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Waiting reveals waning weight: Monitoring over 54 years shows a decline in body condition of a long-lived reptile (tuatara, *Sphenodon punctatus*)

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ABSTRACT

Knowledge gained from monitoring has been the basis for many critical decisions in threatened and endangered species and ecosystem management. Long-term monitoring has been recognized as a necessity for elucidating population trends and community interactions, particularly for long-lived species or ecosystems with slow rates of change. We examine seasonal and annual cycles of morphological changes in a threatened, long-lived, insular reptile, the tuatara (*Sphenodon punctatus*), on Stephens Island, New Zealand. We used body condition indices as a surrogate measure of fitness, and examined seasonal fluctuations, using data from an intensive mark-recapture study, and long-term trends using a dataset that spans 54 years. In spite of seasonal and annual fluctuations, body condition of tuatara has declined significantly between 1949 and 2003; the decline was only evident after >22 years of monitoring. We hypothesize that increasing numbers of tuatara have resulted in a density-dependent population response driven by past habitat modification on Stephens Island. We emphasize the need for long-term monitoring and suggest that potentially costly management decisions, particularly for long-lived species or ecosystems with slow rates of change, should not be based solely on short-term monitoring.

1. Introduction

Many researchers have recognized the value of long-term ecosystem monitoring (Blossey, 1999; Yoccoz et al., 2001), as only long-term data are sufficient to examine annual variation in population parameters and the influence of infrequent events or cyclic phenomena (Tinkle, 1979; Williamson, 1990; Wooller et al., 1992). Only long-term monitoring can provide the baseline data necessary to assess whether species declines are real or due to some natural phenomenon (Blaustein et al., 1994). Long-term datasets are especially important when the rates of change in a system are slow (e.g., long generation time). In the absence of these datasets, research is limited to short-term data that may only resolve fine-scale patterns without any indication of the underlying ecological mechanism (e.g., climate change, Dunn and Winkler, 1999; Connell and Green, 2000; Walther et al., 2002; Chamaille-Jammes et al., 2006).

Long-term monitoring has been recognized as a necessity, but it is often limited by feasibility and funding. Managers frequently need to make critical decisions based on the information that is available, and for minimizing cost and effort monitoring often needs to encompass the shortest time scale that is still biologically relevant (i.e., that accurately reflects the current biological state of the population or ecosystem, Chapman et al., 2000). Long-term trends may not be evident

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or may be misinterpreted if monitoring duration is insufficient (Madsen and Shine, 2001; Thomas et al., 2002), which could result in inappropriate, costly management decisions. Initial monitoring may reveal population trends that are manifested as individual morphological changes (Adler and Levins, 1994; for short-lived species), which would ultimately affect population dynamics.

So how long does a population need to be monitored before trends become evident and appropriate management decisions can be made? We address this question by investigating the seasonal and annual cycles of morphological changes in one population of a threatened, long-lived, insular reptile, the tuatara (*Sphenodon punctatus*). We use intensive mark-recapture data and a dataset spanning 54 years, to interpret body condition responses with respect to climate, reproduction, habitat modification, and monitoring duration.

Tuatara are medium-sized reptiles and the sole extant representatives of the Order Sphenodontia (Benton, 2000). Endemic to New Zealand, they were once widespread throughout the main and outlying islands (Holdaway and Worthy, 1997), but by the early 19th Century, these long-lived reptiles (maximum recorded longevity is 91 years, N.J.N., personal communication) were extirpated on the two main islands, presumably as a result of habitat modification and introduction of rodents (*Rattus exulans*) by human settlers (~750 ya; Anderson, 1996). Much of the habitat on the approximately 30 offshore islands on which tuatara naturally remain has been heavily modified.

Over half of extant tuatara (~30–50,000 individuals) inhabit Stephens Island (known also by its Māori name, Takapourewa; Marlborough Sounds, 40°40′S, 174°00′E), which has been the focus of scientific research since 1949 (Dawbin, 1962, 1982a,b) and is the source island for two translocated populations (Nelson et al., 2002; N.J.N. unpublished data). The 150 ha island supports a lighthouse and has a history of intensive habitat modification. By the mid-1920s, following constant human presence by permanent lighthouse keepers, an estimated 80% of the island's forested habitat had been cleared for farming and speculation was raised over the small number of tuatara remaining after intensive collection for museum specimens (Brown, 2000). Cleared paddocks had been maintained on the island until removal of livestock in 2004, with little natural revegetation since the initial deforestation. Although reforestation efforts have been ongoing, remnant coastal forest now covers less than 15% of the island (Hare and Cree, 2005), and in forest remnants, the average density of tuatara is about 2015 per hectare, which is five times greater than in the artificial paddocks (Carmichael et al., 1989), and at least 20 times greater than on any other island where tuatara naturally occur (Cree and Butler, 1993).

In order to reveal demographic patterns and potential impacts to this biologically significant source population, we examine seasonal and long-term trends in body condition (a measure of mass relative to body size). Specifically, the following questions are addressed: (1) Are long-term trends or cycles in body condition evident, and do these vary between the sexes? (2) Does body condition of tuatara fluctuate seasonally, or with respect to sex or climate? (3) How many years of monitoring may be necessary to reveal significant long-term trends?

2. Materials and methods

2.1. *Long-term body condition trends*

Mark-recapture data were collected from Stephens Island tuatara from 25 separate years, spanning the period 1949–2003. In most sampling years, data were collected during multiple sampling trips, and the times of the sampling trips varied by year. Tuatara caught between 1949 and 1992 were given permanent individual marks by toe-clipping when first captured, and recaptures were recorded. After 1992 toe-clipping was no longer used to permanently mark individuals. During the 2003 trip, a unique number was written on the side of each animal with a permanent marker pen, which was legible for the duration of the sampling period only.

From 1983 to 1985, only females were captured, as mark-recapture data are derived from a nesting study (Newman et al., 1994). Therefore we removed these years from intersexual analyses but retained them for subsequent female-only analyses. Morphological measurements taken from captured tuatara included sex, snout to vent length (SVL; mm) and mass (g) (Table 1). The sex of each adult tuatara ($\geqslant 170$ mm SVL) was easily determined by examining secondary sexual characteristics, including crest development, spine shape, head size/shape, and shape of abdomen (Dawbin, 1982a; Cree et al., 1991).

We calculated body condition indices to assess trends in tuatara body condition. Body condition, which is often used as a surrogate measure of fitness, reflects an animal's storage and expenditure of energy, which can sometimes reveal the stresses or limitations affecting those individuals (Doughty and Shine, 1998; Moore et al., 2000; Schulte-Hostedde et al., 2001). Recent debate has raised cautions about generating false relationships between condition and other parameters correlated with body size (Green, 2001; Schulte-Hostedde et al., 2005). However, with proper testing of assumptions, body condition indices provide a powerful, non-destructive technique for examining body mass changes over time, while accounting for allometric growth (Bradshaw et al., 2000; Shine et al., 2001). We defined body condition as the residual values from a linear regression of log(mass) versus log(SVL), because it was the most appropriate for our dataset and meets the assumption of linearity ($r^2 = 0.95$).

Body condition indices were used to assess long-term intersexual trends in tuatara body condition by carrying out a repeated measures analysis of variance (ANOVA) with a linear mixed effects model. The dependent variable was body condition of tuatara. We included sampling period (year) and sex as dependent fixed effects, and individual as an independent random effect. We used Akaike's Information Criterion (AIC; Akaike, 1973; Burnham and Anderson, 1998) for statistical model selection. For these analyses, we used data from all years in which both males and females were caught.

Upon finding a significant effect of sex and time on tuatara body condition, we explored temporal trends in body condition for each sex. We constructed models for adult females and males separately, including data from all sampling years, to assess trends using linear mixed effects models which accounted for individual variability. Models compared were those in which body condition (1) remained constant over

Table 1 – Sample sizes (*N*), mean snout-vent length (SVL, mm), mass (g), and standard errors (SE) for all tuatara (*Sphenodon punctatus*) measured on 25 sampling trips to Stephens Island. Only females were sampled from 1983 to 1985

Year	Females					Males				
		Mean		Mean			Mean		Mean	
	N	SVL	SE	Mass	SE	N	SVL	SE	Mass	SE
1949	14	198	5	361	27	28	235	5	616	39
1950	29	205	3	332	17	82	244	3	596	23
1951	9	212	11	378	33	16	242	8	610	50
1953	37	197	3	314	7	51	235	5	554	32
1954	78	197	2	324	6	77	236	4	583	24
1955	6	211	10	376	10	23	242	7	573	45
1956	12	206	5	348	8	7	239	11	628	89
1957	19	219	8	475	7	29	230	7	558	48
1965	36	204	2	357	5	47	239	3	586	23
1968	21	204	3	351	5	34	249	3	622	20
1971	53	206	2	295	4	71	252	3	569	17
1972	72	201	2	283	5	53	243	3	536	21
1975	21	211	3	354	5	27	239	5	544	33
1976	14	203	4	311	6	18	232	6	472	41
1977	19	202	3	324	5	21	243	4	565	31
1978	5	207	7	295	4	16	235	9	485	51
1980	14	210	4	357	4	20	252	4	623	28
1983	127	201	1	330	4	–	–	–	–	–
1984	87	199	1	333	4	–	–	–	–	–
1985	112	199	1	294	5	–	–	–	–	–
1986	42	217	1	419	2	27	229	4	484	20
1987	165	204	1	305	4	8	231	12	473	60
1988	90	206	1	319	4	8	213	11	375	55
1992	62	199	2	292	4	25	240	6	555	33
2003	133	195	1	256	5	154	229	2	454	11

time, (2) fluctuated through time, and (3) showed a linear increase or decrease over time.

We further explored the long-term dataset (for both males and females) using the same analysis as above, in the following ways (1) all data exclusive of 1949 and 2003 (as these appeared to have a potentially strong influence on the trend), (2) only data from years that were sampled in the same month (to test for a seasonal sampling effect), and (3) all data in 10 year, 30 year, and multiple-year additive blocks (to assess the monitoring duration necessary to reveal consistently significant trends).

We obtained maximum yearly rainfall data for Stephens Island over the last 150 years (C. Allen, unpublished data). These data were analyzed using an ANOVA with a linear mixed effects model to determine whether rainfall has fluctuated significantly through time, or whether any linear trends are evident that may help to explain any patterns in tuatara body condition.

2.2. *Seasonal body condition trends*

Upon finding significant fluctuations in the long-term dataset we investigated potential seasonal cycles in body condition by recording morphological data from Stephens Island tuatara on four trips (November 2004, January, March, May 2005) in three study plots in Keepers Bush (an original forest remnant). The centers of the study plots were randomly located from an accessible track running through the bush. All tuatara within two circular plots 10 m in radius, and one 14 m radius were captured, and their locations in the plot were recorded. Repeated captures of these individuals were made in November 2004 (over seven days, seven nights; austral spring), January 2005 (four days, four nights; austral summer), March 2005 (four days, four nights), and May 2005 (five days, five nights; austral autumn). We marked each individual using a passive integrated transponder (PIT) tag (AVID, Folsom, Louisiana, USA). At each capture, SVL (mm), mass (g), and sex were recorded. These data were not included in the long-term analysis, as they were collected from a different sample of tuatara, and the body condition indices generated from this analysis are relative and not directly comparable to those generated from the long-term analysis.

To assess seasonal trends in tuatara body condition, we carried out a repeated measures ANOVA with a linear mixed effects model. Body condition of tuatara was the dependent variable. Trip, plot, and sex were dependent fixed effects, and individual was included as an independent random effect. Because juveniles were not sampled in all trips, and were only caught in very low numbers, we did not include them in this analysis. Models were screened based on AICs (Akaike, 1973; Burnham and Anderson, 1998), and we then rescaled the values to the lowest AIC, to give relative AIC values (ΔAIC). Those models with the lowest AIC values provide the best explanation of variance.

We used correlation tests with seasonal data to examine the relationship between body condition and (1) maximum monthly rainfall, (2) maximum monthly rainfall from one month prior to sampling month (to test whether there was a delayed response in condition), and (3) average monthly temperature. These climatic data were obtained for Stephens Island, and included maximum monthly rainfall (mm) and average monthly ambient temperature for the period October 04–June 05 (C. Allen, unpublished data).

All data sets satisfied the assumptions of normality and homogeneity of variances. Means are reported as mean ± 1 SE, and significance is assumed at $p < 0.05$. All analyses were carried out using the computer program *R* (www.rproject.org).

Table 2 – Results of linear mixed effects models of body condition index of tuatara (*Sphenodon punctatus*) from Stephens Island, including rescaled AIC (ΔAIC) and degrees of freedom (DF)

	ΔAIC	DF
Seasonal models		
Trip	0.00	6
Trip + sex	4.77	7
Trip + plot	14.65	8
Trip + plot + sex	19.13	9
Trip + sex + (trip * sex)	25.43	10
Trip + plot + (trip * plot)	39.62	12
Null	127.83	3
Sex	131.52	4
Plot	142.09	5
Long-term models		
Sex + year	0.00	25
Year	32.87	24
Sex + year + (sex * year)	115.85	46
Null	501.56	3
Sex	504.83	4

The model with the lowest ΔAIC best explains the variance in the seasonal and long-term dataset.

3. Results

3.1. *Long-term body condition trends*

From 1949 to 2003, there was a 105 g decrease in average female mass, with only a 2 mm decrease in average SVL. Males showed a 162 g decrease in average mass, with only a 6 mm decrease in average SVL (Table 1). Between 1949 and 2003 a total of 2508 captures were made of 1888 adult tuatara. The heaviest tuatara was an adult male captured in 1950, weighing 1020 g (SVL = 285 mm). Three other adult males weighing 1000 g were captured during this period (the same individual, in 1957, and two different individuals in 1954 and 1957; SVL = 270 and 280 mm respectively). By 2003 maximum mass of adult male tuatara had declined to 770 g (SVL = 267 mm). The heaviest female tuatara was captured in 1953 and weighed 690 g (SVL = 267 mm). A further 3 captures of females weighing ⩾550 g have been made, all in the period 1950–1956. By 2003 maximum mass for female tuatara was 480 g (SVL = 240 mm).

Both sex and year were significant main effects identified by AIC model selection (ΔAIC = 0.0, compared with a null model of ΔAIC = 501.6; Table 2). The next best model, where year is included as the single main effect, is a significantly poorer predictor of tuatara body condition (ΔAIC = 32.9). Adult male tuatara had higher body condition than adult females (males, mean = 0.02 ± 0.004; females, mean = −0.02 ± 0.004; Fig. 1). The lack of a significant interaction between year and sex (ΔAIC = 115.9) demonstrates that temporal variation in body condition is not sex-specific.

Body condition fluctuated significantly through time, compared with a model treating body condition as constant with respect to time (males $\chi^2_{13} = 250.1$, $p < 0.0001$; females $\chi^2_{13} = 490.5$, $p = 0.0001$; Fig. 1). Furthermore, from 1949 to 2003 body condition of both adult male and adult female tuatara declined significantly. A linear decline in condition fits

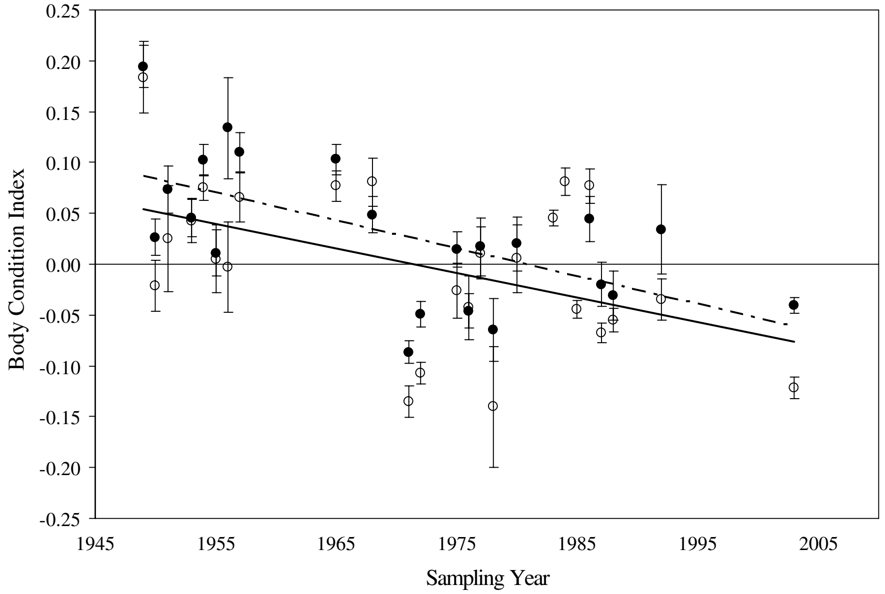

Fig. 1 – Long-term trend of body condition decline for male (●, - -, $r^2 = 0.37$) and female (○, –, $r^2 = 0.22$) tuatara (*Sphenodon punctatus*) from 1949 to 2003 on Stephens Island, New Zealand.

Table 3 – Results of linear mixed effects models of body condition of male and female tuatara of varying sampling periods using reduced datasets collected from Stephens Island over the period 1949–2003

Time span	Females		Males	
	t value	*p* value	*t* value	*p* value
10-year blocks				
1950–1960	−0.6	0.6	0.002	1.0
1960–1970	0.1	0.9	−3.5	0.004*
1970–1980	5.2	<0.0001*	3.0	0.02*
1980–1990	−7.4	<0.0001*	−0.6	0.7
1990–2000	−4.5	0.0026*	−3.0	0.1
30-year blocks				
1950–1980	−8.2	<0.0001*	−7.8	<0.0001*
1960–1990	−3.0	0.006*	−2.7	0.01*
1970–2000	−4.7	<0.0001*	1.0	0.3

Direction of *t*-values (positive or negative) indicates the direction of the linear trend over time, and asterisks indicate significance ($p < 0.05$).

the data better than a model where condition is constant over time in adult tuatara of both sexes (males $\chi^2_7 = 79.6$, $p < 0.0001$; females $\chi^2_7 = 67.8$, $p < 0.0001$; Fig. 1). The decline remained significant even when the analyzed dataset did not include data from 1949 and 2003 (indicating that these years did not disproportionately skew the results), and when the dataset only included years that were sampled in the same month (indicating no effect of sampling season).

A consistently significant decline in body condition only became evident after including >22 years of data (starting in 1949). When each decade of data was analyzed separately, no clear patterns were evident and results varied from significant linear increases (e.g., females 1970–1980, $t = 5.2$, $p < 0.001$) to periods with constant body condition indices (e.g., females 1950–1960, $t = -0.6$, $p = 0.58$; males 1980–1990, $t = -0.6$, $p = 0.7$) to significant linear declines (e.g., females 1980–1990, $t = -7.4$, $p < 0.0001$; males 1960–1970, $t = -3.5$, $p < 0.01$). Regardless of the starting date, datasets that included at least 30 years of data all revealed significant declines in body condition, with the exception of males from 1970 to 2000 (Table 3). Annual rainfall has remained relatively constant over time, and did not exhibit any significant linear trends ($F_{1,52} = 1.7$, $p = 0.2$).

3.2. *Seasonal body condition trends*

From the three study plots, we recorded 461 captures, from 201 individual tuatara (107 males, 87 females, 7 juveniles),

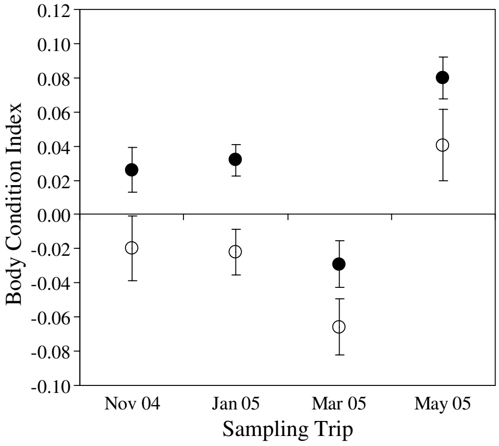

Fig. 2 – Mean seasonal body condition (±1 SE) of male (●) and female (○) tuatara (*Sphenodon punctatus*) sampled from four trips to Stephens Island.

over four trips between November 2004 and May 2005. Individual recaptures increased with time, and new captures decreased with time until they approached zero (Table 4). We found a significant positive relationship between body mass and SVL (linear regression, $r^2 = 0.95$, $P < 0.001$). Snout-vent length averaged 196.6 ± 0.9 mm (female) and 261.7 ± 3.7 mm (male), and mass averaged 231.8 ± 1.5 g (female) and 473.8 ± 9.0 g (male). Body condition was significantly higher in males (mean = 0.02 ± 0.009) than in females (mean = −0.03 ± 0.006) or juveniles (mean = −0.08 ± 0.006).

The univariate model including trip explained the greatest amount of variance in body condition (AIC = −929.1, ΔAIC = 0.0), followed by trip + sex (ΔAIC = 4.8; Table 2). However, because the trip + sex model is not within two AIC units of the best model, we did not consider it to be competitive with the top model (Burnham and Anderson, 1998). Body condition was significantly lower in March (mean = −0.06 ± 0.01; $p < 0.001$) and higher in May (mean = 0.06 ± 0.006) than at other times of the year (Fig. 2).

The warmest months during the sampling period were February 05 (mean temp = 18.0 °C), followed by March 05 (mean temp = 16.0 °C). There was no significant correlation between mean body condition and mean monthly temperature ($r = -0.6$, $p = 0.3$). The maximum rainfall was highest in May 05 with 136.1 mm, and lowest in April 05 with 4.1 mm. There was also no significant correlation between body condition and maximum monthly rainfall ($r = 0.4$, $p = 0.6$), or maximum monthly rainfall one month prior to the sampling month ($r = -0.2$, 0.8).

Table 4 – Frequency of new captures and recaptures, and mean body condition index of all tuatara (*Sphenodon punctatus*) sampled on four trips to Stephens Island (M = males, F = females, and J = juveniles)

Trip	New captures			Recaptures			Mean body condition index
	M	F	J	M	F	J	
November 04	62	38	2	0	0	0	0.009
January 05	34	39	0	41	34	0	0.002
March 05	7	7	3	48	48	1	−0.070
May 05	4	3	2	50	37	1	0.052

4. Discussion

Over the past 54 years, tuatara body condition has decreased significantly over time, with adult male tuatara having consistently higher body condition than adult females, although both sexes have declined at a similar rate. Body condition of both sexes of tuatara appears to fluctuate seasonally and is lowest in March (austral autumn).

The most obvious cause of a seasonal decline in body condition during the mating season (March) is from increased energetic costs of reproductive activity. Plasma levels of oestradiol in female tuatara from Stephens Island are highest in February - March, which is indicative of vitellogenesis (Cree et al., 1992). Furthermore, Cree et al. (1992) found a peak in testosterone of female and male tuatara, and a peak in corticosterone in males (Tyrrell and Cree, 1998) at this time. High testosterone levels are known to increase mobility and social contact of reptiles during mating (Wada, 1982; Ketterson and Nolan, 1992; Denardo and Sinervo, 1994). In tuatara, mite infestation (*Neotrombicula sphenodonti* and *N. naultini*, Acari: Trombiculidae, Goff et al., 1987) also peaks during the breeding season, and is evident by obvious orange patches on the skin that are absent at other times of the year (S. Godfrey, unpublished data; J.A.M., personal observation). Testosterone, in addition to increased physical contact, could therefore have a similar effect of lowered body condition and increased ectoparasite intensity of tuatara. Further research is needed to confirm this hypothesis and because our seasonal dataset is somewhat limited, our conclusions remain speculative.

Despite monthly and annual fluctuations, rainfall levels on Stephens Island have remained constant over the past 150 years, with no significant increases or decreases. A long-term decline in body condition was also found for neighboring North Brother Island tuatara, *S. guntheri* (an island which is very similar to Stephens in habitat modification history and geographic locale). After fully exploring potential climatic influences (including long-term cyclic events), Hoare et al. (2006) found no significant correlations between climate and body condition. Although there is no source of fresh water on Stephens Island, and the animals are highly dependent upon rainfall, because rainfall levels have remained steady over time it does not appear that climate changes are responsible for the body condition decline.

A more likely hypothesis is that the decline may be a density dependent response to resource competition from a steadily increasing number of tuatara. There is anecdotal evidence of intensive collection pressure on Stephens Island tuatara in the late 19th to early 20th centuries. This, coupled with the clearing of over 80% of the forest for farming (likely their preferred habitat, as evidenced by the much higher densities in the forest than in cleared areas; Carmichael et al., 1989) could have caused a temporary bottleneck in this population (Brown, 2000). With time, female tuatara took advantage of the clearings and moved into these areas to nest (females on forested islands naturally nest in open areas such as cliff edges and rocky outcrops with temperatures appropriate to support full egg development; Nelson et al., 2004). The resultant steady increase in nesting activity would have increased recruitment. With a population increasing and the existing adults potentially being displaced to forest remnants, where food is more abundant (Carmichael et al., 1989), food resources (including threatened invertebrates, e.g., Cook Strait giant weta, *Deinacrida rugosa*; Cook Strait click beetle, *Amychus granulatus*) may have been limited.

Tuatara, like many reptiles, may have high phenotypic plasticity (Dufty et al., 2002), allowing them to survive in conditions that other animals may not. Whereas density-dependence can cause decreased survivorship and population declines in, for instance, some mammals (Brown et al., 2001), long-lived reptiles may respond phenotypically (Sumner et al., 1999). In species of reptile that are long-lived, and have slow generation times (like tuatara) these changes may take years to manifest themselves in a population. We speculate that this population rebound is having negative morphological impacts on the individuals.

Adding further evidence to this hypothesis are the morphological responses that accompany newly translocated tuatara individuals (Nelson et al., 2002). Animals used for translocations have been sourced from Stephens Island, or neighboring North Brother Island. In all cases where tuatara have been moved to a new island, the translocated individuals show massive weight gain even after years of stable mass on the source island (averaging 41% mass increase for tuatara translocated from North Brother to Titi Island in 1993, Nelson et al., 2002; N.J.N., unpublished data). This provides strong evidence for competitive release, which, in addition to the very high densities, suggests that resources are limited on source islands. However, because pre-habitat modification morphological data are lacking, this hypothesis remains speculative.

When analyzing our dataset, the significant decline was only apparent after including at least 22 years of data. Ten year datasets revealed conflicting results, and in this species, these short-term datasets are most likely only encompassing natural fluctuations that may reflect food abundance or reproductive activity (e.g., female tuatara only nest on average, once every four years (Cree et al., 1992) and if there is any nesting synchrony there may be an associated population increase following a productive year). Significant body condition increases in earlier decades (e.g., 1970–1980) were apparently not sufficient to reverse the overall declining trend. The reverse may also be true for other populations or species. If a short term decline is severe enough, it may bring a population below the recovery point, thus having a major impact on the viability of that population.

Many studies are conducted within the span of a normal research grant (3–5 years), but this may only represent a minor blip on the evolutionary radar of a long-lived species (Likens, 1989; Madsen and Shine, 2001). Although in some cases short-term datasets are appropriate (e.g., to detect annual or seasonal fluctuations, or when declines are abrupt), it may be inappropriate to make drastic population level management decisions for long-lived species based on a five, 10 or even 15 year dataset. At least 30 years of sampling seems sufficient to reveal consistent trends in our dataset, and the results become more consistent with increasing monitoring. One anomaly, however, is the non-significant linear decline for male tuatara from 1970 to 2000. This could indicate that the decline in body condition of males in this population is stabilizing, and with current reforestation of Stephens Island, it is possible that this trend is beginning to reverse itself.

Numerous ecological studies revealing significant population trends have been based on 20–30 year datasets (Likens, 1989). This monitoring time span seems especially effective at detecting changes in (1) long-lived species with slow rates of change (generation times and/or recruitment events; Wooller et al., 1992; Connell and Green, 2000; Walther et al., 2002), (2) ecosystems subject to long-term or infrequent climatic events (Elliott et al., 1997; Visser et al., 1998; Dunn and Winkler, 1999; Hughes and Connell, 1999; Walther et al., 2002; Connell et al., 2004), (3) species or ecosystems that are slow to respond to disturbance (Westemeier et al., 1998; Chapman et al., 2000), and (4) newly created or restored ecosystems (Mitsch and Wilson, 1996).

In addition to detecting declines, a 25 year monitoring period has been sufficient to reveal population rebounds, even in long-lived species where it had been suggested that such rebounds would not be evident for 100+ years (Chaloupka, 2002). Balazs and Chaloupka (2004), Troeng and Rankin (2005), and most recently Antworth et al. (2006) have all been able to conclude with relative certainty that sea turtle nesting activity is increasing significantly, and that these once depleted populations are responding positively to conservation efforts that began in the 1970s. Likewise, Iverson et al. (2006) have detected a rapid recovery, from near extirpation, of Allen Cays Rock Iguana (*Cyclura cychlura inornata*) populations over the past 25 years, further concluding that these long-lived, insular lizards may now be nearing their carrying capacity.

In conclusion, our results, which reveal a long-term decline in morphological characteristics in spite of seasonal and annual fluctuations for the largest extant tuatara population, further emphasize the need for long-term monitoring (30+ years) when considering threatened and endangered species management. This decline may be a density dependent response to increases in tuatara numbers due to past habitat modification for this long-lived, insular species. At present, this biologically significant population is undoubtedly stable in numbers, albeit representing over half of the world's remaining tuatara. With ongoing reforestation of Stephens Island, we expect that with continued monitoring, a reversal of this decline will become evident in the future. We suggest that conservation management decisions, for this and other long-lived reptiles, should be based on the longest datasets possible, and caution should be used when prescribing conservation solutions based on short-term datasets (<15 years) alone.

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