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Isotopic evidence of saber-tooth development, growth rate, and diet from the adult canine of *Smilodon fatalis* from Rancho La Brea

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Abstract

The large size of canines in saber-toothed cats suggests implicitly that they took longer to grow than "normal" canines. If this were the case, then juveniles may not have been able to use them for hunting. Consequently, juvenile *Smilodon fatalis*, for example, may have had to remain in a social group and be fed by adults longer than is the case for modern large cats. Analysis of the stable carbon and oxygen isotope ratios within the enamel of the sabertooth provides a reasonably direct method to determine development and growth. Variation in the oxygen isotope ratios during the ontogeny of a particular tooth has been reported in many animals, and has been shown to correlate with temperature variation related to seasonality. Variation in the carbon isotope ratios typically reflects differences in diet, and can be used to determine if a carnivore preferred a prey that ate predominantly C_3 or C_4 plants.

This study analyzed stable carbon and oxygen ($\delta^{13}C$, $\delta^{18}O$) isotope ratios from sequential, closely spaced samples of enamel carbonate obtained from upper canines of *S. fatalis*. A sequential change in $\delta^{18}O$ through canine ontogeny for two specimens (which averaged approximately -4‰) is consistent with nearly 1 year being sampled. The results suggest that the canines of *S. fatalis* grew about 80 mm during a 12-month period, or about 7 mm/month, and the total duration of growth for this species was about 18 months. *S. fatalis* apparently achieved its long canine by combining the canine development strategies of extant lions and tigers: a quick growth rate, and growth over a long time. Mean carbon isotope values of -10.1‰ and -11.3‰ suggest consumption of animals eating a C_3 diet.

Keywords: *Smilodon*; Enamel; Canine development; Stable isotopes; Diet

1. Introduction

Evolution of the saber-toothed canine morphology in carnivorous mammals represents an extreme case of hypsodonty, resulting from very different selective pressures than those of hypsodont herbivores. Saber-toothed morphology in the upper canines of mammalian carnivores has evolved convergently at least four times, within the marsupials, creodonts, nimravids, and felids (Simpson, 1941; Emerson and Radinsky, 1980). Much of the research on this morphology has focused on determining the function of the upper canine and its use during prey capture, especially in the Machairodontine species *Smilodon fatalis* (Simpson, 1941; Gonyea, 1976; Emerson and Radinsky, 1980; Akersten, 1985).

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Further work has concentrated on determining the timing and eruption sequence for the saber-toothed canine morphology (Rawn-Schatzinger, 1983; Tejada-Flores and Shaw, 1984; Bryant, 1988, 1990). These studies yielded information about behavior and social dynamics within the particular taxa analyzed. Because of the large size of the canines in saber-toothed groups, it has been suggested that the teeth took longer to grow and erupt. For *S. fatalis*, comparison is generally made to modern lions (Tejada-Flores and Shaw, 1984). The suggestion that saber-toothed canines have a longer duration of growth was based on relative size of the tooth and not on data relating to the timing and rate at which teeth erupt. Stable isotope analyses provide a means for determining the rate and length of tooth eruption in mammalian teeth and also for determining ancient diets.

This study investigates the rate and duration of growth in the upper canine of the Machairodontine species *S. fatalis*, and determines whether *S. fatalis* shows a preference for feeding on C_3- or C_4-feeders using data from stable carbon and oxygen isotope ratios found in tooth enamel.

2. Background

2.1. Rancho La Brea

The asphalt deposits at Rancho La Brea from within the city of Los Angeles in southern California contains over 5800 individuals of birds, 3400 individuals of large mammals, and collections of reptiles, amphibians, and fish. The fauna from this locality also serves as the type locality of the Rancholabrean Land Mammal Age (Marcus and Berger, 1984). Of the mammals at Rancho La Brea, about one-third are specimens of *S. fatalis*, a saber-toothed felid. Because this species is represented by all age classes and ontogenetic stages (Marcus and Berger, 1984; Tejada-Flores and Shaw, 1984), Rancho La Brea provides a unique opportunity to study the ecology of this late Pleistocene carnivore. To place the deposits in time, ^{14}C dates from various bones range from about 35,000 to 9000 years before present (Woodard and Marcus, 1973; Marcus and Berger, 1984), spanning across the height of the last glacial maximum and into the current interglacial. The popular hypothesis for the abundance of *S. fatalis* and other carnivores at Rancho La Brea is that a herbivore became mired within an asphalt seep and attracted a group of carnivores, some of which would subsequently get caught in the asphalt and die (Marcus and Berger, 1984).

2.2. Isotopes in mammals

Variation in the oxygen isotope ratio during the ontogeny of a particular tooth has been noted in many ancient animals (Koch et al., 1989; Cerling and Sharp, 1996; Fricke and O'Neil, 1996; Feranec and MacFadden, 2000; Balasse et al., 2002). In general, higher oxygen isotope ratios ($^{18}O/^{16}O$) within the tooth enamel of a particular organism suggests the ingestion of water during a warmer period (summer), while lower isotope ratios suggest ingestion when the water was colder (winter). The variation in oxygen isotope ratios may also be due to differences in source for the meteoric waters, but source variation may also be temperature dependant as in the seasonal rains of the central United States arising from the Gulf of Mexico or the Pacific Ocean (Amundson et al., 1996). If the duration of tooth and enamel growth extends over several warm and cold periods (seasons), one would expect cyclic variation within the oxygen isotope ratio of enamel apatite. However, the oxygen isotopic value of tooth enamel may not necessarily reflect a one to one ratio with the ingested meteoric water. The ratio can be affected by the physiology or specific behavioral characteristics of a particular individual (Kohn, 1996). Carnivore enamel $\delta^{18}O$ values are generally more negative than the $\delta^{18}O$ values of herbivores occupying the same habitat (Sponheimer and Lee-Thorp, 1999, 2001). Consequently, because of the physiological and behavioral influences, the absolute $\delta^{18}O$ values of ancient enamel may not be interpretable, but the pattern, however dampened, does reflect seasonal variation in meteoric water values (Kohn et al., 1998).

The carbon isotope ratio of mammalian body tissue, including tooth enamel and bone, reflects the isotopic ratio in the food of the particular animal (DeNiro and Epstein, 1978; Lee-Thorp et al., 1989; Cerling et al., 1997). Much related research has concentrated on determining whether a herbivore fed on a plant that used either the C_3 or C_4

photosynthetic pathway, but carbon isotope studies also have been applied to determining the diets of carnivores (Lee-Thorp et al., 1989, 2000; Bocherens et al., 1994). Because herbivores can be classified as employing a C_3- or C_4-feeding strategy (DeNiro and Epstein, 1978; Vogel, 1978, Quade et al., 1992), and the tooth enamel reflects the isotope value of the forage, taking into account the further fractionation of $+14.0$‰ from forage into large herbivore tooth enamel (Cerling and Harris, 1999), it is possible to use carbon isotopes to indicate if a carnivore preferred prey that were either C_3-feeders or C_4-feeders. In herbivores, isotopic values more negative than -8.0‰ are indicative of a pure C_3 diet, values more positive than -2.0‰ indicate a pure C_4 diet, and values between -8.0‰ and -2.0‰ suggest a mixed C_3–C_4 diet (MacFadden and Cerling, 1996). Due to differences in fractionation of isotopes between the food and tooth enamel, carnivores will reflect the same isotopic values as the prey (Lee-Thorp et al., 1989, 2000). For instance, a *S. fatalis* individual that consumes only animals having foraged on C_3 plants would display $\delta^{13}C$ values more negative than -8.0‰. And although post-depositonal diagenesis can overprint isotopic values in bone (Schoeninger and DeNiro, 1982), tooth enamel reliably reflects isotopic values derived from feeding, and is not generally subject to diagenetic alteration (Quade et al., 1992; Wang and Cerling, 1994; Koch et al., 1997).

2.3. Modern cat canine growth rate and length

Understanding the rate and length of growth in modern large felid canines may aid in the determination of those parameters in the canines of *S. fatalis*. Smuts et al. (1978) showed that the upper canine in *Panthera leo*, a social cat, appears in the alveoli between 9 and 11 months of age and finishes growing between 28 and 36 months. Thus, for modern lions, duration of growth for the canines takes between 17 and 27 months. Smuts et al. (1978) also show crown heights for individuals in Kruger National Park, Africa (KNP) to be between 37 and 56 mm. The fastest growth rate in the lion canines at KNP is therefore 3.3 mm/month, while the slowest growth rate is 1.3 mm/month. For the modern tiger, *Panthera tigris*, average crown heights of 53 mm have been shown for males, while female tigers have average crown heights of 47 mm (Gittleman and Van Valkenburgh, 1997). Developmentally, the permanent dentition of *P. tigris* begins to erupt between 8.5 and 9.5 months of age and finishes erupting between 12 and 14 months of age (Mazak, 1981). Based on the average crown heights and if the canines developed as eruption of the permanent teeth begins, commencing eruption with upper incisor 1 and following with i1, I2, I3, i2, i3, P4 and m1, then the canines, and lastly by P3, P2 and M1, and p3 and p4 (Mazak, 1981). The average minimum growth rate is 8.5 mm/month, while the average maximum growth rate is 21.2 mm/month (Mazak, 1981; Gittleman and Van Valkenburgh, 1997). The canines of tigers are the longest among the living felids with canine crown heights of 75 mm or longer (Mazak, 1981). Thus, maximal growth rates would be between 13.6 and 30.0 mm/month. In order for the average canine growth rate in tigers to equal that of lions, the crown of the adult canine needs to start growing before the birth of the individual, which seems unlikely.

3. Methods

Two upper canines of *S. fatalis* (UCMP 173179 and UCMP 158250) from Rancho La Brea were obtained from the University of California Museum of Paleontology to be sampled for both carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotope values. Mammal teeth grow and develop disto-proximally, from tip to root, such that the distal portion is formed when the individual is younger, while the proximal portion is formed when the individual is older. Even though there is a delay in the time of final enamel crystallization from the time of initial enamel matrix deposition (Passey and Cerling, 2002), a reliable seasonal isotopic signature is still present (Kohn et al., 1998). The two canines were ontogenetically sampled perpendicular to the growth axis of the tooth along visible growth increments from the root-enamel junction toward the tip of the canine. Sampling involved drilling ~ 5 mg of pristine enamel along visible growth increments using a 0.3 mm inverted cone carbide drill bit and a variable speed Dremel™ rotary tool (Fig. 1). The pristine enamel powder collected

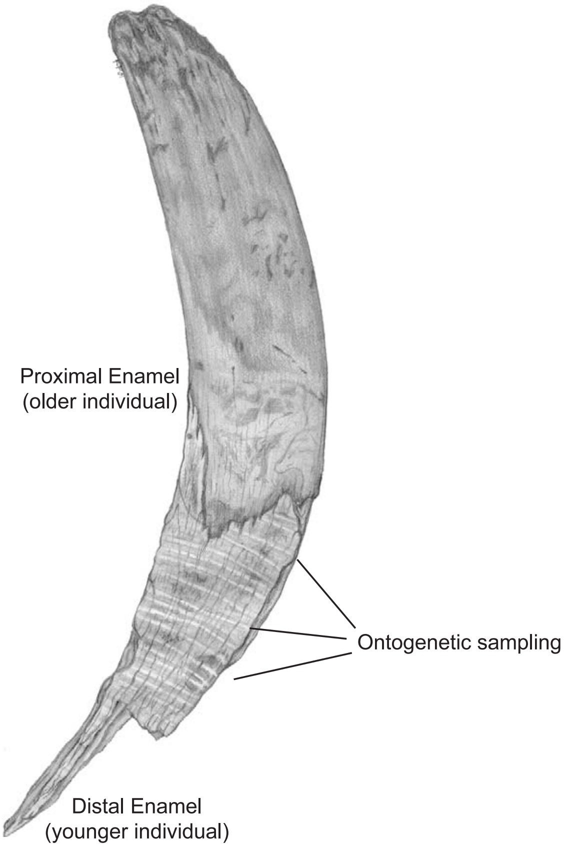

Fig. 1. The upper canine of *S. fatalis* (UCMP 173179), which has been sampled ontogenetically for stable carbon and oxygen isotope analysis. Samples were taken along enamel growth increments perpendicular to the growth axis of the tooth using a Dremel™ rotary tool. Samples were taken about every 3 mm. The total length of the enamel on the canine is ∼ 120 mm.

from the ontogenetic sampling was prepared following protocols similar to those described in MacFadden and Cerling (1996) and Koch et al. (1997). The powder was first treated with 35% hydrogen peroxide for 24 h to remove organics, then decanted and washed with distilled water, soaked in 0.1 N acetic acid for 24 h to remove any diagenetic carbonate, decanted and washed again with distilled water, rinsed with 100% ethyl alcohol, and dried overnight. A total of 37 samples (19 for UCMP 173179; 18 for UCMP158250) were collected and prepared from the *S. fatalis* canines.

After treatment, the samples were analyzed using an ISOCARB automated carbonate preparation system attached to a Micromass Optima gas source mass spectrometer within the Department of Earth and Ocean Sciences at the University of California, Santa Cruz. The ∼ 1 mg samples were dissolved in 100% phosphoric acid at 90 °C to create CO_2. The results are compared using the standard delta notation following equation $X=[(R_{\text{sample}}/R_{\text{standard}})-1]\times 1000$ where X is the $\delta^{13}C$ or $\delta^{18}O$ value, and $R={}^{13}C/{}^{12}C$ or ${}^{18}O/{}^{16}O$, and all isotope values are reported relative to V-PDB. The precision for the analysis was 0.1 ‰ for carbon and 0.1 ‰ for oxygen.

4. Results

4.1. S. fatalis oxygen isotope values

For UCMP 173179, the oxygen isotope values ranged from − 5.0 ‰ to − 2.9 ‰, with a mean value of − 3.9 ‰ (Fig. 2A, Appendix A). The oxygen isotope pattern displayed by the ontogenetic sampling suggests tooth growth during two seasons, including seasons when warmer (more positive) and colder (more negative) water was ingested. The oxygen isotope pattern indicates that nearly 1 year was sampled, suggesting, by the pattern, that about 80 mm of growth occurred over a 12-month period, or ∼ 7 mm/month (Fig. 2). The total length of the enamel on specimen UCMP 173179 was about 120 mm. If the tooth eruption rate and enamel growth remained constant, the entire canine would have taken about 18 months to grow. For UCMP 158250, $\delta^{18}O$ values ranged from − 8.0 ‰ to − 2.5 ‰ with a mean of − 4.0 ‰. The length of the canine and the isotopic pattern displayed is nearly identical to that of UCMP 173179 (Fig. 2B), such that coincident portions of the *S. fatalis* teeth appear to be isotopically similar. This pattern also indicates nearly a year was sampled over 80 mm of tooth, suggesting a growth rate of about 7 mm/month and growth spanning about 18 months.

4.2. S. fatalis carbon isotope values

The carbon isotope values for UCMP 173179 ranged from − 11.9 ‰ to − 8.8 ‰, and averaged

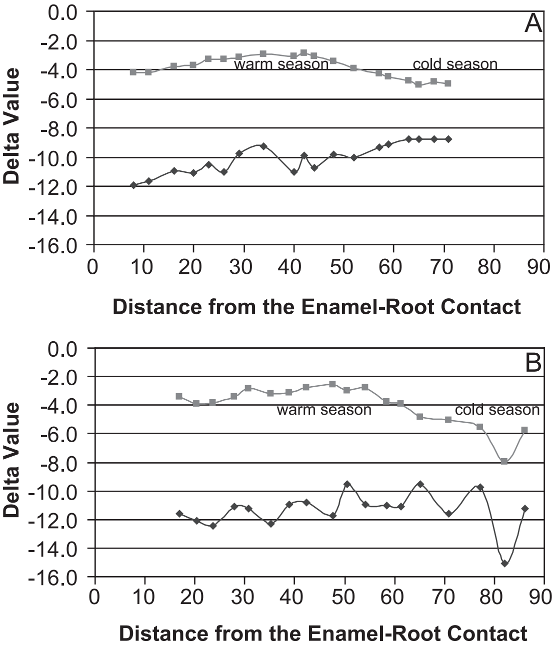

Fig. 2. Oxygen, ■, and carbon, ◆, isotope data for the canines of *S. fatalis* (A, UCMP 173179; B, UCMP 158250). Distance is in mm, and δ values are compared to the V-PDB. The oxygen isotope data suggest about 1 year worth of growth and an estimated 7 mm/month growth rate for the enamel. This rate suggests an enamel growth length of about 18 months, similar to the rate seen in *P. leo*. The carbon isotope ratios suggest a diet of prey having a C_3 forage preference.

− 10.1 ‰, which suggests that *S. fatalis* predominantly ate animals that in turn had a predominantly C_3 diet. The carbon isotope values apparently do not reflect the same (possibly) annual variation as the oxygen isotope values. For this specimen, $\delta^{13}C$ values became more negative as the animal aged. In UCMP 158250, the carbon isotope values ranged from − 15.1 ‰ to − 9.5 ‰ and had a mean value of − 11.3 ‰. Like UCMP 173179, ingestion primarily of prey dependent on a C_3 diet is indicated. However, unlike the other *S. fatalis* specimen, $\delta^{13}C$ values do not trend toward more negative values with age, but instead fluctuate around the mean.

4.3. Combined isotope values of S. fatalis

The pattern in $\delta^{18}O$ values for both *S. fatalis* specimens did not display a full year in either case. Because of the similarity between the oxygen isotope values in the two *S. fatalis* specimens, the $\delta^{13}C$ and $\delta^{18}O$ values were combined to determine if a longer growth signal or dietary signal was present due to differences in sampling more on the proximal or distal end of the individual canines (Fig. 3). A longer sampling length is noted, but the overall isotopic patterns remained.

Using the longer growth length of the combined sample, a two-point running average revealed that the most positive $\delta^{18}O$ value occurred at 48 mm from the enamel–root contact. A second order polynomial curve through the $\delta^{18}O$ values revealed the most positive point at 36 mm from the enamel–root contact. The most negative point for both the two-point running average and polynomial curve was at 86 mm from the enamel–root contact. Using the $\delta^{18}O$ maximum and $\delta^{18}O$ minimum as a warm season high and a cold season low that occur 6 months apart, the growth rate is 6.33 mm/month using the two-point running average and 8.33 mm/

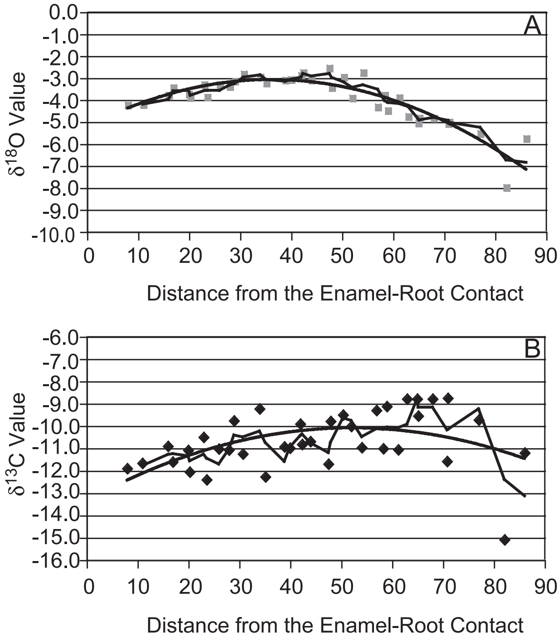

Fig. 3. Combined oxygen (A), ■, and carbon (B), ◆, isotope data for the canines of *S. fatalis* (UCMP 173179 and UCMP 158250). Trendlines represented by a two-point running average, and a smoothed second order polynomial curve. Distance is in mm, and δ values are compared to the V-PDB.

month using the polynomial curve (Fig. 3A). These data agrees with the estimated 80 mm of growth over 12 months. This figure shows that there is cyclicity in the δ^{18}O values consistent with the ~ 7 mm/month growth rate and the suggested 18-month growth period. The two-point running average and second order polynomial curve of the δ^{13}C values did not reveal similar trends. This also concurs with the individual δ^{13}C data, which suggests no dietary cyclicity over the growth of the canine.

5. Discussion

The results provide a promising method to analyze the growth rate, duration of growth, and diet in ancient sabertooth taxa. The preliminary data set of two *S. fatalis* canines suggests a growth rate of about 7 mm/month and duration of growth of about 18 months. The suggested growth rate of the adult canine in *S. fatalis* is faster than that found in modern lions; that is, a longer canine grew in the same amount of time. In comparison to extant tigers, the growth rate for *S. fatalis* appears to be the same as or slower but the canine grows for a longer period of time. *S. fatalis* apparently achieved its long canine by combining the canine development strategies of extant lions and tigers: a quick growth rate, and growth over a long time.

Because we know the δ^{13}C value of *S. fatalis*, if we can determine the δ^{13}C values of the herbivores of Rancho La Brea, it should be possible to determine on what prey *S. fatalis* fed, or at least exclude taxa that *S. fatalis* could not have used as prey. MacFadden et al. (1999) presented carbon isotope vales for *Equus* from Rancho La Brea. The δ^{13}C values for *Equus* range from $-7.7‰$ to $-2.0‰$, with a mean value of $-5.4‰$ suggesting that *Equus* fed on both C_3 and C_4 plants. The δ^{13}C values in the *S. fatalis* canines suggest that its prey fed predominantly on C_3 plants. Research by Akersten et al. (1988) on dental boli from Rancho La Brea shows that *Equus* consumed about 44% monocots and 56% dicots. Included in the diet of *Equus* were *Bouteloua* and *Hilaria*, C_4 genera (Watson and Dallwitz, 1992 onwards), which support the isotopic data for an intermediate diet in *Equus*. Further isotopic analysis of the herbivores of Rancho La Brea would refine knowledge of the possible prey taken by *S. fatalis*. If the carbon isotope values for *Equus* are representative of the entire population of *Equus* at Rancho La Brea, then horse can be excluded from the diet of *S. fatalis*, at least during the time that it took for the adult canine in *S. fatalis* to grow.

6. Conclusions

This study shows that an analysis of oxygen isotope values provides a promising methodology for determining the growth rate and duration of growth of sabertooth. The data gathered so far suggest that the rate of growth in *S. fatalis* was about 7 mm/month, while the length of growth was about 18 months. The data also suggest that *S. fatalis* preyed upon individuals that had a predominantly C_3 diet, at least during the time while the adult canines of the analyzed individuals were growing. Isotopic data from horses of Rancho La Brea suggest that *Equus* did not compose a significant portion of the diet of *S. fatalis* during the time that the canine was forming. Further isotopic analysis of the herbivores at Rancho La Brea would add to our knowledge of the prey of *S. fatalis*.

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Appendix A

Sample number, genus, distance from enamel–root contact, and isotopic values for each specimen. Distance is given in mm, while δ-values are compared to the PDB.

Sample number	UCMP #	Distance from the enamel–root contact	$\delta^{13}C$	$\delta^{18}O$
RSF0022A	173179	8	−11.9	−4.2
RSF0022B	173179	11	−11.7	−4.2
RSF0022C	173179	16	−10.9	−3.8
RSF0022D	173179	20	−11.1	−3.7
RSF0022E	173179	23	−10.5	−3.3
RSF0022F	173179	26	−11.0	−3.3
RSF0022G	173179	29	−9.8	−3.1
RSF0022H	173179	34	−9.2	−3.0
RSF0022I	173179	40	−11.0	−3.1
RSF0022J	173179	42	−9.9	−2.9
RSF0022K	173179	44	−10.7	−3.1
RSF0022L	173179	48	−9.8	−3.4
RSF0022M	173179	52	−10.0	−3.9
RSF0022N	173179	57	−9.3	−4.3
RSF0022O	173179	59	−9.1	−4.5
RSF0022P	173179	63	−8.8	−4.7
RSF0022Q	173179	65	−8.8	−5.0
RSF0022R	173179	68	−8.8	−4.8
RSF0022S	173179	71	−8.8	−5.0
RSF0108A	158250	17	−11.6	−3.4
RSF0108B	158250	20	−12.1	−3.9
RSF0108C	158250	24	−12.4	−3.9
RSF0108D	158250	28	−11.1	−3.4
RSF0108E	158250	31	−11.3	−2.8
RSF0108F	158250	35	−12.3	−3.2
RSF0108G	158250	39	−10.9	−3.1
RSF0108H	158250	42	−10.8	−2.8
RSF0108I	158250	48	−11.7	−2.5
RSF0108J	158250	50	−9.5	−3.0
RSF0108K	158250	54	−11.0	−2.8
RSF0108L	158250	58	−11.0	−3.8
RSF0108M	158250	61	−11.1	−3.9
RSF0108N	158250	65	−9.6	−4.8
RSF0108O	158250	71	−11.6	−5.1
RSF0108P	158250	77	−9.7	−5.5
RSF0108Q	158250	82	−15.1	−8.0
RSF0108R	158250	86	−11.2	−5.8

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