

EFFECTS OF GROWTH-RATE VARIATION ON FLEDGING OF RHINOCEROS AUKLETS (*CERORHINCA MONOCERATA*)

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ABSTRACT.—I examined the effects of variation in growth rate on the time of fledging of nestling Rhinoceros Auklets (*Cerorhinca monocerata*) on Pine Island, British Columbia, in 1989 and 1990. In both years, among unmanipulated nestlings, age at fledging was inversely related to growth rate, whereas mass at fledging was positively related to growth rate. The results of a supplementary feeding study in 1989 showed that food-supplemented chicks grew faster and fledged at a younger age and heavier mass than did unsupplemented chicks, replicating the patterns observed in unmanipulated nestlings. These results are consistent with the predictions of models that consider the fledging decision in alcids is made at the best time for the nestling to shift between two habitats (land and sea) with different fitness characteristics (growth and mortality). Interannual comparisons did not provide the same results. Chick growth rate was higher in 1989 than in 1990 and mass at fledging was correspondingly higher. Age at fledging, however, was the same in both years. I present several possible explanations for the discrepancy between the intra- and interannual comparisons. Received 16 April 1993, accepted 19 August 1993.

AMONG SPECIES in the family Alcidae, there is high intraspecific variability in juvenile life histories (reviewed in Gaston 1985, Harris and Birkhead 1985, Ydenberg 1989). Developmental parameters such as nestling growth rate, peak mass, age at fledging, and mass at fledging may vary over a breeding season, within and among colonies, and between years. Rhinoceros Auklets (*Cerorhinca monocerata*), for example, fledge between 40 and 70 days of age at 45 to 85% of adult body mass (Vermeer and Cullen 1979, Wilson and Manuwal 1986, Harfenist 1991). The observed variation in juvenile development often is characterized as a proximate response to factors such as variations in food availability and quality, nest-site quality, or ambient temperature (e.g. Nettleship 1972, Vermeer and Cullen 1979, Gaston 1985). Few researchers, however, have discussed how selective pressures might influence the evolution of behavior in response to this environmental variation.

Life-history theory provides an evolutionary perspective on the patterns in the time of fledging found in alcids. For the purposes of this discussion, fledging will be considered as the time at which a nestling makes a transition between two habitats with contrasting fitness

characteristics: the nest and the ocean (Ydenberg 1989). Assuming that the chick faces a trade-off between a relatively safe nesting habitat with low growth and a more dangerous ocean habitat with potentially higher growth, the optimal time of fledging can be calculated as the best time (i.e. that which maximizes the chick's probability of survival to breeding) to make that transition (Ydenberg 1989, Clark and Ydenberg 1990a).

The predicted optimal time of fledging for alcids is sensitive to the chick growth rate in the nest. When growth in the nest varies, a negative relationship between mass and age at fledging is expected, with faster-growing chicks fledging heavier and younger than slower-growing chicks (see Ydenberg 1989:fig. 5). This negative relationship has been predicted consistently by models developed using data from the Common Murre (*Uria aalge*; Ydenberg 1989), Atlantic Puffin (*Fratercula arctica*; Clark and Ydenberg 1990a) and Rhinoceros Auklet (Ydenberg et al. 1995).

Rhinoceros Auklets exhibit one of the widest ranges of growth rate, age at fledging, and mass at fledging of alcids; these parameters vary both within and among years (Vermeer and Cullen 1979, Wilson and Manuwal 1986, Bertram et al. 1991). My study was designed to examine the variation in the time of fledging in Rhinoceros Auklets at one colony, using three comparisons:

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(1) natural intra-annual variation in 1989 and 1990; (2) experimentally induced variation in growth rate in 1989; and (3) natural interannual variation between 1989 and 1990. The predictions tested were that faster-growing nestlings would fledge earlier and at a higher mass than slower-growing young, thus producing an overall negative relationship between the age and mass at fledging.

METHODS

In mid-June of 1989 and 1990, I excavated Rhinoceros Auklet burrows on Pine Island, British Columbia (50°58'N, 127°41'W). Excavation involved digging holes through the roof of burrow tunnels until the entire burrow was accessible; between visits access holes were covered with cedar shingles, soil, and moss. I weighed all chicks found to the nearest 2.5 g on a 500-g Pesola scale and measured wing length, from the wrist to the tip of the flattened wing, to the nearest millimeter using Vernier callipers or, after the primaries began to emerge, a ruler. Nestlings were aged using a regression of age on wing length derived from data on nine known-age chicks in 1989; aging was accurate to within one day (Harfenist 1991). Wing length is considered a reliable estimator of chick age because it is relatively independent of the nutritional status of the chick (Vermeer and Cullen 1979). Only burrows that held chicks less than two weeks of age upon first excavation were used because variation in wing length with age increases after this point (Wilson 1977).

Supplementary feeding experiment.—In 1989, when chicks in five study plots reached 13 days of age and were capable of swallowing experimentally proffered fish, they were assigned alternately to one of two experimental groups: (1) Supplemented referred to chicks between 13 days of age and fledging that were weighed, measured, and then fed 30 g of freshly thawed surf smelt (*Hypomesus pretiosus*) every second day as a supplement to the food delivered to them by their parents ($n = 55$). An average of about 30 g of fish were brought per trip by provisioning adults to their chicks on Pine Island in July 1985 and 1986 (Bertram and Kaiser 1988). Only a few chicks had to be force fed when they were very young. (2) Unsupplemented chicks were weighed and measured every second day, but not fed supplementary fish ($n = 55$).

The growth rate for each chick was calculated as the slope of the regression line relating chick age and mass between the beginning of the experiment (13 days) and 37 days of age. This interval corresponds closely to the linear portion of the chicks' sigmoidal growth curve. I used the first day that I failed to find a chick in its burrow as the date of fledging and the mass on the last day that the chick was weighed as the mass at fledging.

Intra- and interannual growth comparisons.—In 1989, an additional 65 burrows in relatively undisturbed areas of the colony were used for intra- and inter-annual comparisons of chick growth and fledging. I weighed and measured the nestlings at 10 days of age and again at 42 days of age, but did not disturb the chicks during the interim. Once the chicks reached 42 days of age, they were weighed and measured every second day until fledging. Age and mass at fledging were determined as described above. In 1990, a similar protocol was followed to monitor a group of 70 unmanipulated burrows. In both years, I calculated the daily growth rates for each bird by subtracting the mass at 10 days of age from that at 42 days, and then dividing by 32. This measure of growth might be biased because the interval used extends slightly beyond the linear portion of the growth curve.

Statistical analysis.—I compared the back-calculated hatching date, mass at various ages, growth rate, peak mass, mass at fledging, age at fledging, and date at fledging using a one-way analysis of variance (ANCOVA). Analysis of covariance (ANCOVA) was used to compare the regression statistics describing chick growth parameters. All statistical analyses were performed using SYSTAT 5.03 (Wilkinson 1989).

In both 1989 and 1990, some study burrows became inaccessible during the breeding season. In addition, six chicks disappeared when only partly feathered. All data from these burrows were excluded from all analyses.

RESULTS

The inverse relationship between mass at fledging and age at fledging for unmanipulated chicks was significant in both 1989 and 1990 (Fig. 1); the slope of the regression line was steeper in the latter year (ANCOVA; homogeneity of slopes, $F = 4.44$, $df = 1$, $P = 0.037$). There were significant negative relationships between age at fledging and growth rate in both years (Fig. 2), confirming that the younger-fledged chicks were the fastest growers. Mass at fledging and growth rate were significantly positively related in both 1989 and 1990 (Fig. 3).

The supplementary feeding significantly increased the growth rate of supplemented chicks above that of unsupplemented chicks (Table 1). Mass at fledging was significantly greater in the supplemented birds. In contrast, the age at fledging was significantly lower in the supplemented nestlings. Hatching date and mass at 13 days did not differ between treatments, which indicates that chicks in the two groups were of similar age and condition at the start of the experiment.

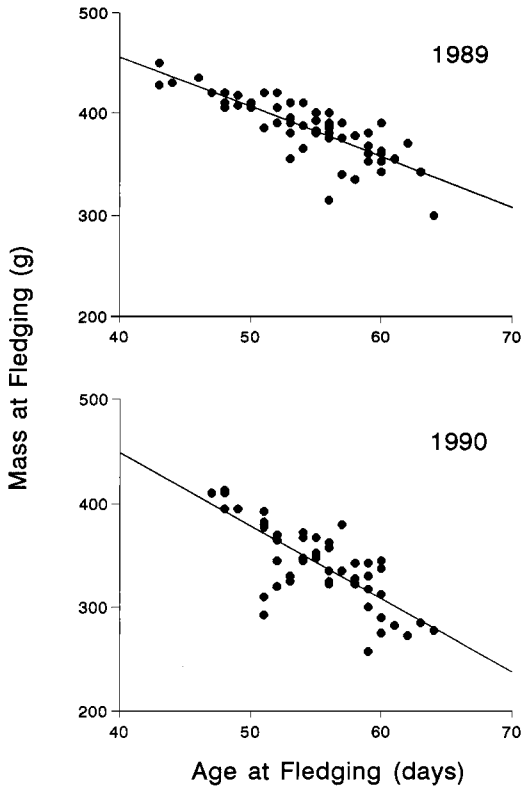


Fig. 1. Relationship between mass and age at fledging in unmanipulated burrows in 1989 ($Y = 663.4 - 5.1X$; $r^2 = 0.70$; $F = 125.2$, $df = 1$ and 54 , $P < 0.001$) and 1990 ($Y = 729.4 - 7.0X$; $r^2 = 0.60$; $F = 76.4$, $df = 1$ and 51 , $P < 0.001$).

A significant inverse relationship existed between mass and age at fledging within both the supplemented and unsupplemented groups (Fig. 4). The slopes and intercepts of the two regression lines are statistically indistinguishable (ANCOVA; homogeneity of slopes, $F = 0.58$, $df = 1$, $P = 0.449$; homogeneity of Y -intercepts, $F = 0.14$, $df = 1$, $P = 0.715$).

The mean growth rate for the supplemented chicks was lower than that for the unmanipulated birds in the same year ($F = 16.78$, $df = 1$ and 99 , $P < 0.001$). Presumably, the extensive handling of chicks involved in the experimental procedure had a negative influence on chick growth.

Growth parameters of unmanipulated nestlings in 1989 and 1990 are given in Table 2. Mass at 10 and 42 days, growth, and mass at fledging were significantly higher in 1989 than in 1990. Hatching dates, fledging dates, and age

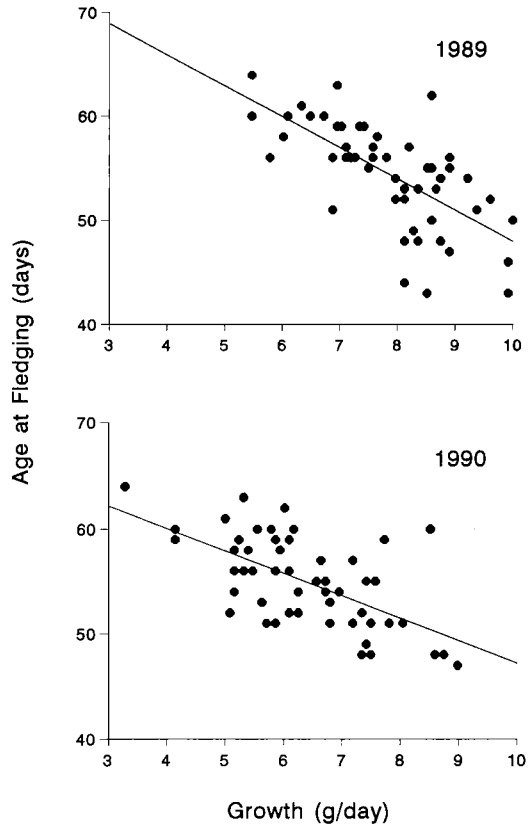


Fig. 2. Relationship between age at fledging and growth rate in unmanipulated burrows in 1989 ($Y = 77.9 - 3.0X$; $r^2 = 0.46$; $F = 46.4$, $df = 1$ and 54 , $P < 0.001$) and 1990 ($Y = 68.6 - 2.1X$; $r^2 = 0.37$; $F = 29.6$, $df = 1$ and 51 , $P < 0.001$).

at fledging, however, were the same in both years.

DISCUSSION

Models of alcid fledging behavior from the chick's perspective (i.e. that maximize the chick's survival to breeding) predict that the mass and age at fledging should vary with growth rate; faster-growing chicks should fledge at a younger age and heavier mass than slower-growing chicks (Ydenberg 1989, Ydenberg et al. 1995). These trends should produce an inverse relationship between mass at fledging and age at fledging. This negative relationship arises from the relative costs and benefits to the chick of staying versus leaving the nest (Ydenberg et al. 1995). Slower-growing chicks will be smaller at a given age and should continue to take ad-

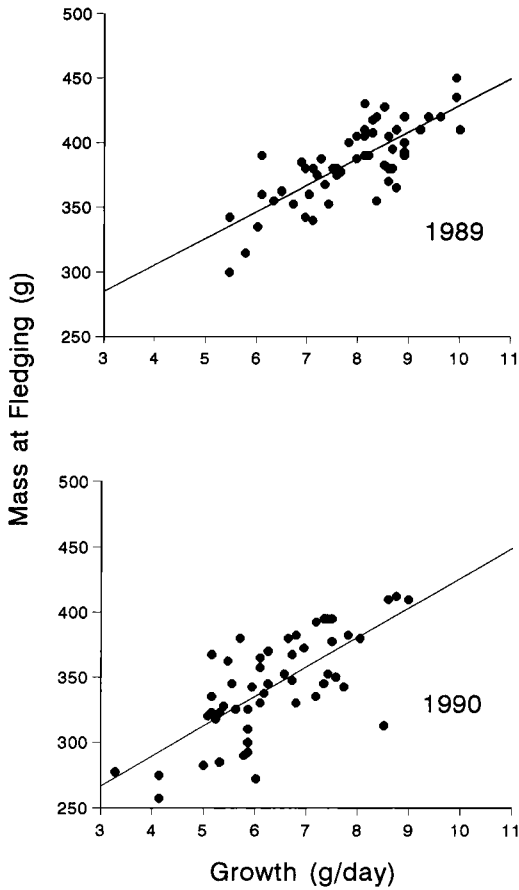


Fig. 3. Relationship between mass at fledging and growth rate in unmanipulated burrows in 1989 ($Y = 212.5 + 21.8X$; $r^2 = 0.65$; $F = 100.7$, $df = 1$ and 54 , $P < 0.001$) and 1990 ($Y = 198.1 + 22.8X$; $r^2 = 0.51$; $F = 52.7$, $df = 1$ and 51 , $P < 0.001$).

vantage of the safety of the nest, whereas faster-growing chicks should forego the safety of the nest for potentially higher growth at sea. The assumption of declining nest growth rate with

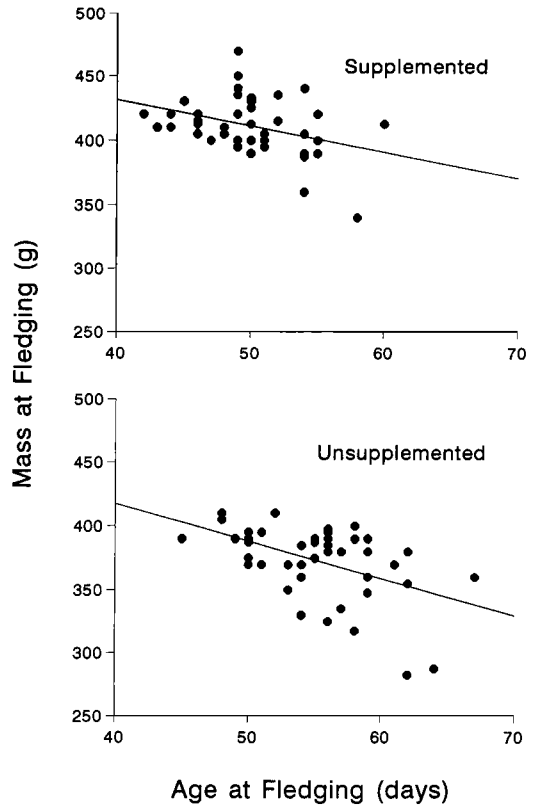


Fig. 4. Relationship between mass and age at fledging for supplemented ($Y = 511.6 - 2.0X$; $r^2 = 0.12$; $F = 5.5$, $df = 1$ and 40 , $P = 0.024$) and unsupplemented ($Y = 534.9 - 2.9X$; $r^2 = 0.23$; $F = 12.8$, $df = 1$ and 43 , $P = 0.001$) Rhinoceros Auklet chicks in supplementary feeding study.

increasing body size as the chick approaches fledging, found in Rhinoceros Auklets (e.g. Wilson 1977, Vermeer and Cullen 1979, Watanuki 1987), is essential to this prediction.

The natural intra-annual variation in growth rates in both 1989 and 1990 produced the pre-

TABLE 1. Growth parameters ($\bar{x} \pm SD$) of Rhinoceros Auklet chicks in supplementary feeding study on Pine Island in 1989.

	Supplemented ($n = 42$)	Unsupplemented ($n = 45$)
Hatching date ^a	17.0 \pm 5.14	16.8 \pm 4.88
Mass at 13 days (g)	170.5 \pm 16.96	164.6 \pm 15.79
Growth (g/day) ^{***}	7.4 \pm 0.75	6.3 \pm 0.85
Peak mass (g) ^{***}	415.8 \pm 19.65	381.3 \pm 31.41
Mass at fledging (g) ^{***}	411.1 \pm 22.67	372.3 \pm 28.54
Age at fledging (days) ^{***}	50.0 \pm 3.91	55.4 \pm 4.65

^a day 1 = 1 June.

^{***}, $P < 0.001$.

TABLE 2. Growth parameters ($\bar{x} \pm SD$) of Rhinoceros Auklet chicks from unmanipulated burrows on Pine Island in 1989 and 1990.

	1989 (n = 56)	1990 (n = 53)
Hatching date ^a	15.7 ± 4.27	16.4 ± 5.19
Mass at 10 days (g) ^{***}	128.8 ± 12.94	117.8 ± 18.81
Mass at 42 days (g) ^{***}	380.3 ± 33.09	321.7 ± 43.11
Growth (g/day) ^{***}	7.9 ± 1.12	6.4 ± 1.21
Mass at fledging (g) ^{***}	383.9 ± 30.35	343.5 ± 38.68
Age at fledging (days)	54.4 ± 4.94	55.0 ± 4.27
Fledging date ^a	70.1 ± 6.62	71.4 ± 7.01

^a day 1 = 1 June.

^{***}, $P < 0.001$.

dicted patterns. Fledging mass was positively related to growth rate and fledging age was negatively related to growth rate. These patterns produce the inverse relationship between mass and age at fledging predicted by the model and found in both years of my study. Thus, in the intra-annual comparisons, Rhinoceros Auklet chicks that grew faster fledged at a heavier mass and younger age than those that grew more slowly.

The supplementary feeding study was designed to evaluate experimentally the effects of growth on the chick's fledging decision. The supplemented chicks grew faster and, as predicted, had a higher mean fledging mass and a lower mean fledging age than did the unsupplemented controls. The two regression lines were statistically indistinguishable, which suggests that one line adequately describes the optimum time of fledging for all of the nestlings used in this experiment, but that different parts of that boundary were reached by the two groups of chicks.

In two other studies, investigators have manipulated the growth rate of Rhinoceros Auklet nestlings. In one case, growth was increased by cross-fostering auklet chicks with Tufted Puffins (*Fratercula cirrhata*; Vermeer and Cullen 1979) and, in the second, the growth rate was decreased by twinning chicks (Summers and Drent 1979). In both studies, faster-growing nestlings fledged at a heavier mass; the age at fledging was not reported in either case.

Data from the literature on alcids suggests that the trends described by my results are not confined to Rhinoceros Auklets. A positive relationship between growth rate and fledging mass is characteristic, whereas an inverse relationship between growth rate and age at fledging is less prevalent (Table 3). "Fledging" used in this context refers to the time when chicks

leave their colonies and is not truly fledging in all cases. The studies summarized in Table 3 include intraseasonal comparisons, feeding and fostering manipulations, and a single-parent study. Inconsistencies in methodologies and in reporting significance values make it difficult to compare and evaluate some of the results.

The interannual comparison of chick growth parameters of Rhinoceros Auklets on Pine Island did not exhibit the same patterns as did the intra-annual and experimental comparisons. Although mass at 10 days, growth, and mass at fledging were significantly higher in 1989 than in 1990, the age at fledging was the same in the two years. The interannual comparison is the weakest of my three tests because other environmental variables are not controlled between years.

In contrast to the results of my interannual comparisons, interannual studies of Rhinoceros Auklets on Triangle Island (British Columbia), Protection and Destruction islands (Washington), and Teuri Island (Japan) found the patterns predicted by the models. In years of higher chick growth, chicks fledged at a higher mass and after a shorter nestling period than in poorer growth years (Vermeer and Cullen 1979, Wilson and Manuwal 1986, Watanuki 1987). Comparisons of data from widely separated Washington colonies within the same year produce similar results (Wilson and Manuwal 1986), as do intercolony comparisons of growth data from the closely related Atlantic Puffin in Norway (Barrett and Rikardsen 1992).

Further evidence for the generality of the inverse relationship between mass and age at fledging in alcids is provided by compilations of chick growth data for two species from several colonies over many years. Data have been summarized for the Atlantic Puffin (Harris 1984: 211) and the Thick-billed Murre (*Uria lomvia*;

TABLE 3. Reported relationships of growth rate with mass and age at fledging in alcids.

Comparison	Relationship ^a between growth rate and		Source
	Mass at fledging	Age at fledging	
Thick-billed Murre (<i>Uria lomvia</i>)			
Intra-annual	+ ^b	- ^b	Gaston and Nettleship 1981
Intra-annual	+	NR	Birkhead and Nettleship 1982
Common Murre (<i>U. aalge</i>)			
First vs. replacement clutch	+	0	Hedgren and Linnman 1979
Pigeon Guillemot (<i>Cephus columba</i>)			
Position in brood	+	- ^c	Emms and Verbeek 1991
Cassin's Auklet (<i>Ptychoramphus aleuticus</i>)			
First vs. second brood	+	-	Manuwal 1979
Atlantic Puffin (<i>Fratercula arctica</i>)			
Twinned chick vs. control	+	-	Corkhill 1973
Single parent vs. control	+	-	Harris 1978
Supplementary feeding experiment	+ ^c	0	Harris 1978
Single parent vs. control	+ ^d	- ^d	Ashcroft 1979
Supplementary feeding experiment	0	0	Hudson 1979
Twinned chick vs. control	- ^d	- ^d	Harris 1984
Tufted Puffin (<i>F. cirrhata</i>)			
Fostered chick vs. control	+	NR	Vermeer and Cullen 1979
Rhinoceros Auklet (<i>Cerorhinca monocerata</i>)			
Twinned chick vs. control	+ ^d	+ ^d	Summers and Drent 1979
Fostered chick vs. control	+	NR	Vermeer and Cullen 1979
Supplementary feeding experiment	+	-	This study
Intra-annual	+	-	This study

^a Significant ($P < 0.05$) unless otherwise noted. NR = not reported.

^b Relationship with mass at fledging significant in two of four years and not reported in other two years; relationship with age at fledging significant in one of four years.

^c Significance unknown.

^d Significant at one of two sites; unlikely that growth rates significantly changed with supplementary feeding.

Ydenberg et al. 1995). A significant negative regression of mass on age at fledging is apparent for both species.

The models discussed above consider fledging from the chick's perspective, with the assumption that the chick controls the time of fledging. The validity of this assumption, however, is debatable. Wilson (1977) reported that Rhinoceros Auklet chicks may refuse food as they approach fledging. In addition, fish are often found in Rhinoceros Auklet burrows after the chicks have fledged (pers. obs.), indicating that, in some cases, the chicks leave even though at least one parent is still delivering food. This suggests that nestlings leave when they are ready, and are not abandoned by their parents. Citing similar evidence, Harris (1976) concluded that nestling Atlantic Puffins desert their parents and not vice versa. However, Bertram (1988) reported that Rhinoceros Auklet parents

seemed to provision according to their own schedule and not according to the needs of the chick in the latter half of the nestling period. Thus, parents also may control fledging through food deliveries. Clark and Ydenberg (1990b) compared the optimal time of fledging from the perspectives of parents and chicks. Because of different fitness costs and benefits to nestlings and parents, the optima are expected to differ. Calculations of the optimal time of fledging from either perspective, however, predict a negative relationship between age and mass at fledging and a dependence of time of fledging on nestling growth rate (Clark and Ydenberg 1990b).

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