

Variation in the reproductive rate of bats

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Abstract: In many respects, bats have relatively slow life histories. However, the reproductive rate of bats (i.e., the proportion of females that reproduce in any breeding season) has not been critically examined. We compiled data on the reproductive rates of bats to test predictions based on life-history theory. Among 257 samples from 103 species, reproductive rate varied considerably and was typically under 100%. Temperate-zone species had significantly lower and more variable reproductive rates than did tropical species. Reproductive rate also varied among families, with species in the Vespertilionidae having particularly high rates. As predicted based on life-history theory, reproductive rate was negatively correlated with longevity, and among vespertilionids, species with larger litters had higher reproductive rates. Thus, the data suggest that bats have relatively slow reproductive rates and, as in other life-history traits, fall at the "slow" end of the fast-slow life-history continuum found among mammals. Female bats, especially those in temperate regions, appear to adjust their allocation of resources to reproduction, and at times forego reproduction, perhaps in relation to their body condition, prey availability, and weather conditions.

Résumé : Les chauves-souris ont, à plusieurs titres, des cycles biologiques relativement lents. Cependant, leur taux de reproduction (i.e., la proportion des chauves-souris qui se reproduisent dans une saison donnée de reproduction) n'a jamais été examiné de façon critique. Une compilation des données sur les taux de reproduction des chauves-souris nous a servi à vérifier certaines prédictions basées sur la théorie démographique. Dans 257 échantillons contenant 103 espèces, le taux de reproduction varie considérablement et il est typiquement inférieur à 100 %. Les espèces de la zone tempérée ont des taux de reproduction significativement plus bas et plus variables que les espèces tropicales. Les taux de reproduction varient aussi d'une famille à l'autre et les Vespertilionidae ont des taux particulièrement élevés. Tel que prédit par la théorie démographique, le taux de reproduction est en corrélation négative avec la longévité et, chez les vespertilionidés, les espèces à portées plus nombreuses ont aussi des taux de reproduction plus hauts. Ces données indiquent que les chauves-souris possèdent des taux de reproduction relativement lents et, comme leurs autres caractéristiques démographiques, leurs taux de reproduction se situent à l'extrémité « lente » du continuum rapide-lent des cycles biologiques trouvés chez les mammifères. Les chauves-souris femelles, particulièrement celles des régions tempérées, semblent ajuster l'allocation de leurs ressources à la reproduction et, à certains moments, elles s'abstiennent de se reproduire, peut-être en relation avec leur condition physique, la disponibilité des proies et les conditions climatiques.

[Traduit par la Rédaction]

Introduction

Among mammals, life-history characteristics tend to vary with body size. Small mammals generally have large litters of small neonates that grow and mature rapidly but live a short life. Large mammals have small litters, and young that grow and mature slowly but have a long reproductive life-span (Western and Ssemakula 1982; Read and Harvey 1989). Bats are unusual in that they are small mammals with a slow life history (Barclay and Harder 2003). The majority of bats weigh less than 100 g, and yet most have one litter per year of one or two young that develop slowly. Longevity records

for several well-studied species exceed 30 years (Wilkinson and South 2002), with the current record being 38 years for a Brandt's bat, *Myotis brandtii* (Eversmann, 1845) (Khiritankov and Ovodov 2001). As predicted by life-history theory (Promislow and Harvey 1990), the slow life history typical of bats is associated with low rates of extrinsic mortality. Reduced mortality may be one of the advantages provided by flight (Pomeroy 1990), but flight may also impose constraints on the life-history options available to bats (Barclay 1994; Barclay and Harder 2003).

Although some aspects of the life histories of bats have received attention (e.g., Austad and Fischer 1991; Barclay 1994; Holmes and Austad 1994; Kunz and Stern 1995; Wilkinson and South 2002), a recent review of the evolution of bat life histories (Barclay and Harder 2003) identified fecundity (reproductive rate) as one aspect that has not been examined critically. Life-history theory predicts that in species such as bats, in which adult survival is high and higher than that of juveniles (e.g., Humphrey and Cope 1976; Thompson 1987; Hoyle et al. 2001), fitness is maximized by foregoing reproduction when conditions are unfavourable. Thus, if weather conditions reduce the availability of food or

Received 13 August 2003. Accepted 28 April 2004. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 22 June 2004.

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a female is in poor body condition, the optimal strategy is to allocate resources to self-maintenance rather than reproduction. Females should enhance their own chance for survival and future reproduction rather than investing in young that have a relatively low chance of surviving to reproduce.

Although life-history theory leads to the prediction that bats should have relatively low reproductive rates, several studies have suggested that virtually all adult females reproduce (Humphrey and Cope 1970; Humphrey 1975; Racey 1982; Lumsden and Bennett 1995). This impression could be due, in part, to sampling females at maternity roosts where reproductive females congregate because of thermal and other benefits (e.g., Chruszcz and Barclay 2002; Kunz and Lumsden 2003). Such samples may not be representative of entire populations (e.g., Pearson et al. 1952), and other studies indicate that in at least some species a considerable proportion of females do not reproduce each season (e.g., Grindal et al. 1992; Cryan et al. 2000). No comprehensive analysis of fecundity among bats has been conducted. Thus, the goals of our study were to compile data on the reproductive rate of bats and to test predictions regarding its variation in accordance with life-history theory.

We predicted that bat reproductive rates correlate with other life-history traits. In particular, reproductive rate should correlate with the mortality rate of adults and with litter size or the number of young produced per year. Factors that favour increased production of young should also favour high reproductive rates. For several reasons, we also predicted that reproductive rate correlates negatively with latitude. Populations of bats at higher latitudes are more likely to encounter conditions that compromise the survival of both adults and young because the breeding season is relatively short and weather conditions vary from year to year. In addition, species in which individuals hibernate have longer life-spans than those that do not (Wilkinson and South 2002), although the mortality rate of hibernating juveniles over their first winter is particularly high (Humphrey and Cope 1976; R.M.R. Barclay, unpublished data). Thus, the difference between adult and juvenile mortality rates may be greater than in species at lower latitudes that do not hibernate. This should favour reduced resource allocation to reproduction in populations at higher latitudes, and thus lower reproductive rates.

Methods

We gathered data on the reproductive rates and life histories of bats from published papers, government reports, theses, and unpublished data (through personal communications).² Some reproductive rates were available from tabular data, whereas in other cases we extracted values from graphical representations of seasonal patterns. We included a reproductive rate from a study if it was based on at least 10 adult females during the reproductive season. We defined reproductive rate as the proportion of adult females that were either demonstrably pregnant, lactating, or post lactating during a particular reproductive season. Because pregnancy

can be difficult to detect early in the season, we only included females caught after the first lactating female was caught, by which point we assumed that pregnancy should be obvious. Some detectably pregnant females may abort and lactating females may abandon their young (Wimsatt 1945; Schowalter et al. 1979). Therefore, our measure of reproductive rate likely overestimated reproductive success. We used this measure because information regarding weaning success of bats is almost nonexistent. We distinguished data obtained from captures at maternity roosts (e.g., buildings, tree roosts, and caves) from data obtained from females captured at more "random" sites such as foraging grounds. This allowed us to test the prediction that estimates of reproductive rates from maternity colonies are biased. When there were multiple studies on the same species and sample type (roost or random), we averaged the reproductive rates and latitudes. For two species, *Eptesicus fuscus* (Palisot de Beauvois, 1796) and *Pipistrellus pipistrellus* (Schreber, 1774), litter size varies across the species' range and we thus included samples from populations with litters of one and with litters of two.

We analyzed data using SAS version 8.01 (SAS Institute Inc., 2000). We arcsine square-root transformed the reproductive rate values to meet assumptions of normality (Zar 1984), but present back-transformed values for graphical purposes. We present means \pm SE. SEs of back-transformed values are asymmetrical about the mean (Zar 1984). We analyzed the effect of latitude and various species' characteristics (i.e., body mass, diet, number of young per year) using general linear models (PROC GLM). For all analyses, we used an α value of 0.05.

Results

We obtained data² for 103 species from 12 families of bats, although species of Vespertilionidae dominated the sample (47 species). The data included 257 datum points, representing samples from different locations for some species and multiple years for some. Measures for all life-history traits were not available for all species, and thus, analyses used different sample sizes depending on which variables were included in the statistical model.

Reproductive rate varied significantly among species ($F_{[12,113]} = 3.31$, $P < 0.001$, $r^2 = 0.26$). Values for specific species ranged from 32.3% to 100% and were as low as 0% for samples from specific years and latitudes. In 52 of the 257 samples (20.2%), 100% of the females were reproductive in a particular year at a specific location. In the initial ANOVA, we included body mass, diet (animal or plant), family, latitude, number of young produced per year, and whether the sample came from roost or random captures. Diet, mass, and young per year had no significant effect on reproductive rate ($P > 0.05$), and thus, we removed them sequentially from the model. Whether samples came from roosts or random captures also had no effect ($P > 0.05$), and thus, we pooled them by latitude per species for the final model. The final model included family affiliation and the

²Supplementary data for this article are available on the Web site or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Ottawa, ON K1A 0S2, Canada. DUD 3586. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 1. Relationship between the latitude (°) of individual studies and the reproductive rate (i.e., proportion of females that reproduce in any breeding season) of female bats.

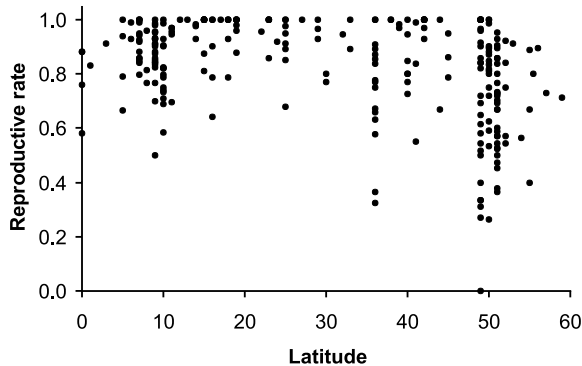
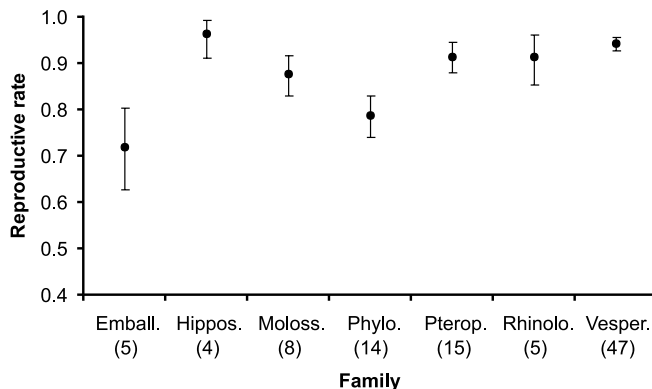


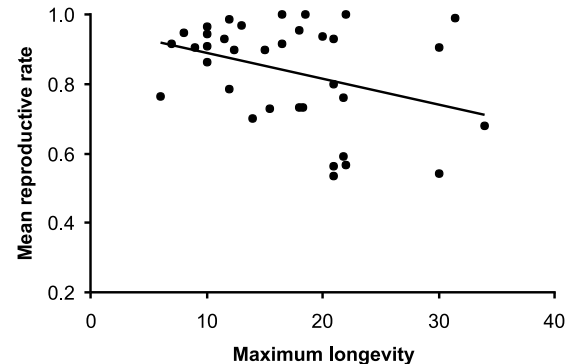
Fig. 2. Mean (\pm SE) reproductive rate (i.e., proportion of females that reproduce in any breeding season) for various families of bats. Emball., Emballonuridae; Hippos., Hipposideridae; Moloss., Molossidae; Phyllo., Phyllostomatidae; Pterop., Pteropodidae; Rhinolo., Rhinolophidae; Vesper., Vespertilionidae. Sample sizes (i.e., number of species) are in parentheses and SEs are asymmetrical as a result of back transformations from log-transformed values.



square of the sample's latitude. We used latitude-squared because latitude had a curvilinear relationship with reproductive rate. Reproductive rate declined with latitude ($F_{[1,113]} = 23.82$, $P < 0.001$; Fig. 1). The family that a species belonged to also significantly affected reproductive rate ($F_{[11,113]} = 2.27$, $P = 0.015$; Fig. 2). We compared the least-squared mean reproductive rate for the seven families with sample sizes of at least four species, using the Bonferroni adjustment to the α value ($\alpha = 0.0024$; Sokal and Rohlf 1995). Vespertilionids had a significantly higher mean reproductive rate than did phyllostomatids when latitude was accounted for ($t = 3.55$, $P < 0.001$). The difference between emballonurids and vespertilionids was almost significant ($t = 2.97$, $P = 0.0036$; Fig. 2).

Because almost half the data came from species of Vespertilionidae, and that family has the greatest latitudinal range of any family of bats, we analyzed variation in reproductive rates of vespertilionids separately. We also analyzed rates for all other families combined. Among vespertilionids ($n = 63$ samples), once nonsignificant effects were removed from the model, the reproductive rate varied significantly

Fig. 3. Relationship between the maximum-recorded longevity (years) for species of bats and their mean reproductive rate (i.e., proportion of females that reproduce in any breeding season). The line represents the best fit linear regression.



($F_{[2,60]} = 16.94$, $P < 0.001$) with latitude-squared ($F_{[1,60]} = 30.85$, $P < 0.001$) and the body mass (log-transformed) of the species ($F_{[1,60]} = 8.31$, $P = 0.006$). Samples from higher latitudes again had lower reproductive rates, and smaller species had lower rates. Samples from latitudes below 33° had significantly higher reproductive rates ($n = 130$; mean \pm SE: $96.7 + 1.2\%$ and $96.7 - 1.5\%$) than did those from higher latitudes ($n = 30$; $80.2 + 2.0\%$ and $80.2 - 2.1\%$) ($t = 6.01$, $P < 0.001$). In addition, samples from higher latitudes had significantly greater variation than those from lower latitudes ($F_{[29,129]} = 1.94$, $P = 0.04$).

Among species in families other than Vespertilionidae, reproductive rate varied significantly ($F_{[13,50]} = 2.29$, $P = 0.018$). As with the overall sample, families differed significantly ($F_{[10,50]} = 2.27$, $P = 0.028$) and reproductive rate declined with latitude-squared ($F_{[1,50]} = 5.74$, $P = 0.020$). There was also a significant interaction between latitude-squared and whether the sample came from roost or random captures ($F_{[1,50]} = 8.10$, $P = 0.006$).

To test predictions regarding correlations between life-history traits, we analyzed the relationship between the number of litters per year or young per litter and reproductive rate. Among vespertilionids, the only family of bats with species having litters of more than one young (Barclay and Harder 2003), species with litters of one had significantly lower reproductive rates ($n = 36$; mean \pm SE: $84.7 + 3.1\%$ and $84.7 - 3.4\%$) than did species with larger litters ($n = 26$; $95.6 + 1.5\%$ and $95.6 - 1.9\%$) ($t_{[60]} = 2.96$, $P = 0.004$). Among species in other families, reproductive rate did not differ between those with one litter per year ($n = 31$) and those with more than one litter per year ($n = 27$) ($t_{[56]} = 0.77$, $P = 0.45$). There was also no significant relationship between a species' reproductive rate and either length of gestation or length of lactation ($P > 0.05$ in each case).

There was a significant negative relationship between a species' reproductive rate and its maximum-recorded life-span when mass was included as a covariate ($F_{[2,32]} = 3.43$, $P = 0.045$, $r^2 = 0.18$; Fig. 3). Species with higher reproductive rates have shorter maximum longevity ($F_{[1,32]} = 5.27$, $P = 0.028$; arcsine square-root transformed reproductive rate = $1.38 - 0.012(\text{maximum longevity})$; $n = 35$).

For a limited number of species, we obtained data for reproductive rates of samples from different latitudes or for more than 1 year at the same latitude. In 6 of 21 temperate-

zone species with data for more than 1 year, the proportion of females that were reproductive varied significantly from year to year (χ^2 tests, $P < 0.05$). These included *Lasionycteris noctivagans* (LeConte, 1831) (3 years, range 33.3%–100% at 50°N; M. Vonhof, personal communication), *Myotis lucifugus* (LeConte, 1831) (4 years, 27.5%–100% at 49°N; Fenton et al. 1980; Herd and Fenton 1983; Grindal et al. 1992; R.M.R. Barclay, unpublished data), *Myotis bechsteinii* (Leisler in Kuhl, 1818) (3 years, 26.3%–80.0% at 50°N; Kerth and Konig 1999), *Myotis ciliolabrum* (Merriam, 1886) (5 years, 50%–100% at 51°N; G. Holloway personal communication; C. Lausen, personal communication), *Myotis yumanensis* (H. Allen, 1864) (4 years, 31.3%–100% at 49°N; Fenton et al. 1980; Herd and Fenton 1983; Grindal et al. 1992; R.M.R. Barclay, unpublished data), and *Pipistrellus hesperus* (H. Allen, 1864) (3 years, 65.7%–89.1% at 36°N; M. Herder, personal communication). The reproductive rate of two of nine tropical species also varied significantly among years (*Leptonycteris curasoae* Miller, 1900: 2 years, 69.4%–96.9% at 11°N (Martino et al. 1998); *Artibeus jamaicensis* Leach, 1821: 5 years, 82.5%–93.2% at 9°N (Bonaccorso 1979; Wilson et al. 1991)).

Three species had significantly lower reproductive rates at higher latitude (*P. pipistrellus*: 98.8% at 41°N and 84.5% at 53°N (Deanesley and Warwick 1939; Rakhmatulina 1971; Racey 1969), although the reproductive rate is complicated by variation in litter size); *M. lucifugus*: 98.4% at 40°N and 69.4% at 50°N;² *Tadarida brasiliensis* (I. Geoffroy Saint-Hilaire, 1824): 96.4% at 29°N and 32.3% at 36°N (Davis et al. 1962; M. Herder, personal communication)). One species had a significantly higher reproductive rate at higher latitude (*Mops condylurus* (A. Smith, 1833): 88.0% at 0° and 100% at 25°S (Mutere 1973; Vivier and van der Merwe 1997)), whereas the rate for the other 17 species did not differ significantly among populations at different latitudes.

In four of nine polyestrous species for which we had appropriate data, reproductive rate varied significantly (χ^2 tests, $P < 0.05$) among reproductive events within a year. For example, lactation rate among *Sturnira lilium* (Geoffroy, 1810) in May was 83%, but only 55% in September (Dinerstein 1986). In 2 years of data, reproductive rates of *Coleura afra* (Peters, 1852) in Kenya were near 100% during the long rainy season, but only 58% and 38%, respectively, during the short rainy season (McWilliam 1987).

Although overall roost and random samples did not differ in reproductive rate, there were only five instances in which we had data from roost and random samples of the same species in the same year and location. In two of these (*E. fuscus*, Bindloss, Alberta, C. Lausen, personal communication; *M. lucifugus*, Cypress Hills, Saskatchewan, M. Brigham, personal communication), the reproductive rate of females in the random samples was significantly lower than that in the maternity roost samples. In the other three situations, there was no significant difference in reproductive rate.

Discussion

Data from a broad spectrum of species support the idea that bats have variable reproductive rates and that typically not all females reproduce at every opportunity. Contrary to some previous studies (e.g., Humphrey and Cope 1970;

Lumsden and Bennett 1995), only rarely are all females in a population reproductive during a breeding season. Indeed in some cases the majority of females forego reproduction. This pattern is consistent with the relatively slow life histories of bats (Read and Harvey 1989; Barclay and Harder 2003).

Life-history theory predicts reduced allocation of resources to reproduction, and thus, low reproductive rates in organisms with high adult survival, especially when juvenile survival is lower than that of adults (Promislow and Harvey 1990). This is the pattern of survival among bats (Humphrey and Cope 1976; Thompson 1987; Hoyle et al. 2001; R.M.R. Barclay, unpublished data). In such situations, females should forego reproduction and allocate resources to their own maintenance and survival when resources are limited and the probability of survival of their young is particularly low. Fitness is maximized by increasing the probability of future reproduction rather than jeopardizing survival by investing limited resources in offspring with a low chance of surviving to reproductive age.

Contrary to our prediction, reproductive rates were not significantly higher at maternity roosts than in more random samples of females. However, in two of five cases in which we had data for roost and random samples from the same species, year, and location, females in maternity colonies had a significantly higher reproductive rate than in random samples. Thus, caution should be taken when assessing reproductive rates from colonies and extrapolating to the entire population.

As we predicted, reproductive rate declined with latitude, whether we considered all families of bats or only species of Vespertilionidae. Other life-history characteristics of bats also vary with latitude (Schowalter et al. 1979; Kunz et al. 1998; Barclay and Harder 2003), as do the life histories of other organisms (e.g., Lack 1954; Barkalow 1962; Cardillo 2002; Olsson and Agren 2002; Morrison and Hero 2003). The reduced reproductive rate of temperate-zone bats is part of a general pattern of slower life histories in temperate species. Temperate-zone bats have longer gestation lengths, fewer young per year, and longer maximum longevities than tropical species (Barclay and Harder 2003). With higher adult survival rates, the resource threshold below which the optimum strategy is to forego reproduction may be higher for temperate species than for tropical ones. The fact that there is also greater variation in reproductive rate among temperate species, and that reproductive rate varies within individual species, suggests that females adjust their allocation to reproduction depending on prevailing conditions, including early season weather, insect abundance, and their own fat reserves. Cool wet springs delay parturition in some species (Racey and Swift 1981) and result in lower reproductive rates (Grindal et al. 1992; Lewis 1993). Indeed, in extreme cases no females in a population reproduce (T. Luszcz, personal communication).

Another explanation for the correlation between latitude and reproductive rate could be that sexual maturity is delayed in temperate species and sexually immature females are included in samples because age cannot be determined. However, there is no significant difference in the age of sexual maturity between temperate and tropical species (Barclay and Harder 2003), and some reproductive rates

were too low to be explained simply by inclusion of immature females. Nonetheless, year-to-year variation in reproductive rates of 1-year-old females can be greater than that for older females (Holroyd 1993), and the reproductive rate for 1st-year females of various species is lower than that of older females (e.g., Schowalter and Gunson 1979; Holroyd 1993; Hoyle et al. 2001). In hibernating species, 1st-year females often enter hibernation with lower fat reserves than older females do, and this may preclude reproduction the following spring (Kunz et al. 1998). If young females in temperate-zone species are more susceptible to variation in conditions than older females, the latitudinal decline in reproductive rate may be less pronounced among older females. Unfortunately, age-specific reproductive rates are not available for the vast majority of bat species.

Variation in reproductive rate of bats is associated with variation in some other life-history traits, as we predicted based on life-history theory. Bats with greater maximum-recorded longevity have lower reproductive rates, whether we analyzed all bats together or only species of vespertilionids. This pattern could be interpreted as selection favouring lower allocation to reproduction when extrinsic mortality is low or as support for the notion that there is a survival cost to increased allocation to reproduction.

Among vespertilionids, species with litters of one had lower reproductive rates than species with larger litters. This observation again is as predicted if life histories are viewed as varying along a fast–slow continuum (Promislow and Harvey 1990). Factors that favour greater reproductive investment may act on both litter size and reproductive rate.

Although bats generally have relatively slow life histories, there are significant differences among families (Barclay and Harder 2003). The life histories of vespertilionids, for example, are relatively fast (i.e., litter size varies, gestation and lactation are brief, and birth mass is small; Barclay and Harder 2003). The fact that vespertilionids have relatively high reproductive rates, and significantly higher than those of phyllostomatids, fits this pattern. Of all the families of bats, Vespertilionidae is the most widespread and speciose and perhaps has the most extreme life history. Whether the success of the family is related to their relatively fast life history remains to be determined.

Acknowledgements

We thank the following for generously providing us with unpublished data: S. Banack, M. Brigham, B. Chruszcz, L. Crampton, P. Faure, B. Fenton, D. Happold, M. Happold, P. Heideman, M. Herder, L. Hollis, G. Holloway, S. Holroyd, T. Kunz, C. Lausen, T. Luszcz, K. Patriquin, E. Pierson, L. Reddy, T. Schowalter, D. Solick, H. ter Hofstede, M. Vonhof, and J. Wilson. G. Wilkinson alerted us to some pertinent literature. C. Pavey and two anonymous reviewers provided helpful comments regarding an earlier version of the manuscript. R.M.R.'s research has been supported by grants from the Natural Sciences and Engineering Research Council of Canada.

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