

# Survival consequences of sex-biased growth and the absence of a growth–mortality trade-off

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## Summary

1. Growth rate is of considerable importance to the life histories of indeterminately growing organisms. Its determination of size at age can generate positive associations with several traits, although the rate at which size increases with time has been negatively linked with survival. Such a trade-off may not, however, be evident at growth rates considerably less than species-specific maxima, nor need links between growth and life history be similar for both sexes.

2. Based on a 5-year, mark–recapture study of an unexploited population of Brook Trout (*Salvelinus fontinalis*) near the edge of the species' range, I tested the null hypotheses that seasonal growth does not differ between sexes and that survival is independent of growth rate. Both hypotheses were rejected.

3. Faster growth by males during summer, and by females during winter, can be explained by seasonal differences, by sex, in the proportional allocation of energy to gonads and soma.

4. Survival increased with growth rate per se, independently of the latter's effects on size at age; survival among males appears more dependent on growth than that of females.

5. The results indicate that there can be fitness costs associated with slow growth, that these costs can differ between sexes, and that they may be exacerbated during periods of energetic stress. Trade-offs between growth and survival may depend on the behavioural and developmental contexts in which they are examined, need not be ubiquitous and may vary throughout a species' geographical range.

*Key-words:* Brook Trout, costs of reproduction, energy allocation, life history, seasonal variation

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## Introduction

Few parameters are of greater import to the fitness of indeterminately growing organisms than growth rate. Reflecting both individual size at age and the rate at which that size is attained, growth can significantly influence several life-history traits, such as age and size at maturity, most notably through its effects on fecundity and survival (Roff 2002). In fish, for example, fast-growing individuals generally mature earlier in life than slower-growing individuals (Alm 1959), and larger individuals produce greater numbers of eggs, often at larger sizes, than smaller individuals (Hutchings 1993; Wootton 1998; Roff 2002). Also, the larger size at age achieved by faster-growing individuals often leads to lower mortality because of the survival benefits associated with large body size (Shuter & Post 1990; Conover 1992; Hutchings 1994).

However, it is not clear how growth rate might affect

survival independently of its influence on body size. To some extent, this depends on the scale at which the association is examined. The mortality effect of a high growth rate is reflected by one of the classic life-history invariants in fish, denoted by  $K/M$ . Representing the ratio of a metric of growth (from the von Bertalanffy growth equation) to the instantaneous rate of mortality, its invariance across taxa implies that species or populations characterized by rapid individual growth are also characterized by high mortality (Beverton & Holt 1959; Charnov 1993; but see Purchase, Hutchings & Morgan 2006). At the individual level, negative consequences to survival may be effected by physiological, metabolic and developmental costs associated with compensatory growth, defined as accelerated growth following a period of retarded growth (Metcalf & Monaghan 2001). For example, rapid growth during larval development is associated with delays in cranial ossification in Pumpkinseed Sunfish (*Lepomis macrochirus*), leading to reduced survival early in life (Arendt & Wilson 2000). Based on correlations observed among species, increased metabolic rate (one metric of growth)

is associated with reduced longevity (Fenchel 1974; Southwood 1976). From an ecological perspective, faster-growing individuals may place themselves at greater risk of predation if faster growth can only be achieved by longer foraging times or riskier foraging behaviour (Holtby & Healey 1990; Werner & Anholt 1993; Biro *et al.* 2004; Yurewicz 2004).

Fitness costs associated with rapid growth may be realized only at specific stages of life, such as those during early development, or at ages or sizes at which vulnerability to predation is greatest. At rates considerably less than species-specific maxima, growth rate may well be a surrogate of fitness (Schluter 1995), particularly when growth rate is a reliable metric of individual condition (Rowe & Thorpe 1990).

A long-term study of individually marked Brook Trout (*Salvelinus fontinalis*) in south-eastern Newfoundland, Canada, provided an opportunity to test the null hypothesis that survival is independent of growth rate. Indeed, if a positive association is more likely to be observed in environments in which the prospects for growth are poor, then it may well be realized near the edge of this species' native distribution, where populations are characterized by the smallest minimum size at maturity known for the species (62 mm for males; 70 mm for females; Hutchings 1996) and by annual rates of individual growth that are not infrequently nil (Hutchings 1993; Wilson, Hutchings & Ferguson 2003).

These mark-recapture data can also be used to examine the degree to which any association between growth and survival differs among seasons and between sexes. Under the assumption that female reproductive success is limited primarily by fecundity, while that of males is limited primarily by number of mates, it is reasonable to hypothesize that sexual differences in seasonal growth can arise from differences in the rates at which energy is allocated to gonadal tissue and somatic tissue. If survival is associated with growth, independent of body size, then sexual differences in seasonal growth may differentially affect the postreproductive survival of males and females.

## Materials and methods

### THE STUDY POPULATION

The population inhabiting Freshwater River on Cape Race, south-eastern Newfoundland, having previously been the subject of life-history (e.g. Hutchings 1991, 1993, 1994; Hutchings *et al.* 1999), behavioural (Hutchings & Gerber 2002) and genetic research (Ferguson, Danzmann & Hutchings 1991; Hutchings & Ferguson 1992; Wilson *et al.* 2003), has many attributes for ecological study. Brook Trout is the only species of fish in the river and the population is not subjected to avian forms of predation, negating the potential influence of interspecific competition and predation on survival and growth (neither predatory

birds nor mammals have been observed at this site since studies began in 1987). The population is unexploited and is otherwise unaffected by anthropogenic disturbance. The 50-m cliff at which the river enters the sea effectively prevents migration to other rivers, rendering the population closed and genetically distinct. Freshwater River is 2.2 km in length; average width and depth measure 3.14 m and 16.8 cm, respectively. From a life-history perspective, Freshwater River trout typically mature at small sizes (80–100 mm) and at young ages (2–3 year). Females are distinguished by the production of fewer than 100 relatively large eggs (4–5 mm diameter) and a high proportional allocation of body tissue to gonads (15–20% of total body weight), relative to other populations on Cape Race.

### MARK-RECAPTURE STUDY

Passive Integrated Transponder (PIT) tags (Biomark Inc., Boise, Idaho, USA) were inserted into 943 trout between 11 and 17 June 1995 ( $n = 354$ ) and between 11 and 13 June 1996 ( $n = 589$ ). The PIT tags, small ( $12.0 \times 2.1$  mm<sup>2</sup>) glass cylinders comprising a coil and an integrated circuit programmed to transmit one of some billions of codes, were inserted into the body cavity of anaesthetized individuals through a 3-mm long incision immediately anterior to the base of the anal fins. The adipose fin was marked by a fin clip to identify tagged individuals upon recapture. Trout were initially captured by electrofisher from one of 38 sections of river averaging  $27.5 \text{ m} \pm 3.3 \text{ m SE}$  in length. All fish were returned to the stream section in which they were captured once they had fully recovered from the tagging procedure. Post-tagging mortality was nil prior to the return of fish to the river.

To resample marked individuals, the entire length of the 2.2-km long unobstructed section of river upstream of the mouth was electrofished twice annually in spring (between 26 May and 13 June) and in autumn (between 26 September and 3 October) from 1995 until 2000, when the number of recaptures had declined to nil. During the resampling phase, the river was divided into 59 sections, averaging  $33.9 \pm 2.7$  SE metres in length. Section lengths did not differ between the tagging and resampling periods ( $F_{1,95} = 2.21$ ,  $P = 0.14$ ). The timing of the autumn sampling periods coincided with spawning, which allowed mature individuals to be sexed by external characteristics (extrusion of milt, visible evidence of eggs beneath the body wall, shape of the urogenital opening). In addition to being sexed, all individuals were measured for fork length.

### DATA ANALYSIS

To examine the influence of season and sex on individual growth, I compared the proportional increase in body length of males and females at different time periods throughout the year. To quantify growth rate,

I compared the lengths of marked individuals recaptured in October of year  $x$  and in June of year  $x + 1$  with their lengths in June of year  $x$ . This permitted a direct comparison of seasonal growth between the sexes during summer (June to October) and throughout the year (June to June), and an indirect comparison of growth during winter/early spring (i.e. October to June), based on growth differences experienced during the other two periods. Although growth might also be estimated from seasonal and annual differences in body mass, data on individual weights are not available for the fish examined in the present study. However, proportional changes in length are typically reflected by even greater proportional changes in body weight (Wootton 1998). As a consequence, the use of proportional differences in length might then be considered to provide a conservative estimate of growth.

To examine the effect of growth rate on survival, I undertook two different analyses. Firstly, I analysed the degree to which growth experienced during summer affected survival from October to the following June. In the second analysis, I assessed the influence of growth between year  $x$  and year  $x + 1$  on the probability of survival between years  $x + 1$  and  $x + 2$ , where  $x$  was the year of tagging (1995 or 1996). For example, for a fish marked with a PIT tag in June 1995, annual growth rate was quantified as the proportional increase in length between June 1995 and June 1996, and survival was monitored from June 1996 to June 1997. Given that sampling for recaptured fish continued biannually until October 2000, there were nine and seven separate occasions during which the presence of marked fish could have been ascertained for fish tagged in 1995 and 1996, respectively. If a fish had not been recaptured during any of the resampling occasions after year  $x + 1$ , it was assumed to have been dead at the beginning of year  $x + 2$ . If a fish had been recaptured either at the beginning of year  $x + 2$ , or at any resampling occasion thereafter, it was assumed to have been alive at the beginning of year  $x + 2$ . Fish identified as being dead or alive at the beginning of year  $x + 2$  were coded 0 and 1, respectively, for analysis.

In addition to growth rate, I also examined the degree to which sex, body size at the beginning and end of the growth periods, year of tagging, resampling location in the river and age influenced seasonal and annual survival. The age of each fish was estimated from age-length keys developed for trout in Freshwater River by Hutchings (1993) and by Wilson *et al.* (2003).

#### STATISTICAL ANALYSIS

Given that survival is a binary variable (individuals being either dead or alive), the effects of the aforementioned explanatory variables on survival were estimated with the use of a generalized linear model, permitting linear modelling of a binary response variable (McCullagh & Nelder 1989). Following Crawley (2002), I began the analysis with a fully saturated

model, i.e. one that included all the factors, covariates and interactions of interest, using the *glm* function of S-Plus. To simplify the model, I then excluded the least significant parameter estimate in a step-wise fashion, examining the Akaike information criterion (AIC) associated with the model at each step. When deletion of a parameter resulted in an insignificant increase in the residual deviance of the fitted model, reflected by a decrease in the AIC associated with that model, the parameter was excluded from the model. The final model was the one that included nothing but statistically significant variables.

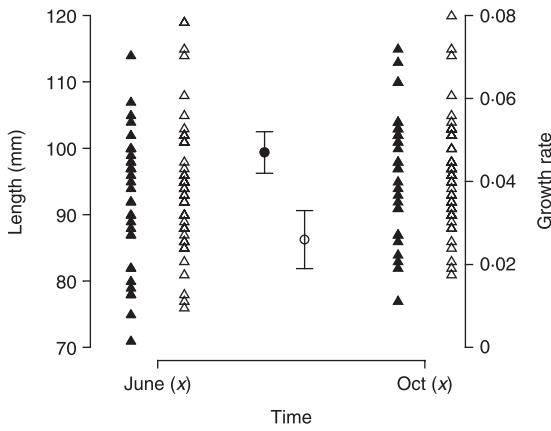
## Results

#### EFFECT OF SEX ON SEASONAL GROWTH

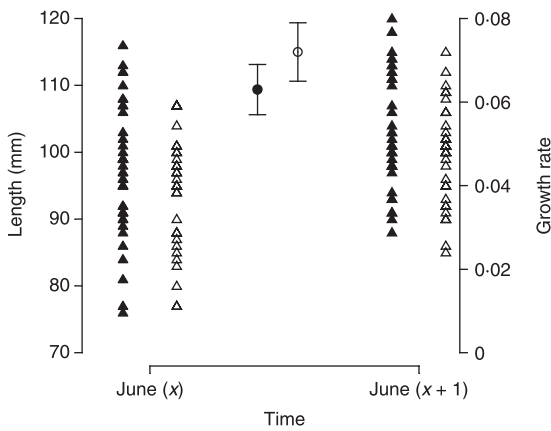
There was no significant difference in body length between males and females. Among individuals for which growth between June and October could be estimated, males ( $n = 36$ ) and females ( $n = 48$ ) were equal in body size, being  $94.8 \text{ mm} \pm 2.2 \text{ mm SE}$  and  $94.5 \text{ mm} \pm 1.4 \text{ mm SE}$ , respectively, in June ( $F_{1,82} = 0.01$ ,  $P = 0.92$ ), and  $99.3 \pm 2.1 \text{ mm}$  and  $97.0 \pm 1.3 \text{ mm}$ , respectively, in October ( $F_{1,82} = 1.10$ ,  $P = 0.300$ ). The estimated age of marked individuals did not differ between sexes ( $F_{1,82} = 0.01$ ,  $P = 0.99$ ), averaging  $2.36 \pm 0.14$  year for males and  $2.11 \pm 0.09$  year for females. Among individuals for which annual growth could be estimated, males ( $n = 40$ ) and females ( $n = 34$ ) were again equal in body size, being  $97.2 \text{ mm} \pm 1.2 \text{ mm SE}$  and  $93.9 \text{ mm} \pm 1.0 \text{ mm SE}$ , respectively, in June of year  $x$  ( $F_{1,72} = 2.63$ ,  $P = 0.109$ ), and  $103.3 \pm 1.3 \text{ mm}$  and  $100.7 \pm 1.1 \text{ mm}$ , respectively, in June of year  $x + 1$  ( $F_{1,72} = 2.82$ ,  $P = 0.098$ ). Among these individuals, for which annual growth could be estimated, the age of marked individuals did not differ between sexes ( $F_{1,72} = 0.31$ ,  $P = 0.577$ ), averaging  $2.29 \pm 0.10$  year for males and  $2.22 \pm 0.09$  year for females.

Growth rate during summer differed between sexes. Between June and October, the proportional increase in length by males was almost twice ( $4.7 \pm 0.5\%$ ) that of females ( $2.6 \pm 0.4\%$ ) ( $F_{1,93} = 12.53$ ,  $P = 0.001$ ) (Fig. 1). By comparison, the proportional increase in length between June in one year and June the following year did not differ between males and females ( $F_{1,117} = 0.93$ ,  $P = 0.337$ ), being  $6.3 \pm 0.6\%$  and  $7.2 \pm 0.7\%$ , respectively (Fig. 2). Taking the difference in these average annual and summer growth rates, females grew  $4.6\%$  between October and the following June compared with only  $1.6\%$  for males. Age, body size or year of tagging had no significant effect on growth rate for either males or females ( $P > 0.05$ ).

Among the 11 individuals (7 females) for which length data were available for all three time intervals (i.e. June and October of year  $x$  and June of year  $x + 1$ ), there was no correlation between growth during summer (June to October) and growth experienced during winter/early spring (October to June) ( $r = -0.24$ ,  $P = 0.486$ ).



**Fig. 1.** Summer growth rate of male (closed symbols) and female (open symbols) Brook Trout from Freshwater River, Newfoundland, Canada. Triangles represent fork lengths measured in June and in October for the same individuals. Circles represent the average proportional increase in length between June and October (error bars represent 1 SE about the mean).

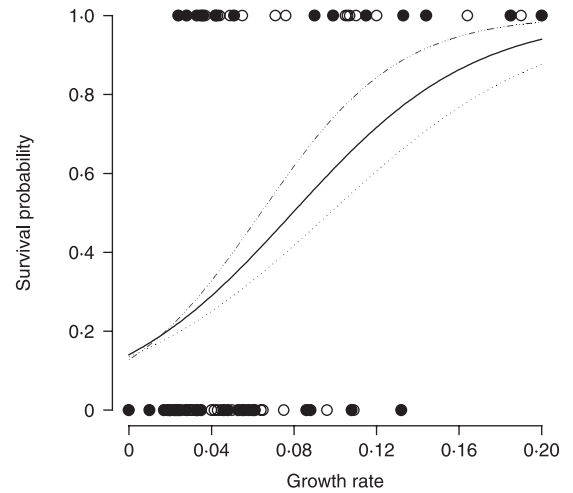


**Fig. 2.** Annual growth rate of male (closed symbols) and female (open symbols) Brook Trout from Freshwater River, Newfoundland, Canada. Triangles represent fork lengths measured in June of year  $x$  and in June of year  $x + 1$  for the same individuals. Circles represent the average annual proportional increase in length (error bars represent 1 SE about the mean).

**EFFECT OF GROWTH ON SURVIVAL**

Several independent variables were initially included in the fully saturated binary regression model used to identify factors responsible for influencing seasonal survival from October to the following June. These explanatory variables included: (1) growth rate between June and October; (2) body length in June; (3) body length in October; (4) year of tagging; (5) age; (6) sex; and (7) resampling location within the river. Based on the model simplification procedure outlined previously, none of these factors was significantly associated with survival during winter and early spring ( $P > 0.05$  for all variables).

To study the influence of many of the same variables on annual survival, the fully saturated model included: (1) growth rate between years  $x$  and  $x + 1$ ; (2) body length at the beginning of year  $x$ ; (3) body length at the beginning of year  $x + 1$ ; (4) year of tagging; (5) age; (6)



**Fig. 3.** Binomial regressions between annual survival probability and proportional increase in length throughout the previous year for male (closed symbols; dashed line) and female (open symbols; dotted line) Brook Trout from Freshwater River, Newfoundland, Canada (solid line is for all data combined).

sex; and (7) resampling location within the river. Based on the stepwise deletion of variables from the saturated model, the only variable significantly associated with survival was growth rate (Fig. 3). Annual growth rate was positively associated with survival during the following year for both males ( $t_{40} = 2.28, P = 0.014$ ) and females ( $t_{32} = 2.36, P = 0.012$ ). The binomial regressions between annual survival ( $Y$ ) and growth rate ( $X$ ) were:

$$Y = \exp(-1.92 + 30.01X) / [1 + \exp(-1.92 + 30.01X)]$$

for females, eqn 1

and

$$Y = \exp(-1.86 + 19.09X) / [1 + \exp(-1.86 + 19.09X)]$$

for males. eqn 2

Although the regression coefficients and the plots of growth vs survival (Fig. 3) suggest that females experienced higher survival rates per unit of growth than males, an ANCOVA failed to detect significant differences between the models for the two sexes. Accordingly, the data for males and females were pooled. Again, among the factors initially included in the saturated model, growth rate was the only variable that significantly influenced survival ( $t_{74} = 3.26, P < 0.001$ ). The binomial regression between survival and growth rate for both sexes combined was  $Y = \exp(-1.81 + 22.82X) / [1 + \exp(-1.81 + 22.82X)]$ .

**Discussion**

**SEX-BIASED SEASONAL GROWTH AND ENERGETIC TRADE-OFFS**

Season and sex can influence the growth rate of mature Brook Trout, and growth can in turn influence survival.

For the unexploited population studied here, males grow faster than females during summer, while females experience more rapid growth in winter and early spring. Among males, growth during summer is three times greater than that during the autumn, winter and spring. Among females, the reverse is true, growth during non-summer months being almost twice that experienced in summer. Although growth rate during summer does not appear to influence survival through the following winter, growth rate averaged throughout one year is positively associated with the probability of surviving the following year. Seasonal differences in the influence of growth rate on survival suggest that growth during winter is of greater importance to annual survival than growth during summer.

Although reports of sex-biased growth are unusual in salmonid fish, they are not unprecedented. Based on length-at-age comparisons of Coho Salmon (*Oncorhynchus kistutch*) returning from sea to spawn, females are often larger at a given age than males (Holtby & Healey 1990; Spidle, Quinn & Bentzen 1998). Coupled with the observation that such populations tend to be male-biased (thought to be indicative of higher at-sea mortality of females), the faster growth experienced by females may be the result of a trade-off balancing the mortality costs of a risk-prone foraging strategy with the growth benefits of ultimately achieving a large size (Holtby & Healey 1990).

Notwithstanding evidence of sex-specific foraging strategies in other fishes, such as Masu Salmon (*O. masou*) (Nagata & Irvine 1997) and American Plaice (*Hippoglossoides platessoides*) (Swain 1997), it is not clear that this provides a sufficient explanation for the sex bias in seasonal growth documented here for Brook Trout, given that annual growth rates were statistically equal between males and females. Instead, the sexual difference in summer growth may be attributed to a sex bias in the allocation of resources between skeletal growth and the storage of reserves. Seasonal differences in this physiological trade-off have been documented by Metcalfe, Bull & Mangel (2002), based on responses by fully fed immature Atlantic Salmon (*Salmo salar*) to previous experimental reductions in body fat. In summer, salmon allocated resources to both the restoration of lipid reserves and to growth in length. In winter, fish restored their lipid reserves but experienced negligible growth in length.

Seasonal differences in the allocation of energy to growth and to energy reserves may explain the sex bias in seasonal growth reported here. Given the polygynous mating system of salmonid fish, coupled with an absence of parental care, it is reasonable to assume that female mating success is limited primarily by the number of eggs she produces, which is a function of lipid reserves, whereas males are limited primarily by the number of individuals with whom they can mate. All else being equal, one might expect females to allocate proportionately more energy to gonadal tissue in the months immediately preceding spawning, and less

to skeletal growth, than males (Jonsson, Jonsson & Hansen 1991; Jonsson & Jonsson 2003). Indeed, among female trout in another Cape Race river, gonadal tissue comprises more than twice the total body lipids (19%, as a percentage of total body weight) than it does in males (8%) (Hutchings *et al.* 1999). Such a discrepancy in the proportional allocation of energy to the gonads may account for the sex bias in growth observed among Freshwater River females during the summer months preceding autumnal spawning.

By contrast, their considerably reduced growth during winter and early spring suggests that males are allocating proportionately more energy to the replenishment of lipids during this period, and less to skeletal growth, than females. The hypothesis that males have a greater energy deficit to make up during winter than females is supported empirically by the observation that postreproductive males in Watern Cove River, Newfoundland, lose proportionately more lipids during winter (58% reduction) than postreproductive females (42% reduction) (Hutchings *et al.* 1999).

#### ABSENCE OF A GROWTH-MORTALITY TRADE-OFF

The present study indicates that growth rate can be positively associated with survival in fish. The discrepancy between this observation and those documented or inferred in other studies requires explanation. Reports of a negative association between growth rate and survival tend to be associated with growth experienced very early during development (Arendt & Wilson 2000; Metcalfe & Monaghan 2001) or with growth hypothesized to be concomitant with risky foraging behaviour (Holtby & Healey 1990; Werner & Anholt 1993; Spidle *et al.* 1998; Metcalfe & Monaghan 2001). However, growth experienced later in life may not be similarly burdened with early developmental costs to survival. Correspondingly, faster growth need not always be associated with greater risks of predation, particularly for territorial species that can select habitats based on their susceptibility to predation and for fishes, such as salmon and trout, that feed on drifting invertebrates while maintaining a relatively stationary position in rivers and streams.

Among studies that have reported a positive association between growth and survival, there is evidence that faster-growing Atlantic Salmon experience higher survival at sea (Friedland *et al.* 2000; but see Crozier & Kennedy 1999) and that faster-growing individuals have a higher probability of surviving winter than slower-growing individuals (Shuter & Post 1990; Conover 1992). However, the causal basis for these positive associations appears to be a function of the larger size attained by faster-growing individuals, coupled with the benefits of large size to survival, rather than any benefit accruing from faster growth per se.

Thus, what distinguishes the present study is the finding that growth rate, independent of body size, can

have a positive influence on survival. The question remains whether it is growth experienced throughout the entire year, or that experienced during a particular season, that is of import to survival. Although annual growth rate was significantly associated with survival in Freshwater River Brook Trout, growth experienced during summer was not. Also, there was no correlation between growth experienced during the summer and that in the following winter within the same individual. These associations between growth and survival suggest that winter and early spring are the seasons during which growth has the greatest influence on annual survival. This may not be unreasonable, given that winter is probably the most energetically stressful season for northern temperate fish that spawn in autumn (Cunjak & Power 1986), a hypothesis supported by Metcalfe *et al.*'s (2002) observation that energy is allocated preferentially to replenishing lipid reserves in winter and by the finding that mortality among trout on Cape Race is highest during the winter months (Hutchings 1993, 1994).

From a life-history perspective, the positive correlation between growth rate and survival documented here identifies a direct association between size-at-age and fitness. Given the slow rates of growth observed among Brook Trout in Freshwater River, the present results could also be interpreted as one of identifying the survival costs of not growing at all. The sex bias in seasonal growth can be explained by sexual differences in the proportional allocation of energy to growth, suggesting that fitness costs associated with slow or minimal growth differ between sexes and may well be exacerbated during periods of energetic stress.

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