Monitoring and Managing the Harvest of Tegu Lizards in Paraguay

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Abstract

*Despite the ongoing worldwide trade in reptiles, monitoring and management systems are only recently being developed for exploited lizards and snakes. We studied the tegu lizard (*Tupinambis *spp.) management and harvest monitoring program in Paraguay as a model for commercially exploited reptile management. Tegu lizards are among the most exploited reptiles in the world, with current quotas for Paraguay and Argentina of 300,000 and 1,000,000, respectively. We analyzed demographic data obtained from harvested skins of 2 species of tegu lizards at 2 trade levels (i.e., check stations and tanneries) over an 8-year period. There was significant annual variation in the number, size, and sex ratios of harvested tegus. Sex ratios were consistently male biased. The proportion of small skins in the harvest decreased over time, indicating compliance with the policy to ban commerce of small tegu skins. However, disparities among check stations and tanneries indicated that small skins might have been restretched by middlemen as they were bartered up the trade chain. Our results support the conclusion that tegu lizards are withstanding the harvest in Paraguay. There was no chronological trend of increased take or decreasing size that would indicate overharvest, and there were no indicators of local population decline. However, data on hunter effort are lacking, and it is important to implement a system for quantifying hunter effort and incorporate those data into harvest models. This is the first study to report long-term data on a harvested lizard. The approach we used here can serve as a model for monitoring and management of other commercially exploited terrestrial reptiles.* (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1723–1734; 2006)

Key words

harvest monitoring, Paraguay, reptile management, skin trade, tegu lizards, Tupinambis.

Management of harvested species depends on feedback from information systems designed to assess population trends (Creed et al. 1984, Getz and Haight 1989, Beissinger and Bucher 1991). In many instances, harvest monitoring is the most feasible and cost-effective approach to gathering demographic information on species whose populations are difficult and expensive to study directly over large geographic areas (Getz and Haight 1989, Fitzgerald et al. 1991, Shine et al. 1996). Furthermore, harvest monitoring systems enable managers to evaluate the effectiveness of harvest policies (i.e., harvest quotas, size limits) and improve them through time (Creed et al. 1984, Bailey et al 1986, Pfister and Bradbury 1996, Kyle et al. 1997, Weeks and Berkeley 2000).

Management programs are lacking for most exploited reptiles; the exception is crocodilians, whose populations can be estimated with eye-shine counts and nest surveys (Webb et al. 1987). Although tegu lizards (*Tupinambis* spp.), monitor lizards (*Varanus* spp.), pythons (*Python* spp.), boa constrictors (*Boa constrictor*), iguanas (*Iguana iguana*), rattlesnakes (*Crotalus* spp.), and other snakes and lizards (squamates) have been used for meat and leather markets for many decades, sustained-yield management and monitoring systems are only recently being established in a few situations (Luxmoore et al. 1988, Fitzgerald et al. 1991, Fitzgerald et al. 1994, Shine et al. 1998, Fitzgerald and Painter 2000). Large-bodied squamate populations are difficult to measure. Squamate reptiles are extremely variable in their activity and observability, making transect counts and mark–recapture studies inefficient, and also making the results questionable for population estimates (Rodda et al. 1999, 2001). Difficulty in detection and measurement does not, however, make reliable monitoring information any less necessary. There is a clear need to develop monitoring systems that enable managers to manage harvested reptile populations.

Tegu lizards from southern South America have been commercially exploited for their skins for >25 years, and they are among the most exploited reptiles in the world (Norman 1987, Fitzgerald 1989, Fitzgerald 1994*a*). During the 1980s, the world trade averaged 1.9 million tegu skins per year (Fig. 1). Large numbers of skins accumulate at different levels of the commercial trade, and it should be feasible to obtain demographic information from the harvest. Prior experience (Fitzgerald 1990) gave us reason to believe that harvest monitoring would prove an efficient means of gathering large amounts of data on demographics of harvested tegus, as well as information on hunting and trade patterns.

We used long-term harvest data to understand trade practices and population structure of 2 species of harvested tegu lizards in Paraguay. We predicted that tegu demographics would vary not only through time but also by location. Therefore, we examined variation in the number, size, and sex ratios of tegu harvest data collected over an 8-year period at locations throughout Paraguay where tegus are hunted. We predicted trade practices at different levels of the trade (i.e., hunter, middleman, and tannery) would

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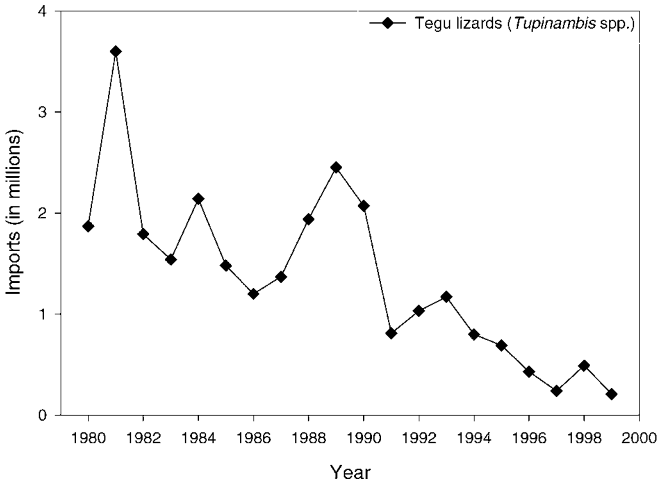

Figure 1. Worldwide imports of tegu lizards (*Tupinambis* spp.) from 1980 to 1998. (Source: World Conservation Monitoring Centre).

result in differences in the makeup of the harvest at each level. To test this idea, we collected harvest data at 2 levels of the trade: at check stations where hunters sell skins and at tanneries where skins accumulate after passing through a trade chain of several middlemen. We predicted that comparisons between these 2 trade levels would enable us to verify compliance with harvest regulations, specifically the policy to ban commerce of small tegu skins. Differences in the proportions of small skins in the harvest at check stations and tanneries, for example, would indicate re-stretching of small skins as they passed through the trade chain.

Despite the general need to manage a variety of exploited terrestrial reptiles, this is the first study that we are aware of to report the workings of an established management program and long-term harvest data for a commercially exploited lizard. We are hopeful the approach used here can serve as a model for monitoring and management of other commercially exploited terrestrial reptiles.

Study Area

Tegu Trade and Management Program

Three species of tegu lizards, the black-and-white tegu (*Tupinambis merianae)*, the red tegu (*T. rufescens.*), and *T. duseni* (no English name), occur in Paraguay (Fitzgerald et al. 1999). The pattern of rectangular, juxtaposed ventral scales of tegu lizards (characteristic of the Teiidae family) makes their skins desirable to the exotic skin trade. Hunters capture tegus with trained dogs that track lizards to their burrows where they are dug out, caught, and killed. Skins are valued for the belly skin and are traded by belly width according to 3 width classes: class 1, >30 cm; class 2, 25–29 cm; and class 3, <25 cm. Hunters sell skins to middlemen, who may restretch them to increase their width into the next size class (i.e., class 3 skins into class 2 and class 2 skins into class 1). Skins accumulate at tanneries where they are processed into finished leather or semitanned crusts. Essentially all tegu skins are exported to exotic leather markets in the Northern Hemisphere (Donadio and Gallardo 1984, Norman 1987, Fitzgerald et al. 1991).

Tegu lizard species were included on Appendix II of the Convention on International Trade of Endangered Species of Wild Fauna and Flora (CITES) before 1980, and information was available on worldwide imports of lizard skins. Political changes in Paraguay in 1989 provided a way for the terms of the CITES convention to be enforced, and Paraguay legalized commercial trade in tegu skins in 1991. Argentina and Paraguay implemented similar management plans in 1991.

Management of tegu lizards consists of policies aimed at influencing population growth rate by targeting large adult males and avoiding harvest of subadults. The basic components of the management scheme in Paraguay consist of 1) a mandatory harvest monitoring program, 2) incentives to reduce the take of juvenile animals (only 3% of the harvest could consist of skins <25 cm wide), and 3) yearly export quotas of 300,000 skins for Paraguay. Additionally, an awareness campaign was begun to inform hunters that there was no market for skins <25 cm wide. This program is the model of wildlife management in Paraguay. Tegu lizards are the only wildlife that is actively managed in Paraguay.

There were several levels of the tegu skin trade in Paraguay, with hunters at the starting point of trade. Tegu skins were stretched and dried by hunters in the field and sold to traveling middlemen or to local store owners. Mobile middlemen and middlemen located in towns or small cities resold skins to major middlemen contracted by tanneries located in or near the capital city of Asunción. Middlemen and tanneries often stockpiled thousands of skins, and major middlemen usually waited to sell skins until the middle or end of the harvest season when prices tended to rise (Fitzgerald et al. 1991, Mieres 2002). Hundreds of skins accumulated in tanneries each month during the buying period when there was a backlog of skins waiting to be tanned. After tanning, skins were exported either 1) whole, as semitanned crusts or as dyed and polished skins, or 2) in precut patterns.

Methods

Data Collection

Legal trading of tegu skins began each year in October and continued throughout the austral warm season until May. Thus, we classified harvest data taken during a season as belonging to the year at the beginning of the season (e.g., data from Oct 1991 to May 1992 were classified as 1991, and so on through the 1998 season). We collected data at all tanneries in operation from 1991 to 1998. Depending on the year, 1–4 tanneries were in operation. For instance, in 1991, there was only one tannery, while in 1998 4 tanneries were operating. All tanneries were located in Asunción, the capital city, and Villa Hayes (Fig. 2). Trading locations used by middlemen in 9 small towns or cities along the principal trade routes served as our check stations for sampling harvested skins in the field (Fig. 2). We visited these check stations monthly during the harvest season from 1993 to

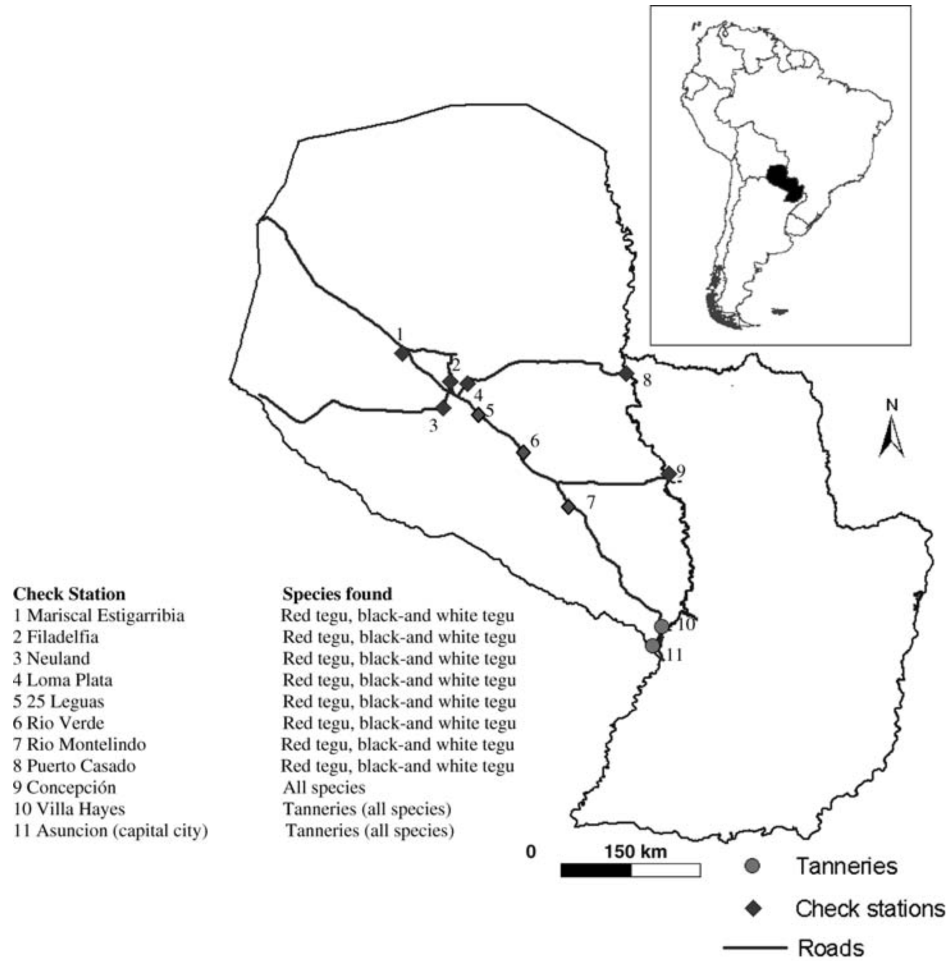

Figure 2. Map of Paraguay showing locations of check stations and tanneries where tegu lizards skins were measured monthly during the harvest season from 1991–1998.

1998. We selected locations of check stations because they formed a linear transect along the Trans-Chaco Highway that bisects the major skin-producing region of the country. We chose 2 other locations along the Paraguay River because we had prior knowledge that tegu skins were traded there.

At each check station, we counted, measured, and determined species and sex of all the tegu skins present. Actual capture locations of lizards were not available. During monthly visits to tanneries we measured a minimum of 300 skins from the thousands of skins present, being careful not to use the same samples on subsequent visits. We determined species based on color and scale patterns. We identified males by the presence of enlarged scales in the cloacal region (Fitzgerald et al. 1991, 1999). We measured snout-to-vent length of dried skins (SVL_{dry}) from the most anterior sublabial scale to the cloacal fold, and we measured skin width at the midpoint of the longitudinal section. We recorded linear measurements to the nearest 1.0 mm.

Body Size Estimation

The length of stretched, dried skins is not the same as SVL measured from a fresh skin or an intact tegu specimen. To obtain a realistic measure of body size of harvested tegus, we quantified the relationship between SVL_{dry} and whole-animal SVL. Dried skins were soaked during the tanning process, so they regained their original shape and could not be distinguished from the skins of freshly harvested animals.

We conducted a measure and remeasure experiment to obtain a regression for estimating SVL of harvested tegu skins from Paraguay. We recorded SVL_{dry} and sex of 1,421 individually marked black-and-white tegu skins and 166 red tegu skins, and we repeated the measurements after the skins were soaked for 48 hours. We calculated regression equations for black-and-white tegus ($SVL_{est} = 95.19103 + 0.880308 \times SVL_{dry}$ [mm], $r^2 = 0.71$, $n = 1{,}421$) and red tegus ($SVL_{est} = 110.86804 + 0.853129 \times SVL_{dry}$ [mm], $r^2 = 0.77$, $n = 166$), and we used these equations to reconstitute the SVL (estimated snout-to-vent length or SVL_{est}) of harvested tegu lizards.

Analyses

We classified individual skins as adult or subadult based on SVL_{est}. Skins $\geq$350-mm SVL_{est} and $\geq$325-mm SVL_{est} corresponded to adults of red tegus and black-and-white tegus, respectively (Quintana 1991, Fitzgerald et al. 1993).

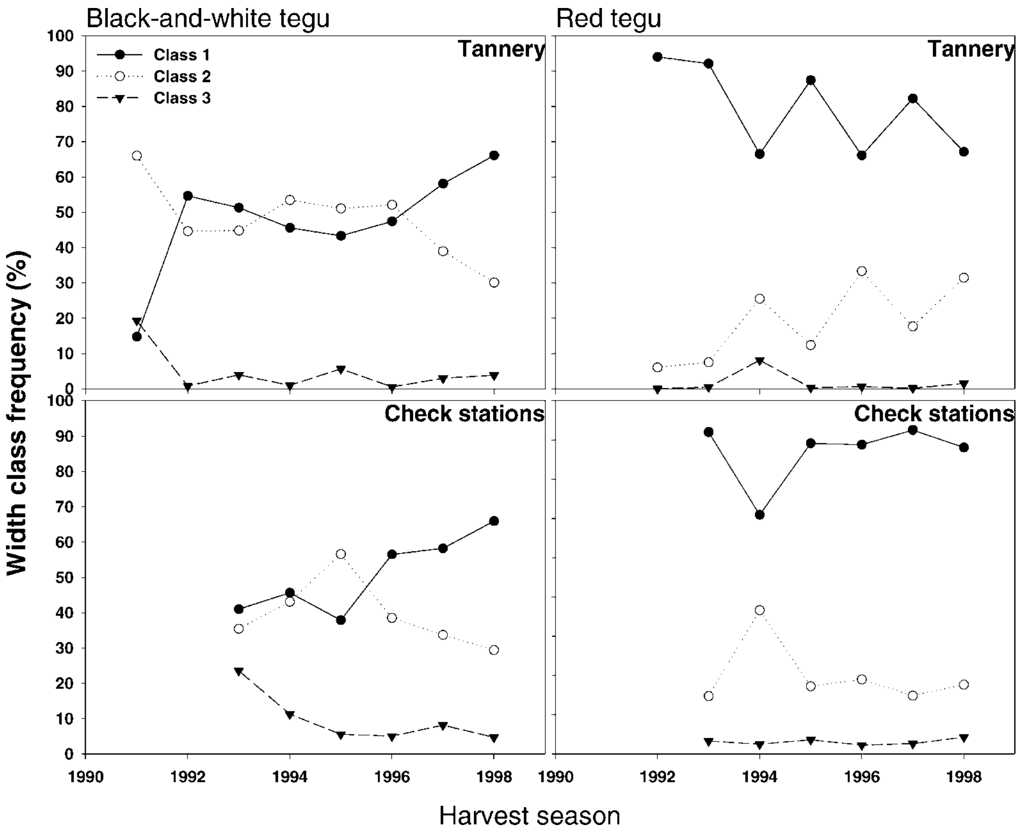

Figure 3. Proportions of width classes of black-and-white tegu and red tegu skins measured in tanneries and at check stations, Paraguay, 1991–1998.

We grouped skin width data according to standard industry width classes (i.e., class 1, class 2, class 3). To visualize trends in these data, we graphed frequencies of industry width classes for each species among years at check stations and tanneries. We did not report results of statistical hypothesis tests on width-class frequency data because contingency analyses conducted with our large sample sizes ($n > 25{,}000$) were of sufficient power to reject the null hypothesis in all cases, even when yearly differences in width-class frequencies were as small as 1%. Therefore, statistically significant results, in this case, did not add explanatory power to patterns of industry width-class differences through time.

We applied general linear models (2-factor and 3-factor ANOVA) to test the null hypotheses of no significant differences in mean size of males and females of each species among years and among check stations. For analysis of data from tanneries, we used separate 2-factor ANOVAs, with interaction (year and sex as factors), for each species to test the hypotheses that body size varied by year and sex. To test for size variation in tegu skins sampled in the field, we used 3-factor ANOVAs, with interaction (year, sex, and check station as factors), to test the hypotheses that body size varied by year, sex, and check station. We followed the ANOVAs with Tukey's post hoc tests to identify statistically distinguishable subsets of mean SVL_{est} among years for each sex and among check stations. We calculated sex ratios (M/F) for each species for all harvest years, and we used contingency analyses to test the null hypotheses that sex ratios did not differ from one among years and among check stations. We chose the alpha level 0.05 for rejecting the null hypotheses in all tests. We used statistical software (SAS [SAS Institute Inc., Cary, North Carolina] and SPSS [SPSS Inc., Chicago, Illinois]) for the statistical analyses.

Results

We measured 26,300 black-and-white tegu skins and 6,915 red tegu skins at tanneries, and we measured 7,335 black-and-white tegu skins and 6,157 red tegu skins at check stations. Black-and-white tegus represented 72% of the overall sample, while red tegus accounted for the remaining 28%. We found 165 *T. duseni* skins in tanneries and 29 skins at the Concepción check station in 1994. In 1995, we found 4 *T. duseni* skins in tanneries and 9 at Concepción. After 1996, numbers of *T. duseni* skins remained low, and every skin of *T. duseni* found in tanneries or check stations was confiscated. We did not include data from *T. duseni* skins in statistical analyses.

We found red tegus and black-and-white tegus at all check stations (Fig. 2). We found red tegu skins primarily at 6 check stations: Filadelfia, Loma Plata, Mariscal Estigarribia, Neuland, 25 Leguas, and Montelindo. We found black-and-white tegu skins in the largest numbers only at 4 check stations: Concepción, Puerto Casado, Montelindo, and Rio Verde.

Trends in Width Classes

The proportion of class 1 black-and-white tegu skins in tanneries increased substantially from 14.7% in 1991 to 66.1% in 1998. The trend in width class 2 skins was the inverse of class 1, not surprising as classes 1 and 2 combined made up 99.5% of all skins in tanneries. Width class 3 skins decreased from 19.3% in 1991 to 3.8% in 1998 (Fig. 3). At check stations, skins of black-and-white tegus in width class 1 increased from 41% in 1993 to 65.9% in 1998. Width class 2 skins increased from 35.5% in 1993, and then decreased to 29.4% in 1998. Width class 3 skins decreased from 23.6% in 1993 to 4.7% in 1998 (Fig. 3).

Red tegu skins in width class 1 in tanneries decreased from 1992 to 1994 then fluctuated yearly between 70% and 90%. Class 2 skins of red tegus showed an inverse pattern to class 1, fluctuating in the opposite pattern from class 1. We also expected this because classes 1 and 2 comprised more than 95% of the red tegu harvest in all years except 1994. Class 3 skins remained relatively stable throughout the years for red tegus in both tannery and check station samples (Fig. 3). At check stations, the proportion of red tegu skins in class 1 remained relatively stable throughout the years ranging from 82% in 1993 to 78.1% in 1998. The proportion of skins in class 2 was also stable at check stations (Fig. 3).

Annual Variation in Body Size

Size variation at tanneries.—The monitoring data reflected known differences between the species and patterns of sexual size dimorphism. Red tegus were larger on average (F: $\bar{x}$ $SVL_{est} = 400.7$, SD = 35.36; M: $\bar{x}$ $SVL_{est} = 455.7$, SD = 52.28), than black-and-white tegus (F: $\bar{x}$ $SVL_{est} = 351.0$, SD = 29.69; M: $\bar{x}$ $SVL_{est} = 384.9$, SD = 39.82; Table 1).

Mean SVL_{est} of adult black-and-white tegu males and females measured at tanneries was significantly different among years and by sex (2-factor ANOVA $F_{15,1} = 293.01$, $P < 0.0001$). There was a statistically significant interaction between year and sex ($F_{7,1} = 13.28$, $P < 0.0001$) indicating that part of the variation in body size among years was also due to size differences among sex during the time period. Mean SVL_{est} of adult black-and-white tegus was smallest in 1995 and 1994 and largest in 1997. Although Tukey's post hoc tests identified 6 groups of distinct subsets ($P < 0.05$), there was no apparent temporal trend in the mean size of black-and-white tegu skins (Fig. 4). Mean SVL_{est} of subadult black-and-white tegu males and females measured at tanneries also differed among years and by sex (2-factor ANOVA $F_{15,1} = 293.01$, $P < 0.0001$). There was no statistically significant interaction between year and sex ($P = 0.553$) in this analysis of subadults, because sexual size dimorphism was not manifested in subadult animals. Again, Tukey's post hoc tests grouped 3 sets of years as significantly distinct subsets ($P < 0.05$) without any chronological pattern in mean size (Fig. 4).

Mean SVL_{est} of adult red tegu males and females measured at tanneries was also statistically significant among years and by sex (2-factor ANOVA $F_{13,1} = 149.59$, $P < 0.0001$). Tukey's post hoc tests grouped different years as distinct subsets ($P < 0.05$). Mean SVL_{est} of adult red tegus was smallest in 1992 and largest in 1995 and 1997. Adult size of red tegus in tanneries oscillated by 20 mm between years (about 4.4% of overall $\bar{x}$ SVL_{est}) for no obvious reason (Fig. 4). There was a statistical interaction between year and sex ($P < 0.0001$), indicating that part of the variation among years was due to changes in sex-based size variation. Differences in mean SVL_{est} of subadult red tegu males and females measured in tanneries were also significant among years and by sex ($F_{13,1} = 3.15$, $P < 0.0001$). As in black-and-white tegus, there was no significant interaction between year and sex for subadult red tegus ($P = 0.178$). Mean SVL_{est} of subadult red tegus in tanneries remained stable through time (Fig. 4).

Size variation at check stations.—We rejected the null hypotheses that mean SVL_{est} of adult black-and-white tegus at check stations was similar among years, among check stations, and by sex according to a 3-factor ANOVA (3-factor ANOVA $F_{33,1} = 47.53$, $P < 0.0001$; Table 2). There was significant interaction between year and check station ($F_{8,3} = 4.21$, $P < 0.0001$), indicating some of the variation among years was also due to variation in body size at check stations. There was no interaction between year and sex ($F_{5,1} = 0.69$, $P > 0.634$) nor between check station and sex ($F_{3,1} = 0.11$, $P > 0.953$), indicating sex-based size differences did not contribute to the annual pattern of variation in size among check stations. Tukey's post hoc tests grouped different years as distinct subsets ($P < 0.05$) with no clear chronological pattern (Fig. 4). Tukey's post hoc tests also grouped check stations into distinct subsets. Mean SVL_{est} of adult black-and-white tegus was smallest and similar at Rio Verde, Concepción, and Casado ($P > 0.05$), and largest in Montelindo (Table 2).

The SVL_{est} of subadult black-and-white tegus at check stations also varied significantly by year (3-factor ANOVA $F_{27,1} = 1.69$, $P = 0.016$). The large dataset provided sufficient power for Tukey's post hoc tests to detect 2 statistically similar ($P > 0.05$), but overlapping subsets of yearly mean SVL_{est} (Table 2). There were no statistically significant interactions between year and check station ($F_{5,1} = 0.31$, $P = 0.93$), year and sex ($F_{5,1} = 1.46$, $P = 0.20$), or check station and sex ($F_{3,1} = 0.60$, $P = 0.62$; Table 2). Mean SVL_{est} of subadult black-and-white tegus remained stable through time (Fig. 4).

Mean body size of adult red tegus varied among years, among check stations and by sex (3-factor ANOVA $F_{84,1} = 26.63$, $P < 0.0001$). Tukey's post hoc tests grouped different years as 3 distinct subsets ($P < 0.05$) with no clear chronological pattern (Fig. 4). There was a statistical interaction between year and check station ($F_{30,7} = 2.01$, $P = 0.001$), but not between year and sex ($F_{5,1} = 1.50$, $P = 0.186$) nor between check station and sex ($F_{7,1} = 1.05$, $P = 0.394$). Tukey's post hoc tests grouped different check stations into distinct subsets ($P < 0.05$). Mean SVL_{est} was smallest in Rio Verde and largest in Montelindo (Table 2).

The SVL_{est} of subadult red tegus measured at check stations showed no significant variation by year, by check station, or by sex (3-way ANOVA $F_{51,1} = 1.09$, $P = 0.33$;

Table 1. Mean size (estimated snout-to-vent length [SVL$_{est}$] in mm) of harvested black-and-white tegus and red tegus from check stations and tanneries in Paraguay measured from 1991–1998.

	Black-and-white tegu						Red tegu					
	F			M			F			M		
Site and yr	$\bar{x}$ SVL$_{est}$	*n*	SD	$\bar{x}$ SVL$_{est}$	*n*	SD	$\bar{x}$ SVL$_{est}$	*n*	SD	$\bar{x}$ SVL$_{est}$	*n*	SD
Tanneries combined	358.7	7,657	27.7	390.2	18,643	41.2	394.9	2290	38.7	451.9	4,625	57.6
1991	367.6	222	26.1	395.8	1,675	27.1						
1992	361.7	1,697	25.6	387.2	2,158	38.8	390.8	220	34.7	439.4	280	53.6
1993	359.7	757	27.5	388.7	1,154	39.5	406.6	246	34.6	463.5	410	50.8
1994	352.3	1,500	30.3	380.1	3,674	43.9	386.1	656	42.8	444.4	1,036	58.9
1995	355.6	1,611	26.7	380.4	2,669	38.1	406.8	191	36.8	462.6	507	49.5
1996	360.7	846	26.3	392.9	1,885	42.7	393.1	514	34.9	444.7	986	57.9
1997	362.3	246	25.8	407.2	1,479	44.3	405.7	158	39.1	467.9	562	52.5
1998	364.3	778	28.7	398.1	3,949	41.0	398.0	305	36.4	451.1	844	65.3
Check stations combined	351.0	2,017	29.6	384.9	5,317	39.8	400.7	1956	35.3	455.7	4,201	52.2
Casado												
1996	345.9	181	22.5	386.9	591	28.4	434.5	5	22.0	492.5	12	38.4
1997	336.8	86	21.6	371.6	246	39.0	409.5	1				
1998	351.5	70	24.5	386.5	456	37.5	430.7	1		424.4	6	55.8
Concepción												
1993	334.2	322	28.9	370.5	417	42.6	361.7	2	1.2	406.7	11	49.5
1994	343.3	261	26.9	373.5	819	40.3	395.3	12	31.9	463.5	24	55.7
1995	347.2	218	24.9	374.7	451	37.2	418.6	3	13.6	492.6	12	32.8
1996	360.6	201	26.9	393.9	560	32.2	428.3	17	31.2	469.9	63	43.4
1997	361.2	61	26.5	397.1	262	39.9				465.2	8	43.5
1998	366.2	46	23.4	401.6	196	40.4	460.7	2	8.4	473.3	11	44.9
Filadelfia												
1993				328.5	1		404.4	16	44.3	424.2	40	46.1
1994				330.2	1		394.1	56	30.4	447.2	105	51.5
1995							413.1	40	25.3	452.8	80	45.1
1996							414.5	56	31.2	469.2	137	46.6
1997				396.3	2	19.9	409.7	21	36.0	466.8	47	55.7
1998	435.9	1		437.9	5	34.9	402.2	57	36.1	455.2	180	49.3
Leguas												
1993	352.4	28	22.1	386.8	97	36.0	399.7	176	39.6	468.5	330	51.8
1994	362.4	2	49.1	390.7	9	45.8	388.1	47	44.2	439.5	82	64.4
1995	293.3	1		293.1	5	21.3	393.3	1		494.9	6	61.7
1996	339.9	1		369.7	10	43.7	399.8	13	31.9	446.9	44	54.2
1997	370.5	16	41.0	394.6	127	29.3	411.5	161	31.6	459.7	360	46.3
1998	395.4	6	43.2	397.5	7	46.5	406.9	98	35.5	465.7	254	49.1
Loma Plata												
1994				311.8	1		414.7	21	22.5	446.8	28	49.1
1995	375.8	7	34.1	383.8	15	34.0	396.2	80	39.3	469.3	103	43.6
1996	371.8	8	30.9	408.5	13	35.6	404.8	54	33.4	465.6	117	52.5
1997	345.9	4	26.3	358.5	13	30.0	397.7	34	29.3	454.5	84	54.2
1998	354.6	6	26.6	369.1	15	41.9	407.3	91	41.0	450.7	203	58.4
Mariscal Estigarribia												
1993				383.9	1		407.5	3	9.2	465.9	11	21.9
1994							390.3	83	31.1	441.5	167	50.6
1995							397.8	19	35.7	476.5	39	47.0
1996							398.7	19	15.6	448.5	37	57.0
1997							400.9	58	27.4	456.9	172	49.0
1998	371.6	1					392.4	98	29.8	452.0	199	53.1
Montelindo												
1995	353.7	6	15.6	362.7	7	48.8	419.8	9	28.5	496.7	47	40.3
1996	358.4	131	24.9	390.8	342	38.4	431.8	15	23.4	473.6	41	48.6
1997	368.1	46	21. 8	406.8	129	35.5	420.4	34	33.2	475.2	74	45.8
1998	379.4	24	27.1	411.6	128	30.0	429.4	13	30.9	486.5	32	50.7
Neuland												
1993							393.8	166	32.3	440.2	255	49.4
1994	389.2	1					379.7	29	36.1	435.5	27	56.3
1995							394.0	54	35.1	448.4	86	50.7
1996							397.3	56	26.6	440.7	150	42.6
1997							381.6	30	29.2	428.4	39	48.1
1998							399.2	153	35.2	453.4	399	52.8

Table 1. continued.

	Black-and-white tegu						Red tegu					
	F			M			F			M		
Site and yr	$\bar{x}$ SVL$_{est}$	*n*	SD	$\bar{x}$ SVL$_{est}$	*n*	SD	$\bar{x}$ SVL$_{est}$	*n*	SD	$\bar{x}$ SVL$_{est}$	*n*	SD
Rio Verde												
1994	318.9	6	24.4	344.1	7	46.2	385.1	5	70.6	432.8	3	113.8
1995	356.9	3	20.1	359.3	4	23.5	413.9	5	36.5	485.4	2	7.2
1996	357.1	33	33.9	392.9	33	45.9	379.9	20	44.3	416.9	25	67.0
1997	330.6	15	23.5	352.6	32	51.2	377.6	22	36.7	414.8	49	66.1

Table 2). Mean SVL$_{est}$ of subadult red tegus remained stable through time (Fig. 4).

Annual Variation in Sex Ratio

The sex ratio was consistently male biased for both species. The proportion of black-and-white tegu males in tanneries varied from 56% to 88.3% in different years, and sex ratio was significantly different among years (Table 3; $\chi^2 = 997.9$, df = 7, $P < 0.001$). Samples of black-and-white tegus at check stations were also male biased from 1993 to 1998 (Table 3), and there was a significant association between sex ratio and year ($\chi^2 = 224.0$, df = 5, $P < 0.001$).

A similar but less pronounced pattern of male bias was observed in red tegu sex ratios. There was a higher proportion of red tegu males in tanneries, ranging from 56.0% to 78.1% in different years (Table 3), and the association between sex ratio and year for red tegu in tannery samples was statistically significant ($\chi^2 = 131.52$, df = 5, $P <$ 0.05). At check stations, the proportion of male red tegus ranged from 63.3% to 71.5%, again with a statistically significant association between sex ratio and year ($\chi^2 = 33.9$, df = 5, $P < 0.05$; Table 3).

Discussion

Our study demonstrates that long-term harvest monitoring of tegu lizards was an effective means for obtaining demographic information about tegu populations that cannot be obtained with direct estimation methods over large geographic areas. Harvest monitoring for exploited squamates has only previously been reported in short-term studies (Fitzgerald et al. 1991, Shine et al. 1998, Fitzgerald and Painter 2000).

The presence of species at check stations did not correlate with their known geographical distributions. Black-and-white tegus were present at 4 check stations outside the species' range (Filadelfia, Loma Plata, Mariscal Estigarribia, and Neuland). Similarly, red tegus were present at 3 check stations outside their range (Concepción, Montelindo, and Casado). Both species are known to occur in sympatry only at Rio Verde and 25 Leguas (Fitzgerald et al. 1999). The occurrence of skins at check stations outside the distribution of the species was presumably due to the movement of skins by hunters and traders. The greater percentage of black-and-white tegus in the harvest can be attributed to the fact that black-and-white tegus have a much larger geographic distribution than red tegus (Presch 1973, Avila-Pires 1995). Black-and-white tegus occur in approximately two-thirds of Paraguay, whereas red tegus occur in the relatively unpopulated semi-arid Chaco.

Variation in Width Classes

The decrease in number of small (i.e., class 3) skins during the monitoring period indicated compliance with the policy to ban small skins from commerce. However, there was a higher proportion of class 3 skins at check stations than in tanneries. Differences in the proportions of width classes in tanneries and at check stations may be explained by 2 reasons. First, the ban on small skins may be less effective in the field compared to tanneries. It is possible that hunters collected small tegus and succeeded in trading them at check stations, but the same skins were refused farther up the trade chain. The disappearance of class 3 skins was not intuitive because a seller would lose money if small skins were simply discarded. Trading small skins outside the Paraguayan market was also unlikely. Small skins have only 1/4 the value of large skins, and there was no evidence that large skins, much less small ones, were being smuggled.

The second, more likely, explanation of the disparity in class 3 skins at check stations and in tanneries is that some class 3 skins were restretched by middlemen and sold to tanneries as class 2 skins. In fact, we observed that middlemen frequently restretched small skins to increase their width into the next size class (i.e., class 3 skins into class 2 and class 2 skins into class 1). Middlemen softened skins with soap and then restretched them. Our datasets are consistent with the idea that class 3 skins at check stations were restretched. In particular, the proportions of class 1, 2, and 3 skins of black-and white tegus at check stations did not match the proportions sampled in tanneries. We should expect the disparity to be greater in black-and-white tegu samples than in red tegu samples because red tegu is the larger of the two species, its skins were larger on average, and there were naturally fewer class 3 skins of red tegus. There would be no incentive to restretch red tegu skins that were already in the most valuable size category. Indeed, there were almost no class 3 red tegus skins in tanneries, and there were <5% at check stations (Fig. 3).

The practice of restretching skins results in several negative management implications. By restretching skins, middlemen essentially fool traders into paying high prices for small skins, take economic advantage of hunters by confusing the width standards, and damage the resource in

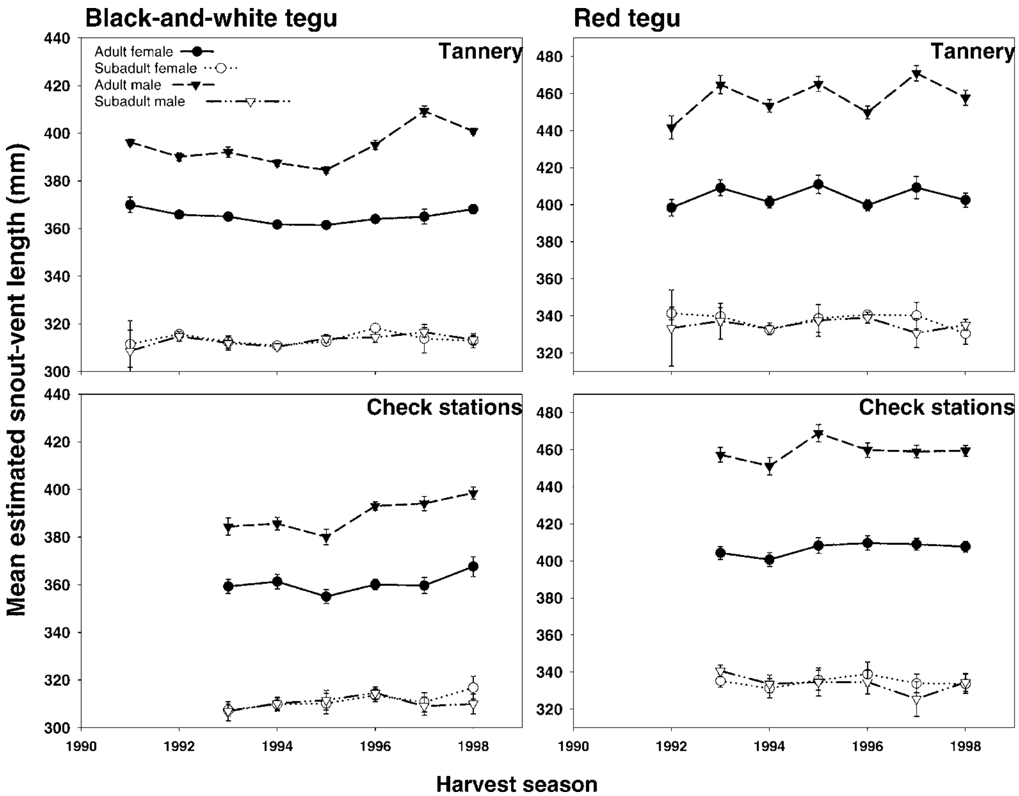

Figure 4. Mean estimated snout-vent length (SVL_{est}) of adult and subadult black-and-white tegus and red tegus for both sexes in tanneries and at check stations. Vertical bars indicate ±1 SE.

the process. The practice of restretching does not help remove hunting pressure from small animals, so long as middlemen continue to buy small skins from hunters. As explained by a professional tanner, restretched skins are often severely damaged during tanning because they are thin and weakened. Damaged skins are discarded and have no export value. Because the current management model and quota depends on monitoring the international export trade according to CITES regulations, discarded skins do not figure into the export quota. This is a problem because it creates a disparity between the actual number of tegus harvested and the number of skins exported. Most wildlife management systems include policies designed to avoid needless waste of the natural resource, and future work on the tegu trade system should be aimed at reducing the problems caused by restretching skins.

The increase in class 1 skins, especially in the case of black-and-white tegu, could be related to low demand for tegu lizard skins in the international market for exotic leather for the period 1996–1999 (Fig. 1). We hypothesize that lower prices during periods of less demand may have caused middlemen to concentrate on buying large skins.

Variation in Sex Ratios

Lizards are tracked to burrows where they are excavated, and it is not possible for hunters to know the sex of the lizard (Fitzgerald et al. 1991). The consistently male-biased sex ratio of harvested tegus was presumably because males were more vulnerable than females to hunters. Male tegus exhibit elevated activity during the breeding season and leave scent marks when they are courting females. Dogs track lizards by their scent; therefore it is logical that they may be more likely to find males (Fitzgerald 1994*a*). Similar male-biased sex ratios are commonly observed in collections of squamates, included other harvested species (Shine et al. 1996, Fitzgerald and Painter 2000).

The most strongly biased sex ratios (M/F) were 6.0 and 5.1 in 1997 and 1998, respectively. The international trade in tegu skins was also low in the same years (Fig. 1), and we observed the largest average sizes in the harvest at the same time. It is plausible that because of low demand and low prices for skins, buyers selected large skins for the trade. Because males are larger than females, selective trading of large skins should result in an increase of male lizards in the harvest.

Variation in Body Size

Although statistically significant, it was difficult to explain interannual variation in body size of harvested tegus in terms of how tegu hunting may be affecting population structure of the lizards. There was no apparent chronological pattern of size increase or decrease, except for a 20 mm increase in male black-and-white tegu skins from 1996 to 1998. Although we did observe a pattern of yearly fluctuations in body size of the red tegu in tanneries only, we did not observe similar patterns in samples from check stations, nor did we observe patterns in any of the data for the black-and-white tegu. We were careful to randomize our samples from

Table 2. Results of 3-factor ANOVAs by year, sex, and check station for adults and subadult black-and-white and red tegus in Paraguay, 1991–1998.

Source	df	Mean square	*F*	*P*	Multiple comparisons[a]										
					Check stations							Yr			
Adult black-and-white tegus															
Overall corrected model	33	46,336.94	47.52	0.000											
Yr	5	16,309.99	16.73	0.000	Rio Verde	A						1995	A		
Check station	3	26,713.97	27.4	0.000	Concepción	A						1993	A		
Sex	1	90,318.31	92.63	0.000	Casado	A						1994	A		
Yr × check station	8	4,103.90	4.21	0.000	Montelindo		B					1996		B	
Yr × sex	5	669.09	0.69	0.634								1997		B	
Check station × sex	3	109.23	0.12	0.953								1998			C
Error	5691	975.01													
Subadult black-and-white tegus															
Overall corrected model	27	287.41	1.70	0.016											
Yr	5	434.53	2.57	0.026	Rio Verde	A						1993	A		
Check station	3	257.77	1.52	0.207	Concepción	A						1997	A	B	
Sex	1	152.88	0.90	0.342	Casado	A	B					1994	A	B	
Yr × check station	6	52.33	0.31	0.932	Montelindo		B					1998	A	B	
Yr × sex	5	247.60	1.46	0.200								1995		B	
Check station × sex	3	101.49	0.60	0.615								1996		B	
Error	653	108.35													
Adult red tegus															
Overall corrected model	84	48,772.87	26.63	0.000											
Yr	5	6,942.28	3.79	0.002	Rio Verde	A						1994	A		
Check station	7	17,332.36	9.46	0.000	Neuland		B					1993	A	B	
Sex	1	59,0541.61	322.46	0.000	Mariscal Estigarribia		B	C				1997		B	C
Yr × check station	30	3,863.69	2.01	0.001	Filadelfia		B	C	D			1996		B	C
Yr × sex	5	2,750.93	1.50	0.186	Loma Plata			C	D			1998			C
Check station × sex	7	1,921.13	1.05	0.394	25 Leguas				D	E		1995			C
Error	5,767	1,831.35			Concepción					E					
					Montelindo						F				
Subadult red tegus															
Overall corrected model	51	191.51	1.09	0.330											
Yr	5	219.880	1.25	0.286	Rio Verde	A						1994	A		
Check station	6	406.107	2.31	0.035	Concepción	A						1993	A		
Sex	1	2.543	0.01	0.904	Mariscal Estigarribia	A						1995	A		
Yr × check station	18	112.889	0.64	0.864	Loma Plata	A						1998	A		
Yr × sex	5	112.208	0.64	0.671	25 Leguas	A						1997	A		
Check station × sex	5	184.290	1.05	0.390	Neuland	A						1996	A		
Error					Filadelfia	A									

[a] Multiple comparisons show significantly distinct subsets according to Tukey's tests ($P < 0.05$).

tanneries, so we have no basis for interpreting the pattern. The magnitude of all changes in size we observed was small in relation to the adult body size of tegus at sexual maturity (325 mm SVL for black-and-white tegus, 350 mm SVL for red tegus), and there was no consistent temporal pattern of increasing and decreasing size throughout the study. Therefore, we suggest that the effects of hunting did not readily explain size variation in the hunted tegus.

We suggest size variation among check stations was attributable to natural geographic variation. Geographic variation in size and sexual dimorphism is common in lizards and snakes, and we were not surprised to find such variation among the harvested tegu samples (Michaud and Echternacht 1995, McCoy et al. 1997, Fitzgerald and Painter 2000). However, our analyses also revealed statistically significant interactions between check stations and year for body size variation, indicating that important variation in skin size was due to patterns of temporal variation in body size among check stations. Hence it appears that geographic variation in body size does not always vary the same through time at different places. This realization is important because it implies that monitoring systems for tegu lizards, and probably all squamates, should rely on site-specific datasets to disentangle natural geographic variation in demography from demographic effects due to hunting.

Movement of skins by hunters would not cause the observed size variation among check stations. Although we know that middlemen and hunters transported some skins, there was no evidence that large or small skins were preferentially transported. There were no differences in skin prices among check stations that would create an incentive to transport either large or small skins. Hence, movement of skins by hunters or middlemen would actually work to randomize the patterns of geographic variation that we observed.

The patterns of body size variation were complex and probably caused by many factors. It is important to note that

Table 3. Sex ratios of black-and-white tegu and red tegu samples from tanneries and 9 check stations, from 1991 to 1998.

Site and yr	Black-and-white tegu n	Black-and-white tegu Sex ratio (M/F)	Red tegu n	Red tegu Sex ratio (M/F)
Tanneries				
1991	1,897	7.6		
1992	3,855	1.3	500	1.3
1993	1,911	1.5	656	1.7
1994	5,174	2.5	1,692	1.6
1995	4,280	1.7	698	2.7
1996	2,731	2.2	1,500	1.9
1997	1,725	6.0	720	3.6
1998	4,727	5.1	1,149	2.8
Casado				
1996	772	3.3	17	2.4
1997	332	2.9	1	
1998	526	6.5	7	6
Concepción				
1993	739	1.3	13	5.5
1994	1,080	3.1	36	2
1995	669	2.1	15	4
1996	760	2.8	80	3.7
1997	323	4.3	8	—
1998	242	4.3	13	5.5
Filadelfia				
1993	1		56	2.5
1994	1		161	1.9
1995			120	2
1996			193	2.5
1997	2		68	2.2
1998	6		237	3.2
Leguas				
1993	125	3.5	506	1.9
1994	11	4.5	129	1.7
1995	6	5	7	6
1996	11	10	57	3.4
1997	143	7.9	521	2.2
1998	13	1.2	352	2.6
Loma Plata				
1994	1		49	1.3
1995	22	2.1	183	1.3
1996	21	1.6	171	2.2
1997	17	3.3	118	2.5
1998	21	2.5	294	2.2
Mariscal Estigarribia				
1993	1		14	3.7
1994			250	2.0
1995			58	2.1
1996			56	1.9
1997			230	2.9
1998	1		297	2.0
Montelindo				
1995	13	1.2	56	5.2
1996	473	2.6	56	2.7
1997	175	2.8	108	2.2
1998	152	5.3	45	2.5
Neuland				
1993			421	1.5
1994	1		56	1.1
1995			140	1.6
1996			206	2.7
1997			69	1.3
1998			553	2.6
Rio Verde				
1994	13	1.2	8	0.6
1995	7	1.3	7	0.4
1996	82	1.5	45	1.3
1997	47	2.1	71	2.2

although statistically significant, changes in mean body size were relatively small in relation to the average body size of adult lizards. The observed yearly changes of 20–40 mm for these lizards that averaged >350 mm SVL probably would not result in measurable changes in demographic processes such as reproductive output or adult survival. Natural fluctuations in body size may be related to unpredictable variation in resources used by tegus. It is known, for example, that growth and reproduction in lizards may be affected by resource abundance. Ballinger (1977) found reproductive output in *Urosaurus ornatus* decreased during years of low precipitation that, in turn, reduced food abundance. Interestingly, natural stochastic population fluctuations may easily mask effects of hunting on demography and population growth. For species with life histories that are characterized by high rates of young-of-the-year mortality (e.g., tegus) and females that do not reproduce every year, relatively small amounts of random variation in annual reproductive output results in stochastic population fluctuations that make it difficult to detect changes in population growth due to hunting (Fitzgerald 1994*b*).

Tegu lizards have been harvested according to demand for several decades and there is no evidence of persistent population decline wherever habitat remains (Fitzgerald et al. 1991). Considering the worldwide trade in skins decreased during the monitoring period due to less demand (Fig. 1; Fitzgerald 1994*a*), the harvest monitoring results indicate the tegu population in Paraguay was probably not declining due to hunting. Black-and-white tegus and red tegus possess a life history that makes them resilient to overharvest, characterized by relatively large clutch sizes, onset of maturity in 3 to 4 years, and a lifespan of 10 years or more (Fitzgerald 1994*a*). Tegu lizards occur in almost all habitats throughout their geographic distribution, and vast areas of the country where both species occur are not hunted.

Although encouraging, the overall pattern of the tegu harvest in Paraguay does not mean the tegu trade is automatically sustainable. Since the beginning of the management program in 1991, the export quotas of 300,000 or 350,000 have been well within the international demand for Paraguayan tegu skins during most years. However in 1994, demand exceeded the quota of 350,000 skins and the Paraguayan government allowed 412,636 skins to be exported (Mieres 2002). Therefore, it is unclear whether the management program could deal with situations where demand for skins exceeds the established quota during sustained periods. Peaks in demand for tegu skins, such as in 1981, 1989, and 1993 have been short lived (Fig. 1), and it is unclear how tegu populations might respond to extended periods of high demand, particularly if quotas were not respected.

Management Implications

The overarching recommendations for management that emerge from our study are: 1) that harvest monitoring continues, and 2) a call to implement a system to quantify hunter effort. Demographic characteristics of harvested animals through time can be used to help determine population trends (Getz and Haight 1989), and we made great strides toward understanding effects of harvest on exploited tegu lizards at regional scales. Unfortunately, corresponding quantitative information on hunting effort that could be linked to changes in tegu population structure is lacking. Gathering this information should be a top management priority. Very long-term datasets and detailed information on growth, resource availability, and hunting patterns would be required to disentangle sources of variation in temporal patterns of body size in tegu lizards. The monitoring program will remain limited until information on the number of hunters and variation in hunter success is available. Norman (1987) reported an average of 15 skins per hunter per year, but his sample was for only 1 year and there was considerable variation around the mean. Hunter effort fluctuated with demand for western diamondback rattlesnakes and the distribution of rattlesnakes/hunter was skewed (Fitzgerald and Painter 2000). Because the life history of tegu lizards is similar to that of western diamondback rattlesnakes, we suggest similar patterns would hold for tegu lizards. Catch-per-unit-effort data are a basic requirement for most harvest models (Hilborn and Walters 1992), and it is critical that such data be incorporated into harvest models for exploited lizards.

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