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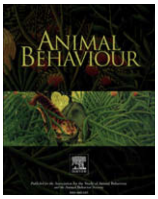

Good neighbour, bad neighbour: song sparrows retaliate against aggressive rivals

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Many territorial animals, despite being in direct competition for resources such as space, food and mates, show reduced aggression towards their neighbours. This situation is called the Dear Enemy effect. One explanation of the Dear Enemy effect is that it is due to a conditional strategy like Tit for Tat where territory holders cooperate by reducing aggression towards neighbours that also show reduced aggression, but retaliate against aggressive neighbours. Previous research found evidence for such a conditional strategy in migratory species but not in species with long-term association between neighbours, suggesting that long-term neighbours might be engaged in more 'forgiving' strategies. We tested this hypothesis in male song sparrows, *Melodia melospiza*, which are resident year-round in our population (leading to long-term associations between neighbouring birds) and display the Dear Enemy effect. We found that following a simulated intrusion by a neighbour, song sparrow males responded more strongly to playback of this neighbour than to playback of a neutral neighbour from their respective boundaries, consistent with a conditional retaliation strategy. We suggest that the primary effect of an intrusion by a neighbour might be to increase the perceived risk of cuckoldry by the intruding male, and increased aggression and vigilance towards this neighbour might be a strategy to prevent cuckoldry.

Territory holders engage in repeated interactions with their neighbours over the period of their residency. These interactions can involve high levels of aggression, as animals are in direct competition with their neighbours in the division of space, food and mates. In fact, territory holders may often be each other's strongest competitors, especially in competition for fertilizations (Yezerinac et al. 1995; Webster et al. 2001; Segelbacher et al. 2005). In many species, however, territory holders actually show reduced aggression towards their neighbours, a phenomenon called the Dear Enemy effect (Fisher 1954; Temeles 1994).

There are benefits to reduced aggression as animals can then use more of their time in other activities such as foraging or mate guarding instead of fighting, thus avoiding the risk of injury and energy expenditure associated with fighting. Reduced aggression, however, may also involve costs. For starters, reduced aggression may involve forgoing an opportunity to enlarge the territory. Also, a nonaggressive individual might suffer losses to a neighbour that chooses to behave aggressively.

The interaction between two neighbours can be modelled as a Prisoner's Dilemma (PD) game (Getty 1987; Godard 1993). In this view, a territory owner that acts nonaggressively towards a neighbour can be thought of as cooperating, while a territory owner that acts aggressively towards its neighbour can be considered to have defected. A necessary condition for the PD game to hold is that an aggressive individual should enjoy greater benefits than a nonaggressive individual when each is faced with a nonaggressive opponent. This stipulation is plausible, as an aggressive individual might enlarge his territory or steal food or matings from a nonaggressive individual. In one dramatic example, Wingfield (1984) found that song sparrows implanted with testosterone (T) showed increased aggression compared to controls, and had territories almost twice as large as control birds, and, in many cases, became polygynous. This finding suggests that increased aggression can lead to significant benefits, since the increase in territory size as a result of T implants appears to have been mediated by territorial aggression.

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If it is true that the payoffs to territorial neighbours parallel the PD game, a possible explanation for the Dear Enemy effect emerges (Getty 1987): territorial animals might be playing a conditional strategy such as Tit for Tat or one of its variants in their repeated interactions. Tit for Tat (or some variant of it; Nowak & Sigmund 1992) involves retaliation against defecting individuals, which in this case would mean retaliating against neighbours that act aggressively. Thus, the Dear Enemy effect should be conditional upon the neighbour's level of aggression towards the subject; that is, a bird should be tolerant of his neighbour if that neighbour is nonaggressive, but show aggression towards his neighbour (retaliate) if that neighbour is aggressive.

Three studies with songbirds have examined whether territorial animals adopt these conditional strategies (Godard 1993; Hyman 2002; Olendorf et al. 2004). In the first such study, Godard (1993) asked whether male hooded warblers, *Wilsonia citrina*, retaliate against intruding neighbours. She found that after a simulated intrusion by a neighbour, aggression towards playback of the neighbour's songs from the boundary increased relative to the aggression level before the simulated intrusion. No increase in aggression towards neighbour song was found in control trials following a simulated intrusion by a stranger, controlling for arousal effects. Thus, the retaliation seemed to be directed towards the particular neighbour that was simulated to defect, supporting the notion that territory holders indeed seem to be playing a conditional strategy like Tit for Tat.

In a second study using the same basic design as Godard (1993), Olendorf et al. (2004) found that red-winged blackbirds, *Agelaius phoeniceus*, also retaliated against a defecting neighbour, again supporting a conditional strategy. Curiously, however, intrusion by a stranger (control condition) evoked a significantly weaker response than intrusion by the neighbour, implying that territorial neighbours were not in a Dear Enemy situation to begin with (see also Temeles 1994; Stoddard 1996).

Finally, a study by Hyman (2002) tested the idea of conditional strategies in a population of Carolina wrens, *Thryothorus ludovicianus*. Carolina wrens are year-round residents and have long-term associations between neighbouring territory holders. They also show the Dear Enemy effect in the spring (Hyman 2005). However, despite using a very similar experimental design to Godard (1993) and Olendorf et al. (2004), Hyman found that Carolina wrens did not show increased aggression towards intruding neighbours. He suggested that the lack of retaliation might indicate that these birds were using a more forgiving variant of Tit for Tat (Nowak & Sigmund 1992), one that might work better between neighbours with long-term associations than a less forgiving strategy. In other words, long-term neighbours might be better off if they refrain from retaliation on some occasions when their neighbours defect. Support for this hypothesis comes from the observation that in the two studies supporting retaliation, both species were migratory, with shorter-term associations between neighbours.

In summary, of the three previous studies examining whether territory holders use a strategy of conditional cooperation with neighbours, two found evidence of the predicted pattern of retaliation against defecting neighbours. Of the two studies finding evidence for retaliation, the Olendorf et al. (2004) study found no evidence for a Dear Enemy effect, as subjects responded more strongly to their neighbours than to strangers. Therefore, to date, only hooded warblers seem to fit the Tit-for-Tat hypothesis in explaining the Dear Enemy effect.

In the present study we asked whether male song sparrows retaliate against intruding neighbours. In our study population in Seattle, WA, U.S.A., song sparrows show a stronger response to playback of stranger song than to playback of neighbour song when playbacks are broadcast from the correct boundary (Stoddard et al. 1991). Thus, song sparrows show the Dear Enemy effect. Also, these song sparrows are resident year-round, with neighbours often sharing a boundary over multiple years. Therefore, song sparrows present a case similar to the Carolina wrens. If long-term associations do result in more forgiving conditional strategies (Hyman 2002), then song sparrows should similarly not show evidence for retaliation. On the other hand, if song sparrows show evidence for retaliation, then long-term relationships with neighbours need not lead to forgiving strategies.

Recent studies have found that song sparrows respond to individual differences in aggression of their neighbours, responding more aggressively to their aggressive neighbours (Hyman & Hughes 2006). This result suggests that song sparrows might be playing a conditional retaliation strategy such as Tit for Tat, which would lead to higher aggression levels towards their aggressive neighbours. Experimental evidence for a conditional retaliation strategy is lacking, however, as the Hyman & Hughes (2006) study did not manipulate aggression between neighbours but rather took advantage of natural variation in aggressiveness between neighbours.

We addressed the question of whether song sparrows retaliate against aggressive neighbours using the following design. We used song playback to simulate a neighbour intruding on the subject's territory, then performed two additional playbacks. One of the two playbacks simulated the intruding neighbour singing from his shared boundary with the subject, whereas the other playback simulated a second 'neutral' neighbour singing from his shared boundary with the subject. The comparison between these two boundary playbacks allowed us to assess whether subjects show higher levels of aggression towards intruding neighbours than towards neutral neighbours. A conditional retaliation strategy predicts that subjects should show higher levels of aggression towards an intruding neighbour.

METHODS

Study Area and Subjects

We conducted the study in an undeveloped 3 km^2 park in Seattle, Washington, U.S.A., where our laboratory has been conducting a long-term study of song sparrows since 1986. This population of song sparrows is resident year-round and includes approximately 150 territorial males. We selected 12 males, whose territory boundaries were mapped through extensive observations of singing sites and movements, to be subjects in the present experiment. All of the subjects, their mates and their neighbours were individually marked with colour leg bands for individual identification. Subjects had a median number of four neighbours (range 3–6).

Stimuli and Apparatus

The repertoires of subjects and their neighbours were recorded with Marantz PMD660 solid-state recorders and Sennheiser ME66/K6 shotgun microphones and were examined in Syrinx (John Burt, www.syrinxpc.com, Seattle, WA, U.S.A.), and stimulus songs were selected based on recording quality.

For each subject we selected at random two neighbours to serve as stimulus birds, one of which was assigned to be the intruder and the other to be the neutral neighbour, again chosen at random. For each stimulus bird, a single song type was selected to be the stimulus song. We made an audio file containing 10 repetitions of a single rendition of the song, with 10 s between each repetition of the song, and standardized the amplitude with 'Maximize' function in Syrinx. Song sparrow songs are about 3 s long, and thus the playback stimuli (from the onset of the first song to the offset of the last repetition) lasted about 120 s.

Six of the stimulus birds were used once as a neutral neighbour and once as an intruder, on different trials (to different subjects). One bird was used twice as a neutral neighbour, and one additional bird was used twice as neutral neighbour and once as intruder. For these birds, we selected a different song for each trial.

Procedure

We tested 12 birds during 27 May–9 June 2008. The trials were conducted between 0700 and 1100 hours. On some days we tested multiple subjects, but we never tested neighbours on the same day. Before each trial, the nondirectional speaker to be used in the simulated intrusion was placed in the middle of subject's territory. We marked a 4 m circle around the speaker by tying flagging on vegetation to help with distance estimation. One experimenter controlled the playback from the laptop and recorded the trial on the recorder about 20 m away from the speaker using the same recording gear as above. A second observer in a different location helped monitor the subject's behaviour. A third observer was responsible for monitoring the stimulus bird's behaviour, in case the stimulus bird started singing or otherwise interfered with the trial. However, no such instances of interference occurred during this study. Each observer was equipped with a walkie-talkie so that observations could be relayed to the first observer for recording.

We waited to start the trial until the subject and the stimulus bird were both quiet and the subject was away from the vicinity of the speaker (>20 m). We started each trial with the intrusion playback, using a nondirectional speaker with a built-in amplifier (Pignose Model No. 7-100R). The intrusion playback lasted 2 min, after which we continued recording and observing the subject's behaviour for a post-trial period of 3 min. Playback volumes were adjusted to normal amplitudes of song sparrow singing by ear before each trial.

Following the post-trial period, we waited for 45 min, after which we presented the subject with two boundary playbacks. These were done just inside the stimulus bird's territory, within 2 m of the shared boundary with the subject, with a directional speaker (see Burt et al. 2001 for a description) facing into the subject's territory. As in the intrusion playback, boundary playbacks consisted of 2 min of playback and 3 min of post-trial observation. For half of the subjects, the first boundary playback was the intruder playback from the intruder's normal territory boundary, using the same song type as in the intrusion. For the other half, the first playback was from the neutral neighbour's boundary, using the neutral neighbour's songs. The order of boundary playbacks was determined by flipping a coin in the first trial, and by alternating the order for every subsequent trial. The first boundary playback started 45 min after the post-trial period of the intrusion playback. The second boundary playback started 15 min after the end of post-trial period of the first boundary playback.

Response Measures

We measured the subject's response to each playback using four behavioural measures: latency to approach, closest approach, number of flights and number of songs sung during the playback period. Latency to approach was defined as the latency of the first flight towards the speaker. During six of the neutral neighbour playbacks and one of the intruder playbacks, the subject did not make any flights towards the speaker; in these cases, we assigned a latency of 120 s, which is equal to the duration of the playback period. If we could not locate the subject during the playback (3 of 6 neutral neighbour playbacks), we used 40 m, which corresponds to the average distance from the shared boundary to the territory centre of the subject, as the closest approach distance. Note that these latter cases of no response represent the lowest possible response strength that the subjects could show. In all these cases, the same subject responded to the corresponding intruder playback trials.

Data Analysis

All response variables except number of songs were highly correlated with each other (Pearson correlation: $r_{34} > 0.60$, $P < 0.0005$). Song rate was significantly correlated only with closest approach distance (Pearson correlation: $r_{34} = -0.371$, $P < 0.05$). Therefore, we analysed song rates separately. We performed a principal components analysis (PCA) to generate a single measure of aggressive response using the remaining three measures described above. The first principal component explained 76.4% of variance (see Table 1 for loading coefficients).

We used the PCA aggression scores and number of songs in separate repeated measures ANOVAs to assess differences between playback conditions (three levels: intrusion, intruder boundary, neutral boundary). The critical prediction of the Tit-for-Tat hypothesis is that subjects should respond more strongly to the boundary playback of the intruder neighbour than to the boundary playback of the neutral neighbour. We evaluated this hypothesis with post hoc analyses when appropriate. All analyses were done in SPSS 14.0 statistical package (SPSS Inc, Chicago, IL, U.S.A.). We also tested for consistent individual differences across playback conditions by looking at pairwise correlations between the aggression scores in response to the playback condition. Statistical test were two tailed unless otherwise noted.

RESULTS

The repeated measures ANOVA on the aggression scores revealed significant differences between the three playbacks ($F_{2,22} = 43.27$, $P < 0.0005$). Subjects responded most strongly to the intrusion, followed by the intruder boundary playback and then the neutral boundary playback (Figs 1, 2). Critically, among the boundary playbacks, subjects responded significantly more strongly to the intruder than to the neutral neighbour (within-subjects contrast: $F_{1,11} = 19.10$, $P < 0.001$).

As noted above, individual song sparrows differ in aggressiveness (Nowicki et al. 2002; Hyman & Hughes 2006). We therefore tested for consistent individual differences in subjects' responses during each playback condition. There was a significant positive correlation between subjects' responses to intrusion and to neutral boundary playbacks (Pearson correlation: $r_{10} = 0.641$, one-tailed $P < 0.02$) and between their responses to intruder boundary and to neutral boundary playbacks (Pearson correlation: $r_{10} = 0.480$, one-tailed $P = 0.05$). There was also a nonsignificant tendency for subjects' responses to intrusion and to intruder boundary playbacks to be positively correlated (Pearson correlation: $r_{10} = 0.473$, one-tailed $P = 0.06$).

If, despite our random assignment of birds to the intruder or neutral neighbour condition, we chose as intruders birds that were

Table 1
Loading coefficients of song sparrow response measures onto the first principal component in the principal components analysis

Response measure	Loading coefficient
Number of flights	0.882
Closest approach	−0.872
Latency to approach	−0.868

Higher values on the aggression score indicate higher aggression.

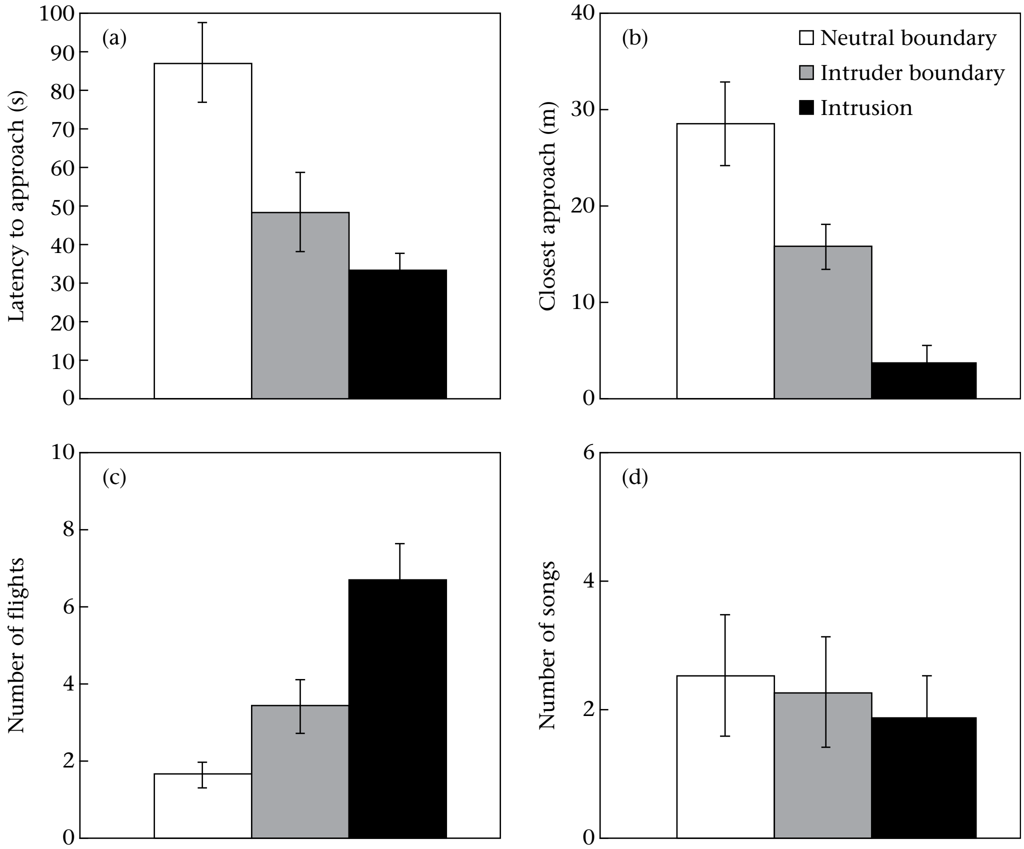

Figure 1. Mean ± SE response measures of song sparrows across playback conditions. Number of songs did not differ across playback conditions. The other three response measures were highly correlated with each other and were entered into a PCA.

consistently more aggressive than the birds we had chosen as neutral neighbours, this could lead to the same result of subjects responding more strongly to the intruder playback, without any effect of the simulated intrusion. We tested this hypothesis by using the subset of data including stimulus birds that were used both as an intruder for one subject and as a neutral neighbour for another subject ($N = 7$). We took the subject's aggression scores from the boundary playbacks involving these birds (for the bird that was used twice as a neutral neighbour, we took the average of the two scores) and analysed them using a two-tailed, independent samples *t* test. The results revealed that subjects responded significantly more strongly to a particular stimulus bird at the territory boundary when that bird was an intruder neighbour than when it was a neutral neighbour ($t_6 = 3.94$, $P < 0.01$; Fig. 3). Therefore, the difference between the two boundary playbacks resulted from the simulated intrusion manipulation and not from intrinsic differences of the aggression levels of birds that were used as intruders and neutral neighbours.

The number of songs given in response to playbacks did not differ significantly between the three conditions (repeated measures ANOVA: $F_{2,22} = 0.54$, $P = 0.60$; Fig. 1).

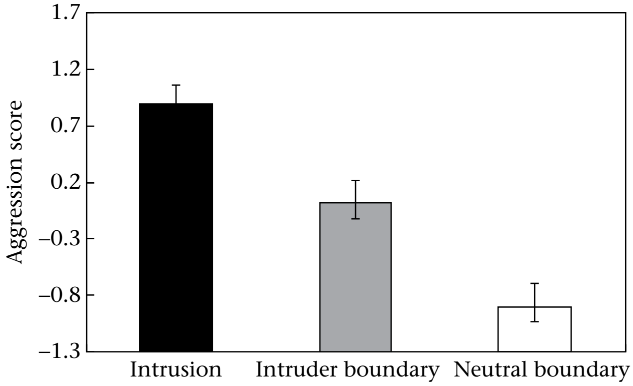

Figure 2. Mean ± SE aggression scores of song sparrows across playback conditions.

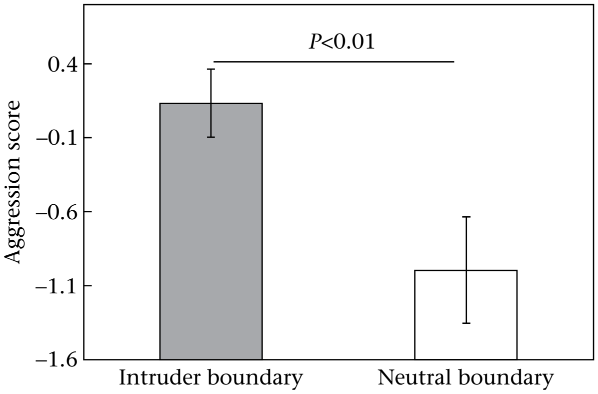

Figure 3. Mean ± SE aggression scores in response to playbacks of the seven song sparrows that were used both as an intruder and as a neutral neighbour on different trials (for different subjects).

DISCUSSION

We found that a male song sparrow responded more aggressively to a neighbour that had recently intruded on his territory than to a neutral, nonintruding neighbour. Our finding that subjects did not respond very strongly to neutral neighbours (only half of the subjects approached the speaker in response to neutral neighbour playback) supports earlier work (Stoddard et al. 1991) showing that song sparrows are in a Dear Enemy relationship with their immediate neighbours. These results suggest that song sparrows are engaged in a conditional strategy in which they retaliate against their aggressive neighbours and tolerate their nonaggressive neighbours. The results also extend previous findings showing that song sparrows respond to individual differences in aggressiveness of their neighbours (Hyman & Hughes 2006). Our subjects also showed consistent individual differences in their response strength to different playback conditions. This finding suggests that neighbouring males in our population also differ individually in their aggressiveness. Furthermore, increased aggression towards intruders suggests that males not only respond to intrinsic aggressiveness of their neighbours, but also to short-term changes in aggression levels.

Our results are compatible with the idea that territory holders are in a Prisoners Dilemma-like game, where they play a Tit-for-Tat strategy. These results corroborate results of previous studies that have found evidence for retaliation against aggressive neighbours (Godard 1993; Olendorf et al. 2004). However, in one of these previous studies (Olendorf et al. 2004) there was no evidence for a Dear Enemy relationship between red-winged blackbird neighbours (birds responded more strongly to neighbours than to strangers), making it unclear whether the conditional retaliation led to a decrease in aggression towards neighbours. Note, however, that an earlier study of red-winged blackbirds in a different population did find the Dear Enemy effect (Yasukawa et al. 1982). The difference between this study and Olendorf et al.'s (2004) study might result from population differences in the relative threat of strangers versus neighbours to territory holders in usurping their territory or their mate (Temeles 1994).

In contrast, Hyman (2002) found that Carolina wrens did not increase aggression towards their neighbours after an intrusion by that neighbour. The explanation he proposed was that long-term associations with neighbours might lead to more forgiving strategies among territory holders. Song sparrows in our population, however, also have long-term associations with their neighbours but still showed retaliation to intruders, thus indicating that this explanation may not be generalizable.

Hyman (2002) suggested another factor that might be of importance in determining whether neighbours retaliate. Carolina wrens appear to be one of the rare genetically monogamous songbird species (Haggerty et al. 2001). In contrast, extrapair copulations (EPCs) are prevalent in the song sparrow (24% of offspring in our population result from EPCs; C. E. Hill, Ç. Akçay, S. E. Campbell & M. D. Beecher, unpublished data). Furthermore, most of the EPCs occur with an immediate neighbour. This finding suggests that males might be retaliating against an intruding neighbour to decrease the risk of cuckoldry by that neighbour. There are at least two possible reasons why an intruding neighbour might pose a higher risk of cuckoldry to a male than a nonintruding neighbour: (1) females might have a preference for aggressive males as extrapair mates, and an intruding male might be perceived as aggressive; (2) intruding males may pose a more direct threat of initiating extrapair mating attempts (Westneat & Stewart 2003). Evidence for either possibility in song sparrows is meager at this point and requires further research effort into behavioural events leading to extrapair mating.

The cuckoldry risk hypothesis outlined above is not necessarily an alternative to a Prisoner's Dilemma game. Rather, it can be viewed as a Prisoner's Dilemma game where the payoffs are determined not only by the location of territory boundaries, but also by mating interactions (i.e. winning an EPC versus losing an offspring). The cuckoldry risk hypothesis nevertheless makes some new predictions. For starters, males should respond more aggressively towards neighbours that are likely to cuckold them (Olendorf et al. 2004). Also, if we carried out an experiment like the present one, we would expect to see changes in female and male behaviour in response to a simulated intrusion, such as an increase in female forays into the aggressive neighbour's territory and an increase in mate guarding by the male.

Further research is needed to understand the nature of interactions between territory holders. We believe that such research should focus on understanding the behavioural mechanisms of boundary negotiations and mating interactions. Species differ in whether they are in dear enemy relationships (Temeles 1994), and differences between Carolina wrens and song sparrows suggest that even when neighbours are dear enemies, species might differ in the strategies through which they cooperate.

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