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Sexual Selection on Morphology in an Explosive Breeding Amphibian, the Columbia Spotted Frog (*Rana luteiventris*)

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ABSTRACT.—It is well documented that sexual selection acts on morphological differences between individuals and can lead to sexual dimorphism in species with male combat and female choice. However, the effect of sexual selection on the evolution of morphological traits is poorly understood in species with scramble competition in which males race for access to females during a brief pulse of breeding activity. Because male access to females may be more random in scramble mating systems, male morphological traits may not strongly influence mating success. To investigate the influence of sexual selection on male morphology in a species with a scramble mating system, we collected detailed morphological measurements from male and female Columbia Spotted Frogs (*Rana luteiventris*), which have an extreme scramble mating system. Male Columbia Spotted Frogs have enlarged thumb (nuptial) pads and muscular forearms, which may help them grasp females. As predicted, we discovered that males found in amplexus with females had proportionately larger nuptial pads and thicker forearms than did unpaired males, but mating success was not related to overall body size. Although many single males attempted to dislodge males already in amplexus with females, no attempted takeovers were successful. Therefore, we suggest that the advantage of thick forearms and large nuptial pads occurs during the initial phase of securing a female when she first enters the breeding area. These findings suggest that sexual selection may influence morphology even in a species with scramble mating.

Sexual selection is a form of selection that arises from differences in mating success (Futuyma, 1998). Sexual selection has long been recognized to influence morphological evolution in sexually reproducing species (Darwin, 1871), especially in those species with one of two types of reproductive strategies (Small, 1992). First, competition among males in the form of direct physical combat can lead to the development of physical traits that are used as weapons or armor during contests over females (Gould and Gould, 1989; Andersson, 1994). In a second form of sexual selection, successful males are chosen by females (Andersson, 1994). In many bird species, for example, females choose their partners based on their plumage or coloration, which can lead to the development of exaggerated or showy traits (Petrie et al., 1991; Safran and McGraw, 2004). And in many frog species, females choose males based on their advertisement calls (Ryan, 1980, 1985). Both male combat and female choice can lead to the development of sexually dimorphic traits, and the degree of sexual dimorphism is generally thought to reflect the intensity of sexual selection (Shuster and Wade, 2003).

However, some species have neither physical combat among males nor female choice. Scramble competition is one such mating system in which individuals race for access to mates, and there appears to be little opportunity for male combat or female choice. Species with scramble mating systems often have sexually dimorphic traits, although these traits are usually less pronounced than those found in species with male-male combat or female choice (Gould and Gould, 1989). The presence of these sexually dimorphic traits suggests that sexual selection nonetheless may play a role in scramble mating systems as well. Although relatively little is known about the effects of sexual selection on the morphology of species with scramble mating systems, it is hypothesized that, in these species, reproductive success is determined more by chance compared to species with male combat or female choice. In his renowned treatise on sexual selection, Andersson (1994) writes, "More work also needs to be done on scramble competition and endurance rivalry, the importance of which has become clear only recently."

Many anuran species have short, intense scramble mating systems, known as explosive breeding. Explosive breeding generally lasts from one day to two weeks (Wells, 1977a; Pough et al., 2004). Males usually congregate at breeding areas first and begin calling and searching for females. Females arrive later and

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in smaller numbers at any given point in time; hence, the sex ratio at the breeding pond is usually male-skewed (Turner, 1960; Wells, 1977a; Pough et al., 2004). Because all males are not reproductively successful, there is competition among males for access to females, but in only an estimated 5.4% of anuran species does this competition take the form of direct physical combat (Shine, 1979). In many explosive breeding ranids and bufonids in Western North America, however, there can be male-male contact in the attempt to displace other males that borders on "combat" (Olson et al., 1986; Davis and Verrell, 2005). Because of the short duration of the breeding season and the nature of the scramble system, it has been suggested that there is also little opportunity or time for female choice (Wells, 1977a).

Despite the absence of female choice and direct male combat in anurans with explosive breeding, sexual selection may still act on male morphology. For example, most explosive breeding anurans are sexually dimorphic. Males of many species are smaller than females and have muscular forearms and enlarged areas of textured skin on their thumbs or chest called nuptial pads (Duellman, 1970; Lynch, 1971). Specifically, it is hypothesized that large body size, nuptial pads, or muscular forelimbs may help males achieve amplexus (the mating embrace) and hold on to females until oviposition (Duellman and Trueb, 1994).

In this study, we investigated the extent of sexual dimorphism and the effect of morphological variation on male mating success in Columbia Spotted Frogs (*Rana luteiventris*). Columbia Spotted Frogs are pond-breeding frogs native to the western United States, western Canada, and southeastern Alaska (Stebbins, 2003). They have an explosive mating system lasting a few days to a couple of weeks at each breeding site (Turner, 1958; Bull and Shepherd, 2003). Male Columbia Spotted Frogs are generally smaller than females and have enlarged, muscular forearms and nuptial pads at the base of the thumbs, but it is not known whether these traits influence mating success. Here, we addressed the following two questions. (1) Are there significant morphological differences in shape between males and females that could be related to sexual selection? (2) Does body size, relative size of nuptial pads (independent of overall body size), or relative width of forearms affect the mating success of male Columbia Spotted Frogs?

MATERIALS AND METHODS

This study was conducted at a small lake on the north side of Spruce Mountain (hereafter

referred to as Spruce Mountain Lake), Lincoln County, in the Cabinet Mountains of Montana (48°19'12"N, 115°58'51"W; referred to as pond 1 in Funk et al., 2005a). Spruce Mountain Lake has a surface area of approximately 1 ha and a maximum depth of 4 m. The lake is structurally simple, with relatively little cover for frogs, making it easy to survey. The elevation of the lake is approximately 1,570 m. The breeding season for Columbia Spotted Frogs at Spruce Mountain Lake lasted for only four days in 2002, from 13–16 June. During that time, a total of 92 egg masses were deposited under approximately 1 m of water at three main areas along the northwest shore of the lake.

We began observing the breeding areas and capturing frogs on June 14, at which time only several egg masses had been deposited, and ended on June 16, when no more egg masses were laid and no amplexant pairs were observed. During these three days, two people observed the main breeding areas and searched the perimeter of the lake from 0700 h to approximately 1800 h, although most frogs were captured from approximately 0700–1000 h, which was when almost all breeding activity took place. Both amplexant pairs and single males were captured, and one person continued watching the breeding area, while the other person measured frogs. We captured 33 amplexant pairs (66 frogs) and 24 single males at Spruce Mountain Lake during the sampling period. Three females were not measured (two escaped and one was injured). Therefore, total $N = 87$. Males found in amplexus (paired males) were likely successful in fertilizing eggs, because we saw no evidence that males were dislodged once in amplexus (see details in Results). Amplexus can last several days in Columbia Spotted Frogs (Svihla, 1935; Turner, 1958; Bull, 2005; Davis and Verrell, 2005).

Once frogs were captured, each amplexant pair was placed in an individual plastic container to prevent possible displacement of the original male, and single males were placed in a container with other single males. Fourteen morphological measurements were taken from each male and 10 measurements were taken from each female (specific measurements defined in Fig. 1). Measurements were taken with plastic dial calipers accurate to ± 0.0015 mm by a single observer (AEG) for consistency. Several frogs were measured twice to assure accuracy. Snout-vent length (SVL), chest width, and left and right upper arm length, forearm length, upper arm width, and forearm width were measured for both males and females. Arc length was calculated as the sum of left and right upper arm lengths, left and right forearm lengths, and chest width. The length and width

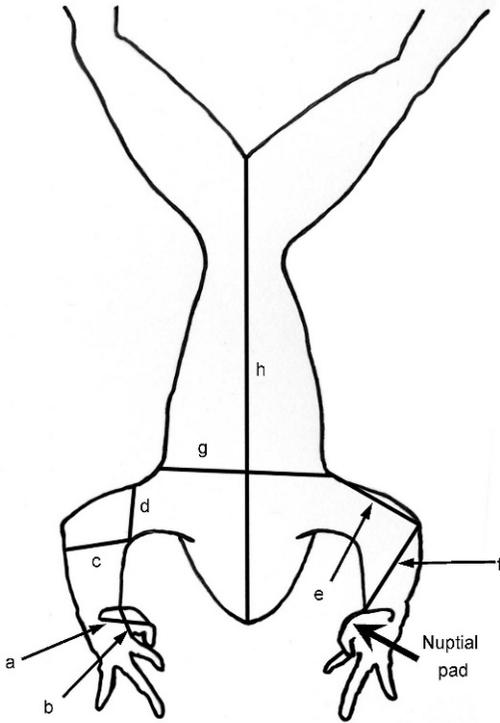


FIG. 1. Morphological measurements taken from each frog captured: (a) length of nuptial pad (males only), measured from end to end of nuptial pad; (b) width of nuptial pad (males only), measured from point where thumb meets forearm to point where thumb pad meets first finger; (c) forearm width, as there were no points of reference that could be found on every frog, we measured the forearm width by continuing the line of the leading edge of the upper arm; (d) upper arm width, similar to (c), we measured the upper arm width by continuing the line of the leading edge of the forearm; (e) upper arm length, measured from the point of the axilla to the point of the elbow; (f) forearm length, measured from the point of the elbow to the point where the nuptial pad meets the forearm; (g) chest width, measured from axilla to axilla; (h) snout-vent length, measured from end of snout to vent. The thick arrow shows the location of a male's nuptial pad. All measurements were taken with frogs in a relaxed position with arms at an approximately 90° angle.

of left and right nuptial pads were also measured for each male. All measurements were taken with the frogs in a standard position in which they were held upside down with the arms relaxed at a 90° angle from the body axis (as shown in Fig. 1). Each frog was also given a unique toe-clip code for later identification as described previously (Heyer et al., 1994; Funk et al., 2005b).

To measure each frog, amplexant pairs were separated. After frogs were processed, original pairs were placed back together in a plastic container. All original pairs immediately resumed amplexus and all pairs and individuals were released in the area where they were captured. Our methods did not seem to disrupt the natural breeding behavior of the frogs, because we never observed a single male dislodge a previously captured amplexant male, amplexant pairs immediately resumed mating, and single males resumed calling and searching for mates immediately upon return to the water.

Morphological data were log-transformed to normalize data. Averages of left and right measurements were calculated for bilaterally symmetric traits prior to log-transformation. We tested for differences between males and females and between paired and unpaired males in each morphological trait using one-way ANOVA. Because many of the traits measured are strongly correlated with overall body size, we also used multivariate principal component analysis (PCA) to test for differences in shape independent of size between males and females and between paired and unpaired males. Principal component analysis is a standard method for analyzing morphometric data (e.g., Schneider et al., 1999; Ron et al., 2005; Funk et al., 2008a). In PCA of morphological data, the first axis is generally a size axis, and the remaining axes describe orthogonal axes of variation in shape. Differences between males and females and between paired and unpaired males in principal component (PC) scores for each PC axis were also tested using one-way ANOVA. Analyses were conducted using MINITAB 15.

RESULTS

Males captured in amplexus appeared to successfully remain in amplexus until oviposition. During our daily observation period of 11 hours, we observed approximately 30 attempted takeovers in which a single male tried to clasp a female already in amplexus with another male. None of these attempts was successful. Furthermore, three previously captured pairs were recaptured on a later day, and all pairs had the same male and female as on the first day of capture. None of the males captured in amplexus were later recaptured without a female, and no males were recaptured with a different female. Conversely, males initially captured without a female were never recaptured in amplexus. During our observation period, no single gravid females were found in the lake.

TABLE 1. Morphological measurements of male and female Columbia Spotted Frogs. *P*-values were determined using one-way ANOVA of log-transformed data. *N* = 30 females and *N* = 57 males.

Variable	Sex	Mean (mm)	SD	<i>P</i>
Snout-vent length	F	72.1	5.6	<0.001
	M	63.3	3.0	
Upper arm width	F	5.4	0.7	<0.001
	M	6.0	0.6	
Upper arm length	F	10.2	1.0	<0.001
	M	12.0	1.2	
Forearm width	F	6.5	0.7	<0.001
	M	8.0	0.8	
Forearm length	F	11.4	0.9	0.092
	M	11.1	0.8	
Chest width	F	24.0	2.3	<0.001
	M	20.8	1.4	
Arc length	F	67.2	5.6	0.744
	M	66.8	3.7	

There were several statistically significant differences between females and males in log-transformed morphological traits (Table 1). Although females tended to have larger snout-vent lengths and wider chests than males, males had significantly wider forearms, wider upper arms, and longer upper arms. There were also significant morphological differences between paired and unpaired males (Table 2). Paired males had thicker nuptial pads, wider upper arms, and narrower chests than unpaired males.

Principal components analysis showed significant differences in shape as well as size

TABLE 2. Morphological measurements of paired and unpaired male Columbia Spotted Frogs. *P*-values were determined using one-way ANOVA of log-transformed data. *N* = 33 paired and *N* = 24 unpaired males.

Variable	Amplexus?	Mean (mm)	SD	<i>P</i>
Snout-vent length	Yes	62.9	3.0	0.232
	No	63.9	3.0	
Upper arm width	Yes	6.2	0.6	0.010
	No	5.8	0.5	
Upper arm length	Yes	12.0	1.1	0.835
	No	11.9	1.3	
Forearm width	Yes	8.1	0.7	0.134
	No	7.8	0.9	
Forearm length	Yes	11.0	0.8	0.111
	No	11.3	0.7	
Chest width	Yes	20.4	1.6	0.012
	No	21.3	0.9	
Arc length	Yes	66.2	3.5	0.151
	No	67.6	3.9	
Nuptial pad width	Yes	3.5	0.4	0.014
	No	3.3	0.3	
Nuptial pad length	Yes	6.8	0.6	0.111
	No	6.5	0.6	

TABLE 3. PCA loadings of log-transformed morphological variables for male and female Columbia Spotted Frogs.

Variable	PC 1	PC 2	PC 3
Snout-vent length	0.732	-0.232	0.641
Forearm width	-0.125	0.879	0.461
Arc length	0.670	0.417	-0.614
Eigenvalue	1.527	1.186	0.288
% of variance	50.9	39.5	9.6

between males and females (Table 3; Fig. 2). Principal component axis one (PC 1) explained 50.9% of the variation in male and female morphology and had high positive loadings for SVL and arc length. Principal component axis two (PC 2) explained an additional 39.5% of the variation and had a high positive loading for forearm width. Females had significantly higher PC 1 scores than males ($N = 87$, $F_{1,85} = 31.83$, $P < 0.001$) and significantly lower PC 2 scores ($F_{1,85} = 91.96$, $P < 0.001$). Therefore, males were smaller overall than females but had proportionately thicker forearms independent of body size.

There were also significant differences between paired and unpaired males in shape and size (Table 4; Fig. 3). Principal component one (PC 1) explained 45.1% of the variation in male morphology and was largely a size axis, with all variables showing high positive loadings. Principal components two (PC 2) and three (PC 3) explained an additional 19.7% and 17.2% of the variation, respectively, and are both largely shape axes. PC 2 had high negative loadings for nuptial pad length and width and a high

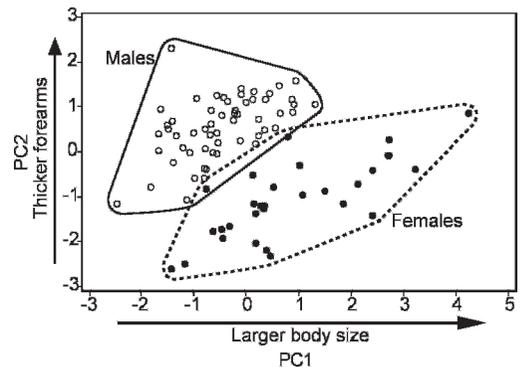


FIG. 2. Morphological differences between males ($N = 57$; open circles) and females ($N = 30$; solid circles) revealed by principal components analysis. PC 1 had high positive loadings for snout-vent length (SVL) and arc length, and PC 2 a high positive loading for forearm width (Table 3). The range of data points for females is shown with a dotted line and the range for males is shown with a solid line.

TABLE 4. PCA loadings of log-transformed morphological variables for paired and unpaired male Columbia Spotted Frogs.

Variable	PC 1	PC 2	PC 3
Snout-vent length	0.449	0.612	-0.050
Forearm width	0.422	0.247	0.637
Arc length	0.462	0.170	-0.663
Nuptial pad width	0.457	-0.417	0.332
Nuptial pad length	0.444	-0.601	-0.207
Eigenvalue	2.253	0.985	0.858
% of variance	45.1	19.7	17.2

positive loading for SVL. PC 3 had a high positive loading for forearm width and a high negative loading for arc length. There was no significant difference in PC1 between paired and unpaired males ($F_{1,55} = 0.69$, $P = 0.41$), but paired males had significantly lower PC 2 scores than unpaired males ($F_{1,55} = 7.58$, $P = 0.008$) and significantly higher PC 3 scores than unpaired males ($F_{1,55} = 7.88$, $P = 0.007$). Thus, paired males had proportionately larger nuptial pads and thicker forearms than unpaired males independent of body size. Paired males also had shorter snout-vent lengths and arc lengths than unpaired males independent of overall body size. In other words, paired males were stouter, with more exaggerated nuptial pads and forearms.

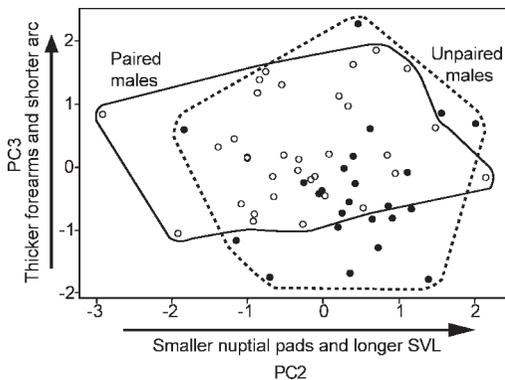


FIG. 3. Morphological differences between paired ($N = 33$; open circles) and unpaired ($N = 24$; solid circles) males revealed by principal components analysis. PC 2 had high positive loadings for snout-vent length (SVL) and high negative loadings for nuptial pad length and width. PC 3 had high positive loadings for forearm width and high negative loadings for arc length (Table 4). The range of data points for paired males is shown with a solid line and the range for unpaired males is shown with a dotted line.

DISCUSSION

We found significant morphological differences between male and female Columbia Spotted Frogs, as suggested by previous observations. Females greatly exceeded males in overall size and snout-vent lengths (SVL), but males had wider forearms (Table 1; Fig. 2). Several other studies have shown that female Columbia Spotted Frogs are larger than males (Turner, 1960; Licht, 1975; Cuellar, 1994; Bull, 2005; Davis and Verrell, 2005), but this is the first study of which we are aware to quantify morphometric variables and show significant differences in shape, specifically in forearm width, between male and female Columbia Spotted Frogs. Turner (1960) suggested that larger female size is caused by faster growth rates in females not lower survival rates in males. Larger female size is consistent with other studies of *Rana* species that show that larger female body size is related to increased fecundity (Salthe and Duellman, 1973; Elmberg, 1991). Significantly wider forearms in males than females shown here is consistent with the hypothesis that forearms of males are under sexual selection.

Principal component analysis also revealed small but statistically significant differences in morphology between males found in amplexus with females versus unpaired males. Although a male's overall body size was not important in influencing mating success (as shown by no significant differences in PC 1 scores), paired males had proportionately larger nuptial pads and wider forearms independent of body size, as shown by statistically significant differences in PC 2 and PC 3 scores, respectively (Fig. 3). This result also suggests that forearms and nuptial pads of males are under sexual selection. Males with thicker forearms and larger nuptial pads may be better able to clasp and hold onto a female as she first enters the breeding area. Previous work in *Bufo marinus* also shows that males with more robust forearms have greater mating success (Lee, 2001). In addition, amplexant males have proportionately longer forelimbs than unpaired males in four out of five anuran species examined by Lee (1986).

The quantitative differences in morphological traits between paired and unpaired males were small. Paired males had forearms an average of 0.3 mm (3.8%) wider than those of unpaired males and nuptial pads an average of 0.3 mm (4.6%) longer and 0.2 mm (6.1%) wider than those of unsuccessful males (Table 2). Nonetheless, these minute morphological differences between paired and unpaired males are apparently important for male reproductive success,

because there were statistically significant differences in these traits in the principal components analysis between paired and unpaired males. Natural selection has been found to influence subtle variation in morphology, because minute morphological differences between individuals can have a tremendous impact on an individual's survival (for example, as seen with beak size in Darwin's finches; Grant and Grant, 2002). Here, we show that sexual selection may also act on such minute variations in morphology; a frog's reproductive success or failure can be determined by a difference as small as 0.2 mm.

We hypothesize that the benefit of larger, more muscular forearms and larger nuptial pads occurs during the initial attempts to secure amplexus with females. While observing breeding activities, we noted approximately 30 attempted takeovers of amplexant females by single males, and none of these attempts was successful. Thus, once a male successfully grasps a female, he is difficult to dislodge. Particularly intense male-male competition may occur when a single female first enters the breeding area, and males with thicker forearms and larger nuptial pads may be able to acquire a stronger grip on the female than males with thinner forearms and smaller nuptial pads. Alternatively, exaggerated male secondary sexual characteristics could simply reflect male hormone levels. For example, a male with relatively thick forearms and large nuptial pads may have high hormone levels and, therefore, may try more vigorously to secure amplexus.

It is interesting that we found no significant difference in the overall size of paired versus unpaired males given the large body of literature showing a large male advantage in securing amplexus with females (Wells, 1977b; Howard, 1980; Berven, 1981; Woodward, 1982; Howard and Kluge, 1985; Olson et al., 1986). These studies show that males found paired with females tend to be larger than unpaired males. One potential reason why no large male advantage was observed in Columbia Spotted Frogs is that mating patterns often vary spatially and over time in explosive breeding species (Olson et al., 1986). Our study only examined mating success during a single breeding season in one population; yet there is substantial genetic divergence and ecological variation across the range of Columbia Spotted Frogs (Green et al., 1996; Bos and Sites, 2001; Funk et al., 2008b), suggesting that populations may also differ in mating patterns. Additional populations should be analyzed to test whether a large male advantage is seen in other populations or in other years. Alternatively, the large male advantage seen in other species

may be a by-product of a correlation between body size and other morphological traits that directly influence male mating success. Lee (1986) first suggested this possibility after morphological analysis of explosive breeding anurans showed that amplexant males had longer forelimbs than unpaired males independent of body size. More detailed morphological studies that examine body shape, not just SVL, are necessary to tease apart the relative importance of size and shape in mating success of explosive breeding anurans.

It is possible that some males found in amplexus were later dislodged by other males and, therefore, were unsuccessful. Conversely, some unpaired males found early in the four-day breeding period may have later acquired females and, therefore, were ultimately successful. In general, however, three lines of evidence suggest that paired males were successful during the 2002 breeding season, and unpaired males were not. First, in the three cases in which amplexant pairs were recaptured on subsequent days, the same male and female were found in each pair. Second, of 30 attempted takeovers, no single males successfully dislodged an amplexant male. Finally, none of the 24 single males was later found in amplexus. Moreover, even if some unpaired males did eventually secure amplexus and had the opportunity to mate on later days, these males are still less successful in the sense that it took them longer to acquire mates. In either case, the observed differences in forearm width and nuptial pad sizes between paired and unpaired males suggest that these morphological traits are important in quickly achieving amplexus with females.

The morphological effects of sexual selection on species with male combat or female choice are relatively well documented (Duellman and Savitzky, 1976; Wells, 1977a,b; Kluge, 1981; Lee and Crump, 1981; Duellman and Trueb, 1994). However, scramble mating systems are thought to be much more random, and the degree to which sexual selection affects the morphology of a species with a scramble mating system is poorly understood (Wells, 1977a; Olson et al., 1986). Our results suggest that small morphological differences between male Columbia Spotted Frogs may be important in influencing mating success. In fact, sexual selection for traits that enable a male to reproduce successfully may be especially intense in scramble systems because males only have a brief opportunity to mate each year.

Furthermore, the morphological traits that influence the reproductive success of male Columbia Spotted Frogs serve an entirely different function than traits selected through

direct male-male combat or female choice. Wide forearms and large nuptial pads of successful males are not used to fight with other males and do not appear to be chosen by females. Typically, males of species with scramble mating systems have larger eyes or sensory organs and better locomotor abilities than females to locate and reach a female more effectively (Andersson, 1994). In contrast, the traits we found to be advantageous for males are not used for finding females or for locomotion. Instead, they are used for grasping and holding on to a female until oviposition. This suggests that sexual selection may act on a broader array of traits than often appreciated.

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