indicated by fat scores) increased wing loading in all age/sex classes, but females and adults showed significantly greater fat-related increases in wing loading than males and immatures. Increasing from lean body mass to a full fat load added approximately 14 to 16% to an individual's wing loading. Wing loading increased allometrically with lean body mass in juncos (heavier individuals have relatively greater wing loading). We found sex- and fat-related variation in wing loading that is probably sufficient to affect flight performance and, therefore, susceptibility to predation, strategies of fattening, and distribution among individual Dark-eyed Juncos. *Received 7 December 1990, accepted 10 January 1992.*

Wing loading, a fundamental component of avian wing design, affects speed, maneuverability, and energy expenditure during flight (Rayner 1988, Pennycuick 1989, Norberg 1990 and references therein). Because wing loading is an important determinant of flight performance, interspecific differences (particularly large-scale taxonomic differences) in wing loading can be associated with ecological and behavioral variation among taxa (Greenewalt 1962, 1975, Norberg 1979, 1986, 1990:241, Norberg and Norberg 1988, Rayner 1988). Within species, wing loading can exhibit age- and sex-specific variation (e.g. Blem 1975, Mueller et al. 1981). Furthermore, widespread intraspecific variation in wing length (e.g. Alatalo et al. 1984) and wing shape (Gaston 1974, Tiainen and Hanksi 1985, Hedenström and Pettersson 1986, Mulvihill and Chandler 1990) suggests that variation in wing loading within species is common. This raises the possibility of ecologically significant covariation of aerodynamically important traits such as wing loading with foraging behavior, susceptibility to predation, or migratory dynamics within a population.

We analyzed intraspecific variation in wing loading in a passerine bird, the Dark-eyed Junco

(*Junco hyemalis*). Predicting the extent or direction of possible differences in wing loading among age/sex classes of juncos is difficult, because wing loading is the result of an interaction among body mass, wing length, and wing shape (all of which are characters that show age- and sex-related variation in juncos; Nolan and Ketterson 1983, Mulvihill and Chandler 1990). Furthermore, the body mass of juncos is subject to considerable temporal variation (e.g. during migratory or winter fattening) that will influence wing loading (Nolan and Ketterson 1983, Chandler and Mulvihill, unpubl. data). In fact, increased wing loading may be an important cost of carrying extra body fat (Blem 1975, Stuebe and Ketterson 1982, Nolan and Ketterson 1983), placing constraints on viable strategies of migratory or winter fattening (Lima 1986, Alerstam and Lindström 1990). Because of the potential ecological significance of age- and sex-specific variation in wing loading, and the hypothesized role of increased wing loading in constraining migratory and winter fattening, our objectives were: (1) to quantify age- and sex-related differences in wing area and wing loading among Dark-eyed Juncos; (2) to determine the aerodynamic cost (in terms of increased wing loading) of increasing fat levels in a passerine bird; and (3) to characterize the intraspecific relationship between wing loading and body mass.

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TABLE 1. Body mass, wing dimensions, and wing loading ($\bar{x} \pm$ SE) of age/sex classes of Dark-eyed Juncos. Ranges in parentheses.

Age and sex	n	Wing length (mm)	Body mass (g)	Wing area (cm²)	Wing loading (Nm⁻²)
Adult male	16	79.4 ± 0.30 (78.0–82.0)	20.6 ± 0.27 (18.5–22.4)	105.1 ± 0.83 (98.7–109.6)	19.3 ± 0.25 (17.1–20.8)
Adult female	9	73.9 ± 0.45 (71.5–76.0)	19.1 ± 0.36 (18.0–21.2)	90.5 ± 1.24 (85.1–95.7)	20.7 ± 0.29 (19.5–22.3)
Immature male	11	77.5 ± 0.36 (76.0–80.0)	20.3 ± 0.42 (18.2–22.7)	103.7 ± 1.22 (98.3–109.8)	19.2 ± 0.45 (17.2–21.4)
Immature female	15	72.7 ± 0.26 (71.0–74.5)	18.9 ± 0.29 (17.4–21.3)	91.6 ± 0.71 (88.0–96.9)	20.3 ± 0.28 (18.6–22.3)
Age[a]		***	ns	ns	ns
Sex[a]		***	***	***	***

[a] Two-way analysis of variance; ns, $P > 0.05$; ***, $P < 0.001$.

METHODS

Data collection.—Juncos were captured during the 1989 autumn migration at Powdermill Nature Reserve, field station of the Carnegie Museum of Natural History, Westmoreland County, Pennsylvania (for a detailed description of the study area, see Mulvihill and Chandler 1990). For each individual ($n = 51$), we carefully traced the outline of the fully extended right wing onto graph paper. We assumed that any measurement error associated with the tracing process was random with respect to age or sex of the bird. We also recorded the unflattened wing length (to the nearest 0.5 mm), body mass (to the nearest 0.1 g) on an electronic balance, and fat score (ranked from 0 to 3; Leberman 1967). All measurements were performed by the same person (Mulvihill). Although fat scores are subject to many sources of error, they are relatively reliable when assigned by a single, experienced observer working within a species (Krementz and Pendleton 1990).

Wing tracings were digitized (by Chandler) using Sigmascan, and total wing area was calculated as twice the area of the right wing (Pennycuick 1989:12). Wing area as used in this paper does not include the area of the body between the wings (cf. Norberg 1990:61, Pennycuick 1989:12). Wing loading is a measure of the body weight (body mass times gravitational acceleration, $g = 9.81$ m·s⁻²) per unit wing area (Pennycuick 1989:14, Norberg 1990:62). Wing loadings are reported in Newtons (N) per square meter (1 N = 1 kg m·s⁻²; SI units).

To quantify more precisely the relationship between body mass and fat scores (and thus wing loading), we supplemented the data from the 51 juncos for which we measured wing areas with data on body mass and fat scores from a sample of 1,107 fall-migrating juncos (382 adult males, 232 adult females, 204 immature males, 289 immature females) captured at Powdermill from 1987–1989. We weighed these birds and scored their fat levels exactly as we did for the 51 birds for which we measured wing areas.

Statistical analysis.—Variances in wing length, body mass, wing area, and wing loading among age/sex classes did not differ significantly from homogeneity (F-max test; $F_{max} = 1.7$, 1.6, 2.2, and 2.9, respectively; $P > 0.05$). The distribution of these variables within age/sex classes did not deviate significantly from normality (Kolmogorov–Smirnov test against standard normal distribution). Although sample sizes were small for rigorous tests, there was no evidence of pronounced deviation from homogeneity or normality.

We used two-way analysis of variance to assess differences among means for ages and sexes. Predictive equations relating body mass to fat score for each age/sex class were calculated using Model I least-squares regression. Exponents for the allometric equations relating wing area and wing loading to body mass were estimated as the slope of linear regressions from log-log plots. Although body mass is subject to natural variation and was measured with error (appropriate for Model II regression; Sokal and Rohlf 1981:460), we used a least-squares regression line because of its superior ability to predict wing area or wing loading for a particular body mass (Sokal and Rohlf 1981:549). We used analysis of covariance (ANCOVA) to compare the relationship of wing area and wing loading to lean body mass in male and female juncos.

RESULTS

Wing length differed significantly between ages and sexes of juncos, but body mass, wing area, and wing loading differed only between the sexes (Table 1). Although male juncos were significantly heavier than females, their relatively larger wing area resulted in smaller wing loadings (Table 1). There were no significant interactions between age and sex for these variables.

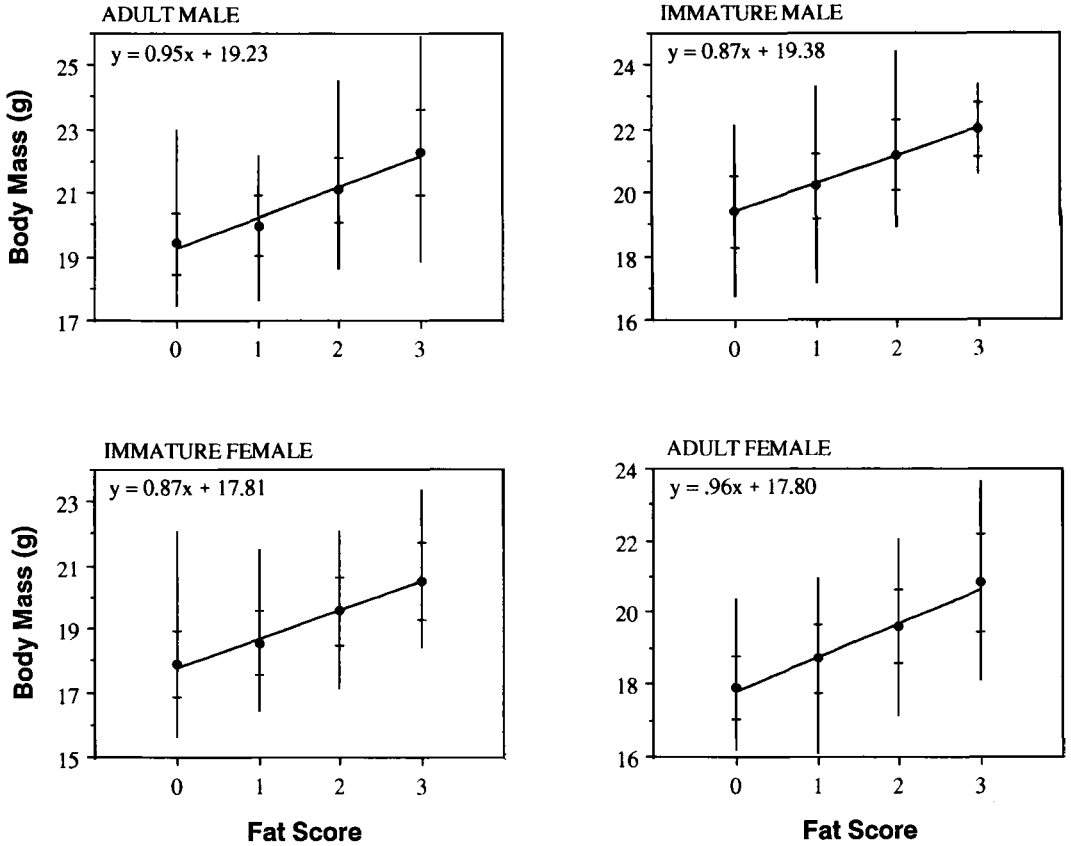Wing area was correlated with body mass in

Fig. 1. Relationship between body mass and fat score (ranked from 0 to 3) within classes of fall-migrating Dark-eyed Juncos captured at Powdermill Nature Reserve (1987–1989). Black dot, horizontal mark, and vertical line show mean, standard deviation, and range, respectively. Regressions fitted to raw data, and all four regression lines highly significant ($P < 0.001$).

female ($r = 0.50$, df = 22, $P = 0.01$, ages pooled), but not male ($r = 0.21$, df = 25, $P = 0.30$, ages pooled) juncos. Wing loading was correlated with body mass in both females ($r = 0.81$, $P < 0.001$, ages pooled) and males ($r = 0.83$, $P < 0.001$, ages pooled). These correlations, however, may obscure two distinct sources of variation in body mass—short-term variation due to differences in body fat (fat scores) and intrinsic differences in "size" (i.e. lean body mass). We used a sample of 1,107 juncos to quantify more precisely the relationship between body mass, fat scores, and wing loading.

Wing loading and fat levels.—For each age/sex class, there was a significant linear relationship between body mass and fat score (Fig. 1); fat scores explained approximately 45% of the variation in body mass among adult juncos (males, 45.6%; females, 45.0%) and approximately 37%

among immatures (males, 37.1%; females, 37.8%). On average, adult juncos add slightly more body mass per unit fat score than immatures (Fig. 1). Using the slopes of these predictive equations as an estimate of the change in body mass with a change in fat score (as scored at Powdermill), we calculated the expected change in wing loading (i.e. how much increasing fat scores would increase wing loading) for each individual in our sample given its wing area (Table 2). In each age/sex class, individuals accumulating body fat sufficient to result in a change in fat score of one unit would add approximately 0.9 to 1.0 Nm^{-2} to their wing loading (Table 2). Based on the changes in body mass predicted by the mass-fat regressions (Fig. 1), adult and female juncos show significantly larger increases in wing loading per unit increase in fat score than immatures and males (Table 2).
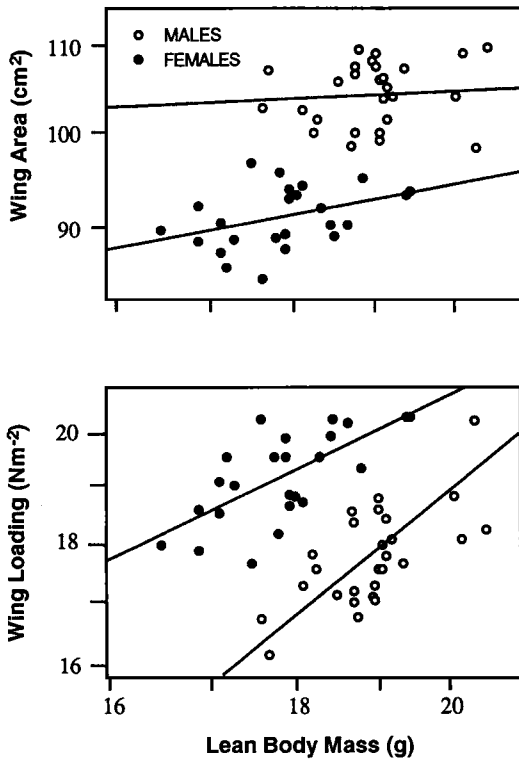
Fig. 2. Log–log plots of wing area and minimum wing loading against lean body mass in male and female Dark-eyed Juncos. Slopes of regression lines do not differ between sexes (ANCOVA; $F = 0.45$, df $= 1$ and 47, $P = 0.50$), but elevation of lines does (ANCOVA; $F = 106.7$, df $= 1$ and 48, $P < 0.001$). Slopes of lines estimate exponents for allometric relationships between wing dimensions and body mass.

Wing loading and body size.—Overall body size among the individuals in our sample, as measured by body mass, was confounded by variations in fat score. However, the predictive equations relating body mass to fat score (Fig. 1) can be used to estimate a lean body mass (i.e. body mass at a fat score of 0) for each individual. We estimated this mass by the equation:

$$Y = a - bX, \qquad (1)$$

where Y is lean body mass (in grams), a is body mass (in grams), b is the slope, and X is the fat score. The slope of the regression line (b) was appropriate for the age/sex class (Fig. 1). Wing loading was then recalculated using lean body mass in place of body mass (minimum wing loading; Table 2). There was little or no relationship between wing area and lean body mass

for both male ($b = 0.15$, $P = 0.44$, $r^2 = 0.02$, $n = 27$) and female ($b = 0.33$, $P = 0.05$, $r^2 = 0.15$, $n = 24$) juncos (Fig. 2). Because wing area showed little or no increase with increasing lean body mass, minimum wing loading increased strongly and significantly with lean body mass in both sexes (males, $b = 0.85$, $P < 0.001$, $r^2 = 0.45$; females, $b = 0.67$, $P < 0.001$, $r^2 = 0.45$; Fig. 2).

The estimated increase in wing loading resulting from a unit increase in fat score (Table 2) represents approximately 4.8% of minimum wing loading in males (adults $= 4.97\%$, immatures $= 4.59\%$) and approximately 5.1% in females (adults $= 5.37\%$, immatures $= 4.87\%$). Thus, a male junco going from lean body mass (fat score $= 0$) to a full fat load (fat score $= 3$) would add approximately 13.8 to 14.9% (depending upon age) to its wing loading. A female would add about 14.6 to 16.1%.

DISCUSSION

Wing area and body mass—the determinants of wing loading—differed between male and female juncos (Table 1). Although male juncos have greater body mass, their wing area also is relatively large, resulting in smaller wing loadings than females. Higher wing loading in females has been reported for other species as well (House Sparrow, *Passer domesticus*, Blem 1975; Sharp-shinned Hawk, *Accipiter striatus*, Mueller et al. 1981). It appears that the common pattern of intersexual differences in wing loading among these species exists despite distinctly different patterns of sexual dimorphism (males larger in juncos and House Sparrows, Blem 1975; females larger in Sharp-shinned Hawks, Mueller et al. 1981; see also Andersson and Norberg 1981). Unfortunately, however, patterns of intraspecific variation in aerodynamic traits are poorly documented relative to interspecific variation (e.g. Greenewalt 1962, 1975).

At the relatively slow flight speeds characteristic of small emberizids, low wing loading allows more maneuverable flight (Norberg 1979, Rayner 1988) and, presumably, greater abilities in predator avoidance (Blem 1975, Alerstam and Lindström 1990). The intersexual differences in wing loading reported here are similar in magnitude to differences interpreted as having consequences for maneuverability within a guild of foliage-gleaning birds (Norberg 1979). Blem (1975) reported detectable effects on the flight capability of House Sparrows over a range of

TABLE 2.   Effect of fat score on wing loading, lean body mass, and minimum wing loading ($\bar{x} \pm$ SE) in Dark-eyed Juncos. Ranges in parentheses.

Age and sex	n	Δ wing loading/ Δ fat score	Lean body mass (g)	Minimum wing loading (Nm^{-2})
Adult male	16	0.89 ± 0.007 (0.85–0.94)	19.1 ± 0.16 (18.0–20.3)	17.8 ± 0.18 (16.5–19.0)
Adult female	9	1.04 ± 0.014 (0.98–1.11)	17.9 ± 0.23 (17.0–19.3)	19.4 ± 0.24 (18.1–20.2)
Immature male	11	0.82 ± 0.010 (0.78–0.87)	19.4 ± 0.24 (18.2–21.0)	18.3 ± 0.29 (17.2–20.5)
Immature female	15	0.93 ± 0.007 (0.88–0.97)	17.9 ± 0.21 (16.5–19.6)	19.2 ± 0.22 (17.7–20.5)
Age[a]		*	ns	ns
Sex[a]		***	***	***

[a] Two-way analysis of variance; ns, $P > 0.05$; *, $P < 0.05$; ***, $P < 0.001$.

wing loadings comparable to the maximum differences observed among individual juncos (the sparrows were weighted artificially). Small differences in wing loading also contribute significantly to interspecific variation in maneuverability of bats (Aldridge 1986a, b). These results suggest that the sex-specific differences in wing loading among juncos are likely to be ecologically significant, with males enjoying a maneuverability advantage relative to females.

Because of their higher wing loading, female juncos should be less maneuverable. Other things being equal, this could result in sex-specific differences in predation risk, foraging behavior (e.g. proximity to cover) or social interactions (e.g. group size). This interpretation is complicated by the fact that the wing shape of female juncos differs significantly from that of males (i.e. all other things are not equal). Specifically, females have shorter, more rounded wings than males (Mulvihill and Chandler 1990), and these traits enhance rapid takeoff and maneuverability at slow flight speeds (Savile 1957, Alatalo et al. 1984, Norberg 1990:238). Thus, the wing shape of female juncos may compensate partially for maneuverability losses due to high wing loading.

Although some of the aerodynamic consequences of intersexual differences in wing loading are clear, the ultimate cause of these differences is not. Low wing loading may allow males to carry higher fat loads and, thus, winter closer to the breeding grounds (Nolan and Ketterson 1983), or it may minimize the allometric constraints that wing loading places on large size in males (see below). However, lower wing loading in males also occurs in species without sexual segregation on the wintering grounds (Blem 1975) and in species where males are smaller than females (Mueller et al. 1981). Thus, the potential adaptive significance of intersexual differences in wing loading and wing shape in Dark-eyed Juncos is uncertain (Mulvihill and Chandler 1990).

Wing loading and fat levels.—Unlike aerodynamic traits such as wing length or wing shape, wing loading can show considerable short-term variation due to fluctuations in body mass (via changes in body fat). Furthermore, the effects of increased body mass on wing loading may constrain viable strategies of migratory and winter fattening in birds (Blem 1975, Stuebe and Ketterson 1982, Nolan and Ketterson 1983, Lima 1986, Alerstam and Lindström 1990). In juncos, increased fat score results in increased body mass (Fig. 1) and an appreciable addition to wing loading (Table 2). Juncos accumulating body fat sufficient to go from a lean body mass (no visible fat) to a maximum fat load (fat score = 3) add approximately 14 to 16% to their wing loading. Artificial increases in wing loading of this approximate magnitude (16–19% increase via added weights) result in slower flight with increased wingbeat frequency and amplitude in Eurasian Kestrels (*Falco tinnunculus*; Videler et al. 1988a, b). House Sparrows also showed reduced flight capabilities (i.e. they were less able to avoid capture in an aviary) when their wing loading was increased by 15 to 20% (Blem 1975).

The results of Blem (1975) and Videler et al. (1988a, b) suggest that, at their maximum, the fat-related increases in wing loading of juncos are sufficient to affect flight capabilities and, possibly, predator avoidance. Fattening in jun-

cos appears to carry a significant aerodynamic cost (Lima 1986, Alerstam and Lindström 1990). Unexpectedly, this cost differs among both ages and sexes (Table 2). Future researchers should consider that equal increases in fat score do not necessarily result in equal increases in wing loading among ages or sexes.

The effects of fat on wing loading also may have implications for the differential winter distribution of age/sex classes of juncos (Ketterson and Nolan 1976, 1979). Although all age/ sex classes experience increased wing loading at higher fat levels, females begin with higher minimum wing loading and show the greatest increase in loading per unit fat score (Table 2). Within a sex, adults show significantly greater fat-related increases in wing loading than immatures (Table 2). Thus, females and adults pay a higher cost than males and immatures (in terms of increased wing loading) to maintain high levels of body fat. Because wintering at high latitudes requires the maintenance of higher fat levels than wintering farther south (Nolan and Ketterson 1983), female and/or adult juncos may be at an aerodynamic disadvantage at high latitudes (cf. Blem 1975). Perhaps not coincidentally, females and adults winter, on average, south of males and immatures (Ketterson and Nolan 1976, 1979). Although sex- and age-specific differences in the relationship between fat levels and wing loading are unlikely to explain completely patterns of differential migration in juncos (conceivably, differential winter distributions may permit these differences rather than result from them), intraspecific variation in aerodynamic traits such as wing loading may play an under-appreciated role in affecting habitat use and distribution in birds.

Wing loading and body size.—Wing area and wing loading increase with increasing body mass in birds (Greenewalt 1962, 1975). For these increases to be isometric (i.e. with no change in relative proportions), wing area should increase as the 0.67 power of body mass, and wing loading should increase as the 0.33 power of body mass (Norberg 1990:169). With the exception of hummingbirds, broad interspecific comparisons have yielded exponents similar to these (Norberg 1990:168–172).

Scaling relationships observed at the interspecific level, however, are not reflected at the intraspecific level in juncos (also, see Norberg 1990: fig. 10.1). Although wing area and wing loading increase with lean body mass in juncos,

calculated exponents (estimated as the slope of regressions from log–log plots; Fig. 2) deviate substantially from those based on interspecific comparisons. Wing area increases slowly with increasing body mass in both male and female juncos (Fig. 2). As a result, larger (heavier) juncos have relatively greater wing loading than smaller ones in both sexes (Fig. 2). Although large size is an advantage in dominance interactions among juncos (Ketterson 1979), the allometric relationship between wing loading and body mass is probably one constraint on the advantages of large size (Blem 1975). If so, the lower absolute wing loading of male juncos (Fig. 2) may minimize this constraint.

Several studies have shown that slight differences in aerodynamic traits can have important effects on ecology and behavior (e.g. Blem 1975, Feinsinger and Chaplin 1975, Norberg 1979, 1981, Aldridge 1986a, b, Norberg and Rayner 1987, Norberg and Norberg 1988, Videler et al. 1988a, b). The differences in wing loading observed among juncos of differing sex and fat scores are similar in magnitude to differences interpreted as ecologically significant among species or shown to affect flight performance within species. Although the specific effects of wing-loading variation in juncos may be complicated by patterns of age- and sex-related variation in wing shape (Mulvihill and Chandler 1990), there is clearly considerable potential for intraspecific variation in flight morphology to affect ecology and behavior within populations of Dark-eyed Juncos.

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