



Not putting all their eggs in one basket: bet-hedging despite extraordinary annual reproductive output of desert tortoises

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Bet-hedging theory makes the counter-intuitive prediction that, if juvenile survival is low and unpredictable, organisms should consistently reduce short-term reproductive output to minimize the risk of reproductive failure in the long-term. We investigated the long-term reproductive output of an Agassiz's desert tortoise (*Gopherus agassizii*) population and conformance to a bet-hedging strategy of reproduction in an unpredictable but comparatively productive environment. Most females reproduced every year, even during periods of low precipitation and poor germination of food plants, and the mean percentage of reproducing females did not differ significantly on an annual basis. Although mean annual egg production (clutch size × clutch frequency) differed significantly among years, mean clutch size and mean clutch frequency remained relatively constant. During an El Niño year, mean annual egg production and mean annual clutch frequency were the highest ever reported for this species. Annual egg production was positively influenced by maternal body size but clutch size and clutch frequency were not. Our long-term results confirm earlier conclusions based on short-term research that desert tortoises have a bet-hedging strategy of producing small clutches almost every year. The risk of long-term reproductive failure is minimized in unpredictable environments, both through time by annually producing multiple small clutches over a long reproductive lifespan, even in years of low resource availability, and through space by depositing multiple annual clutches in different locations. The extraordinary annual reproductive output of this population appears to be the result of a typically high but unpredictable biomass of annual food plants at the site relative to tortoise habitat in dryer regions. Under the comparatively productive but unpredictable conditions, tortoises conform to predictions of a bet-hedging strategy of reproduction with relatively small but consistent clutch sizes. Published 2015. This article is a U.S. Government work and is in the public domain in the USA, *Biological Journal of the Linnean Society*, 2015, ●●, ●●–●●.

ADDITIONAL KEYWORDS: annual plant biomass – clutch size – clutch frequency – *Gopherus agassizii* – productivity – renewable energy – Sonoran Desert – turtle – wind energy – winter rainfall.

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INTRODUCTION

Reproductive output is a fundamental life-history trait that profoundly affects population stability and persistence (Cole, 1954; Stearns, 1976). Despite the importance of reproductive output, measured as brood or clutch size, wide variation in resource availability can cause similar fluctuations in the amount of energy available for oviparous organisms to allocate to reproduction in a given year (Congdon, 1989). If resource availability allows for increased reproductive output in oviparous species, theoretically, they can produce larger eggs, more eggs per clutch, more clutches or a combination of those attributes including more and larger eggs (Smith & Fretwell, 1974; Brockelman, 1975). Concomitantly, reduced resource availability can reduce reproductive output. Deserts are well known for the harsh conditions that they impose on organisms. The spatial and temporal unpredictability of rainfall (Noy-Meir, 1973) is but one hardship with which desert-dwelling animals must cope (Flesch & Steidl, 2006; Lovich *et al.*, 2014a). This backdrop of unpredictability can cause wide variation in resource availability in arid ecosystems. Under such variable conditions, smaller clutches should be favoured in long-lived organisms because they reduce the chance of total failure for a given bout of reproduction (Stearns, 1976).

Reproductive adaptations to unpredictable environments have been reviewed by Shine & Brown (2012). One pre-ovipositional strategy is for an organism to make a decision to reproduce in a given year or not. If resources are inadequate, it may be better to skip an opportunity to reproduce. Because reproduction for iteroparous organisms is not an ‘all or none’ situation, they can modify their allocation of annual available energy to reproduction among the competing demands for growth, development or storage (Stearns, 1976). It is also possible for organisms to alter the onset and termination of reproduction (Lovich *et al.*, 2012), although synchronization with resource availability may be all but impossible in unpredictable environments.

Life histories interact with the environment and resource availability in ways that allow for theoretical predictions about reproductive output (Stearns, 1976). For example, in environments with high and unpredictable juvenile survivorship, selection is predicted to favour increased longevity, iteroparity, late maturity, and a smaller reproductive effort with fewer young per brood but more broods (Stearns, 1976; Congdon, Dunham & Tinkle, 1982). This strategy has been referred to as a ‘bet-hedging’ approach and it maximizes the long-term probability of producing surviving offspring during otherwise unpredictable periods of high juvenile survivorship (Congdon *et al.*,

1982). Thus, reducing present reproductive output can lead to higher reproductive output over time (Venable, 2007).

Agassiz’s desert tortoise (*Gopherus agassizii*) is a model organism for studying the effects of spatial and temporal variation of resource availability on a species that produces small clutches of relatively large eggs with large yolk reserves (Morafka, 1994) and has life-history traits that are predicted under a bet-hedging strategy or tactic (Stearns, 1976; Congdon *et al.*, 1982). The long lives, iteroparous reproduction, low annual reproductive output, and production of multiple clutches seen in many turtle species, such as the desert tortoise, reduce the effect of low and unpredictable juvenile survivorship on the reproductive success of females (Cunnington & Brooks, 1996; Averill-Murray, Allison & Smith, 2014).

Absolute resource availability is an important proximate constraint on the energetics of desert reptiles (Congdon, 1989). One might expect that, as obligate herbivores (Ernst & Lovich, 2009), the energy available to desert tortoises for reproduction should be directly linked to the annual productivity of food plants and indirectly to the quantity and timing of winter rainfall as a strong determinant of annual plant production in the North American deserts (Beatley, 1974; Bowers, 2005). For example, during their 1980–1981 studies in Ivanpah Valley, California, Turner, Medica & Lyons (1984) observed lower clutch frequencies in 1981 and assumed that the phenomenon was related to lower winter rainfall and differences in the availability of food plants relative to 1980. However, later short-term studies, combining data from Ivanpah Valley and Goffs, California, demonstrated that desert tortoise annual egg production is not as dependent on rainfall or biomass of annual food plants as might be expected. Turner *et al.* (1986) found that desert tortoise mean clutch frequency varied little during five consecutive years at the two widely separated study sites, even when estimated dry biomass of annual food plants varied by over two orders of magnitude. Nevertheless, regression of clutch frequency on estimated dry biomass was significant, although Turner *et al.* (1986) acknowledged that data on clutch frequency from one of their two study sites were of ‘questionable quality’. They concluded that ‘The evidence presently available implies some role of winter rainfall in mediating egg production . . .’ in desert tortoises.

We studied the reproductive ecology of a population of *G. agassizii* at an operating wind energy facility near Palm Springs, California, for eight field seasons over 16 years of widely varying weather conditions (Lovich *et al.*, 2012) to collect data on annual variation in egg size, clutch size, clutch frequency, annual egg production, and annual reproductive frequency as

they relate to rainfall and annual plant biomass production. Assessing reproductive output and its relationship with fitness in the long-lived desert tortoise requires long-term studies that encompass both ‘good’ and ‘bad’ years (McCoy *et al.*, 2014). In the present study, we provide the first long-term perspective of the environmental determinates of reproductive output of this species, and a critical test of their dependence on rainfall and annual plant biomass for egg production over a period matching the mean time to maturity (14–15 years; Germano, 1994) and approaching one generation time (approximately 25 years) for long-lived tortoises (U.S. Fish and Wildlife Service, 1994; Edwards *et al.*, 2004). In addition, we re-evaluate the bet-hedging hypothesis posited for desert tortoise reproductive output in one of the most productive habitats occupied by *G. agassizii* (Lovich *et al.*, 2011a), albeit an industrial landscape developed for wind energy generation (Lovich & Daniels, 2000).

MATERIAL AND METHODS

STUDY SITE

The study site, known locally as ‘Mesa’, is located (33.95168°N, 116.667295°W, WGS84) at a wind energy generation facility in the southeastern foothills of the San Bernardino Mountains, Riverside County, California. The location is at the extreme western edge of the Sonoran Desert ecosystem where it interdigitates with elements of both Mojave and coastal plant communities (Lovich *et al.*, 2011a, b). Mesa is heavily impacted by anthropogenic structures associated with the facility including 460 turbines, a workshop and maintenance yard, electrical substations, transformers, culverts (Lovich *et al.*, 2011a), and an extensive network of unpaved roads that were established after the project was permitted in 1983. Few published wildlife studies are available for wind energy facilities (Lovich & Ennen, 2013). In addition, large portions of the site have been affected by fires during the period of study but with no demonstrable long-term effects on the annual reproductive output of the population (Lovich *et al.*, 2011b). More detailed site descriptions are provided in Lovich & Daniels (2000) and Lovich *et al.* (2011a, b).

Weather conditions varied greatly across years (Lovich *et al.*, 2012), including both drought and wetter El Niño conditions (Ennen, Meyer & Lovich, 2012a), the latter of which can trigger large germination events of annual plants (Bowers, 2005). Precipitation at the site is delivered primarily from Pacific frontal storms during the winter months (October to March). Summer rainfall is rare in the western Sonoran Desert. Estimated mean winter pre-

cipitation at Mesa from 1997–2013 using WestMap PRISM data (<http://www.cefa.dri.edu/Westmap/>) was 15.2 cm (range 2.9–44.1 cm). The wet and productive nature of our study site (Lovich *et al.*, 2011a) is a result of its proximity to the coastally-moderated climate of southern California. Winter precipitation at Mesa is more reliable, and received in substantially greater amounts, than at drier more typical tortoise habitats in interior desert locations such as Rock Valley, Nevada, where long-term data (Medica *et al.*, 2012) on mean winter precipitation are available for comparison (45-year mean = 10.7 cm).

FIELD TECHNIQUES

Over a 16-year period (1997–2013), we used X-radiography to monitor the reproductive output of adult female *G. agassizii* during eight reproductive seasons (April to July). Sample sizes in this analysis varied annually (Table 1) based on a total sample size of 22 individual females across years. Not all females were included every year because they could not be found in subsequent years, or because of funding limitations or mortality (with mortality being unrelated to our research) (Lovich *et al.*, 2011a). To facilitate serial recaptures of individuals within a given year, and in some cases among years, tortoises were fitted with radios that weighed approximately 50 g (model R1540; Advanced Telemetry Systems) or less than 2% of the weight of a typical adult female tortoise. Radios were affixed to tortoise carapaces using the technique described by Boarman *et al.* (1998).

Generally, females were located every 7–10 days and X-radiographed in the field (HF80; MinXray) from 1997–2010 using Rare Earth Cassettes (3M) and either Kodak or Imation film. In 2011, we used a MinXray, TR-80 generator connected to a fully digital Canon custom X-radiography system. The vast majority of exposures were taken in the field at a setting of 60 kV for 0.08–0.10 s at a focal distance of 69.6 cm. These settings expose females and eggs to very low levels of radiation (Hinton *et al.*, 1997). We used X-radiography to measure the annual percentage of reproducing mature females, clutch size, clutch frequency (number of clutches produced by a female annually), and annual egg production (AEP) per individual (total number of eggs produced/female/year). X-ray egg width (XREW) was measured from X-radiographs (with dial calipers for film and K-PACS, version 1.6.0; <http://www.k-pacs.net>). Additional parameters related to clutch phenology were reported by Lovich *et al.* (2012). When females were captured, we measured their midline carapace length (MCL) using tree calipers (± 1 mm) and weighed them with spring scales (± 10 g). Mean \pm SD female MCL was 25.1 ± 1.5 cm; range 21.60–27.00 cm).

Table 1. Summary statistics (mean \pm SD) of reproductive characteristics for eight years of reproductive data from a population of female *Gopherus agassizii* inhabiting a utility-scale renewable energy facility near Palm Springs, California

Years	N*	X-ray egg width (mm)	Clutch frequency	Annual egg production	Clutch size			CV clutch size, frequency	% Reproductive females*
					First	Second	Third		
1997	10	38.29 \pm 2.19	2.00 \pm 0.58	9.00 \pm 3.42	4.29 \pm 1.50 (7)	5.00 \pm 1.90 (6)	3 (1)	0.37, 0.29	100
1998	14	38.89 \pm 2.16	2.36 \pm 0.50	11.9 \pm 2.64	4.83 \pm 2.04 (12)	5.73 \pm 1.62 (11)	3.25 \pm 1.26 (4)	0.39, 0.21	100
1999	13	39.67 \pm 2.24	1.64 \pm 0.50	7.00 \pm 2.05	4.33 \pm 1.15 (12)	4.43 \pm 1.40 (7)	-	0.28, 0.31	92.3
2000	17	38.21 \pm 2.80	1.93 \pm 0.46	8.33 \pm 3.24	4.20 \pm 1.57 (15)	4.46 \pm 1.81 (13)	4 (1)	0.38, 0.24	100
2009	7	38.95 \pm 3.35	2.00 \pm 0.82	8.25 \pm 3.50	4.00 \pm 2.58 (4)	5.33 \pm 2.08 (3)	1 (1)	0.60, 0.41	100
2010	10	38.10 \pm 2.17	2.00 \pm 0.63	7.75 \pm 3.10	4.25 \pm 0.96 (4)	3.60 \pm 0.89 (5)	5 (1)	0.24, 0.32	75
2011	11	39.29 \pm 3.07	1.70 \pm 0.48	6.80 \pm 2.74	3.80 \pm 1.55 (10)	4.14 \pm 1.46 (7)	-	0.37, 0.28	100
2013	7	39.88 \pm 2.76	1.86 \pm 0.69	6.86 \pm 2.97	3.43 \pm 0.79 (7)	4.2 \pm 1.10 (5)	3 (1)	0.26, 0.37	100

Mean egg width is based on all clutches in a year. Sample sizes used in statistical analyses are shown in parentheses. Some clutches were not included as a result of indistinct X-radiographs. Coefficients of variation (CV) are given for both clutch size and clutch frequency.

*Some individuals were not included in several analyses and descriptive statistics as a result of the lack of complete reproductive history within a year

The quantity and timing of winter precipitation (October to March) is important for germination of desert annual plants that constitute the bulk of the diet of desert tortoises (Ernst & Lovich, 2009). As detailed further in Ennen *et al.* (2012a), annual aboveground plant biomass was estimated in the spring of 1997, 1998, and 1999 by clipping all species of annual plants and herbaceous perennials (except cacti) within 0.1-m² quadrats along 10 randomly located 100 m transects (Strong, 1966; McCleary & Wagner, 1972) as close as possible to the period of peak production. Because portions of the study site were affected by a large fire in 1995 (Lovich *et al.*, 2011b), half of the transects were located in previously burned areas to better represent tortoise habitat heterogeneity. Quadrats were located randomly in pairs and included one quadrat located in the open (shrub interspaces) and the other in the canopy drip zone of the nearest perennial shrub (Rowlands, 1986). Samples were placed in drying ovens and then weighed to the nearest 0.01 g. Biomass was estimated by dividing the weight by the area sampled (Turner *et al.*, 1986).

STATISTICAL ANALYSIS

Following Wallis, Henen & Nagy (1999), all analyses except those involving the percentage of reproducing females per year included only mature egg-laying females (MCL > 20 cm). We excluded data for one female (even in the analysis of percent of reproductive females) that was well above the size of sexual maturity but never produced shelled eggs (see Results). We tested for a relationship between female body size (MCL) and all measures of reproductive output. We used generalized linear mixed models (GLMM; function `glmer`, package `lmerTest`; Kuznetsova, Brockhoff & Christensen, 2014) to investigate the relationship between female body size (MCL) on clutch frequency and clutch size using individual tortoises as a random effect and assuming a Poisson distribution. Because AEP was a continuous variable, we tested for normality using a Shapiro–Wilks test (function `shapiro.test`, package `stats`). Annual egg production was normally distributed ($P = 0.07$ – 0.89) in every year except 2011 ($W = 0.84$, $P = 0.04$); therefore, we used log-transformation to improve normality and relied on the robustness of analysis of variance to deviations from normality (Schmider *et al.*, 2010). We used linear mixed-effects models (LMM; function `lmer`, package `lmerTest`; Kuznetsova *et al.*, 2014) to investigate the relationship between AEP (log transformed) and MCL (log transformed) using individual tortoise as a random effect. Next, if the GLMMs and LMM testing the relationship between MCL and the reproductive outputs were significant, we used residuals to

investigate the annual variation of reproductive output. To determine whether reproductive output varied annually, we conducted GLMMs for clutch size and clutch frequency with individual tortoise as a random effect. For the clutch size model, we used year and clutch number as fixed effects and tested their interaction. In the clutch frequency and AEP models, we only used year as a fixed effect. We used the analysis of variance (ANOVA) function (car package; Fox *et al.*, 2014) for all our GLMMs and the ANOVA function (lmerTest package; Kuznetsova *et al.*, 2014) for our linear mixed models to calculate P -values. Where appropriate, we conducted post-hoc tests (Tukey's honestly significant difference) using the glht function (package multcomp; Hothorn *et al.*, 2014). We used linear regression analysis to measure the strength of association between estimated precipitation and reproductive output. All statistical analyses were conducted in SYSTAT, version 13 (Systat Software Inc.) or R (R Development Core Team) at an alpha of 0.05.

RESULTS

EGG PRODUCTION, PERCENTAGE OF REPRODUCTIVE FEMALES, AND OVIPOSITION

Shelled eggs were visible via X-radiography from April through late July but clutch phenology varied among years as reported previously (Lovich *et al.*, 2012). The earliest date that shelled eggs were detected in X-radiographs was on 2 April (2013) and the latest was on 28 July (1998), with the latter suggesting that oviposition may occur as late as early August in some years. Mean XREW width of all clutches ranged from 38.10–39.88 mm across years (Table 1). Detailed analyses of data on egg width will be reported elsewhere. Oviposition dates, nest characteristics, and hatchling emergence dates are presented in Ennen *et al.* (2012b). The percentage of reproductive females (including only sexually mature tortoises) ranged from 75–100% each year (Table 1), not including females with unknown reproductive histories within a year or the female discussed next, and did not vary among years (GLMM: $F_7 = 9.54$, $P = 0.22$: assumption of independence may be violated by repeated measures). One adult female (24.2 cm MCL) never produced a clutch of shelled eggs despite being X-rayed in 1997, 1998, and 2009–2013. When examined by ultrasound in 2011, she contained three visible yolless sacs, approximately half the diameter of a normal egg, surrounded by mostly noncalcareous membranes (G. Kuchling, pers. comm.).

CLUTCH SIZE AND CLUTCH FREQUENCY

Clutch size ranged from 1–9. Mean clutch size varied little among years and ranged from 3.25–5.73

eggs/clutch, excluding a single egg clutch and the annual coefficient of variation (CV) ranged from 0.24–0.60 (Table 1). Clutch frequency varied somewhat among years and ranged from 1.64–2.36 clutches/female/year, and the annual coefficient of variation ranged from 0.21–0.41. Clutch frequency was not influenced by MCL (GLMM: $F_1 = 0.16$, $P = 0.67$), and clutch frequency did not differ significantly among years (GLMM: $F_7 = 1.89$, $P = 0.97$). Mean annual CVs for clutch size and clutch frequency were not significantly different (two-sample t -test, pooled variance, $t_{14} = -1.20$, $P = 0.25$), suggesting that one was not more variable than the other. Nine females produced third clutches in six out of eight years (75.0%). Only one of those females produced more than one third clutch during the study. In the El Niño year 1998, four individuals out of 14 produced a third clutch. The mean size of third clutches was 3.22 ($N = 9$; range 1–5; $SD = 1.30$). In only two cases were third clutches larger than both first and second clutches for a given female in the same year. Third clutches contributed to only 6.6% of overall egg production. First clutches accounted for 51.8% and second clutches accounted for 41.6% of total egg production. Clutch size was not influenced by MCL (GLMM: $F_1 = 1.47$, $P = 0.23$). Using only data from years in which third clutches were produced (Table 1), clutch size did not significantly differ between years (GLMM: $F_5 = 3.45$, $P = 0.63$), or clutches (GLMM: $F_2 = 3.55$, $P = 0.17$), and the interaction term between year and clutch number was not significant (GLMM: $F_{10} = 4.85$, $P = 0.90$). Excluding data for third clutches, there were no significant differences among years (GLMM: $F_7 = 4.55$, $P = 0.71$) and clutches (GLMM: $F_7 = 1.33$, $P = 0.25$), and, again, the interaction term between year and clutch number was not significant (GLMM $F_7 = 1.75$, $P = 0.97$).

ANNUAL REPRODUCTIVE OUTPUT

Total AEP ranged from 1–15 eggs/female. Mean AEP ranged from 6.8–11.9 eggs/female/year (Table 1). Two females produced 15 eggs in a year, one with three clutches (four, six and five eggs, respectively in 1998) and one with only two clutches (eight and seven eggs, respectively, in 2000). Maternal body size (MCL) influenced AEP ($F_{1,20.72} = 4.44$, $P = 0.047$) in our population (Fig. 1). The residuals of AEP regressed on MCL differed significantly among years ($F_{7,67.98} = 3.31$, $P = 0.004$), with 1998 differing significantly from 1999 ($Z = -3.56$, $P = 0.008$), 2000 ($Z = -3.05$, $P = 0.046$), 2011 ($Z = -4.17$, $P < 0.001$), and 2013 ($Z = -3.66$, $P = 0.006$) using a Tukey's honestly significant difference (Fig. 2).

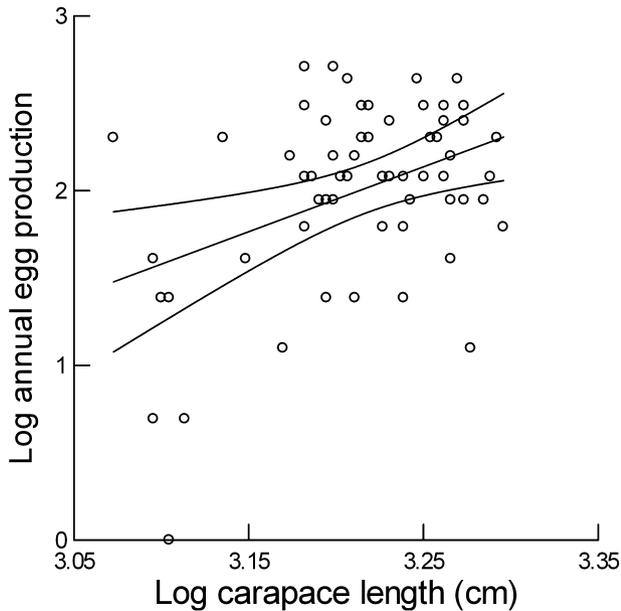


Figure 1. The log-log relationship between annual egg production (total annual number of eggs per female) and body size as measured by carapace length in a population of *Gopherus agassizii* inhabiting a wind energy facility in Riverside County, California. 95% CI shown.

PRECIPITATION AND ANNUAL PLANT PRODUCTIVITY EFFECTS

Winter precipitation varied appreciably during the study (Fig. 3) but had no significant effect on clutch frequency ($F_{1,6} = 0.67$; $r^2 = 0.10$; $P = 0.45$) or AEP ($F_{1,6} = 0.26$; $r^2 = 0.04$; $P = 0.63$) as shown by linear regressions. Similarly, neither mean first ($F_{1,6} = 0.20$; $r^2 = 0.03$; $P = 0.67$), nor mean second clutch sizes ($F_{1,6} = 0.17$; $r^2 = 0.03$; $P = 0.69$) were significantly related to winter precipitation. The percentage of reproductive females did not vary significantly with winter precipitation either ($F_{1,6} = 0.07$; $r^2 = 0.01$; $P = 0.80$). Total corrected mean dry annual biomass sampled in spring was 98.29 g m^{-2} ($N = 40$; $\text{SE} = 16.08$) in 1997, 138.24 g m^{-2} ($N = 36$; $\text{SE} = 32.37$) in 1998, and 0.17 g m^{-2} ($N = 36$; $\text{SE} = 0.11$) in 1999. Plotting our data on annual plant biomass along with data from Mueller *et al.* (1998) and Turner *et al.* (1986) shows an asymptotic relationship between biomass and clutch frequency (Fig. 4) across a wider range of values than previously available.

DISCUSSION

No previously published studies investigating the reproductive ecology of Agassiz's desert tortoise (*sensu* Murphy *et al.*, 2011) have exceeded 3 years at a specific site (Turner *et al.*, 1986; Henen, 1997; Mueller *et al.*, 1998; Lovich *et al.*, 1999; Wallis *et al.*,

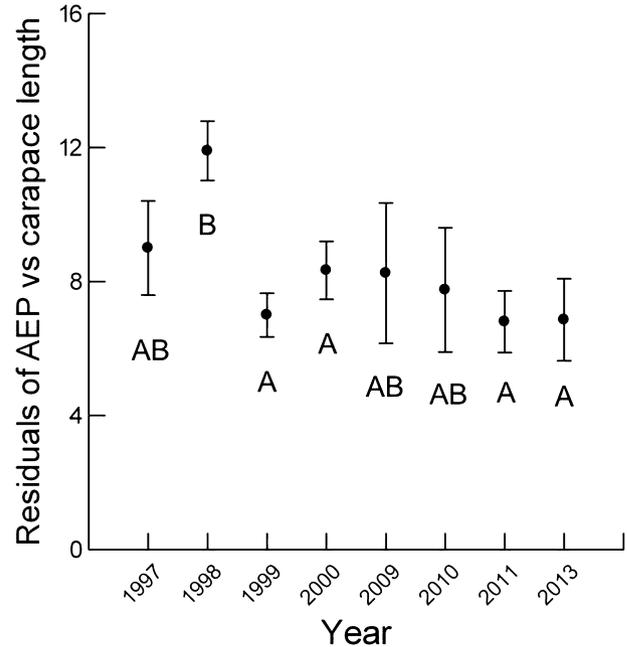


Figure 2. Annual mean values of individual tortoise annual egg production (AEP) in a population of *Gopherus agassizii* inhabiting a wind energy facility in Riverside County, California, based on raw data. Standard error bars of raw data are shown (differences are accentuated when using residuals). The means were significantly different among years when comparing residuals from linear regression of AEP on female carapace length. Years not sharing the same uppercase letter are significantly different based on residual analysis. Note that the *x*-axis is categorical and not continuous to show our years of study.

1999; Bjurlin & Bissonette, 2004). Short-term studies of long-lived animals can make it difficult to identify biologically meaningful relationships between life-history traits such as reproductive output and environmental variables. However, the results of our long-term study largely support conclusions based on earlier short-term research suggesting that desert tortoises show relatively invariant egg production (both clutch size and clutch frequency in our analysis) and iteroparous reproduction in the face of highly variable environmental conditions producing wide variation in resource availability.

It appears that females rarely skip an opportunity to reproduce, even in 'bad' years of resource availability, counter to some predictions for organisms living in unpredictable environments (Shine & Brown, 2012). This behaviour is consistent with a 'bet-hedging' strategy, first applied to the reproductive strategy of *G. agassizii* by Henen (1997) and more recently by Averill-Murray *et al.* (2014). Under this strategy, tortoises 'wager' a small investment (e.g. small clutch size) in reproduction for each clutch,

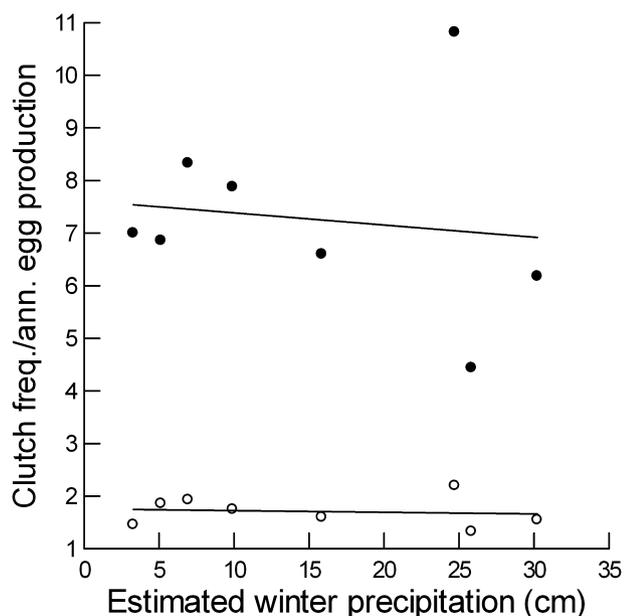


Figure 3. Estimated winter precipitation (October to March) versus both clutch frequency (open circles) and mean annual egg production (solid circles) in a population of *Gopherus agassizii* inhabiting a wind energy facility in Riverside County, California. Precipitation was estimated using WestMap (<http://www.cefa.dri.edu/Westmap/>). The extreme outlier for mean annual egg production represents the El Niño year 1998.

even though they are capable of producing more eggs per clutch. Small clutch sizes minimize the risk of complete reproductive failure in a given year (e.g. to predation), compared to substantial investments in larger clutches (Stearns, 1976). Generating a small clutch every year, regardless of unpredictable resource availability, allows for the possibility of a potential ‘pay-off’ if conditions eventually favour the production of viable hatchlings that survive to reproduce at a later time.

The question of how desert tortoises are able to produce clutches even in years of low rainfall and poor germination of annual food plants was not answered until the pioneering studies of Henen, (1997) who identified the source and timing of energy and resources used by desert tortoises to support egg production. By relaxing the control of water and energy homeostasis (Peterson, 1996) and forfeiting body condition, tortoises are able to produce eggs in lean years, thereby reducing the chance of certain reproductive failure if they forgo an opportunity to reproduce in years of poor resource availability that might otherwise favour the survival of some hatchlings (Seger & Brockman, 1987). In addition, they have the ability to store resources from one year (perhaps a good year) and use them the following year

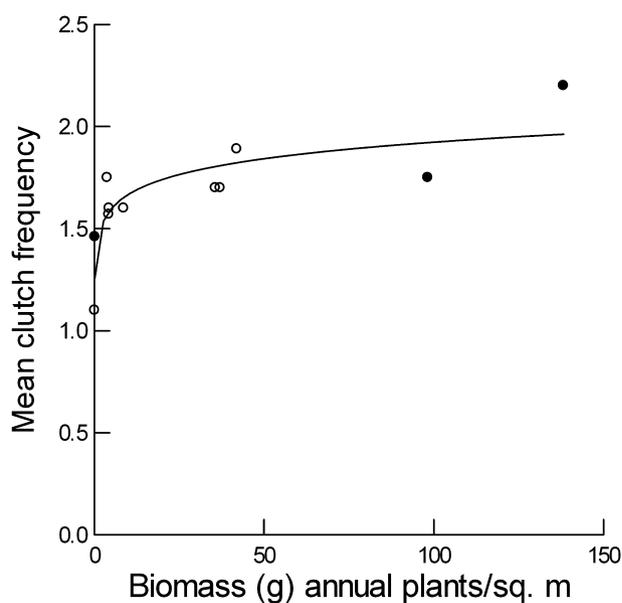


Figure 4. The relationship between estimated dry biomass of annual plants (g m^{-2}) and mean annual clutch frequency for *Gopherus agassizii* populations in Goffs and Ivanpah Valley, California (Turner *et al.*, 1986), the Nevada Test Site (Mueller *et al.*, 1998), and the present study (Palm Springs, California), with the latter shown as black dots. A power function ($y = ax^b$) is fit to the data to visualize the relationship.

(perhaps a bad year) even under extreme drought conditions with a ten-fold variation in resource availability (Henen, 2002). That ability gives tortoises (Henen, 2004) the option to use both stored (capital) and recently harvested (income) reserves of resources to produce a clutch (Van Dyke, Beapre & Kreider, 2012). Evidence suggests that tortoises at Mesa are able to benefit from the effects of El Niño on food plant productivity at least into the next year (Ennen *et al.*, 2012a) via capital income.

However, investing water and energy into reproduction is a delicate balancing act in the highly variable desert environment, with significant negative consequences on adult female survivorship during frequent or protracted droughts (Lovich *et al.*, 2014a). When females do skip an opportunity to reproduce (Tables 1, 2), it is likely that they do so to maintain adequate reserves of water and energy to survive and not compromise substantial future opportunities for reproduction. Given the potential longevity of desert tortoises (Germano, 1992, 1994), their iteroparous reproductive lifespan can extend for approximately 50 years, which is sufficiently long to overlap with favourable environmental conditions for recruitment.

Bet-hedging can spread the risk of reproductive failure both spatially and temporally (Hopper *et al.*,

Table 2. A comparison between reproductive characteristics reported in the present study and for *Gopherus agassizii* throughout the species' range

	Present study	Wallis <i>et al.</i> (1999)	McLuckie & Fridell (2002)	Turner <i>et al.</i> (1984)	Turner <i>et al.</i> (1986)	Rostal <i>et al.</i> (1994)	Baxter, Wilson & Morafka (2008)	Bjurlin & Bissonette (2004)	Henen (1997)	Mueller <i>et al.</i> (1998)
US State	California	California	Utah	California	California	Nevada	California	California	California	Nevada
% Females reproducing	75–100%	75–100%	66.70%	80–86.7%	95.7–100%*	NA	79%	NA	NA	NA
Clutch frequency	1.70–2.36	1.67–1.76	1.33 ± 0.14	1.10–1.60	1.57–1.89	NA	NA	NA	NA	1.5
Clutch size										
First	3.4–4.8	3.9–4.4	5.2 ± 0.47	NA	4.1–4.8	5.1	2.7(1–6)	4.35–5.91***†	3.00–3.56***	5.1 ± 0.3
Second	3.6–5.7	4.0–4.7	5.5 ± 1.55	NA	4.25–5.57	3.7	**	**	NA	4.8 ± 0.4
Third	1–5‡	NA	NA/	NA	2–6	NA	**	**	NA	NA
Annual egg production per female	6.8–11.9	7.0–7.3	7.0 ± 1.16	NA	6.6–9.0*	NA	3.9 ± 0.8***	NA	NA	6.7–7.7

When values are given to the first or second decimal place, they represent means with ranges indicating values between or among years. When those data were not available, simple ranges are given or listed as not available (NA).

*Calculated from Tables 1, 2, 3 of Turner *et al.*, 1986.

**Clutch order not listed.

†Mean clutch size of nests preyed upon by predators listed. Mean clutch size of nests not disturbed by predators = 4.35.

‡Values represents ranges and not means.

2003). Producing multiple clutches in different nest sites (Ennen *et al.*, 2012b) limits unacceptably high losses from nest predators by spreading the risk of reproductive failure among multiple nests (Eckert, 1987), in both time and space, something that has not previously been noted for desert tortoises. In the case of female tortoises, this is accomplished through the temporal separation of multiple clutches (Lovich *et al.*, 2012), oviposited at several different nest sites (Ennen *et al.*, 2012b; Lovich *et al.*, 2014b), with reproduction occurring in almost every year (Henen, 1997) of a long reproductive lifespan (Germano, 1992, 1994). Producing multiple scattered clutches also increases the probability that some offspring will survive during a propitious period of resource availability (Averill-Murray *et al.*, 2014) or in a favourable resource patch.

Even at a highly productive but environmentally variable site such as Mesa, tortoises produce consistently small clutch sizes every year as predicted under bet-hedging theory (Stearns, 1976). However, AEP varies significantly among years, after adjusting for MCL, mostly as a result of the effect of the anomalous El Niño year of 1998 when many females produced third clutches. The fact that both mean clutch size of first and second clutches at our study site are not significantly different emphasizes the consistency of bet-hedging by tortoises. Wallis *et al.* (1999) reported that variation in AEP was a function of clutch size and not clutch frequency. Using our data, CVs for clutch frequency and clutch size among years were not significantly different, suggesting that neither varied more than the other. Also, means for clutch frequency and clutch size did not vary annually. Nevertheless, the impact of clutch frequency on AEP cannot be understated. Because clutch size is relatively invariant, in years when females produce multiple clutches, a second clutch functionally doubles their reproductive output and, in years where three clutches are produced, it is effectively tripled. Collectively, these results suggest that clutch frequency does have an impact on variation in AEP, and that evidence for variation in clutch size impacting AEP is not convincing. It is somewhat puzzling that AEP was related to female body size whereas clutch size and clutch frequency were not. Although that may be related to a lack of statistical power, body size is typically not a reliable predictor of reproductive output in North American tortoises, explaining little of the variation in clutch size within populations (Averill-Murray *et al.*, 2014).

The potential incongruence between the conclusion of Wallis *et al.* (1999) regarding the strong effect of clutch size on AEP and our results may be the result of three factors: (1) some of the study sites of Wallis *et al.* received artificially supplemented water from

irrigation; (2) both of their study years were El Niño years with high rainfall; and (3) third clutches, not observed by Wallis, were observed much more frequently by us than in any other studies. In general, third clutches are uncommon for desert tortoises under natural conditions (Ernst & Lovich, 2009). However, some females at Mesa produced a third clutch in six out of eight years (71.4%) and, in the El Niño year of 1998, approximately one-third of monitored females at Mesa produced a third clutch (Lovich *et al.*, 1999, 2012). The only other published study to report third clutches was Turner *et al.* (1986), who reported only two third clutches in 3 years.

Reproductive output at Mesa was extraordinarily high in comparison with other published studies for tortoises (Table 2). During the El Niño year of 1998 with 217 mm of winter precipitation and high winter annual plant biomass, mean \pm SD annual clutch frequency (2.36 ± 0.50) and annual egg production (11.9 ± 2.64) were the highest ever reported in a *G. agassizii* population (Tables 1, 2). Even in the dry year 2000, with only 54.2 mm of winter precipitation, Mesa recorded a mean \pm SD annual clutch frequency (1.93 ± 0.46) and annual egg production (8.33 ± 3.24) that were greater than the means reported in any previous studies (Tables 1, 2). By comparison, a population of *G. agassizii* at Goffs, California (Turner *et al.*, 1986) exhibited a similar but slightly lower, annual clutch frequency of 1.89 clutches/female/year and annual egg production of 7.79 eggs/female, although more than double (estimated at 120 mm) the amount of winter precipitation observed at Mesa in 2000 was required. Although annual fecundity of the *G. agassizii* population at Mesa is higher than most other populations as a result of the high clutch frequency, they still produce relatively small clutches of eggs in conformance with predictions of bet-hedging.

Although annual egg production of desert tortoises is not always tightly coupled to rainfall or biomass of annual food plants, they are certainly related. Our research demonstrates the capacity for desert tortoises to respond rapidly to large precipitation events and extraordinarily high annual plant biomass with increased clutch frequency from one year to the next, as demonstrated in the El Niño year 1998 (Lovich *et al.*, 1999; Ennen *et al.*, 2012a). However, the allocation of resources to reproductive output is complicated as a result of at least three other factors. The first is the ability of *G. agassizii* to produce clutches even in years of low annual plant productivity by relaxing homeostasis and forfeiting body condition as discussed previously. The second factor is because tortoises are selective foragers, actively seeking out preferred nutritious, easily digestible plant species (Henen, 2002). As a result, biomass estimates of annual plants do not directly represent the nutrients

available to desert tortoises. The third factor complicating the relationship between reproductive output and winter annual dry biomass is a matter of scale. According to Henen (2002), egg production and clutch frequency are highly correlated with biomass at low levels from 0–2 g m⁻². At higher levels of 4–40 g m⁻², both egg production and clutch frequency approach an asymptote, a relationship confirmed recently by Averill-Murray *et al.*, (2014).

Considering the issue of scale, we recorded extraordinarily high dry biomass values (98.29–138.24 g m⁻²) during two wet years, higher than any values previously reported in the tortoise literature. Other studies demonstrate that the biomass of annual food plants in the desert occupied by *G. agassizii* exhibits an asymptotic relationship with winter precipitation. Turner & Randall (1989) measured the relationship between winter precipitation and biomass of winter annual plants in southern Nevada from 1964–1976 and found that production started to decline after approximately 100 mm of precipitation (September to March) and 10 g m⁻², and approached an asymptote at 200 mm of precipitation and 100 g m⁻². At another site in southern Nevada, Medica *et al.*, (2012) observed that maximum biomass values near 80 g m⁻² occurred when winter precipitation (October to March) exceeded 200 mm. Clutch frequency appears to track the asymptotic relationship with biomass (Fig. 4) and suggests that a physiological limit to clutch frequency is met at Mesa. The observed association supports the conclusion of Henen (2002) regarding a slower increase in clutch frequency as biomass exceeds 40 g m⁻², although a lower threshold of 2–5 g m⁻² was suggested for AEP by McCoy *et al.*, (2014) without including our data. The enhanced AEP output at our study site appears to reflect the high biomass of annual food plants in comparison to dryer, less productive desert tortoise study sites.

Similarly, early on in the present study, we concluded that biomass of food plants affected the percentage of reproductive females and clutch frequency but not clutch size (Lovich *et al.*, 1999). Our conclusions were based on only 2 years of data, although the first year was the end of a short drought and the second year was an El Niño event that doubled winter precipitation (Ennen *et al.*, 2012a). With the accumulation of more data, it is now apparent that the percentage of reproductive females and clutch frequency are less variable among years. Relatively stable clutch sizes among years were still supported by longer-term data. The dramatic difference that we initially reported for clutch frequency appears to be the result of comparing two extreme years (1997 and 1998) as far as winter precipitation is concerned.

Primary productivity at Mesa is at the high end in comparison with other reported measures in dryer

portions of desert tortoise habitat (Fig. 4) and near the asymptote of what is possible (Turner & Randall, 1989; Medica *et al.*, 2012). Thus, because primary production at Mesa in good years is near the maximum reported for the desert habitat of *G. agassizii*, reproductive output is similarly maximized.

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