

# Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China

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## Abstract

In order to use counts of active animals to estimate population parameters (abundance, sex ratio, age structure), we need to understand the factors that bias such counts. For many taxa, the main problems involve behavioural differences among age/sex classes, and the effects of local conditions on activity levels. A unique opportunity to quantify such effects on snakes occurs on Shedao, a small island in the Bohai Sea off north-eastern China. The island contains an extraordinary density of endemic pit-vipers (*Gloydius shedaoensis*), that feed primarily on migrating passerine birds. Over an 8-year period we walked the same 540-m path on 936 mornings during bird-migration periods, counted all pit-vipers within a 3-m-wide transect, and recorded the animals' sex and age class (adult vs juvenile). Total numbers of snakes averaged 40.6 per survey (0.31 per m): thus, the data set contains 37,980 records of sightings of snakes. The total numbers and the composition (sex ratio, age structure) of snakes seen in a morning differed among segments of the path, differed between seasons (spring versus autumn), differed with time within each season, and were influenced by weather conditions (temperature, wind speed, relative humidity). For example, more snakes were seen on days that were hot, with little wind. The proportion of juvenile snakes in the sample decreased on hot, dry, windy days. Sex ratios shifted with time and air temperature. Interactions between these factors were also significant. Overall, census conditions (date, weather) had more influence on total numbers of snakes seen than on age structure or sex ratio in the samples. However, visual censuses strongly under-represented the proportion of adult (vs juvenile) snakes, and the numbers of male compared to female snakes. These analyses provide a strong cautionary message for researchers who use census data to infer underlying demographic traits. At the same time, they show that census data can be informative about abundance and demography as long as one understands the nature and magnitude of biases introduced by conditions prevailing during data acquisition. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

In many circumstances, biologists want to know how many animals exist in a given area, and the composition of the population in terms of traits such as sex and age. Information on these topics is important for purposes such as conservation, control (culling), tourism, and management decisions (e.g. Caughley and Sinclair, 1994). Intuition suggests that the most straightforward way to obtain these data is to simply go out and count the animals. In practice, this technique may provide a

very imprecise estimate of actual numbers and population composition because of behavioural biases that influence which animals are seen and which are not (e.g. Caughley, 1977; Greenwood, 1996; Whiting et al., 1996; Härkönen et al., 1999). These methodological problems are not insuperable, however, and direct counts are frequently used to estimate population parameters — especially for relatively large or conspicuous animals that live in open habitats where they are highly visible (e.g. Cairns and Grigg, 1993). In such cases, raw data from counts can be corrected to allow for known biases associated with differential observability (e.g. Cairns and Grigg, 1993; Caughley and Sinclair, 1994).

Unfortunately, many kinds of animals do not lend themselves to such procedures. The problems of differential activity leading to bias in estimation are exacerbated

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in many ectotherms. These animals typically exhibit frequent periods of prolonged inactivity (Pough, 1980), such that only a small proportion of the population is observable at any one time. Additionally, ectothermy allows a wide range of body sizes of ecologically independent individuals within a population (e.g. Pough, 1980; Greene, 1984; Shine et al., 1998). This range of sizes is likely to increase variation in activity patterns and thus, observability. For example, small individuals within a population will have different thermal and hydric relationships with the environment than will larger conspecifics, and thus may be active in different weather conditions (Hillman, 1969; Vitt et al., 1997). Similarly, different-sized individuals may feed on different prey types, and thus, forage in different ways, at different times or in different places, and may themselves be vulnerable to different kinds of predators (e.g. Mushinsky et al., 1982; Greene, 1997).

If we are to use direct counts as indices of underlying population parameters, we need to validate these procedures by documenting the source and magnitude of biases introduced by differential observability (e.g. Caughley, 1977; Whiting et al., 1996). This is a difficult challenge for some kinds of organisms, such as snakes. Most snakes are relatively rare, highly cryptic and often inactive, leading some authorities to question whether *any* snakes are appropriate organisms for population studies (Turner, 1977). More recent studies clearly show that some snake species are indeed well-suited to such studies, although many are not (Seigel, 1993). Hence, the best strategy may be to take advantage of these potential “model systems” to document the form and magnitude of biases associated with differential observability. The results of such studies can then be extrapolated (with caution) to survey data based on other species. At the very least, such research can suggest which attributes of the environment and the study species are most likely to influence observability, and hence, compromise an investigator’s ability to use direct counts to infer aspects of abundance or population structure.

Although snakes occur in high densities in some areas, many of these systems are poorly-suited to visual census. Some snake aggregations are seasonal, such that most of the population is observable only briefly before dispersing (e.g. Gregory and Stewart, 1975). In other cases, the snakes are difficult to observe because they are fossorial (e.g. Fitch, 1975) or aquatic (Madsen and Osterkamp, 1982; Houston and Shine, 1994), or habitat heterogeneity engenders massive biases in observability (Weatherhead and Charland, 1985). Thus, logistical problems impede sampling. Large diurnal terrestrial species in relatively open habitats would seem the best candidates for direct enumeration, but even here research has found that most snakes are not seen by the observer (Whitaker and Shine, 1999).

The ideal system for such a study would be one with the following characteristics: the snakes are large; they exist at high densities; they occupy a relatively open, homogeneous habitat; they are sedentary rather than migratory; they are easily observable when active, but totally hidden when inactive; and they do not flee from human presence. A species of insular pit-viper from north-eastern China, *Gloydus shedaoensis* (Zhao, 1979) satisfies all of these conditions. This species thus offers a unique opportunity to identify factors that determine the numbers and types (sex, size) of snakes that can be seen by an observer. Chinese biologists accord a high conservation priority to these snakes, and have studied this taxon for >20 years. Results from research on Shedao have been published primarily in Chinese journals (e.g. Wu, 1977; Jiang and Zhao, 1980; Zhao, 1980; Yang, 1986; Sun et al., 1993), with only a few English-language summaries of major results (Huang, 1984, 1989; Li, 1995). We have analysed an extensive data-set on counts of active snakes, with the results below.

## 2. Materials and methods

### 2.1. Study area and species

The island of Shedao (“snake island”) lies in the Bohai Sea 13 km off the southern end of Liaoding Peninsula in north-eastern China (38°57'N, 120°59'E). Also known as Xiaolongshan (“little dragon mountain”), this small (0.73 km<sup>2</sup>) island is steep and rocky, with a covering of bushes and small trees (Huang, 1989). The climate is cool-temperate, with mean monthly air temperatures averaging 24.0°C in midsummer (July) and -4.1°C in midwinter (January; unpubl. data from weather-recording station on the island). The island lies on a major migration route for Asian birds, and hence receives large numbers of passerines in both spring (May) and autumn (September–October). The only reptile species on the island is an endemic pit-viper, *G. shedaoensis*, with adults of both sexes averaging approximately 650 mm snout-vent length (SVL). Adult pit-vipers feed almost exclusively on migrating birds, whereas juvenile snakes feed on centipedes as well as small birds (Huang, 1984, 1989; Li, 1995). The pit-vipers attain high population densities on the island (approximately 20,000 snakes: Huang, 1984).

The snakes spend much of their time hidden, but are easily seen in their foraging sites. Some snakes use terrestrial sites, but most climb into bushes and small trees to ambush birds (Fig. 1). Behavioural studies show that the snakes spend the night on the ground, climbing into foraging sites only during periods of the morning and evening when small passerines are active (e.g. Sun, 1990; Sun et al., 1990). Especially when they are in foraging poses, the snakes virtually ignore the close approach of



Fig. 1. Shedao pit-vipers (*Gloydus shedaensis*) in typical ambush pose on the branches of a small tree.

humans (pers. obs.). During times of the year when there are no migrating birds, the pit-vipers cease activity and are seen only rarely (Sun, 1990). Thus, snakes are encountered frequently only during spring and autumn.

## 2.2. Methods

On most days during these main activity periods in 7 years (1990–1997, except 1995), the Chinese scientists walked a 540-m transect along a cleared path. Observations commenced at approximately 0700 to 0800 h every morning and each survey required about 60 min. to complete. A single observer scanned the path, and all areas within 1 m on either side of the path, for snakes. Thus, the total transect width was 3 m (1-m-wide path plus 1 m either side). Any snakes sighted either on the path itself or on adjacent branches were sexed (by tail shape) and classified as either juveniles (<600 mm SVL) or adults (>600 mm SVL). The snakes were not handled during this process. The same route was walked every day. Data were recorded separately for four sections of the path (lengths 80, 150, 210 and 100 m). The first section ran along the bottom of a small ravine through open woodland dominated by *Robina pseudoacacia*. Two shallow pools of water adjacent to the path attracted many passerines (and hence, snakes). The second section of path ran up a steep south-facing slope through a grassland/shrub mosaic with *Koelreuteria paniculata* as the dominant tree species. The third section ran along the crest of the ridge, through a more thickly wooded area of *Celtis bungeana* and *Securinega suffruticosa*. The fourth section ran back down the slope, roughly parallel to the second segment but through more open grassland with shrubs (*Amorpha fruticosa*). Weather conditions at the time of

data collection were recorded once each morning from a weather-monitoring station set up beside the path. Preliminary analyses indicated that our major results were consistent across years, so we report only analyses on the pooled data set.

Distributions of data were checked for compliance with assumptions of the relevant statistical tests. No transformations were necessary.

## 3. Results

Data were gathered for a total of 936 days (292 in 1990, 152 in 1991, 120 in 1992, 96 in 1993, 76 in 1994, 88 in 1996, and 112 in 1997). The average number of snakes sighted during the 540-m walk each morning was 40.6 (S.D. = 25.4, range 0–124). Thus, a total of 37,980 sightings of snakes were recorded. On average, 68.3% of these animals were classed as adults (S.D. = 17.0%, range 0–100%). The overall sex ratio (proportion male) averaged 45.7% (S.D. = 10.6%, range 0–100%). The total numbers of snakes sighted each morning, and the sex and age composition of that sample, might plausibly be affected by:

- (1) the location of the snake (some areas along the path presumably have higher snake densities than others, and may be more or less suitable for different sexes or ages of snakes);
- (2) the season of year when the survey was conducted (the numbers and composition of samples in spring may differ from those in autumn, because of other seasonal effects such as reproductive activity);

- (3) the time within each season when the survey was conducted (different age and sex groups may become active at different times); and
- (4) weather conditions at the time of the survey (because total activity levels, and patterns within different subgroups, may be differentially affected by local temperature, humidity or wind speed).

### 3.1. Effects of location and season

We first examined spatial and temporal (seasonal) effects, before looking at the effects of within-season timing and weather conditions on survey results. Thus, our first analyses were two-factor ANOVAs with location (segment of the path) and season (spring or autumn) as factors. The dependent variables were total numbers (snakes sighted per m), age structure (number of adults relative to numbers of juveniles) and sex ratio (numbers of males compared to females, in both adults and juveniles).

The total number of snakes recorded during a morning survey differed among locations and between seasons, with a significant interaction between these two factors ( $F_{3,928} = 17.37$ ,  $P = 0.001$ ; Fig. 2a). Numbers of snakes were higher in segment 1 (the area with pools of water) than in the other segments. On average, more snakes were seen in autumn than in spring, but the difference was much greater for segment 1 than for the other areas. Indeed, snake densities were similar in spring and autumn for segment 4 (Fig. 2a).

The proportion of the total sample composed of adults also differed substantially among segments (Fig. 2b). Juvenile snakes were relatively less abundant in segments 2 and 3 than in the other segments. The overall proportion of juvenile snakes did not differ between seasons, but the analysis revealed a significant interaction between season and location. Spatial patterns in age structure were broadly similar in spring and autumn (Fig. 2b), but an ANOVA revealed a significant interaction term ( $F_{3,924} = 7.42$ ,  $P = 0.001$ ). That is, the way in which age structure varied among the path segments differed significantly between seasons (Fig. 2b; and see below).

The overall sex ratio of the surveyed snakes (proportion of the sample comprised of males) averaged 45.7%, significantly less than 50% ( $\chi^2 = 280.9$ , 1 df,  $P = 0.0001$ ). The proportion of males varied among locations ( $F_{3,924} = 6.71$ ,  $P = 0.0002$ ; males were most common in segment 3, least common in segment 1) and was higher in autumn than in spring ( $F_{1,924} = 7.79$ ,  $P = 0.005$ ). Although sex ratios were influenced by both location and season, the interaction between these two factors was not significant ( $F_{3,924} = 0.93$ ,  $P = 0.43$ ; see Fig. 2c).

### 3.2. Effects of time during the season

We analysed data separately for each season, using one-factor ANOVAs with week number as the factor.

These analyses detected highly significant weekly variation in all of the traits that we measured (Fig. 3). The total numbers of snakes per metre of path peaked midway through both seasons, with the decline on either side of

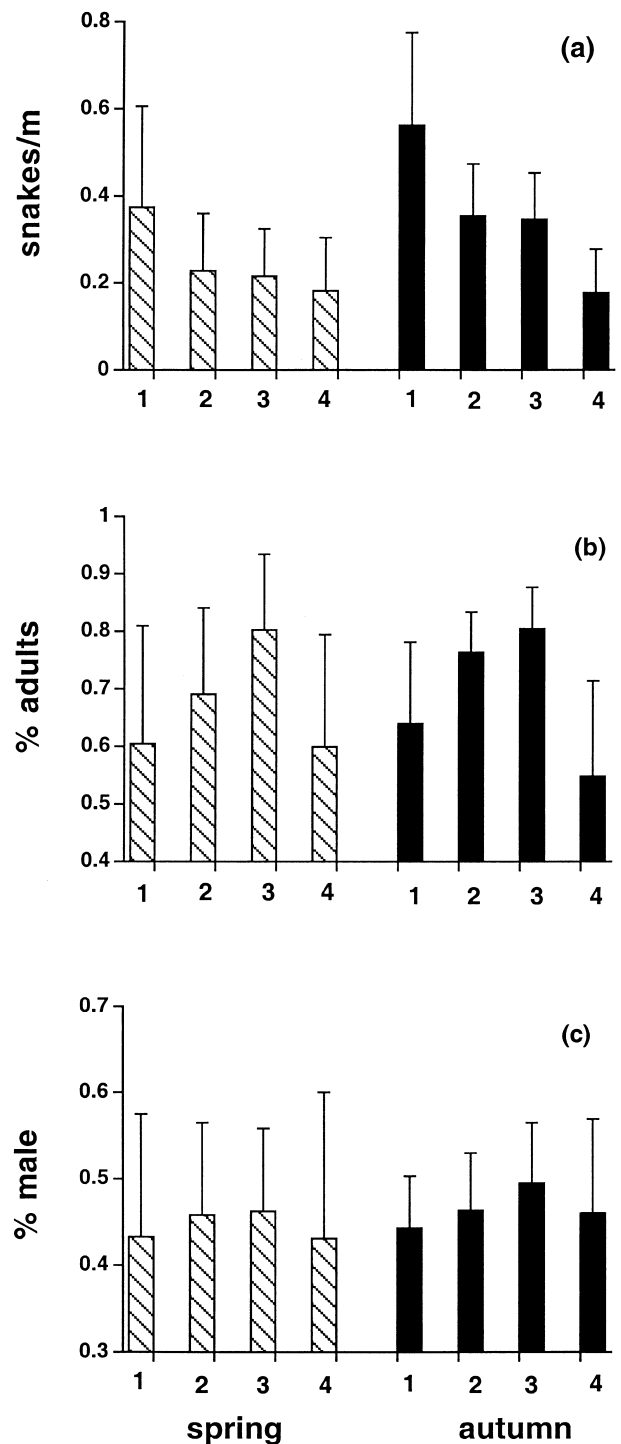


Fig. 2. Effects of location (segment of the path) and season (spring vs autumn) on the numbers and composition of samples of pit-vipers recorded during surveys: (a) total number of snakes; (b) proportion of adult snakes; (c) sex ratio. Numbers on the horizontal axis refer to the four segments of the path. Histograms show mean values  $\pm 1$  S.D. See text for statistical results.

this peak being steeper in spring than in autumn (spring:  $F_{8,387} = 19.14$ ,  $P < 0.0001$ ; autumn:  $F_{7,528} = 4.005$ ,  $P < 0.001$ ; Fig. 3a). The proportion of adult snakes among the samples did not change consistently through time in autumn ( $F_{7,528} = 1.44$ ,  $P = 0.19$ ), but was highest

during the period of peak snake abundance in spring ( $F_{8,387} = 11.04$ ,  $P < 0.0001$ ). That is, the earliest-emerging snakes were mostly juveniles, with adults dominating the sample only during the peak period of bird migration (Fig. 3b). Temporal shifts in sex ratio were less marked,

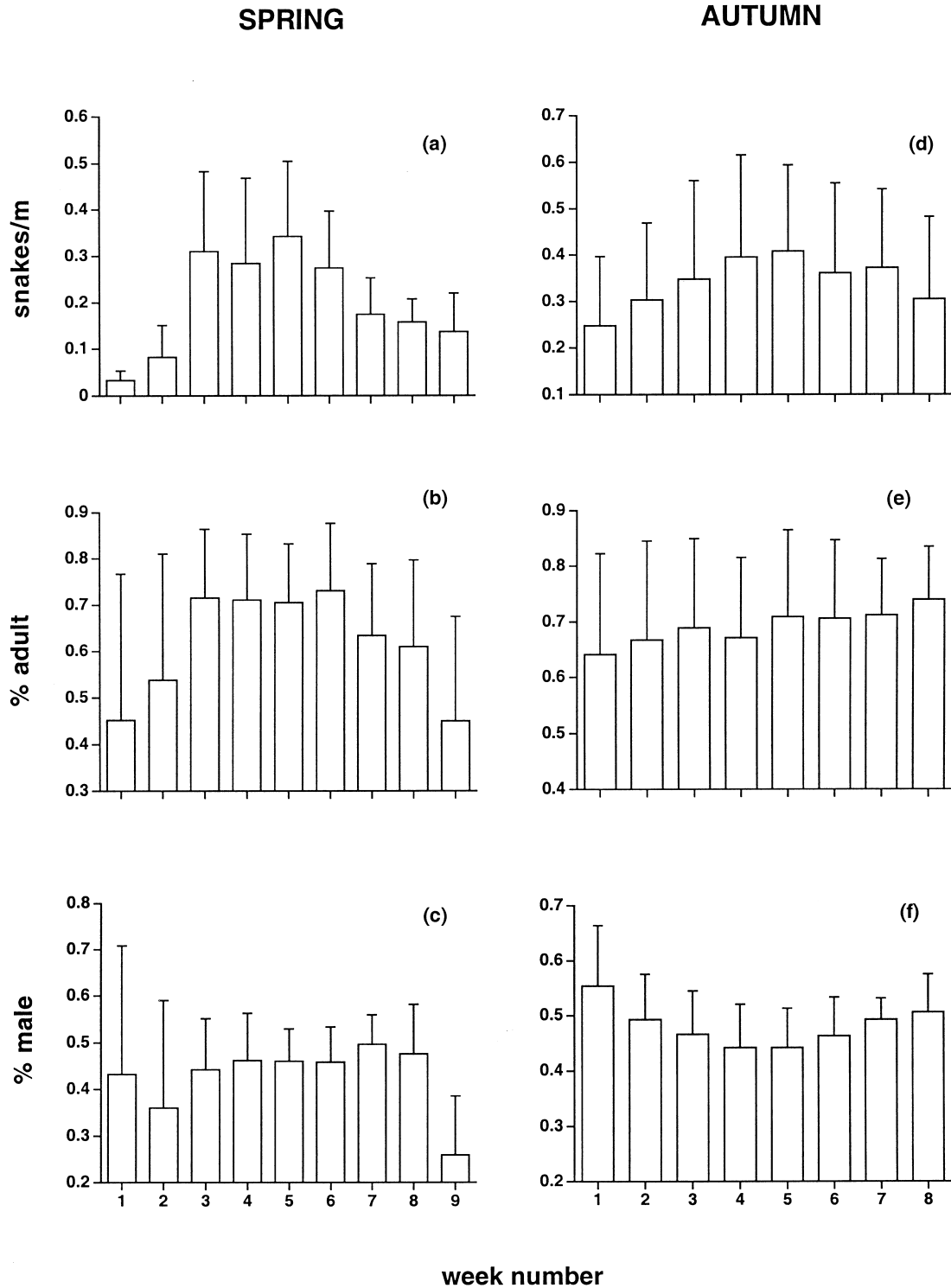


Fig. 3. Shifts in the numbers, size structure and sex ratio of Shedaop pit-vipers during each activity season. Data for the spring period are shown in left-hand graphs (a–c), and those for the autumn activity period on the right-hand side (d–f). The graphs show mean values for samples within each weekly period  $\pm 1$  S.D. See text for statistical results.

but nonetheless highly significant in our statistical tests (spring:  $F_{8,387} = 3.91$ ,  $P < 0.001$ ; autumn:  $F_{7,528} = 8.88$ ,  $P < 0.001$ ). The numbers of males relative to females tended to increase during the peak appearance period in spring, but the reverse pattern was evident in autumn (Fig. 3c).

### 3.3. Effects of weather conditions

Given the significant effects of location and season (or interactions involving these factors) on the numbers, age structure and sex ratio of the snake sample, analyses of the effects of local weather conditions on these attributes need to take such factors into account. We can do this using MANCOVA (multivariate analysis of covariance), with the data from each segment of the path being used as replicates. “Time within season” was not included as a factor in these analyses, because the significant effects of this variable (Fig. 3) might be caused by temporal shifts in weather conditions. These MANCOVA analyses (with the weather variable as the covariate, season as the factor and snake numbers, age structure or sex ratio as the dependent variables) provided the following results.

1. *The total number of snakes sighted* was affected by relative humidity, without any confounding interaction terms or seasonal differences (main effect: Wilk’s Lambda = 0.94;  $F_{4,221} = 3.54$ ,  $P = 0.008$ ). More snakes were seen on days with lower relative humidity. This effect was stronger in spring than in autumn (Fig. 4c), but the interaction between relative humidity and season was not statistically significant (Wilk’s Lambda = 1.00;  $F_{4,228} = 0.30$ ,  $P = 0.88$ ). Air temperature and wind speed also affected the number of snakes sighted, but in both of these cases there was a significant interaction with season (for air temperature, Wilk’s Lambda = 0.91;  $F_{4,227} = 5.82$ ,  $P = 0.0002$ ; for wind speed, Wilk’s Lambda = 0.93;  $F_{4,221} = 2.69$ ,  $P = 0.032$ ). Closer inspection clarifies the nature of these interactions. Higher wind speeds reduced snake numbers in both spring and autumn, but at a greater rate in the former season than in the latter (Fig. 4a). Higher air temperatures increased snake numbers in spring but decreased them in autumn, perhaps because of differences in the range of temperatures experienced during these two seasons. That is, the snakes’ response to air temperature may have been the same in both seasons, with an intermediate optimal temperature for activity. This temperature was rarely reached in spring, but was often exceeded in autumn (Fig. 4b).

2. *The proportion of adult snakes* in the sample was influenced by all three of the weather variables that we measured. The effects were broadly similar in spring and autumn (Fig. 5). The proportion of the sample consisting of adult snakes was reduced on days with higher relative humidity (Wilk’s Lambda = 0.96;  $F_{4,224} = 2.61$ ,  $P = 0.037$ ), and increased on days with strong winds (Wilk’s

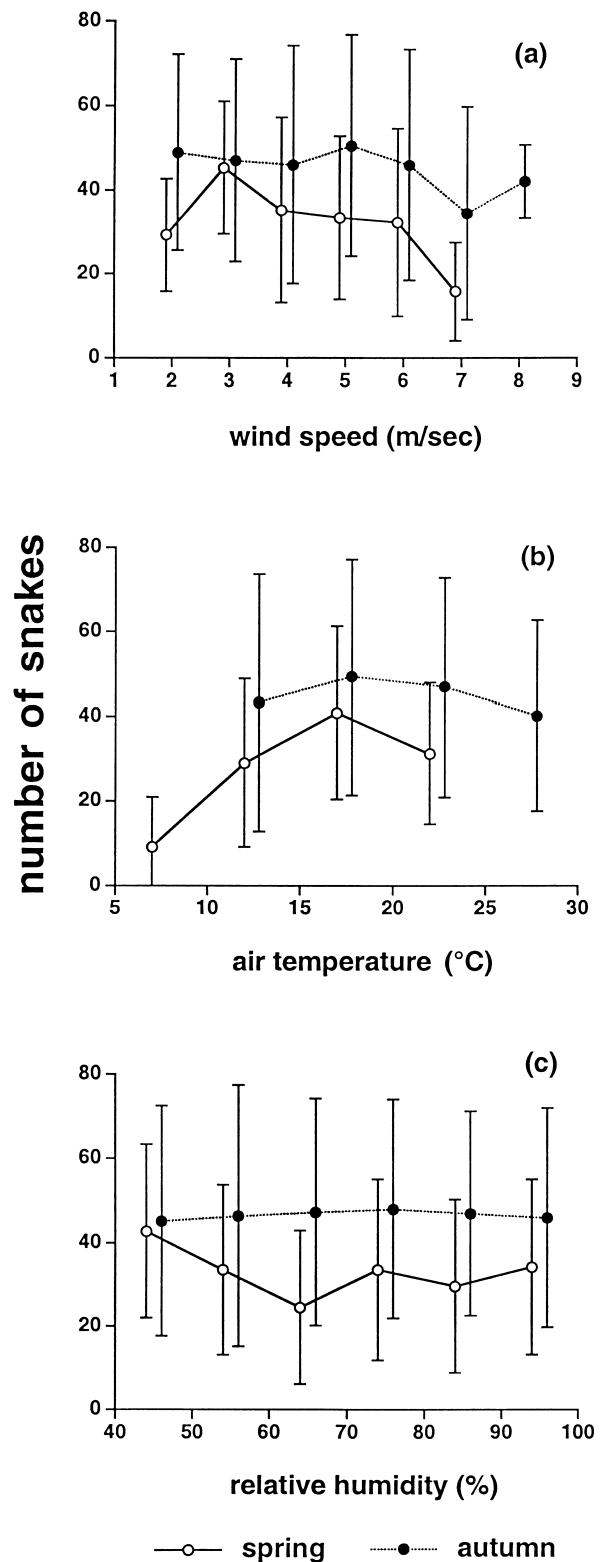


Fig. 4. Seasonal differences in the way in which snake numbers were influenced by weather conditions: (a) wind speed; (b) air temperature; and (c) relative humidity. Least-squares regression lines were fitted separately to raw data from spring and autumn, but (because sample sizes were very large) the graphs show mean values  $\pm 1$  S.D. over intervals for each independent variable. See text for statistical results.

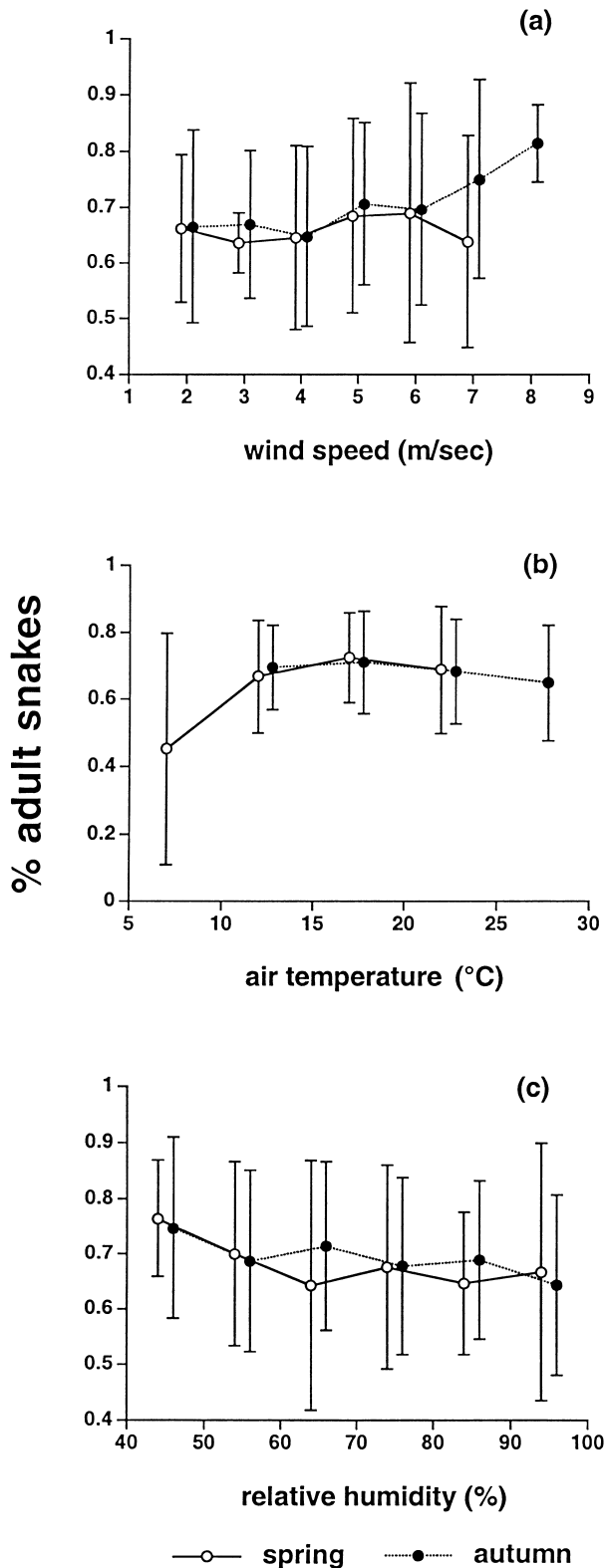


Fig. 5. Seasonal differences in the way in which the proportions of adult pit-vipers in census counts were influenced by weather conditions: (a) wind speed; (b) air temperature; and (c) relative humidity. Least-squares regression lines were fitted separately to raw data from spring and autumn, but (because sample sizes were very large) the graphs show mean values  $\pm 1$  S.D. over intervals for each independent variable. See text for statistical results.

Lambda = 0.94;  $F_{4,219} = 3.30$ ,  $P = 0.02$ ). The association between air temperature and the proportion of adult snakes was similar to its association with total numbers: both peaked at intermediate temperatures, and so tended to increase with temperature in spring (when the weather was generally cool) and decrease with temperature in autumn (when the days were much hotter; see Fig. 5b). Thus, we detected a significant interaction between season and air temperature (Wilk's Lambda = 0.87;  $F_{4,225} = 8.44$ ,  $P = 0.001$ ).

3. *The sex ratio of snakes* in our survey samples was significantly affected only by air temperature: the ratio of males to females was higher on hotter days than in cooler weather (Wilk's Lambda = 0.93;  $F_{4,225} = 4.09$ ,  $P = 0.003$ ; see Fig. 6). Neither of the other variables, or interactions with season, were significant in these MANCOVA analyses.

We also conducted separate (independent) ANCOVAs on data from each path segment. The results were similar to those reported above for the MANCOVAs, and thus will not be presented separately.

### 3.4. Multiple regression analyses

The above analyses show that the numbers and kinds (ages, sexes) of snakes recorded during a survey were significantly linked to at least four variables: location, season, time within season, and weather conditions at the time of the survey (Table 1). Under such circumstances, it is difficult to tease apart causal connections. Some of the "independent" variables will be correlated with each other: for example, weather conditions differ between seasons, and change through time within each season. Similarly, days with higher temperatures may be less windy, and/or less humid. One way to tease such effects apart is to use multiple regression, such that the effects of each variable are evaluated after the effects of other variables have been taken into account.

We performed multiple regressions for each dependent variable (total numbers, proportion of adults, sex ratio) within each season. The independent variables included in these analyses were time within season, air temperature, wind speed and relative humidity. Time within season explained the least variance in five of the six regressions, suggesting that weather conditions may be more important causal influences on snake activity than is time within season. Each of the three weather variables explained significant ( $P < 0.05$ ) variance in at least two of the six analyses, suggesting that all may influence the activity of the snakes.

## 4. Discussion

The survey data from Shedao provide perhaps the most extensive data set ever gathered on activity patterns

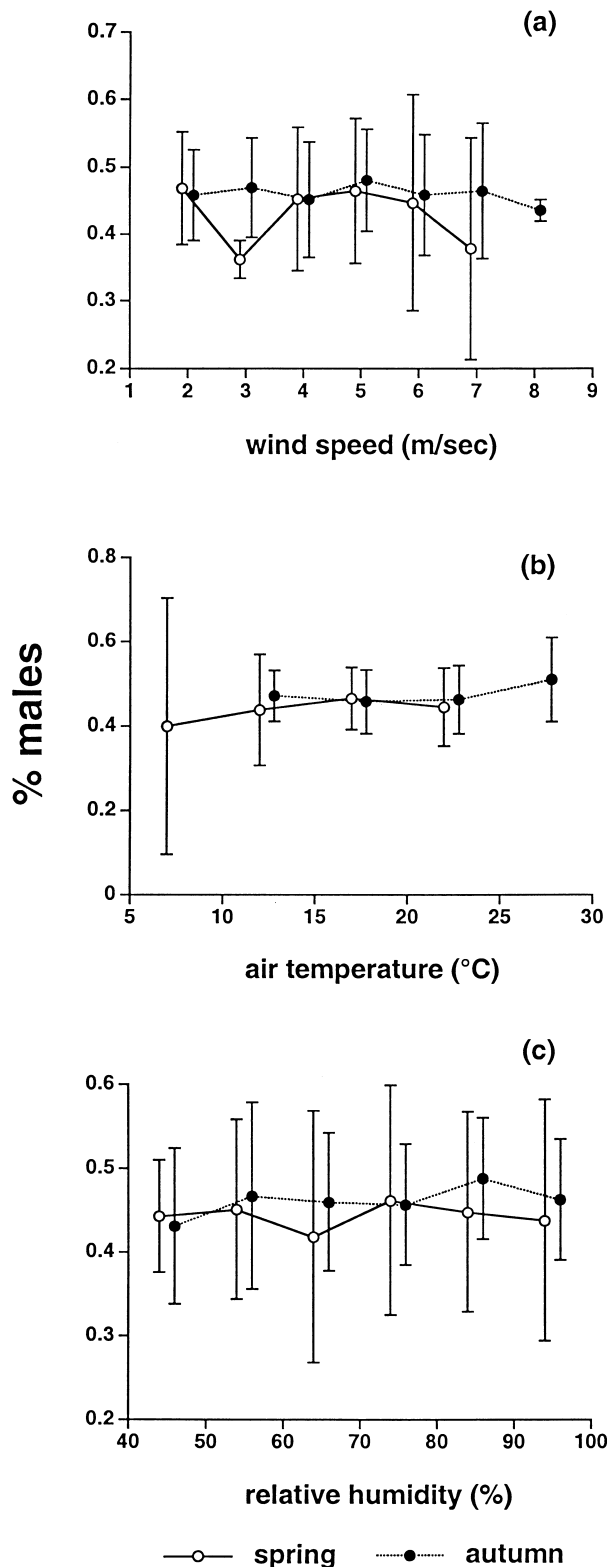


Fig. 6. Seasonal differences in the way in which the proportions of male pit-vipers in census counts were influenced by weather conditions: (a) wind speed; (b) air temperature; and (c) relative humidity. Least-squares regression lines were fitted separately to raw data from spring and autumn, but (because sample sizes were very large) the graphs show mean values  $\pm 1$  S.D. over intervals for each independent variable. See text for statistical results.

in snakes. Several other studies on snakes have spanned much longer periods (e.g. Fukada, 1992; Fitch, 1999), but have not involved snakes that are accessible for visual counts. Indeed, the pit-vipers of Shedao may be almost uniquely suitable for such a study, compared to other snakes (although not to many lizard species). Nonetheless, broadly equivalent data on other snake species can be gained by the use of traps (Gibbons and Semlitsch, 1987; Houston and Shine, 1994; Dodd and Franz, 1995), by collecting snakes on roads (Bernardino and Dalrymple, 1992; Rosen and Lowe, 1994; Bonnet et al., 1999), and from data-sets from community-based “wildlife rescue” groups (Koenig, 1999) or museum collections (Shine, 1994).

The methods used to enumerate the numbers, age classes and sexes of active Shedao pit-vipers were extremely simple. One potential difficulty in terms of statistical analysis of these data, however, is that a significant proportion of these sightings undoubtedly involved repeated records of the same snakes. Mark-recapture studies suggest that there are about 20,000 snakes on the island, whereas the total number of sightings (admittedly, over an 8-year period, with considerable opportunity for mortality and recruitment) involved about twice this many (37,980) records. The animals are highly philopatric and hence likely to be re-sighted in the same area on successive days (Sun, 1990; Sun et al., 1990). Given the very large sample sizes, however, any bias due to a particular individual’s behaviour will be trivial in the extreme. That is, our analyses are based on such large numbers of animals that repeated sightings of any aberrant individuals will have negligible impact on inferences about activity patterns with respect to sex, age, etc.

The clear result from our analyses is that behavioural factors influence the numbers and kinds of snakes that are active (and hence, observable) at any given time. Not only do local weather conditions influence the numbers of snakes sighted, but this number also varies among locations and between seasons. Additionally, the composition of the sample (age classes and sexes) will depend upon all of these factors. Similar kinds of biases have been detected in studies of other kinds of organisms (Härkönen et al., 1999), and are likely to be widespread in snakes also (e.g. Gannon and Secoy, 1985; Gibbons and Semlitsch, 1987; Plummer and Congdon, 1994; Dodd and Franz, 1995). For example, the cues for foraging activity may differ between conspecific adult and juvenile snakes, or between males and females, especially if they feed on prey with different activity cycles (e.g. Gannon and Secoy, 1984; Clarke et al., 1996).

Previous studies on the Shedao pit-vipers, and on other snake species, suggest reasons for some of the patterns that we have documented. For example, location effects (differences among sites in the total densities of snakes, or in their age structure or sex ratio) are likely to occur in almost every ecological system. Although



Table 1  
Potential magnitude of error introduced by behavioural influences on activity patterns in Shedao pit-vipers<sup>a</sup>

Source of error	No. of snakes				% Adults				% Male			
	Max.	Min.	Diff.	%Diff.	Max.	Min.	Diff.	% Diff.	Max.	Min.	Diff.	% Diff.
Location	0.28	0.18	0.30	0.91	0.80	0.57	0.23	0.34	0.48	0.44	0.04	0.09
Season	47.1	31.9	15.2	0.39	0.69	0.68	0.01	0.02	0.47	0.45	0.02	0.04
<i>Time within season</i>												
Spring	51.6	20.1	31.5	0.88	0.82	0.59	0.23	0.33	0.51	0.41	0.10	0.22
Autumn	56.9	39.2	17.7	0.37	0.75	0.64	0.11	0.16	0.49	0.43	0.06	0.13
Air temperature (range 7–30°C)	57.1	21.7	35.4	0.90	0.71	0.65	0.06	0.09	0.48	0.41	0.07	0.16
Wind speed (range 2–8 m/s)	49.2	30.9	18.3	0.46	0.72	0.65	0.07	0.10	0.47	0.45	0.02	0.04
Relative humidity (range 40–100%)	40.7	40.3	0.4	0.01	0.73	0.67	0.06	0.09	0.44	0.44	0.00	0.00

<sup>a</sup> For each potential source of bias, the magnitude of potential error is calculated as the maximum divergence between mean values for samples differing only in that factor. "Location" = differences among the four segments of the path; "season" = differences between spring and autumn; "time within season" = differences from the earliest to latest dates of sampling within a season. Weather variables = range in values predicted from least-squares linear regression at each extreme of the range of independent variables observed during the study. See text for further explanation.

the habitat on Shedao is broadly homogeneous, subtle spatial variation in aspects such as slope, elevation, and vegetation cover undoubtedly influence factors such as the availability of prey or foraging sites, wind speed, temperature and relative humidity. All of these factors may affect the size and structure of the sample obtained by visual census.

Differences in observability due to season are also likely to be widespread in snakes. Many species show highly seasonal activity schedules (e.g. Henderson and Hoovers, 1977; Gibbons and Semlitsch, 1987; Dalrymple et al., 1991). The cues that drive this seasonality may often involve abiotic factors, especially temperature. However, the inactivity of Shedao pit-vipers during summer (Sun, 1990; Sun et al., 1990) strongly suggests that seasonal activity in these snakes is driven primarily by the availability of prey. This situation is seen in a more subtle form in many other snakes, where reduced prey availability results in lowered activity levels (e.g. Andren, 1982; Shine and Lambeck, 1990). In one varanid lizard species, experimental studies in the field showed that activity levels were set directly by prey abundance (Phillips, 1995).

It would be of great interest to know how the Shedao pit-vipers (and indeed, other snake species) assess prey availability. Whatever the cue (visual, chemical?), it may also be responsible for differences in overall activity levels between spring and autumn (Fig. 2). Because the autumn migration includes recently-fledged birds, the numbers of birds migrating to warmer areas at this time is typically much higher than the number of adult birds that fly north in spring (e.g. a 2.5-fold difference in migrating Swedish passerines: S. Svensson, pers. comm.). Seasonal differences in activity levels might

also reflect reproductive activities. For examples, adult males of many snake species do not feed during the mating season, and females often feed ravenously after parturition (Bonnet et al., 1999; Fitch, 1999). Such sex differences may well generate sex differences in foraging rates (and thus, observability) across different seasons.

The snakes of Shedao are not unusual in showing temporal shifts in numbers, sex ratios and age structures across time within a single season. However, the form of this shift in Shedao is rather different to that seen in most other snakes. A review of this topic tentatively concluded that the most common pattern was for adult male snakes to emerge earlier in spring than conspecific females, and for juveniles to emerge later than adults (Gibbons and Semlitsch, 1987). The pit-vipers of Shedao show the opposite pattern in both cases: samples taken early in spring contained a higher proportion of juvenile animals, and a higher proportion of females than of males (see Fig. 3). These unusual trends may reflect particular aspects of the foraging biology of *G. shedaensis*. Because the adult snakes depend upon migrating birds, they may derive little benefit from emergence early in spring before the birds arrive. In contrast, juvenile pit-vipers feed on invertebrates as well as birds, and thus may benefit from emerging as soon as invertebrate prey are available. The delayed emergence of adult males (relative to females) is more puzzling, but may reflect the seasonal timing of spermatogenesis (Olsson et al., 1999). Spermatogenesis in *G. shedaensis* occurs primarily in summer and autumn (Yang, 1983), such that males do not need to bask early in spring to complete sperm maturation.

Weather conditions also affected the numbers and types of Shedao pit-vipers recorded during visual census

periods (Fig. 4). Again, several of these patterns are easily interpretable. Many snake species probably are most active at some specific range of air temperatures and relative humidity (e.g. Peterson et al., 1993; Shine and Madsen, 1996; Daltry et al., 1998). Higher ambient temperatures may facilitate the maintenance of high body temperatures which, in turn, may enhance ecologically relevant performance measures such as strike speed and accuracy (Greenwald, 1974). However, temperatures that are too high may force the snake to seek shade to avoid overheating (e.g. Peterson et al., 1993; Shine and Madsen, 1996). Relative humidity may similarly drive activity times and the choice of foraging sites (Daltry et al., 1998).

In our surveys, wind speed substantially affected snake numbers (Fig. 4). Although many experienced field-workers believe that windy conditions reduce encounter rates with snakes, we are not aware of any previous data to demonstrate such an effect. Strong winds might discourage snake activity for several reasons, especially in a species that uses arboreal foraging sites. Windy conditions may enhance rates of cooling or desiccation, discourage bird activity, and/or make it difficult for the snake to detect or capture prey. Smaller (juvenile) snakes may be affected more than adults, particularly in terms of thermal and hydric exchanges. In keeping with this possibility, the proportion of juvenile snakes in our census samples declined in windy weather. Desiccation may be a serious threat to juvenile pit-vipers, given the lack of freshwater on Shedao.

How important are these biases in terms of our inferences about population parameters? At least three questions are of interest in this respect:

1. *How much do sampling conditions affect our estimates?* We can assess the magnitude of sampling bias by looking at the ranges of values for total abundance, age structure and sex ratio induced by variation in other factors (location, season, time within season, weather conditions). Table 1 shows the size of the effects (and thus, the potential errors) from each source, as indicated by the maximum disparity in mean estimates among various samples that differed only in respect of that factor. The census counts are sensitive to all of these sources of bias, but the pattern is complex. For example, the total number of snakes seen depended heavily upon several factors (air temperature, time within season, season, location, wind speed). The composition of the samples was less strongly affected by sampling conditions, differing mostly with respect to location and time within season (Table 1). Of the weather variables recorded, air temperature had the most effect on sample number and composition, and relative humidity the least (Table 1).

2. *How accurately do our samples reflect underlying ("real") values for the same parameters?* We can evaluate the validity of our sampling by comparing the estimates

from sight records to actual mean values of the population as determined by mark-recapture studies conducted at the same time. Such studies were conducted in September 1989, by paint-marking snakes and then resampling to estimate the proportion of paint-marked snakes within the population (Huang, 1990; Li, 1995).

Comparison shows that the census data (from May 1990) provide a poor estimate of the age and sex structure of the snake population. The proportion of adult animals was 55.4% from the census data, vs 71.9% from the mark-recapture study. The proportion of males in the population was calculated as 40.4% from the census vs 47.6% from the mark-recapture. That is, adult snakes, especially males, were strongly under-represented in visual counts. These biases fit well with the results from behavioural studies, in which observers recorded the proportions of snakes within enclosures that were active on any given day. Juvenile snakes spent more time off the ground (up in branches) than did adults (90 vs 63%: Li, 1995), and would be easier to observe. The proportion of snakes containing prey items was higher in females than in males (26 vs 22%: Li et al., 1990), also suggesting a greater observability for females. Clearly, such differences in activity patterns among age and sex classes of snakes can generate substantial biases in observability.

3. *How general are our results?* The specific features of our results cannot be generalised to other systems. Particular aspects of topography, seasonality, weather conditions and reptile biology will interact in complex ways, such that the determinants of observability will differ even between conspecific populations in adjacent areas (Whiting et al., 1996). Similarly, activity patterns will relate to weather conditions quite differently in different taxa: for example, although air temperature was a more important influence than relative humidity on activity of snakes in Shedao, the opposite result has been reported in another Asian pit-viper (Daltry et al., 1998). Nonetheless, it seems likely that other systems will resemble the Shedao example in that (i) the numbers and kinds of individuals that are seen by an observer will depend upon numerous biotic and abiotic features; and (ii) thus, those counts will give only a rough approximation to the underlying parameters of population size and structure. These caveats do not mean that census data are uninformative, but they do mean that such data need to be interpreted very carefully.

The determinants of activity patterns in free-ranging reptiles are likely to be very complex, and simple generalisations may prove to be elusive. Nonetheless, we suggest that studies on this topic have the potential to reveal important insights into reptile biology. Differences in activity patterns among sex and age classes, and the ways in which these animals respond to environmental variation, can illuminate important issues:

(i) population estimation for conservation purposes, as in the present example. With knowledge of the determinants of sample sizes and composition, census counts can be used to monitor changes in underlying populational traits;

(ii) predicting the times and places that snakes will be active can be of value in reducing the risk of snake-bite, by identifying situations to avoid (Whitaker and Shine, 1999);

(iii) the efficiency of surveys can be maximised by determining the optimal times, places and conditions under which such surveys should be conducted (Dodd and Franz, 1995; Whiting et al., 1996); and

(iv) snakes that are obvious to a human observer are likely to be more vulnerable to attack by other humans, and may also be more vulnerable to other visually-oriented predators such as birds of prey (Peterson et al., 1993; Koenig, 1999). Thus, analyses such as ours may help to predict which segments of the snake population are most at risk, and which times and places are likely to be most important in this respect.

Overall, our analyses provide both a cautionary tale, and encouragement, for conservation biologists who use census data to estimate underlying aspects of abundance and population structure of their study organisms. Clearly, estimates of such parameters can be substantially affected by conditions prevailing at the time of the census, and by minor spatial differences in habitat types and microclimate. Hence, uncritical use of such data, without an understanding of the ways in which census conditions affect parameter estimates, can lead to serious error. On the other hand, our study also suggests that many of these biases are sufficiently consistent that they can readily be taken into account. Thus, censuses may indeed provide valuable insights into biological attributes of the study population, but must be interpreted with great care.

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