LONG-TERM CHANGES IN MOVEMENT PATTERNS OF MASSASAUGAS (*SISTRURUS CATENATUS*)

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ABSTRACT: Snake ecologists have long recognized that life history traits are subject to considerable temporal variation, but that recognition has not extended to studies of movement patterns or habitat selection. To determine whether movement patterns of snakes also are subject to temporal variation, we studied the ecology of Massasaugas (*Sistrurus catenatus*) in northwestern Missouri, from 1979 to1983, and from 1993 to 1998. In our initial studies of these rattlesnakes, individuals were commonly observed crossing a refuge road each spring, apparently moving from a central prairie habitat to outlying upland areas. In the fall, the snakes were observed moving in the opposite direction, apparently returning to the prairie for hibernation. By crossing refuge roads each way, road mortality was common from 1979 to 1983. In 1993, the site was impacted by a major flood, which greatly altered the population and its reproductive ecology. After the flood, both radiotelemetry and mark-recapture studies showed that few Massasaugas crossed refuge roads or left the central prairie. From 1993 to 1998, most individuals observed crossing the roads were neonates, whereas adults comprised the most common age class crossing roads from 1979 to 1983. The reasons for the change in movement patterns are unknown, but may represent either habitat alterations or impacts from road mortality.

INTRODUCTION

Interest in studies of movement patterns and habitat use by snakes have surged since the introduction of implantable radiotransmitters (see review by Reinert, 1993). Viperid snakes have been prime candidates for such studies, since their relatively large body size has eased the problems caused by transmitter size (e.g., Reinert, 1984; Reinert and Zappalorti, 1988; Beaupre, 1995a, b; Beck, 1995; Reinert and Rupert, 1999). As noted by Houston and Shine (1994), the high cost of most radiotransmitters (170–260 U. S. dollars in late 1999) coupled with the time-intensive nature of radio-tracking places severe limits both on the number of snakes that can be monitored at one time and, most notably, the duration of the study itself. For example, of the 13 radiotelemetric studies on snakes published in the three primary North American herpetological journals (*Copeia*, *Herpetologica*, *Journal of Herpetology*) from 1994 to 1999, the longest duration was 48 months and the shortest was one month (median = 18 months).

By contrast, there is increasingly common recognition among workers studying the life-history of snakes that multi-year data are needed to properly characterize such traits as clutch size, clutch frequency, and offspring size (e.g., Andrén and Nilson, 1983; Seigel and Fitch, 1985; Brown, 1991; Madsen and Shine, 1992; Seigel et al., 1995, 1998; Shine and Madsen, 1997; Greene et al., 1999). Many life history studies of snakes last four years or longer (> 30 years), including numerous studies on vipers (e.g., Andrén and Nilson, 1983; Brown, 1991; Madsen and Shine, 1992; Martin, 1993; Fitch, 1999). Taken in this light, most radiotelemetric studies clearly are short-term in nature.

The purpose of our paper is not to denigrate prior studies. We feel that the value of even relatively short-term studies on snake movement patterns is unquestionably significant. Indeed, one of us (Seigel, 1993) has noted that snakes are model organisms for studies of movement patterns and habitat utilization. However, we are unaware of anyone raising a critical question: what constraints, if any, does the relatively short-term nature of projects using telemetry impose on the inferences we can draw from such studies? The answer, also based on lessons from life history studies, depends on the degree of temporal variation present within each population. When there is a high degree of temporal variation in movement patterns and habitat use, as is true in studies on reproductive traits (see above citations), then inferences based on short-term studies must be limited. Conversely, when among-year variation in movement patterns is limited, then short-term studies have fewer constraints.

Clearly, it is difficult to address this question when long-term telemetry studies are so rare. In our review of the papers noted above, however, there is little attention paid to this issue. Instead, most authors imply either that among-year variation is limited (and so can be discounted), or that the inferences drawn from short-term studies are valid even when among-year variation exists.

The best test of this problem is to conduct a long-term telemetric study (> 5 years), but we face the same cost and logistic constraints as other researchers. As an alternative (and less expensive) approach, we here compare the movement patterns of a single popula-

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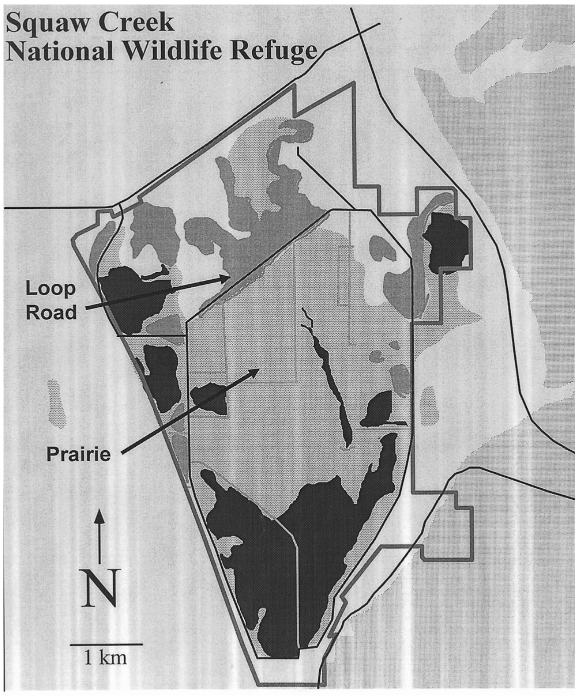

Fig. 1. Map of Squaw Creek NWR, showing major habitats and study areas.

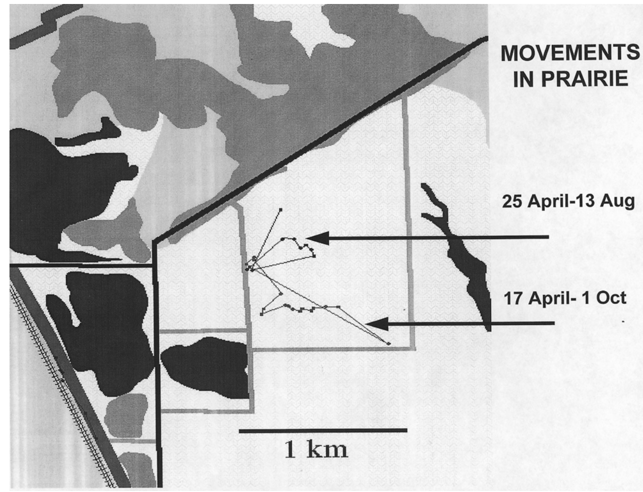

Fig. 2. Movement patterns of selected *S. catenatus* monitored via radiotelemetry. Note that each snake made extensive movements, but neither left the prairie.

tion of the Massasauga (*Sistrurus catenatus*) studied 10 years apart. The first study was conducted by RAS from 1979 to 1983 (Seigel, 1986), and the second part was conducted by MJP and RAS from 1993 to 1997, following a major flood at the site (Seigel et al., 1998). We tested the null hypothesis that broad-scale movement patterns and habitat use will be the same among time periods (thus validating the short-term approach to these topics). Rejecting the null hypothesis would at least limit the inferences that can be drawn from short-term studies using telemetry.

MATERIALS AND METHODS

Study Site

We studied the movements of *S. catenatus* at the Squaw Creek National Wildlife Refuge (SQ) in northwestern Missouri (Fig. 1). Details of the study site are provided by Seigel (1986) and Seigel et al. (1998). Briefly, most *S. catenatus* are found in a moist prairie located in the northern portion of the refuge, where hibernation takes place in crayfish burrows (Fig. 1). The prairie is surrounded by a gravel road (Loop Road) and is crossed by several raised levees where the rattlesnakes both hibernate and bask during the active season (late March to early November).

Squaw Creek was impacted by a major flood in the summer of 1993. This flood impacted both the prairie habitat (creating large mud flats devoid of vegetation during the summer and early fall of 1993) and the Massasaugas (by reducing body condition and apparently eliminating the smaller size classes; for details see Seigel et al., 1998). By 1996, the population was recovering from this event.

Data Collection

In all years, we captured *S. catenatus* crossing Loop Road by driving at a slow rate of speed (ca. 16–24 km/h). Loop Road is fairly wide (ca. 4 m) and is usually devoid of large obstacles that would prevent *S. catenatus* from being seen. Massasaugas cross roads slowly, so missing them is highly unlikely (thus minimizing inter-observer variation). Also, they were captured by hand along refuge levees and in the prairie. All animals were measured (snout-vent length, SVL) to the nearest 10 mm, body mass to nearest 5 g, sexed, marked for identification (via scale-clipping or PIT-tagging), and released at the point of capture within 24 h. (Several pregnant females were kept in outdoor enclosures during the late summer in 1995–1996, but this would not affect our assessment of movement patterns, since most migration occurred before we penned the females.) For details of capture procedures and processing see Seigel (1986) and Seigel et al. (1998).

Movement and Habitat Use

We utilized both mark-recapture and radiotelemetry to determine movement patterns and habitat use. Studies from 1979 to 1983 utilized primarily mark-recapture methods, except for three individuals followed by telemetry in fall of 1981 and 1982. Studies in the 1990s followed the same basic procedures as in 1979–1983, except that we expanded the telemetry component of the study to include a larger sample size, and transmitters were implanted in the spring rather than the fall.

Radiotransmitters (Holohil Co, AVM Inc., and MiniMitter Co.) were implanted surgically in the body cavity following the procedures of Reinert and Cundall (1982); they varied in size, but were < 5% of total snake mass. Snakes were held for 24–72 h after surgery, released at the site of capture, and located every 2–7 days (depending on weather conditions). When subjects could not be located, their location was plotted on a map via triangulation.

Statistical Methods

Data were analyzed using SYSTAT 7.0 (SPSS, 1997). Means are presented as ± one standard deviation. Data for movement patterns use an individual one time per season (i.e., known recaptures were not counted twice within one time period).

RESULTS

Movement Patterns: 1979 to 1982

Massasaugas were commonly seen crossing Loop Road (for the complete years 1980–1982, a mean of 32.0 ± 5.29 individual snakes/year, range = 26–36), but the direction of their movements was highly seasonal. During April and May, nine of 12 *S. catenatus* (whose movement direction could be determined accurately) were moving north, away from the central prairie (many other individuals were observed but were either road-killed, or their direction could not be determined). The reverse pattern was seen in the September and October (late summer and fall), when 13 of 14 snakes observed crossing Loop Road were moving southward, in the direction of the prairie. Differences in the direction moved were significantly different between seasons (Fisher's exact test, P = 0.001). Thus, movements across Loop Road were both common and seasonally predictable, with the majority of movements north (away from the prairie) in spring, and south (toward the prairie) in the late summer and fall.

The seasonal movements of *S. catenatus* were also documented by a limited radiotelemetry program. Three adults (> 50 cm SVL), which were originally captured while crossing Loop Road, were followed by implanted transmitters in late summer and early fall of 1981–1982. After release, all three snakes moved directly south from Loop Road into the prairie; one snake was lost almost immediately, but the other two moved 50–250 m into the prairie where they selected hibernation sites in crayfish burrows.

Of 86 Massasaugas found crossing Loop Road from 1979 to 1982, the ratio of adults (i.e., > 45 cm SVL) to juveniles was 0.95:1. This was almost identical to the overall ratio of adults to juveniles in the population as a whole (0.96:1, Seigel, 1986), suggesting that both adults and juveniles were equally likely to be found crossing Loop Road.

Movement Patterns: 1994 to 1997

Compared with previous data, significantly fewer rattlesnakes were found crossing Loop Road from 1994 to 1997. Using data from 1996 and 1997 (comparable in sampling effort to 1979–1982) only 11.5 ± 0.71 snakes/year were found crossing Loop Road (ANOVA, $F_{1,3}$ = 26.7, P = 0.014). In addition, the sizes and age classes found crossing Loop Road were also significantly different from that found in previous years; individuals found crossing Loop Road in 1979–1983 were an almost equal mixture of adults and juveniles, whereas in 1996–1997 the ratio was 0.29 adults/juvenile (contingency table analysis, G = 5.143, df = 1, P = 0.023). The low ratio of adults is especially noteworthy, since our overall sample at this time (1993–1997) was strongly dominated by adults: 1993–1994, 4.65 adults/juvenile; 1996–1997, 2.13 adults/juveniles (Seigel et al., 1998; M. Pilgrim, unpublished). Thus, the numbers of rattlesnakes crossing Loop Road were highly skewed toward juveniles.

To further document movements (or absence thereof) of *S. catenatus* during this period we implanted 12 individuals with transmitters; seven of these animals were originally captured in or adjacent to the prairie (Table 1). Although many of these snakes made relatively long movements (> 1 km) within the prairie (Fig. 2), none ever left the prairie despite tracking up to 177 days ($\bar{x}$ = 69.9 ± 59.27 days). In addition, we had no evidence that rattlesnakes made major habitat shifts from marsh to prairie, or from prairie to forests.

DISCUSSION

We have three lines of evidence to show that the movement and habitat utilization patterns of *S. catenatus* changed between 1979 and 1982 and 1994 and 1997: (1) significantly lower numbers of rattlesnakes found crossing Loop Road, (2) a significant

Table 1. Movement patterns and habitat use by *Sistrurus catenatus* monitored via radiotelemetry during 1996-1997. Number of days monitored refers to periods when snakes were actually located in the field (through 1 October 1997). * = snakes captured in or near prairie.

Snake ID	SVL (cm)	Capture site	Dates monitored	Number of days monitored	Total distance moved (m)	Mean distance moved per day (m)	Left refuge land?	Habitat used (dominant vegetation)
A *	51.5	Original dike	16 June-30 Aug., 1996	39	76	6.3	No	Reed canary grass, bordering marshes with some trees
B	68.0	Railroad dike	23 July-hibernation (Oct. 1996)	76	39	10.1	Yes (hibernated off refuge)	Marsh (primarily sedges and smart-weed); some cord grass in vicinity
C	73.0	Railroad tracks	12-30 Aug., 1996	19	105	5.5	NA (originally located off refuge)	Cordgrass patch and marsh (primarily sedges and smartweed)
D *	65.7	New burn dike	22-30 Aug., 1996	9	114	12.7	No	Cordgrass prairie with sedges
E *	60.1	Massasauga dike	17 Apr.-1 Oct. , 1997	177	1936	10.9	No	Cordgrass prairie with sedges
F *	59.5	Massasauga dike	17 Apr.-16 May, 1997	22	495	22.5	No	Cordgrass and reed canary grass with sedges
G *	63.5	Massasauga dike	25 Apr.-7 Jun., 1997	44	331	7.5	No	Cordgrass prairie with sedges
H *	66.3	Massasauga dike	25 Apr.-13 Aug., 1997	111	1244	11.2	No	Cordgrass prairie with sedges
I	45.0	Railroad dike	18 May-6 Aug., 1997	81	929	11.4	Yes	Reed canary and cordgrass with sedges
J *	52.4	New burn dike	19 May-13Aug., 1997	87	1098	12.6	No	Cordgrass prairie with sedges
K	49.1	Loop Road	25 May-15 Sept., 1997	114	980	8.6	No	Marsh (sedges, smartweed, and cattail)
L	59.4	Marsh north of original	14 July-1 Oct., 1997	78	1144	14.7	No	Marsh (sedges, smartweed, and cattail); cordgrass patches

shift from a nearly 1:1 ratio of adult to juveniles crossing the road to one largely dominated by juveniles, and (3) an absence of any migratory movements among eight subjects followed by radiotelemetry. Aside from a true change in movement patterns (see below), could these changes be accounted for by sampling or observer bias? We think not. First, it is highly unlikely that large numbers of *S. catenatus* were missed while crossing Loop Road. Not only are they highly conspicuous at such times, but adults are more conspicuous than juveniles. Thus, if we were simply missing snakes, we would have been more likely to see adults rather than juveniles. Since we found the opposite (more juveniles than adults on Loop Road), we reject the possibility that snakes were being overlooked. Second, while it is difficult to assess the ability of different observers to find Massasaugas, the ability of MAP to detect snakes during 1996–1997 was, if anything, better than that of RAS during 1979–1983.

Could the absence of *S. catenatus* be the result of lower sampling effort in 1996–1997? We did not keep rigorous records of the distance traveled each day, but our primary sampling sites at SQ can only be reached along Loop Road, in essence forcing us to sample along this road several times per day. In addition, others have also noticed the absence of *S. catenatus* along Loop Road. For example, the refuge staff has been asked to bring in road kills and/or report Massasaugas found crossing Loop Road for several years, but saw few snakes during the period in question (but see below). Even local residents noticed the absence of rattlesnakes on Loop Road. One resident told us in 1997 that he had been coming to the refuge for many years to watch Massasaugas crossing the road, but had seen none since the 1993 flood (he was relieved that they were still common on the site).

Finally, could the lower numbers of Massasaugas crossing Loop Road be an indicator of lower population numbers? Our data indicate that although population numbers may have decreased immediately following the 1993 flood, by 1995 the population largely recovered, and we found more *S. catenatus* in 1996-1997 than in any comparable period from 1979 to 1983 (Seigel et al., 1998; M. Pilgrim, pers. observ.). In addition, lower numbers of rattlesnakes would not explain that our sampling during 1996-1997 showed an adult-dominated population in the prairie, but that very few adults were found crossing Loop Road.

Explanations, or Why Don't the Snakes Cross the Road?

Explanations for the apparent changes in movement patterns are speculative, especially since we do not clearly understand why *S. catenatus* is often migratory. Although its seasonal movements are well-documented (see review in Johnson et al., 2000), there is considerable geographic variation in the extent of movements and what component of the population makes seasonal movements. Although the "typical" pattern for *S. catenatus* is to utilize drier, more upland areas in the summer and wetlands in the fall, winter, and early spring, in some cases individuals remain in wetlands all year, and in others, only pregnant females are found to make seasonal movements (Johnson et al., 2000:3). Since we did no large scale radiotelemetry at SQ in 1979–1983, we cannot determine how far individuals moved at that time, what exact microhabitats they utilized, or why the movements took place to begin with (e.g., foraging, thermal preferences, etc).

Within these constraints, our explanations for the apparent change in movement patterns at SQ focus on two primary issues: differential mortality rates and changes in habitat.

Differential Mortality.—This explanation relies on two assumptions: (1) migratory *S. catenatus* were a subset of the overall population at SQ, and (2) migratory Massasaugas suffered higher mortality rates than snakes that did not migrate. We lack direct evidence to support the first assumption, which requires behavioral differences among individual snakes (presumably genetically-based), such that some migrate and some remain sedentary. Such variation in tendency to migrate may well exist for snakes, but we are unaware of any tests. Conversely, the assumption that rattlesnakes which migrate suffer high mortality rates is well-supported by data from 1979 to 1983, when road kills from high levels of tourist traffic were common (Seigel, 1986). Indeed, without one of us (RAS) to escort Massasaugas across the road, mortality rates from road kills probably would have exceeded 50% of the snakes crossong the road. We thus propose a scenario where the subset of Massasaugas that left the prairie each year was gradually reduced by road mortality until only non-migratory individuals remained.

A related explanation focuses on the effects of the 1993 flood. Briefly, this scenario entails that the flood differentially killed migratory rather than non-migratory individuals. There was certainly a major shift in population structure (in age classes and sex ratio) following the 1993 flood (Seigel et al., 1998), but there is no evidence that migratory rattlesnakes experienced higher mortality than those that were non-migratory.

Because of the absence of data showing that migratory behaviors in snakes have a genetic basis, we regard these explanations as speculative. However, additional studies examining inter-individual variation in movement patterns might be revealing, especially in species such as *S. catenatus,* with strong patterns of seasonal movements.

Changes in Habitat.—Although we do not know why *S. catenatus* made seasonal movements from 1979 to 1983, in other portions of their range they are thought to make seasonal migrations to enhance foraging ability, improve thermoregulatory ability, or both (see review in Johnson et al., 2000). This suggests that prey and/or thermal requirements cannot be met in the same habitat where hibernation occurs. If that habitat was altered in some way (enhancing either prey availability or the ability to thermoregulate), then seasonal movements would not be necessary.

The prairie habitat at SQ has been altered considerably over the past 40 years. During the late 1960s, herds of cattle grazed on the prairie, resulting in a sharp decrease in the population of *S. catenatus* and the invasion of large amounts of woody vegetation (Seigel, 1986). In the mid-1970s cattle were removed and a program of more frequent prescribed burns was instituted. Although the prairie was partially recovered by the time of our studies (1979–1983), it is in better condition today, with few traces of woody vegetation. Thus, seasonal movements of rattlesnakes in 1979–1983 may have been a response to improper management, forcing snakes to leave the prairie to find suitable sites for foraging and/or basking. Now that the recovery of the habitat is more complete, seasonal movements may no longer be necessary, resulting in the pattern seen in 1994–1997. We consider this to be the most likely explanation for the changes in movement patterns discussed here (but see below).

In addition to habitat restoration resulting from the elimination of cattle and more frequent burning, the extensive flooding in 1993 also impacted the prairie at SQ, which created large open areas of mud flats. However, this was a relatively short-term event, and most noticeable effects of the flood were gone by late 1995. Thus, we are dubious that the flood caused changes in movement patterns, at least as a direct function of habitat alteration.

One way of testing these hypotheses is to determine if the numbers of *S. catenatus* found crossing Loop Road continues to change. For example, an increase in numbers of rattlesnakes found crossing the road would suggest that long-term recovery of the prairie is not a parsimonious explanation, since we would not expect better habitat conditions to result in higher numbers of snakes crossing the road (our explanation above suggests the opposite). Conversely, an increase in the rate of road crossings might suggest that the changes observed were linked to the 1993 flood, and that migration is starting to increase. We are continuing to monitor the rate of road crossings to test these ideas.

Implications of Temporal Variation in Movement Patterns

Telemetry Studies.—We show that movement patterns of *S. catenatus* changed considerably during the 15 years of study. Thus, at least for this population, we reject the null hypothesis that movement and habitat utilization patterns are consistent over time. How general these results are depends to some degree on the explanation for the apparent change. For example, if the changes are a reflection of habitat modification from more appropriate management of the prairie, then these results are likely to be quite general. Although long-term studies on the effect of habitat changes for snakes are rare, the best data available (Fitch, 1999) shows that habitat restoration (recovery of a forest from farming and cattle grazing) has a dramatic impact on snake populations. Other habitat modifications (habitat restoration and habitat alterations for development) may also have a strong impact on the movement patterns of snakes.

Our study provides sufficient evidence to question the use of short-term data for making inferences regarding habitat utilization and movement patterns. Thus, using short-term telemetry studies to assess movement patterns and habitat utilization for snakes may be subject to the same restrictions as using short-term data for life-history studies. Although we recognize the high costs of conducting longer-term or "follow-up" telemetric studies, we suggest that one or two seasons of radiotelemetry data may be insufficient to characterize habitat utilization and movement patterns of a population. Further studies will show if our data have generality for other populations of snakes, or whether environmental changes at SQ represent a unique situation.

Use of Road Surveys to Determine Population Changes

Another implication of our study concerns the use of road surveys for snake populations, a method which is commonly used to assess activity patterns, habitat use, and population changes over time (e.g., Dodd, 1989; Bernardino and Dalrymple, 1992; Mendelson and Jennings, 1992; Rosen and Lowe, 1994). Using road surveys to assess changes in population abundance over time requires an assumption that changes in survey results are strongly correlated with the numbers of snakes present at any moment in time. Our data show that for *S. catenatus* at SQ, such an assumption may not be warranted. In our case, using road surveys to assess population status would have concluded that *S. catenatus* had declined dramatically, an impression shared by the local public, but which was clearly incorrect. This does not mean that road surveys are necessarily biased, but we do caution that long-term changes in movement patterns in snakes can lead to incorrect conclusions if only one method is used to assess population status.

Conservation Implications

The apparent change in movement patterns of *S. catenatus* has at least two implications for conservation and management of this species at Squaw Creek. First, the current low numbers of rattlesnakes found crossing Loop Road decreases the need for managing human visitation in order to prevent road mortality, a serious concern in the 1980s (Seigel, 1986). Naturally, should road crossings increase, this concern would again be valid. Second, since rattlesnakes rarely made major habitat shifts during this study, the need for managing "summer" habitats or migratory corridors is greatly reduced.

Finally, although we recognize the limitations of a single study, temporal variation in movement and habitat utilization patterns also has implications on a more general scale for conservation and management practices. Habitat utilization is clearly a major component of modern conservation biology and wildlife management, with the use of Habitat Conservation Plans (HCP) by the U. S. Fish and Wildlife Service a prime example (Nelson, 1999). Since HCPs often contain a "no surprise" clause that limits future changes in the agreement, having a thorough understanding of the variation in the habitat utilization patterns of a population seems essential before finalizing an HCP. Based on our data, we caution that short-term studies may provide information that is inadequate for making long-term management plans such as HCPs.

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