2005 Progress Report

Population Biology of the psammophilous lizard *Meroles anchietae*

This report summarizes the results of a population census conducted between 28 June and 4 July, 2005. The objectives of this study included the following: 1) To investigate further the basis for the male biased sex ratio that we observed in prior years; and 2) To compare 2005 with the previous demographic profiles of the Helga's Dune population.

There were no mortalities, and no lizards were removed from the population.

MATERIALS AND METHODS

Study Site: Helga's Dune is a small, isolated linear dune near the field station at Gobabeb, Namibia (see Muth and Fisher 1999, Appendix I). As in1999, 2001, 2002, and 2004, we limited the size of the study plot in an effort to enumerate an entire subpopulation, including elusive females, rather than census the entire dune. Our 1997 data indicated that there is a gap in lizard sightings between the southern 1/3 and the northern 2/3 of the dune, and that—at least for the duration of our study—there was no migration across this gap. Thus the population in the southern portion is effectively closed. This portion of Helga's Dune is about 830 m long, and between 52 m and 210 m wide.

Census Protocol: We did multiple surveys to census the southern portion of Helga's Dune between 28 June and 4 July 2005. We surveyed during the lizard's two daily activity periods: one survey per activity period except when too cold and/or windy for lizard activity. We captured all unmarked individuals and individuals new to this year's census, measured their snout-vent length (SVL, ± 1 mm) and mass (± 0.1 g), and marked them by toe clipping (Medica *et al.* 1971). Juveniles were marked temporarily by writing their identification number mid-dorsally with permanent ink. Adults were permanently marked with colored beads (Fisher and Muth 1989). We used ten colors of small "seed" beads (size 14/0), three beads per lizard, to give each individual a unique mark that was identifiable from a distance with binoculars. We recorded the position of each capture and each resighting using a global positioning system (see below). Positions were recorded where an individual was first sighted.

Population Size Estimates: We were unsuccessful in capturing all of the individuals in the subpopulation. Thus, we relied on mark-recapture methods to estimate population size. We used the Closed Captures technique from Program MARK (Version 4.2, White and Burnham 1999) which calculates the probability of initial capture (p), the probability of recapture (c), and estimates the population size (N). This technique allows estimates of N by sex group where the groups can have differing capture probabilities (both p and c). For these analyses we pooled capture data from both morning and afternoon activity periods of a given day resulting in six sample days. Capture histories for each individual are recorded as 0 if not seen and 1 if seen, even if sighted in both activity periods of any given day. The Closed Captures technique allows the groups (in this case males, females and juveniles) to be modeled as being equal, different, or some combination thereof in regards to N, p, and c. We used Huggins (1989, 1991) closed capture model which allowed us to use size (SVL) as an individual covariate.

Spatial Activity: We used the Global Positioning System (GPS) to record the position of each sighting. We also used Trimble Navigation GeoExplorer 3 GPS units to map the perimeter of this portion of Helga's Dune for comparison with previous years. By using two receivers capable of carrier phase processing we were able to obtain an accuracy of less than 1 m. On occasion, signals were degraded by poor satellite geometry and atmospheric conditions. When this occurred the acquisition of position data was repeated until the resulting accuracy was acceptable.

Statistical Analyses. We used SYSTAT® 10.0 for Windows (SPSS Inc., 2000) for all statistical analyses. Parametric statistics were used for data with a normal or transformed normal distribution. The nonparametric statistics were used for data that could not be transformed to a normal distribution using standard transformations.

RESULTS

Capture data: We captured a total of 41 individual *Meroles anchietae* on the southern portion of Helga's Dune. These included 18 males, 16 females, and 7 juveniles (see Table 1). The adult sex ratio, 1.25:1, is not significantly different from 1:1 (Pearson Chi-square = 0.12, P = 0.732, 1 D.F.). However, the frequencies of all adult sightings (initial plus resightings) were significantly skewed in favor of males (1.953:1; Pearson Chi-square = 6.78, P = 0.009, 1 D.F.).

We recaptured 12 individuals marked in previous years. Of these, seven were from the 40 individuals first marked in April 2004, two were from the 64 individuals marked in October-November 2002 and three were from the 216 individuals marked in April-May 2001. This gives a rough estimate of from 6 to 18% annual survivorship. But the sexes and age classes should be treated independently based on the unequal capture probabilities between sexes and the probable lower survivorship of the juvenile age class. Treating males independently refines the rough survivorship estimate to 11 to 14%. These survivorship analyses will be explored intensively at the end of fieldwork on this project.

Body sizes for the three groups, males, females, and juveniles, are tabulated in Table 2. A histogram (Figure 1) shows frequencies at each size (snout-vent length) and the size groupings within sexes suggest age classes.

Table 1: Capture frequencies for *Meroles anchietae* in June-July 2005. Initial Captures include individuals marked in previous years.

	Initial Captures	Recaptures	Total
Males	18	22	40
Females	16	4	20
Juveniles	7	13	20
Total	41	39	80

Table 2. Body sizes by sex group for Meroles anchietae for June-July 2005.

	Median SVL (cm)	N	Range	Median Mass (g)	N	Range
All	4.3	40	3.2 – 5.3	3.0	41	1.2 – 5.3
Males	4.9	17	3.9 – 5.3	4.3	18	1.8 – 5.3
Females	4.1	16	3.2 – 4.6	2.7	16	1.2 – 3.8
Juveniles	3.5	7	3.2 – 4.1	1.6	7	1.2 – 2.0

Table 3. Population estimates (N) and 95% confidence limits for models of 2005 data using the Huggins Closed Captures technique of Program Mark. Models are ranked by their corrected Akaike's Information Criterion (AICc) and those having an AICc that differs from the top model by more than two are considered inferior and thus their estimates are not shown. Model syntax includes terms for group (g), sex when treated differently than by group (m, f, j), size covariate (svl) and whether run using the design matrix (dm) of Program Mark. See Discussion for details.

	N			95% C.I.			Delta
Model	♂♂	♀♀	Juv.	♂♂	♀♀	Juv.	AICc
1. {p(g+pc)+svl*g) dm}	49	121	8	23 - 200	36 - 565	7 - 20	**0.00**
2. {p(g+pc)+svl) dm}	43	143	9	21 - 204	36 - 826	7 - 27	**0.99**
3. {p(g+pc) dm}							2.43
4. {p(g) c(m=j)}							3.79
5. {p(g) c(g)							4.06
6. {p(g)=c(g)							7.53
7. {p(g) c(f)							7.76
8. {p(.)=c(.)							22.55

Population Size. The proportion of small individuals (svl <4.0 cm) in the marked portion of the population was about 19.5% this year. The average of the six survey years is 23.6%, range 6.2 to 52.3%. We estimated population sizes of all three "sex" groups (males, females, and juveniles) using a technique that allowed for this variation in population size as well as in capture probability among the three groups. We postulated that, based on our previous results, the probability of capture (initial and recapture) differs between males and females, and that the population size differs among groups. This year, however, we included body size (svl) as an individual covariate and postulated that the largest males would be seen most often as they defended their territories and searched for females. Smaller males should be buried more often to avoid aggressive encounters. Females on the otherhand should show little size-related differences in sightability once they reach sexual maturity. Using Huggins (1989,1991) Closed Captures model we compared models without a size covariate, models with a size covariate, and models with a size covariate*group interaction. The top model is p(g+pc)+svl*g, the size*group interaction model (Table 3). The estimates of N, p and c for all six years are shown in Table 4 (see Discussion).

DISCUSSION

Male and female individuals were represented nearly equally in the enumerated population. However, females were less likely to be captured than were males as in most previous years. In 2005 males, females, and juveniles comprised 44, 39, and 17 %, respectively, of the enumerated population.

The Huggins Closed Capture technique in Program MARK (Version 2.1) enables the probability of initial capture and the probability of recapture (resighting) for each group to be modeled as independent parameters to derive an estimate of the population size of each group. Furthermore size can be used as a covariate and can be modeled alone or as an interaction with sex group. Based on observations from previous years we postulated that the probability of capture for males would increase with an increase in body size because of aggressive, apparently territorial behavior. Juveniles could show an inverse relationship because the smaller individuals appear to be tolerated by males, perhaps triggered by the yellow juvenile coloration. This yellow color fades as juveniles grow larger and they begin to show adult features at about 4.0 cm svl. We have not observed any size-related differences in sightability of females although they can certainly exist. We correctly picked the model that best represents the data for 2005, which shows a size by group interaction (Table 3). When the Huggins technique was applied to data from previous years this same model was best for three years; a similar model that differed in that size lacked a group interaction was best in one year; and one without a size covariate and that treated the probabilities of initial and of recapture as equal within groups was best for one year (Table 4). The 95% confidence limits of p and c overlap among groups within years. But it is especially noteworthy that there are years with no overlap; for example the 95% C.L. for both p and c for males in 2001 do not overlap those for 2002. Lower calculated probabilities for p and c resulted in broader confidence intervals for the derived parameter N (population estimate). Although our previous work suggests that males and females have a 1:1 sex ratio, and the enumerated sex ratio for 2005 did not differ significantly from 1:1, the estimated population sizes differed substantially between sexes in 2005 and is suspect.

The estimated adult population size for the south 1/3 of Helga's Dune varies substantially among years (Figure 2). Even with the high reproductive output seen in 2001, there was a substantial decline in adult population size in 2002. This suggests that survivorship varies substantially among years, perhaps in response to the quantity of precipitation received since a previous census. Survivorship might also vary by body size. Variation in survivorship and in population size in response to precipitation will be explored in depth after the end of fieldwork on this project.

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Program MARK can be downloaded at: http://www.cnr.colostate.edu/~gwhite/mark/mark.htm

Table 4. (Following page) Population estimates (N), probability of initial capture (p), probability of recapture (c) and 95% confidence limits for the best model as determined by AICc for all models run for a given year. Models were run using the Huggins Closed Captures technique of Program Mark (Version 4.2, White and Burnham 1999). Model syntax includes terms for all three sex groups (g), specific sex groups (m, f, j), size covariate (svl) and whether run using the design matrix (dm) of Program Mark.

Group	**N**	**N 95% C.L.**	**p**	**p 95% C.L.**	**c**	**c 95% C.L.**
Model {p(g+pc) +svl) dm}						
Males	21.7	21.1 - 29.1	0.374	0.208 - 0.575	0.178	0.108 - 0.279
Females	12.7	11.3 - 22.0	0.268	0.139 - 0.454	0.117	0.058 - 0.221
Juveniles	6.6	5.2 - 17.7	0.327	0.094 - 0.695	0.150	0.034 - 0.470
Model {p(g+pc)+svl*g) dm}						
Males	55.0	45.9 - 85.5	0.091	0.053 - 0.151	0.178	0.128 - 0.243
Females	36.8	27.8 - 62.4	0.050	0.019 - 0.125	0.101	0.041 - 0.228
Juveniles	12.7	9.7 - 28.3	0.018	0.004 - 0.077	0.037	0.008 - 0.149
Model {p(g+pc)+svl*g) dm}						
Males	110.5	81.1 - 194.1	0.021	0.007 - 0.063	0.057	0.025 - 0.124
Females	125.6	77.1 - 247.2	0.034	0.016 - 0.070	0.089	0.058 - 0.134
Juveniles	268.8	184.5 - 466.8	0.034	0.017 - 0.067	0.088	0.063 - 0.122
Model {p(g+pc)+svl*g) dm}						
Males	43.6	40.9 - 55.2	0.264	0.166 - 0.392	0.424	0.336 - 0.517
Females	55.9	40.8 - 96.7	0.107	0.052 - 0.208	0.197	0.115 - 0.316
Juveniles	4.9	4.1 - 11.8	0.189	0.002 - 0.959	0.323	0.005 - 0.978
Model {p(g)=c(g)}						
Males	19.6	19.1 - 23.7	0.269	0.210 - 0.337	0.269	0.210 - 0.337
Females	27.6	23.2 - 41.2	0.122	0.079 - 0.183	0.122	0.079 - 0.183
Juveniles	20.0	17.1 - 30.6	0.137	0.087 - 0.209	0.137	0.087 - 0.209
Model {p(g+pc)+svl*g) dm}						
Males	48.5	23.1 - 199.6	0.044	0.008 - 0.222	0.175	0.067 - 0.384
Females	120.6	35.9 - 564.6	0.021	0.003 - 0.121	0.088	0.026 - 0.259
Juveniles	8.5	7.2 - 19.7	0.206	0.018 - 0.785	0.541	0.087 - 0.936

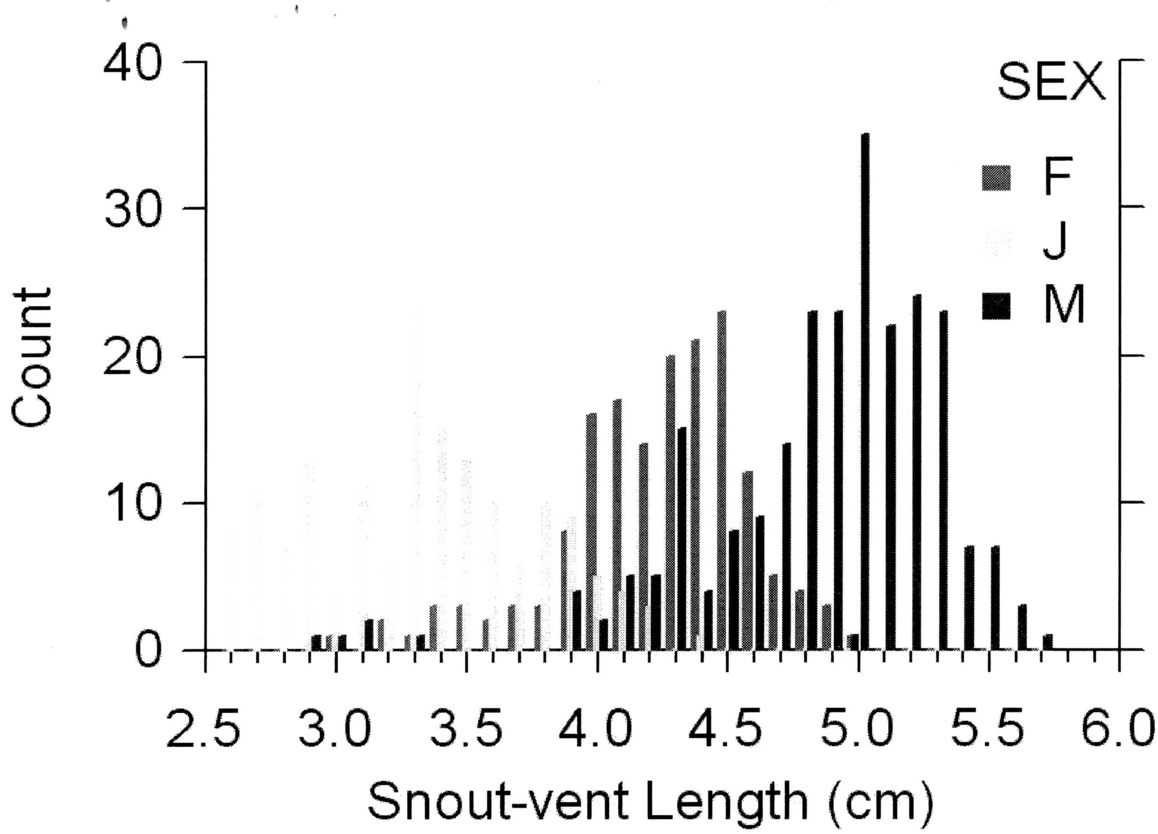

Figure 1. Histogram showing size distribution of *Meroles anchietae* at Helga's Dune for all survey years. A juvenile and one to two adult size classes can be seen. Most individuals exhibit adult characteristics by 4.0 cm.

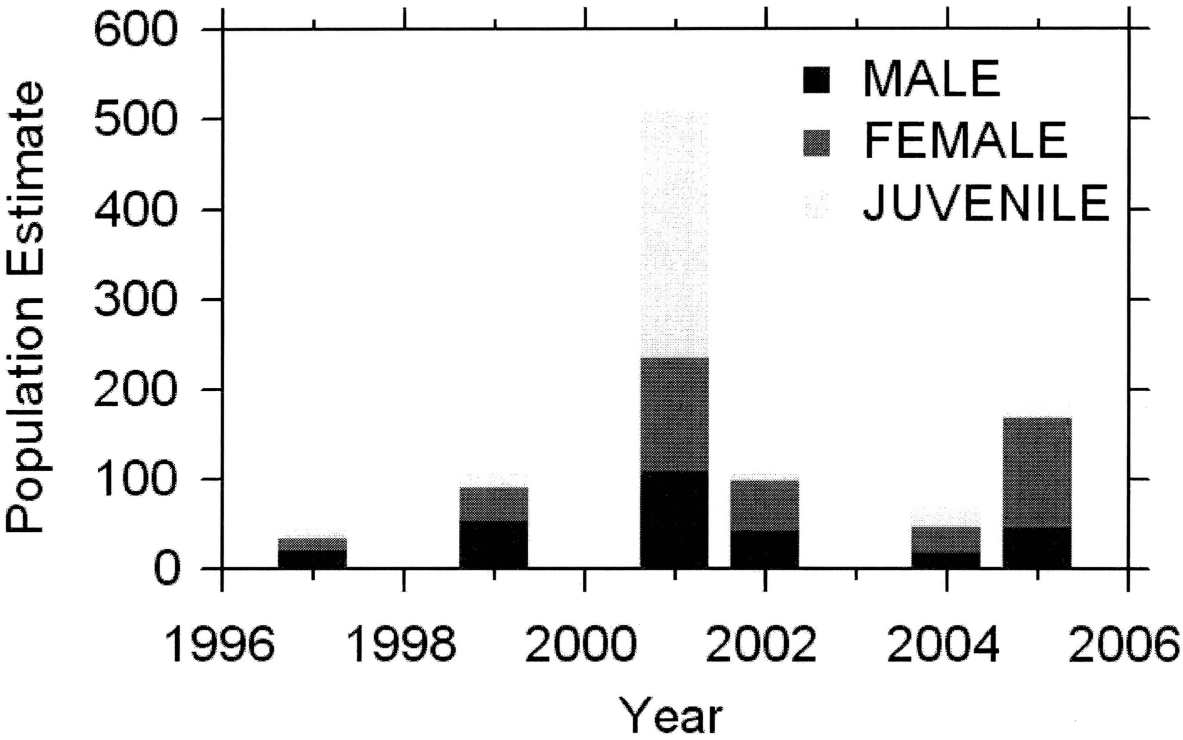

Figure 2. Estimated population size of *Meroles anchietae* per census year at Helga's Dune. Estimates were calculated using the Huggins Closed Captures technique of Program Mark (White and Burnham 1999).