Sexual selection and a secondary sexual character in two *Drosophila* species

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Abstract. Evidence of sexual selection on male body size and on the number and symmetry of sternopleural bristles and of sex comb teeth was sought in natural populations of two *Drosophila* species. Body size did not differ between mating and non-mating males in either species. Mating male *D. simulans* had significantly fewer sex comb teeth than did males not found copulating, and mating male *D. pseudoobscura* had more sternopleural bristles. No difference in fluctuating asymmetry of any bilateral trait was found between mating and non-mating males. These observations suggest that generalizations that large body size and symmetry promote mating success are unfounded.

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A guiding theme in sexual selection research has been the elucidation of general principles underlying mating success. Whether success is achieved through inter- or intra-sexual interactions, large body size in males has emerged as a correlate of success across a range of taxa (Thornhill & Alcock 1983) Recent investigations with *Drosophila* species have indicated, however, that the relationship between body size and male success is complex and may not be as strong as originally believed. As more species are studied, the number of examples where the two are uncorrelated is increasing (Table I). Larger male size has been reported to be associated with mating success in *D. melanogaster* (Partridge et al. 1987; Markow 1987, 1988; Pitnick 1991), *D. nigrospiracula* (Markow 1988), *D. hydei* (Markow 1985; Pitnick & Markow 1994), *D. buzzatii* (Santos et al. 1988), *D. testacea* (James & Jaenike 1992), *D. simulans* and *D. mojavensis* (Markow & Ricker 1992). In contrast with these reports, mating male *D. pseudoobscura* from a two-year field study were no larger than single males (Markow & Ricker 1992), but larger size was associated with male success in certain samples of another field study (Partridge et al. 1987). Our own observations for

natural populations of *D. nigrospiracula* have yielded different associations between size and mating success in different studies (Markow 1988; Polak & Markow 1985), suggesting that directional sexual selection for large male body size is not universal. In *D. montana*, small males showed a reproductive advantage in nature (Aspi & Hoikkala 1992). Finally, there is evidence of stabilizing sexual selection on male size for *D. simulans* (Markow & Ricker 1992), *D. pseudoobscura* (Markow and Ricker 1992), *D. melanogaster* (Markow & Sawka 1991), *D. mojavensis* (Markow & Ricker 1992), *D. buzzatii* (Santos et al. 1988; Ruiz et al. 1991) and *D. silvestris* (Boake 1989).

Another approach to identifying correlates of male mating success has been to seek more general correlates of male quality or fitness as expressed in the developmental stability, or fluctuating asymmetry, of males. This was first examined by Markow (1987) in a study in which developmental stability, as reflected in sternopleural bristle fluctuating asymmetry, was associated with male success in laboratory reared *D. melanogaster*. This approach has subsequently been used to show a positive relationship between symmetry and mating success in natural populations of a number of other taxa (e.g. Møller 1990, 1992; Thornhill 1992). When additional *Drosophila* species were tested, however, no consistent pattern in the relationship between instability and success was observed (Markow & Ricker 1992).

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Table I. Summary of reported associations of male courtship advantages with body size and fluctuating asymmetry

Species	Conditions	Body size	Asymmetry	Reference
D. melanogaster	Lab	+	+	Markow 1987
	Lab/field	+		Markow 1988
	Field	+		Partridge et al. 1987
	Lab	+		Pitnick 1991
	Lab	+	0	Wilkinson 1987
	Lab	+		Markow & Sawka 1992
D. simulans	Field	+	+/0	Markow & Ricker 1992
D. hydei	Lab	+		Markow 1985
	Lab	+		Pitnick & Markow 1994
D. nigrospiracula	Lab/Field	+		Markow 1988
	Field	0		Polak & Markow 1995
D. mojavensis	Field	+	0	Markow & Ricker 1992
D. pseudoobscura	Field	+/0/ −		Partridge et al. 1987
	Field	0	−	Markow & Ricker 1992
D. testacea	Field	+/0		James & Jaenike 1992
D. montana	Field	−		Aspi & Hoikkala 1992
D. buzzatii	Field	+		Santos et al. 1988
D. suboobscura	Lab	−		Steele & Partridge 1988
	Lab	+		Steele 1986

'+' indicates a positive relationship between male success and large size or increased asymmetry, '0' reflects no relationship, ' − ' indicates that success was associated with small size or low asymmetry.

Recently, attention has been drawn to the potential association between developmental stability in secondary sexual traits and male success (Møller & Pomiankowski 1994). These authors predicted that (1) secondary sexual characters, because they are under directional selection, should show greater fluctuating asymmetry than general morphological traits, and (2) low fluctuating asymmetry in secondary sexual characters provide the most reliable indicator to females of general male quality, with greater symmetry in these characters being associated with male success. Although these authors use data on bird spurs and beetle horns to support their first prediction (Møller 1992), and observations on bird feather ornaments to support the second (Møller & Pomiankowski 1994), the broad applicability of this concept has yet to be examined.

A secondary sexual character found in *Drosophila* is the sex comb, seen only in species of the subgenus *Sophophora*. Sex combs are used by males during courtship and mounting. Their expression varies between species, both in the number of teeth in the comb and in the number of rows of combs. In the present study, we used two species, *D. simulans*, in which there is one row of sex combs, and *D. pseudoobscura*, in which males have two rows situated on adjacent tarsal segments.

Spieth (1952) observed a relationship between the sequence in which males of a given species attempt copulation and the presence of sex combs: Sophophoran males attempt intromission before mounting is complete, but males of species without sex combs do not. Using this distinction, Spieth (1952) speculated that the combs are necessary in precopulatory manoeuvrering by males. A number of investigations reported reduced copulatory success for males whose sex combs have been surgically removed (Spieth 1952; Cook 1977; Coyne 1985). The actual role of the sex combs may differ, however, between flies of the melanogaster group in which there is one row of teeth and those of the obscura group in which males have two. Spieth (1952) and Cook (1977) observed that in the melanogaster group, the combs are used in grasping the female, specifically her ovipositor (Coyne 1985), but in the obscura group they may, in addition, assist males in spreading the female's wings. No studies have addressed the evolutionary significance of

intraspecific variation in the numbers of teeth in the sex combs.

The present study had two objectives. First, we accrued additional observations on the relationship between male size and mating success in natural *Drosophila* populations. The major focus, however, was to examine the expression of a secondary sexual character with respect to sexual selection and to compare levels of variation in that character with variation observed in other morphological features of the same males. We chose to study *D. simulans* and *D. pseudoobscura*, because these two species provide a comparison between the melanogaster and obscura species groups in which there are one and two rows, respectively, of sex combs. In addition, our earlier studies on these species (Markow & Ricker 1992) provide comparative data from other years of the same local populations, enabling us to address the issue of the consistency with which certain characters are associated with mating success.

METHODS

Field Collections

We aspirated copulating pairs and single males of *D. simulans* and *D. pseudoobscura* from fallen citrus in Tempe, Arizona in the spring of 1994. Flies were collected at times when courtship and copulation were most prevalent, from 0730 to 0930 hours and from 1630 to 1930 hours. Copulating pairs were found both on the outer skin of fruit, as well as on the fleshy pulp deep within cracks in the fruit. Whenever a copulating pair was collected, we also collected five to six single flies in the immediate vicinity. Prior to mating, a female is typically courted by a group of males, from which the successful contestant emerges. Unsuccessful males remain in the area and court other females. Thus the single males nearby a copulating pair will be fairly representative of unsuccessful males. Because a small number of *D. melanogaster*, the sibling species of *D. simulans*, was also found in our collections, we collected enough single males to ensure that at least one *D. simulans* was in the sample to compare. Flies were taken to the laboratory to be measured and to have their sternopleural bristles and sex comb teeth counted.

Measurement on Flies

Before any measurements were made on flies, we separated mating males from females and coded them in such a way as to obscure their mating status from the investigator performing the measures. We then anaesthetized the single males and placed them in a line. The first *D. simulans* in the line was selected to be measured. A dissecting microscope (Wild) with an ocular micrometer was used to determine thorax length. We also made counts on two bilateral traits, sternopleural bristle and sex comb tooth number; bristles were counted under the dissecting microscope at a magnification of $\times 40$ and comb teeth were counted under a compound microscope at a magnification of $\times 100$, after mounting each male's legs on a glass slide in a drop of white paraffin oil. We measured each bilateral trait three separate times to evaluate the role of measurement error in fluctuating asymmetry analysis. *Drosophila pseudoobscura* has two rows of sex combs, upper and lower, which we counted and recorded separately.

Analysis of Fluctuating Asymmetry

In comparing levels of fluctuating asymmetry in mating and non-mating flies, we followed the guidelines of Palmer (1994). These recommendations include testing for directional asymmetry (i.e. one side typically larger than the other), for a relationship between asymmetry and trait magnitude, and for measurement error, which can lead to an inability to detect significant differences in fluctuating asymmetry between treatments or classes. In the case of the two bilateral traits studied here, the lack of relationship between bristle or tooth number asymmetry with bristle or tooth number, respectively, enabled us to use the value, Right minus Left $(R - L)$, known as Palmer index FA1, as our measure of fluctuating asymmetry.

Bristle number and sex comb tooth number are meristic characters, and as such raise specific concerns with respect to the confounding effect of measurement error (Markow 1994). Palmer (1994) recommended two procedures to test for measurement error when dealing with meristic traits. First, the potential for subjectivity must be ruled out. For sternopleural bristles and sex comb teeth, there are no intermediate or diminished
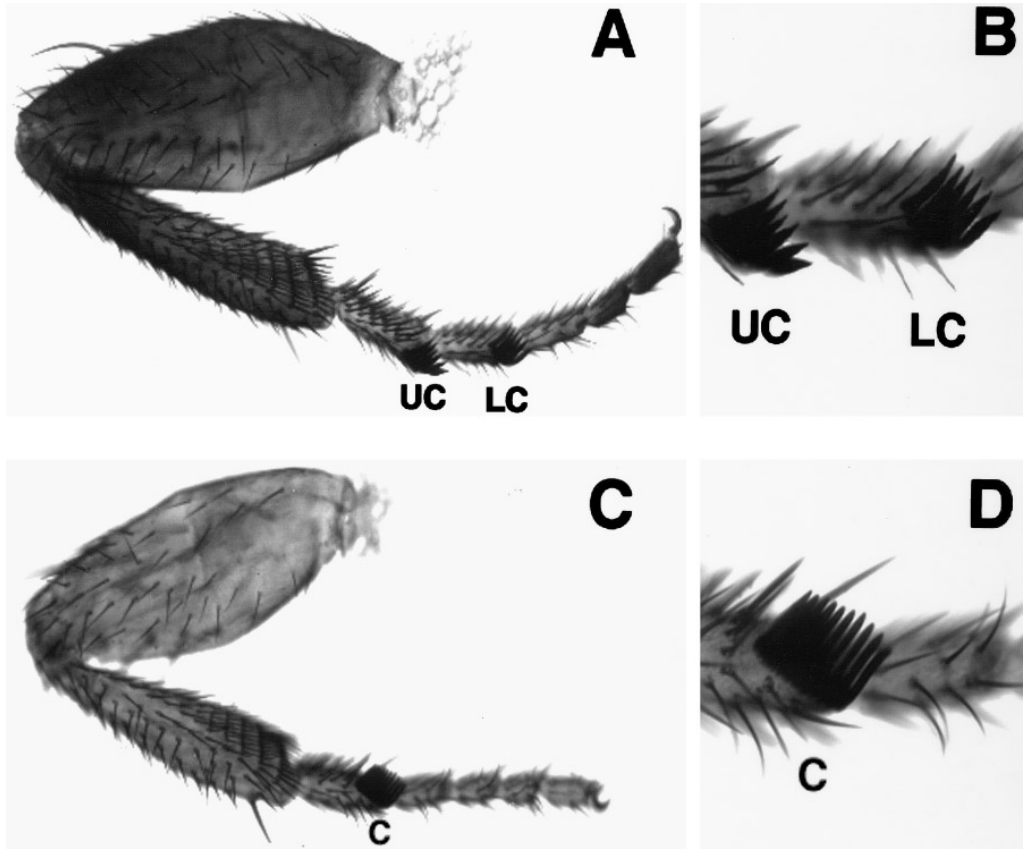
Figure 1. (A) Right prothoracic leg of *Drosophila pseudoobscura*, showing the sex comb located on each of the first two tarsal segments. In magnified view (B), each comb of this leg can be seen to have six teeth. (C) Right prothoracic leg of *D. simulans*, showing the single sex comb located on the first tarsal segment. In magnified view (D), this sex comb can be seen to have 10 teeth. C=sex comb; UC=upper sex comb; LC=lower sex combs.

expressions of the trait, so subjectivity is not an issue. The other issue is observer counting error, which, if low, can be ignored. We addressed this by counting the traits three times on each fly. There were 100 flies of each species. For *D. simulans*, there were two bilateral traits, bristles and one row of sex combs on the right and left sides, respectively, giving a total of 400 data points. In two cases, one of the three counts for a data point was off by a value of one, giving an error rate of 0.005. For *D. pseudoobscura*, the extra row of combs gave 500 data points. In two cases, the count differed by a value of one, which was an error rate of 0.004. Thus measurement error was inconsequential and in those four cases where error was detected, we used the value for the trait in which two of the three counts agreed.

RESULTS

Drosophila simulans

Characteristics of mating and single males are shown in Table II. Mating and single males did not differ in mean thorax length ($F_{1,98}=0.18$, $P=0.67$) or in sternopleural bristle numbers ($F_{1,98}=0.54$, $P=0.46$). However, males found *in copula* showed significantly fewer teeth in their sex combs (right and left combined) than single males ($F_{1,98}=7.16$, $P=0.009$).

We were also interested in whether sex comb tooth number showed more phenotypic variability than sternopleural bristles. The coefficient of variation (CV), because it is standardized by the trait mean, provides a way of comparing levels of variation in different traits from the same

Table II. Measurements from mating ($N=50$) and single ($N=50$) *D. simulans* males

Trait	Mating males		Single males	
	$\bar{X} \pm \text{SE}$	CV	$\bar{X} \pm \text{SE}$	CV
Thorax length (mm)	0.94 ± 0.01	8.01	0.93 ± 0.01	7.49
Bristle number	24.45 ± 0.57	15.92	26.11 ± 0.68	18.41
Sex comb number	20.88 ± 0.29	9.75	21.98 ± 0.29	9.44

Table III. Bristle and sex comb tooth number from the right and left sides of mating ($N=50$) and single ($N=50$) *D. simulans* males and fluctuating asymmetry (FA)

Trait	Mating males $\bar{X} \pm \text{SE}$	Single males $\bar{X} \pm \text{SE}$
Right bristle	12.70 ± 0.31	12.94 ± 0.37
Left bristle	12.76 ± 0.34	13.16 ± 0.37
Right comb	10.32 ± 0.17	10.80 ± 0.17
Left comb	10.56 ± 0.17	11.18 ± 0.16
Bristle FA	1.87 ± 0.15	1.67 ± 0.18
Comb FA	0.96 ± 0.12	0.90 ± 0.12

biological sample (Sokal & Rohlf 1981). Testing the significance of differences in the CV is performed by calculating a *c* value (Woolf 1968). The CV (Table I) for sex comb teeth (all males) was the same as for thorax length ($c=0.02$, $P>0.80$), but the sternopleural bristle CV was twice as variable as that of sex comb teeth and of thorax length ($c=4.83$, $P<0.001$). The CVs did not differ between mating and non-mating males for any trait.

To determine whether males in the two categories differ in developmental stability, we examined the degree of fluctuating asymmetry for both bilateral traits (Table III). Neither trait showed directional asymmetry in mating or single flies. Neither bristle number nor sex comb tooth number showed any relationship between character magnitude and fluctuating asymmetry (bristle *R*-square$=0.02$; sex comb *R*-square$=0.002$). Neither sternopleural bristles ($F_{1,98}=0.70$, $P=0.40$) nor sex comb teeth ($F_{1,98}=0.13$, $P=0.40$) differed in the degree of fluctuating asymmetry in mating or single males, although the tendency was towards greater asymmetry in the mating males.

Drosophila pseudoobscura

Values for thorax length and bilateral traits in mating and single *D. pseudoobscura* males are shown in Table IV. Males from the two groups were identical in size ($F_{1,98}=0.09$, $P=0.77$). Mated males had significantly more sternopleural bristles than single males ($F_{1,98}=4.7$, $P=0.033$). Sex comb tooth number, whether the upper and lower rows were considered separately or pooled (pooled $F_{1,98}=1.25$, $P=0.266$), did not differ between male groups.

As in *D. simulans*, bristles were more variable than thorax length ($c=4.14$, $P<0.001$, all males), but upper combs were more variable than bristles ($c=2.44$, $P<0.02$, all males) and lower combs were more variable than the upper ones ($c=14.4$, $P<0.001$, all males). As observed for *D. simulans*, single males and mating males showed no significant differences in the CV of any trait, even the lower sex comb ($c=1$, 24, $P>0.2$).

Table V shows the bristle and sex comb tooth numbers for the right and left sides of mating and single *D. pseudoobscura* males. No directional asymmetry was detected and none of the traits showed relationships between trait magnitude and asymmetry (bristle: *R*-square$=0.004$; combs: *R*-square$=0.097$). Levels of fluctuating asymmetry in mating and single males was the same for both bristles ($F_{1,98}=1.26$, $P=0.265$) and sex combs ($F_{1,98}=0.14$, $P=0.709$).

DISCUSSION

Thorax length, the most commonly used measure of body size in *Drosophila*, did not show any consistent relationship with male mating status in either species. Mating males of *D. simulans* were characterized by slightly, but not significantly, greater thorax lengths than single males, a difference found to be statistically significant in both years of an earlier study (Markow & Ricker 1992). Single and mating *D. pseudoobscura* males were identical in size, as reported previously (Markow & Ricker 1992). An inconsistent relationship between male size and success also emerged

Table IV. Measurements from mating (*N*=50) and single (*N*=50) *D. pseudoobscura* males

Trait	Mating males		Single males	
	$\bar{X} \pm$ SE	CV	$\bar{X} \pm$ SE	CV
Thorax length	1.01 ± 0.01	7.24	1.05 ± 0.01	6.59
Bristle number	31.93 ± 0.71	15.74	29.62 ± 0.79	19.01
Upper sex comb	12.36 ± 0.41	23.67	11.52 ± 0.42	25.72
Lower sex comb	8.32 ± 0.63	53.67	7.50 ± 0.68	64.04
Total sex comb	20.68 ± 1.01	34.85	19.02 ± 1.08	40.09

Table V. Right and left bristle and sex comb number for mating (*N*=50) and single (*N*=50) *D. pseudoobscura* males and fluctuating asymmetry (FA)

Trait	Mating males $\bar{X} \pm$ SE	Single males $\bar{X} \pm$ SE
Right bristle	15.78 ± 0.39	14.78 ± 0.43
Left bristle	16.14 ± 0.37	14.82 ± 0.42
Right upper comb	6.26 ± 0.21	5.82 ± 0.22
Left upper comb	6.10 ± 0.21	5.70 ± 0.21
Right lower comb	4.26 ± 0.32	3.86 ± 0.34
Left lower comb	4.06 ± 0.31	3.68 ± 0.34
Bristle FA	1.64 ± 0.13	1.83 ± 0.12
Sex comb FA	0.24 ± 0.05	0.20 ± 0.05

between replicates in another study of natural populations of *D. pseudoobscura* (Partridge et al. 1987). All of the above studies were made on natural populations of flies and therefore were unable to control factors such as age, reproductive status, population density, quality of the developmental environment or even parental developmental environment, all of which influence male mating success (Markow et al. 1978; Long et al. 1980; Just & Markow 1989; Markow & Sawka 1992) or territorial success (Zamudio et al. 1995). Zamudio et al. (1995), in controlled laboratory experiments, provided additional evidence that male body size is not necessarily associated with territorial behaviour, and offered a developmental/physiological construct for the interpretation of differences in success of males of different sizes.

Sternopleural bristle number was unrelated to male mating status in *D. simulans* but was in *D. pseudoobscura*. This observation matches previous findings for *D. simulans* (Markow & Ricker 1992). In that study, the relationship between bristle number and mating status in *D. pseudo-* obscura was not examined because we lacked a microscope capable of resolving their very black bristles. There is no reason to expect sternopleural bristle number to be associated with male success, but the argument can be more easily made that male courtship ability, or vigour, is size-dependent. Because studies have differed in their findings with respect to male size, however, any conclusions about the sternopleural bristles should be based upon a larger number of independent investigations.

The sex combs, on the other hand, have a known function in courtship. Mean number of sex comb teeth was associated with mating status only in *D. simulans*, mating males having an average of one fewer teeth than single males. Thus a greater number of teeth does not appear to favour male success. Too many teeth may be disadvantageous in grasping females, or females may find combs with too many teeth to be aversive and may avoid copulation with such males. The fact that no difference was observed in tooth number for mating or single *D. pseudoobscura* males may reflect the different functions ascribed to the combs in these two species (Speith 1952; Cook 1977; see Introduction).

Variation in the traits under study, with the exception of thorax length, may be examined at the levels of inter- and intra-individual variation. Inter-individual variation for the sexual and non-sexual traits may be compared by ranking the coefficients of variation. For *D. simulans*, the ranking, in ascending order, is thorax length< sex comb tooth number<sternopleural bristles. The order for *D. pseudoobscura* is different: thorax length<sternopleural bristles<lower sex combs< upper sex combs. The order is the same regardless of male mating status. Despite the differences between *D. simulans* and *D. pseudoobscura* in

thorax length and bristle number, the coefficients of variation for these two traits are amazingly similar. Total sex comb number for *D. pseudoobscura* is similar to the sex comb number for *D. simulans*, even though the sex combs of the former are arranged in two rows. However, the coefficient of variation for sex combs in *D. pseudoobscura* is comparatively much greater. The mean tooth number we observed for *D. simulans* is virtually identical to the means reported for this species by Coyne (1985).

Comparing the magnitudes of the CVs between mating and single males does not indicate that stabilizing selection is acting on any of the traits. Intra-individual variation, reported as fluctuating asymmetry, reflects developmental instability, or the degree to which the flies were unable to buffer disturbances during their ontogeny (Waddington 1953). Some investigators have interpreted high symmetry to indicate high male quality (Møller & Pomiankowski 1994), although direct support for this assumption is conflicting (discussed in Markow 1994, 1995). With respect to sexual selection in *Drosophila*, only four species have been examined. Low sternopleural bristle fluctuating asymmetry was associated with male success in *D. melanogaster* (Markow 1987), and lower wing fluctuating asymmetry was found in mating *D. pseudoobscura* males (Markow & Ricker 1992). In *D. simulans*, however, successful males showed the greatest fluctuating asymmetry both in their wings and in their aristal branching (Markow & Ricker 1992). In the fourth species, *D. mojavensis*, no differences were found between mating and single males for fluctuating asymmetry in either wing length or bristle number (Markow & Ricker 1992). The present study is consistent with the earlier reports in that sternopleural fluctuating asymmetry did not differ by mating status in either *D. simulans* or *D. pseudoobscura*.

Møller & Pomiankowski (1994) argue that the strongest associations with asymmetry should be seen in secondary sexual characters. On this basis, we would not necessarily expect sternopleural bristles, which are not secondary sexual traits, to show any association with mating success. Our test of their prediction for secondary sexual traits using the sex combs in two *Drosophila* species, however, does not support their hypothesis. Wing length has been related to male mating success via differences in songs produced by artificially shortened wings (Ewing 1964; Bennet-Clark &

Ewing 1969). As described above, however, Markow & Ricker (1992) found that wing symmetry was greater in mating males of only one of three *Drosophila* species, *D. pseudoobscura*, and that it was actually reduced in copulating males in *D. simulans*. In a laboratory study with *D. melanogaster*, surgically created wing asymmetries had no influence on the outcome of sexual selection (Markow & Sawka 1992). Thus, among *Drosophila*, there is no evidence that fluctuating asymmetry in secondary sexual characters typically is greater than for other characters or is associated with mating success. Sex comb tooth number is more variable than the other traits in one of the species examined, *D. pseudoobscura*, but in neither species was there evidence that fluctuating asymmetry in the sex combs is sexually selected.

Several factors could explain our observations. One is that the experimental design, although it is the one typically used by such studies, does not permit consistent detection of differences between successful and unsuccessful males. Alternatively, *Drosophila* may be unusual in some way and therefore are not representative of most taxa. On the other hand, avian systems, with their more elaborate male ornamentation, may not be representative. A final explanation is that the phenomenon proposed by Møller & Pomiankowski (1994) is not a general one. Only studies of other taxa can resolve this question.

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