INTRODUCTION

In most songbirds, young birds learn their songs after they have dispersed from their natal area and are prospecting for and establishing their breeding territories (Beecher, Campbell, & Stoddard, 1994; DeWolfe, Baptista, & Petrinovich, 1989). As a consequence, in these species young birds learn their songs from their eventual neighbors (Beecher et al., 1994; Liu & Kroodsma, 2006; Nelson & Poesel, 2009; Payne, 1983; Wheelwright et al., 2008). This finding suggests that the function of song learning is to share songs with your neighbors (Beecher, 2008; Payne, 1983; Poesel, Nelson, & Gibbs, 2012).

If song sharing with your breeding season neighbors is the main function of song learning, then the timing of learning should evolve such that the bird memorizes songs and actively shapes its song repertoire while establishing a territory. However, early laboratory studies found that song memorization in several species is usually limited to a short period early in the natal summer (e.g., Marler & Peters, 1977, 1987, 1988). This poses a dilemma for species that are close-ended learners (birds that learn their repertoire of songs in their first year of life and subsequently do not modify it): the young bird will need to learn the songs of their neighbors and consequently they show high song sharing with neighbors and use these shared songs preferentially in interactions with them. Males also show significant variation in the timing of territory establishment, ranging from their natal summer to the next spring. Using a three-year dataset, we found that the timing of territory establishment did not systematically affect the composition of the song repertoire of the tutee: early establishers and late establishers learned equally as much from their primary tutors and had a similar number of tutors and similar repertoire sizes, nor did timing of territory establishment affect subsequent survival on territory. Therefore, the song-learning program of song sparrows seems versatile enough to lead to high song sharing even for birds that establish territories relatively late.

Teritory establishment, song learning strategies and survival in song sparrows

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Abstract
In most songbirds, the processes of song learning and territory establishment overlap in the early life and a young bird usually winds up with songs matching those of his territorial neighbors in his first breeding season. In the present study, we examined the relationships among the timing of territory establishment, the pattern of song learning and territorial success in a sedentary population of song sparrows (Melospiza melodia). Males in this population tend to learn their songs from their neighbors and consequently they show high song sharing with neighbors and use these shared songs preferentially in interactions with them. Males also show significant variation in the timing of territory establishment, ranging from their natal summer to the next spring. Using a three-year dataset, we found that the timing of territory establishment did not systematically affect the composition of the song repertoire of the tutee: early establishers and late establishers learned equally as much from their primary tutors and had a similar number of tutors and similar repertoire sizes, nor did timing of territory establishment affect subsequent survival on territory. Therefore, the song-learning program of song sparrows seems versatile enough to lead to high song sharing even for birds that establish territories relatively late.

KEYWORDS
bird song learning, selective attrition, song sharing, song sparrows, survival, territory establishment
songs than they will eventually keep. During this time of overproduction, they interact with older, territorial birds and prune their song repertoire down to just those songs that best match those of these older birds who will be their neighbors. Field and laboratory studies have provided some support for the overproduction and selective attrition model in several species (Nelson, 1992; Nelson & Marler, 1994; Nelson, Marler, & Morton, 1996; Nelson & Poesel, 2009; Nordby, Campbell, & Beecher, 2007).

Another solution to this dilemma is to delay the end of the memorization phase depending on the young bird’s social experience (Kroodsma & Pickert, 1980, 1984; Whaling, Soha, Nelson, Lasley, & Marler, 1998). For instance in marsh wrens, Cistothorus palustris, young males who hatch early in the summer and are exposed to recorded marsh wren songs in the laboratory in the summer and following spring will complete their song learning in the first 60–80 days of life (Kroodsma, 1978). In another laboratory study using recorded song, Kroodsma and Pickert (1980) found that when birds were artificially put on a photoperiod simulating late hatching and did not hear enough novel songs in their natal fall, they were able to add new songs to their repertoire in the next spring. In contrast, birds on an early-hatching photoperiod were not able to learn new songs next spring. This finding suggests that late hatching and under-exposure to song in the summer and fall could extend the period in which a bird can memorize new songs into the following spring.

In this study, we examine the relationship of song learning and the timing of territory establishment in a resident population of song sparrows (Melospiza melodia). Song sparrows are a temperate songbird species in which only males sing; female song is very rare (Arcese, Stoddard, & Hiebert, 1988; Beecher, Campbell, & Stoddard, 1994). Male song sparrows are close-ended learners that develop a repertoire of about 9 songs (range: 5–13 songs) in their first year of life, which they do not modify in subsequent years (Nordby, Campbell, & Beecher, 2002). In our population, songs are often learned from immediate neighbors, and often the repertoire of the tutee is biased towards one particular "primary" tutor who accounts for about 50% of the songs, although this proportion varies between 30%–100% among tutees (Akçay, Campbell, Reed, & Beecher, 2014; Beecher, 2008, 2017; Nordby, Campbell, & Beecher, 1999).

Early laboratory studies of song learning in male song sparrows in an eastern population (M. melodia melodia subspecies) revealed a sensitive period mostly limited to the first summer (Marler & Peters, 1987). Subsequent laboratory studies of our resident population (morphna subspecies) have found that learning of new songs can occur in the fall and following spring as well (Nordby, Campbell, & Beecher, 2001; Nulty et al., 2010; Templeton, Burt, et al., 2012) although how common this "late learning" is in nature is still unknown, and generalizing to natural conditions from laboratory studies is difficult.

Song sparrows also show significant variation in the timing of territory establishment. In our field site and nearby resident populations, young song sparrows are observed to "float" over a wide area until they establish and start defending a territory (Arcese, 1987, 1989; Smith & Arcese, 1989; Templeton, Reed, Campbell, & Beecher, 2012). Territorial behavior of the newly recruited birds starts as early as July of their hatch year (at about 2–3 months of age) and as late as April of the following spring. Variation in territory establishment might have consequences for song learning, especially given that song sparrows in our population sing throughout the late summer and fall (though at a reduced rate).

Tutees establishing territories in their first summer will have more opportunities earlier to hear and interact with their future primary tutors. According to the selective attrition model (Nelson & Marler, 1994) the primary tutor’s influence would manifest itself if this tutor survived into the following breeding season, favoring selective retention of songs previously memorized songs from that tutor. Consistent with this hypothesis, previous studies in our population found that birds learn or retain more songs from tutors who survive the winter (past January 1) than from tutors who do not (Akçay et al., 2014; Nordby et al., 1999), although whether this overall effect depends on the timing of the territory establishment by the young bird is unclear (see also Nordby et al., 2007).

The situation is different for late establishers who might be at a disadvantage in terms of learning the neighbors’ songs. Some young birds may establish their territories late because they have been shut out of the area where they learned songs in their natal summer, as can happen, for example, when none of the tutor-neighbors die over winter (Nordby et al., 1999). In this case, the songs memorized by the young bird in his natal year will generally be poor matches to the songs of his eventual neighborhood. This would require the bird to either learn a new set of songs in short order or to retain through selective attrition the best-matching songs of his already-memorized songs. Other late establishers may simply have hatched late and may not hear enough songs in their natal summer. In that case, they would have to do much of their song learning in the fall or following spring, which might lead to sub-optimal repertoires. A late establisher would also have fewer opportunities to engage in direct interactions or overhear interactions between neighboring males hampering the attrition process (Nelson & Marler, 1994). Finally, evidence suggests that adults respond to tutee songs aggressively in early spring (when the songs are better formed but still plastic, and a late-establishing bird would still need to be practicing) while they respond with reduced aggression towards plastic song heard in the summer and fall when an early establishing tutee would be singing (Templeton, Campbell, & Beecher, 2012). Thus, a late establisher who attempts to directly interact with potential tutors will likely receive an aggressive response which may inhibit de novo song learning (Casey & Baker, 1993).

In the present study, we analyze a three-year dataset on the timing of territory establishment by young birds in our resident population of song sparrows. In three consecutive years starting with 2009, we banded and recorded young males during the period of their song learning and attempted to track their time of territory establishment through systematic surveys. We hypothesized that early establishers would learn a higher proportion of songs from a primary tutor than late establishers, particularly when the primary tutor also survives into the first breeding season. We also tested the hypothesis that early
establishing birds survive longer on territory, either because they are of better quality, as has been suggested for migratory birds (Kokko, 1999) or because early establishing has some other benefit that promotes survival (Bonte et al., 2012; Brown, Brown, & Brazeal, 2008).

2 | METHODS

2.1 | Study site and subjects

This study is part of a long-term study of song sparrows located in Discovery Park, Seattle, Washington, USA, that started in 1986 (Beecher et al., 1994). More information on the specifics of the site can be found in Beecher (2008). This population is resident year-round and males generally defend their territories all year, with the exception of during molting (August) and cold weather periods in November-December, when birds show reduced territoriality (but often are still on their territory). Breeding usually starts in March or April depending on the weather conditions, particularly the El Nino cycle (Wilson & Arcese, 2003), although song sparrows start becoming territorial again and singing after the winter solstice as days start to lengthen (Smith, Brenowitz, Beecher, & Wingfield, 1997). We therefore considered January 1 as the starting point of spring. Each year between 120 and 150 adult males hold territories in the portion of the park under study. Males were caught with mist nets or Potter traps, and each male was fitted with a US Fish and Wildlife Service metal band and three color bands for visual identification. Often multiple juveniles were caught in the same net by herding them into the net as a flock (Templeton, Reed, et al., 2012).

2.2 | Surveying

During the study, we kept track of the arrival and disappearance of males on territory by visiting territories every two weeks throughout the year, with the exceptions noted above of August (molting) and November and December (inclement weather) when we surveyed the study area opportunistically and banded new birds whenever we could. We used either playbacks or observation of singing males to determine whether a territory holder was still present or had been replaced by a new bird.

We counted a bird as territorial if he was observed singing on a territory and approached playback of conspecific song. We took the date of territory establishment of the young bird to be the date of first such observation on a territory if the same area was known to have been held by another bird recently (within a few weeks) and the young bird kept the territory into the spring. In our study site, all suitable areas for song sparrow territories are occupied at any given point in time, and we have rarely observed song sparrows expanding into "no-man's land" areas where there were no song sparrows previously, except for cases where habitat had been significantly changed (e.g., planting or growth of new shrubbery). We classified territory establishment dates into three categories: the summer of the hatch year (before September), fall of hatch year (September to January) and next spring (January to through May, the majority of these birds established their territories in January and February).

In total, we determined territory establishment dates and song learning for 71 young birds who hatched in the years 2009 (n = 30), 2010 (n = 22) and 2011 (n = 19) and established territories in our study site sometime between the summer of their hatch year and the subsequent spring. The majority of the subjects (44 out of 71, 61.9%) were banded either in the summer with juvenile plumage or in the fall with breeding plumage but singing plastic song. Older adults show a slight increase in variability in their crystallized song in fall but this increase is not comparable to plastic song of juveniles seen at the same season (Smith et al., 1997). The rest of the subjects were banded after January 1st of their second calendar year with breeding plumage but were identified as second-calendar year birds from their songs which still showed plastic elements (see Figure 1 for examples of song development at different stages in the first year).

We tracked the territory tenure of birds through 2016 by surveying the area as indicated above. Song sparrows do not move significant distances once they establish a territory, moving at most a few territories over (Hughes & Hyman, 2011). We therefore considered birds to have lost territory if they were not observed on their prior territory, any of the nearby territories or anywhere else in our study area, and if their original territory was being defended by another male (Akçay, Campbell, & Beecher, 2015).

2.3 | Song recording and song-learning analyses

We recorded the repertoire of young males when these were crystallized (between February and June of their second calendar year) and of their potential tutors with a digital recorder and a shotgun microphone (Marantz PMD 660 and Sennheiser ME66/K6). We considered the repertoire fully recorded after at least 16 switches in a continuous recording, which has been shown to be a large enough sample to capture the entire repertoire (Nordby et al., 2002). From these recordings, we carried out song analyses as in our previous studies (Akçay et al., 2014; Beecher et al., 1994; Nordby et al., 1999). Briefly, we made spectrograms of each song in the repertoire of each tutee and potential tutor using Syrinx (John Burt, www.syrinxpc.com). We considered each adult male that held a territory in June of the tutee’s hatch year as a potential tutor. Three judges independently compared the visual match between the songs of the tutee and potential tutors. After this stage, the three judges compared their matches and arrived at a consensus sheet where all judges agreed upon the matches.

If a male was implicated as having the sole best match to a tutee song, he was given a score of 1 (full credit) for that song. For songs where more than one male was judged to have the best match, the score was split among these males (e.g., if there were two males, each received 0.5). Split-credit songs like these happen because of high levels of song sharing within neighborhoods in our population (Hill, Campbell, Nordby, Burt, & Beecher, 1999). For about half of the songs,
tutorship was shared in this way (46.5% in 2009 cohort; Akçay et al., 2014). For each tutee, the tutor with the highest tutoring score was defined as the primary tutor. For this primary tutor, we noted whether he survived past January 1st of the second calendar year of the tutee.

2.4 | Data analyses

From the dates of territory establishment, we classified each tutee as having established a territory in the natal summer, natal fall, or spring (after January 1st of their second year). Our dependent variables were repertoire size, proportion of songs learned from the primary tutor, and number of tutors that accounted for the entire repertoire. We analyzed these dependent variables with linear mixed models with territory establishment season, tutor survival into spring and their interaction as the predictor variables and cohort as a random factor. We analyzed territory tenure of the tutees with a general linear mixed model with Poisson distribution and log-link, adding cohort as a random factor and territory establishment season as a fixed factor. The analyses were carried out in R (R Core Team 2012).

2.5 | Ethical note

The research reported here was conducted in accordance with the ethical guidelines of ABS/ASAB for the use of animals in behavioural studies.
research and teaching and approved by the University of Washington Institutional Animal Care and Use Committee (protocol no: 2207-03) and with United States Fish and Wildlife Service Banding permit (#20220).

3 | RESULTS

Thirteen (18.3%) of the tutees were first observed to be territorial in the natal summer, 20 (28.2%) in the fall, and 38 tutees (53.5%) in the spring (27 in January and February, and 11 in March and April). The season in which the tutees established their territory did not have a significant effect on either the proportion of songs learned from the primary tutor, the number of tutors, or the overall repertoire size (Table 1, Figure 2). Whether the primary tutor survived into the first spring of the tutee had a significant effect on proportion of the repertoire this tutor accounted for (Figure 2): Tutees whose primary tutors survived past January 1st learned a higher proportion of their repertoire from them than did tutees whose primary tutor did not and had a smaller number of tutors, replicating earlier findings in our population (Akçay et al., 2014; Nordby et al., 1999). There also was no interaction effect of territory establishment season and whether the primary tutor survived into spring. Finally, there was no difference in territory tenure depending on the timing of first territory establishment ($\chi^2 = 1.70, p = .43$, Figure 3).

4 | DISCUSSION

We tested whether the timing of territory establishment has any influence on song-learning strategies of male song sparrows. While we replicated our earlier findings that tutor survival into spring increases the tutoring influence of that bird (Akçay et al., 2014; Nordby et al., 1999), we found that whether the young bird established his territory in the summer, fall or spring did not affect either proportion of the song repertoire learned from that tutor, the number of tutors or the final repertoire size of the tutee. We also found no support that early establishing birds experienced a fitness benefit in the long-term as territory tenure did not significantly differ between birds establishing their territories in different seasons.

4.1 | Timing of song learning and territory establishment

The fact that timing of territory establishment does not affect these aspects of song learning suggests at least two possibilities. First, at least some birds that establish their territories late may have been present all along. It is hard to detect juvenile song sparrows that are not territorial as they move about inconspicuously and silently ("float") and therefore may have been present and listening in on singing interactions between adults. Given that eavesdropping on singing interactions is known to be a potent factor in song learning by song sparrows (Beecher, Burt, O’Loghlen, Templeton, & Campbell, 2007; Templeton, Akçay, Campbell, & Beecher, 2010), eavesdropping may compensate for the lack of direct interactions with adults that they would have had, had they been territorial.

Radio-tracking studies of young birds in our study population show that they sometimes cover a large amount of ground (Templeton, Reed, et al., 2012), and during these movements they are likely to overhear many adults singing, including their future primary tutor. Given laboratory studies that failed to detect an upper limit in recognition memory for songs in song sparrows (Stoddard, Beecher,Loesche, & Campbell, 1992), it is plausible that a bird is able to memorize a very large number of songs during this floater phase. This hypothesis predicts that late establishers would sing larger repertoires than early establishers in the spring (i.e. overproduce) which they would then winnow down to a normal-sized repertoire that matches their primary tutor and other neighbors. Overproduction followed by selective attrition does occur in our population (Nordby et al., 2007) although we do not know if it is related to the timing of territoriality. Note that this strategy of memorization and production of a large repertoire may lead to a cost in terms of the quality of learning. For instance in Puget-Sound white-crowned sparrows (Zonotrichia leucophrys pugetensis), young birds that sang large repertoires (e.g., 4 songs) imitated the local songs more poorly than young birds that sang the species-typical repertoire size of a single song (Nelson & Poesel, 2014). Although we did not quantify the match between the tutee and tutor version of the songs, it is possible that late establishers may match their primary tutor songs less well compared to early establishers.

A second, non-exclusive possibility is that song sparrows can memorize new songs until at least the time they establish their territories, whenever this happens. Estimates of the timing of memorization phase comes from laboratory studies of hand-raised birds, typically tutored with recorded songs played from speakers—the so-called "tape tutor" (Marler & Peters, 1987, 1988). Under more naturalistic conditions involving either live birds or song presentation that represent naturalistic bouts of singing, these estimates have proven to significantly underestimate the length of the song memorization period, which often extends into the first spring for some songbirds.

### Table 1

<table>
<thead>
<tr>
<th>Season of territory establishment</th>
<th>Proportion learned from primary tutor</th>
<th>Repertoire size</th>
<th>Number of tutors</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0.08 (0.96)</td>
<td>1.22 (0.54)</td>
<td>1.86 (0.39)</td>
</tr>
<tr>
<td>Primary tutor’s survival into January</td>
<td>4.70 (0.026)</td>
<td>0.31 (0.58)</td>
<td>1.77 (0.18)</td>
</tr>
<tr>
<td>Interaction</td>
<td>0.34 (0.84)</td>
<td>0.04 (0.97)</td>
<td>1.19 (0.55)</td>
</tr>
</tbody>
</table>
Furthermore as discussed above, there is evidence that the memorization phase in some species, like marsh wrens and white-crowned sparrows shows flexibility with respect to hatching date, tutor exposure and the presence of live tutors (Baptista & Petrinovich, 1984, 1986; Kroodsma & Pickert, 1980, 1984; Petrinovich & Baptista, 1987; Whaling et al., 1998). These findings suggest that the sensitive period for song memorization may close in the summer for birds establishing at that time and close the following spring for birds establishing at that time.

One possible mechanism of the closing of the memorization phase is the upregulation of testosterone, which may happen at the time of territory establishment. It is well established that androgens including testosterone regulate territoriality as well as song learning (Alward, Rouse, Balthazart, & Ball, 2017; Bottjer & Johnson, 1997; Marler, Peters, Ball, Dufty, & Wingfield, 1988). For instance, implanting juvenile birds with testosterone crystallizes song rapidly (Marler et al., 1988). This crystallization may also bring about the closure of the song memorization phase. In the field, young males are not likely to experience high levels of plasma testosterone until their breeding season (Wingfield, 1994; Wingfield & Hahn, 1994) but recent studies suggest that aggressive interactions in the non-breeding season do lead to local synthesis of androgens in the brain (Pradhan et al., 2010; Soma et al., 2000). Local production of androgens may in turn affect song-learning circuits in the brain by terminating song memorization phase (Alward et al., 2017). Conversely, late establishers who presumably do not engage in aggressive interactions until later,
may be able to maintain a longer period of song memorization due to the lack of androgen production.

Finally, our finding that tutees learned more from their primary tutors who survived into the spring replicates our previous findings in this population that the presence of tutors in the spring is important in tutoring (Akçay et al., 2014; Nordby et al., 1999). This pattern is consistent with the selective attrition model of Nelson and Marler (1994) which predicts that late interactions with tutors is a crucial factor that determines which of the songs previously memorized are retained for the final crystallized repertoire.

### 4.2 Song learning in sedentary and migratory populations

Our population of song sparrows is sedentary with birds singing year-round. This may result in the evolution of a longer memorization phase. The situation would be different for migratory birds which often travel to a wintering ground where they either do not hear conspecific song or hear songs that are not local to the areas to which they will return next spring. Thus, memorization of songs during the first winter may not be adaptive, in which case birds would be favored to ignore or avoid memorizing these songs. Nevertheless, the song memorization phase might reopen the next spring. Some evidence on this point comes from the previously mentioned study of marsh wrens (Kroodsma & Pickert, 1980, 1984) and a study of chaffinches (Thielcke & Krome, 1991). In the latter study, the authors tutored juvenile chaffinches caught in late summer and early fall with one song in the fall and winter and another song in the next spring. Despite the fact that the birds had significant song exposure in the field before being caught, they nevertheless learned the spring song from tape tutors. None of the birds copied the fall song however, suggesting that chaffinches may be insensitive to song presented in this period. The Nulty et al. (2010) study cited earlier also found evidence in our population that tutors that were heard in summer and fall were less effective tutors compared with tutors heard in summer and spring, suggesting that song sparrows too may be insensitive to fall song.

While our population is sedentary, some nearby populations of song sparrows display altitudinal migratory strategies in which the birds migrate from their high-altitude, snow covered breeding grounds to lower altitudes where they would hear sedentary song sparrows singing that are not necessarily local to their population. In a study of one such population Hill et al. (1999) found that level of song sharing among neighbors was as high as in our sedentary study population, suggesting that song-learning programs are likely to be same in these two populations. Given that final territories in the high-altitude population are not established until next spring, this suggests that the memorization phase either stays open throughout fall and spring or reopens in the spring. A common garden experiment comparing the memorization of songs presented in different seasons to birds from these sedentary, and migratory populations would be required to distinguish between these possibilities.

### 4.3 Timing of territory establishment and fitness

We found no evidence that early establishing males experienced a long-term fitness benefit compared with later establishing males. Given that in our population, almost all areas that are suitable for song sparrows are occupied, the variation in timing of territory establishment is likely to be due to opening of vacancies due to the disappearance of a prior territory owner or the presence of a large territory that may be split into two territories well enough to support two song sparrow pairs. These extra-large territories can arise over the winter or spring when birds are depredated and have their territories taken over by their existing neighbors (Akçay et al., 2012). This fact means that later in the breeding season, there are some territories that used to hold two territories but are now defended by a single song sparrow, and juveniles can insert themselves into these territories more easily.

Most studies on the timing of territorial behavior and subsequent fitness effects have been on migratory species which arrive at their breeding territories from somewhere else (Brooke, 1979; Francis & Cooke, 1986; Kokko, 1999; Lozano, Perreault, & Lemon, 1996). Variation in the timing of territory establishment has been studied in year-round resident species less often (Dixon, 1956; Matthysen, 1989). In one such study, Matthyssen (1989) did not detect any differences in fitness (in terms of survival) and eventual territory quality between early- and late-establishing males in the year-round resident European nuthatches (Sitta europaea), consistent with our present findings.

Variation in the timing of territory establishment has also been studied in a partially migratory population of eastern song sparrows in rural Pennsylvania (Hughes & Hyman, 2011). In this population, some males established their territories early in the spring while...
about a quarter of males established territories later (after the first nest has hatched). Hughes and Hyman (2011) found that timing of first-time territory establishment did not relate to fitness in terms of survival. Indeed, late-establishing males who subsequently moved to a different, non-overlapping territory had the highest reproductive success in terms of number of nests and young fledged. These results too suggest that late-establishing males do not necessarily consist of low-quality individuals.

5 | CONCLUSIONS

In conclusion, in a large multi-year dataset, we found no effect of timing of territory establishment on song-learning strategies as exemplified by the three main parameters that vary across individual song sparrows: proportion of repertoire learned from the primary tutor, repertoire size and how many tutors the tutee learned his songs from. These results indicate that song sparrows are able to match the songs of their neighbors even if they establish their territories late, suggesting a versatile learning program where late establishers have a longer song memorization phase, and/or the capability of memorizing a large number of songs through eavesdropping while not being territorial. We also found no evidence that late-establishing males suffer a fitness cost, consistent with earlier findings in year-round resident species. Future research can experimentally manipulate song experience of birds in the field in realistic ways (e.g. Mennill et al., 2018) to dissociate the different hypotheses regarding how birds can adaptively shape their learned song repertoire and territorial strategies.

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CONFLICT OF INTEREST
The authors declare that they have no conflict of interests.

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