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# Reproduction by *Uta stansburiana* (Reptilia, Lacertilia, Iguanidae) in Southern Nevada

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*ABSTRACT*—Monthly mean clutch sizes of *Uta stansburiana* in southern Nevada were measured over a 10-year period. Overall mean clutch sizes of female *Uta* > 12 months of age were 4.40 (March-April), 3.80 (May), 3.04 (June), and 2.65 (July). Overall means of yearling females (< 12 months of age) were about 82-90% of those of older females between April and June. Reproduction by *Uta* in 1973 surpassed that observed in any of nine previous years. The mean size of the first clutch laid by older females was 5.35, and some females deposited up to eight eggs. The minimum number of clutches laid was four and the maximum seven. The net reproductive rate ($R_o$) estimated for 1973 was 2.34, exceeding an earlier estimate for 1966 (1.65).

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We have worked with populations of *Uta stansburiana* in southern Nevada since 1964, investigating the response of this species to continuous gamma irradiation (Turner, Hoddenbach, and Lannom, 1965; Turner and Lannom, 1968; Turner, Licht, et al., 1973; Turner, 1975), as well as several features of its population biology (Hoddenbach and Turner, 1968; Turner et al., 1970). Currently we are interested in the influences of winter rainfall on available food and egg production by females, and in the development of quantitative models expressing such relationships. The results of field experiments directed to these ends have been previously reported (Turner, Medica, and Smith, 1973, 1974).

Hoddenbach and Turner (1968) analyzed mean clutch sizes of *Uta stansburiana* in southern Nevada for the years 1964-1966. These authors showed that older females produced larger clutches than yearling females (8-10 months of age), and defined distinct differences between years and months. The general seasonal pattern was from larger clutches during March and April to smaller ones in June (see also Tinkle, 1961), although in 1965 the opposite trend was observed. Some follicular atresia occurred among younger females, but clutch sizes of old females estimated from yolked follicles and oviducal eggs did not differ significantly. Differences between years were interpreted in terms of annual differences in winter rainfall as suggested by the work of Mayhew (1966a, b) with species of *Uma*, and Zweifel and Lowe (1966) with *Xantusia vigilis*. In a later paper Turner et al. (1970) analyzed the net reproductive rate ($R_o$) of *Uta* based on clutch size and frequency data recorded during 1966. During that year some females produced as many as five clutches of eggs, and the associated estimate of $R_o$ (1.65) was judged to reflect the maximum capacity for increase by *Uta stansburiana* in southern Nevada. However, events in 1973 suggested the possibility of a higher net reproductive rate.

The purpose of this paper is to extend previous observations relating to *Uta* clutch sizes, to reevaluate the question of net reproductive rate in terms of observations in 1973, and to examine further the influences of age and season on mean clutch sizes. Some of these findings will subsequently be used in a model of the dynamics of southern Nevada populations of this lizard.

## METHODS

The present analysis of mean clutch sizes is based on data collected over a 10-year interval between 1964 and 1973 in Rock Valley, Nye County, Nevada. Clutch size information for 1964-1966 has been reported by Hoddenbach and Turner (1968), but we will treat som( their data differently in the present paper. Data for 1967-1973 were obtained from 1,: females (> 40 mm in snout-vent length) collected between March and July of each year. interval between collections was about 7-10 days in all years. After collection, animals v measured to the nearest mm and weighed to the nearest mg on a Mettler Gram-atic Type balance. Animals were autopsied and the numbers and sizes of oviducal eggs, corpora lutea yolked follicles recorded. Clutch sizes were estimated from the numbers of yolked follicle 2.5 mm in diameter, oviducal eggs and corpora lutea. Females were assigned to two size cla based on snout-vent length: 40-45 mm and > 45 mm. These categories correspond closely v animals 9-12 months of age and animals ⩾ 21 months of age (see Turner et al., 1970: 5( Clutch size estimates for 1967-1973 were based on 1,363 clutches (9 females exhibited b yolked follicles and oviducal eggs—or corpora lutea—and both counts were used).

To estimate the net reproductive rate of *Uta* during 1973 we used i) the same schedul( survivorship given by Turner et al. (1970: Table 8), ii) age-specific clutch size estimate: measured in 1973, and iii) age-specific clutch frequency data as determined in 1973. frequency of clutches was assessed by weekly captures, weighing and examination of mar females in Plot 5 in Rock Valley. Procedures were as described by Medica, Hoddenbach, Lannom (1971: 28 et seq.).

For the purpose of modeling egg production by *Uta*, mean March clutch sizes are questionable relevance because we have rarely observed egg deposition before the month April. As pointed out above, there is some follicular atresia among younger females, but significant loss among older males. Hence, we have used co( from March and April to estir the size of the first clutch laid older females, but only co( from April to estimate this p meter for yearling females. Clu size estimates for the months May, June, and July were basec lizards collected during tl months. Data from July were a\ able only for the years 1965, 1( 1967, 1968, 1969, and 1973.

TABLE 1. Mean clutch sizes of *Uta stansburiana* in Rock Valley, Nevada. Figures in parentheses are sample sizes. Second rows give ranges of observations.

| Year | Size of female | April | Month May | June | July |
|---|---|---|---|---|---|
| 1967 | Large | 3.98 (47) | 3.45 (31) | 2.79 (14) | – |
| | | 3-5 | 1-5 | 2-4 | |
| | Small | 3.46 (59) | 3.00 (68) | 2.31 (29) | 2.50 (4) |
| | | 3-5 | 1-4 | 1-3 | 2-3 |
| 1968 | Large | 4.87 (108) | 3.47 (59) | 2.71 (14) | 3.00 (1) |
| | | 4-7 | 2-5 | 2-4 | 3 |
| | Small | 4.69 (16) | 3.28 (57) | 2.56 (9) | – |
| | | 3-6 | 2-5 | 2-3 | |
| 1969 | Large | 4.94 (51) | 4.50 (38) | 3.74 (38) | 2.80 (10) |
| | | 4-6 | 2-6 | 2-5 | 2-4 |
| | Small | 3.40 (49) | 3.57 (23) | 3.29 (17) | 2.86 (7) |
| | | 3-5 | 2-5 | 2-4 | 2-4 |
| 1970 | Large | 4.10 (29) | 3.18 (11) | 2.60 (5) | |
| | | 3-6 | 2-4 | 2-4 | |
| | Small | 3.18 (28) | 2.82 (33) | 2.00 (12) | |
| | | 2-4 | 2-4 | 1-3 | |
| 1971 | Large | 4.30 (74) | 3.56 (18) | 2.58 (12) | |
| | | 3-6 | 3-5 | 2-3 | |
| | Small | 4.00 (7) | 2.85 (13) | 2.50 (10) | |
| | | 3-5 | 2-3 | 2-4 | |
| 1972 | Large | 4.45 (48) | 3.37 (30) | 2.79 (28) | |
| | | 3-6 | 2-5 | 1-4 | |
| | Small | 3.60 (10) | 2.86 (7) | 2.56 (9) | |
| | | 2-5 | 2-3 | 2-3 | |
| 1973 | Large | 5.35 (46) | 5.03 (37) | 3.67 (27) | 2.33 (6) |
| | | 4-8 | 3-7 | 1-7 | 2-3 |
| | Small | 3.86 (7) | 4.25 (4) | 3.50 (6) | 2.50 (2) |
| | | 3-5 | 4-5 | 3-4 | 2-3 |

## RESULTS

Table 1 gives mean clu sizes for the months of April, M June, and July for the years 1! to 1973. Recall that the A means for older females are ba on animals collected in March April. Comparable means younger females (April, May, June) were given for the years 1! to 1966 by Hoddenbach Turner (1968: Table 1). Means the large females for the month May and June may also be foun( this earlier paper. Revised A means for large females (March April samples combined) dur 1964-1966 have been recalcula as 3.70, 3.83, and 4.45, respectively. It is our ultimate intention to use the April means for older females as the dependent variable in a multiple regression analysis involving rainfall totals and air temperatures as independent variables. Our present purpose is to derive relationships between April clutch sizes of adult females and the sizes of clutches laid later in the season and by younger females. Table 2 gives 10-year (unweighted) means for the age and month categories—based on data given by Hoddenbach and Turner (1968) and Table 1.

TABLE 2. Ten-year mean monthly clutch sizes for *Uta stansburiana* in Rock Valley, Nevada. The April mean for older females is based on samples taken in March and April.

| Age category | Mean clutch sizes April | May | June | July |
|---|---|---|---|---|
| Young (< 12 months) | 3.63 | 3.15 | 2.75 | 2.60 |
| Older (> 12 months) | 4.40 | 3.30 | 3.04 | 2.65 |

Only 55 lizards collected between 1965 and 1973 contributed to the July estimates, and we will arbitrarily take 2.6 as the mean size of any clutches laid this late in the season. In analyzing the data for the months of April, May, and June we examined nine relationships by simple linear regression (with the dependent variable given first in all cases): 1) May and April clutches of older females, 2) June and April clutches of older females, 3) May and April clutches of younger females, 4) June and April clutches of younger females, 5) April clutches of younger and older females, 6) May clutches of younger and older females, 7) June clutches of younger and older females, 8) May clutches of younger females and April clutches of older females, and 9) June clutches of younger females and April clutches of older females.

Mean clutch sizes of older females in May ($X_2$) could be estimated in terms of April mean clutch sizes ($X_1$) as follows:

$$X_2 = 0.881X_1 - 0.078 \quad (1)$$

Mean clutch sizes of younger females in May ($X_5$) could be estimated from those of older females during April ($X_1$) as follows:

$$X_5 = 0.772X_1 - 0.243 \quad (2)$$

Mean clutch sizes of younger females in June ($X_6$) could be estimated from those of older females during the same month ($X_3$) as follows:

$$X_6 = 1.03X_3 - 0.380 \quad (3)$$

The other regression analyses were of no use because the F tests of non-zero slopes were insignificant. Hence, we will simply estimate the mean clutch sizes of young females in April ($X_4$) as 3.63/4.40, or $0.825X_1$, and the mean clutch sizes of older females in June ($X_3$) as 3.04/4.40, or $0.69X_1$. If the size of the first clutch laid by older females in April can be estimated from various abiotic variables, the relationships derived above may be used to estimate egg production by younger females and by older females at later times during the season. We recognize that this approach may obscure some interesting biological subtleties, for mean clutch sizes do not always decline throughout the season, e. g., see Hoddenbach and Turner (1968: 264-265).

We have already commented on the increased reproduction by *Uta* during 1973. This year was unlike any of the previous nine years in total rainfall during the preceding winter and the first four months of the year. Rainfall between October and December of 1972 was 62 mm, and between January and April of 1973 an additional 150 mm was recorded. Bamberg and his colleagues estimated net above-ground primary production by annuals and perennials in Rock Valley during 1971 and 1972 to be about 162 and 186 kg (dry weight) per ha (Turner, 1973: 2-3), but aggregate production in 1973 was estimated at around 1,250 kg/ha (Bamberg et al., 1974). The response of *Uta* to these conditions was in line with expectations based on previous irrigation experiments carried out by Medica and Smith (Turner, Medica, and Smith, 1973, 1974). Mean clutch sizes in 1973 were higher than those recorded in any previous year (Table 1), and three females apparently produced clutches of eight eggs. Two of these lizards were collected in early March and contained 6 mm yolked follicles. The other was collected in early April and contained 8 shelled oviducal eggs.

TABLE 3. Records of the reproductive state of a female *Uta stansburiana* in Rock Valley, Nevada, during the 1973 reproductive season. Asterisks indicate the prior deposition of eggs.

| Date | Snout-vent length (mm) | Weight (g) | Reproductive state inferred from palpation and body weight changes |
|---|---|---|---|
| 7 March 1973 | 50 | 3.71 | Yolked follicles, 2-3 mm |
| 30 March | 50 | 4.16 | 5 yolked follicles, 4-5 mm |
| 6 April | 51 | 4.46 | Eggs |
| 9 April | 50 | 4.54 | Eggs |
| 18 April* | 49 | 3.82 | Small yolked follicles |
| 23 April | 50 | 4.13 | 6 yolked follicles, 3 mm |
| 1 May | 51 | 4.50 | Eggs |
| 8 May | 51 | 4.82 | Eggs |
| 17 May* | 51 | 4.36 | 6 yolked follicles, 4 mm |
| 21 May | 52 | 4.84 | Eggs |
| 4 June* | 52 | 4.52 | 4 yolked follicles, 5 mm |
| 12 June* | 50 | 3.31 | Negative, no follicles |
| 18 June | 50 | 4.10 | 5 yolked follicles, 3-4 mm |
| 2 July* | 50 | 3.39 | Small yolked follicles |
| 9 July | 50 | 4.10 | Eggs |
| 16 July* | 51 | 3.40 | Negative, no follicles |
| 24 July | 49 | 3.96 | 3 yolked follicles, 5-6 mm |
| 31 July* | 49 | 3.06 | Negative |
| 6 August | 51 | 3.65 | Negative |

TABLE 4. Numbers of egg clutches by *Uta stansburiana* in Rock V during 1973. Figures pertain only t females surviving the entire reprodu season.

| Number of clutches | Age of females (mo < 12 | > |
|---|---|---|
| 4 | – | |
| 5 | 7 | |
| 6 | 14 | |
| 7 | 1 | |

Clutch frequency also creased in 1973. Females which out the entire reproductive se usually lay between two and clutches of eggs. However, the n mum number of clutches laid females surviving the entire 1 season was four, and many fem laid six clutches. Table 3 s marizes records pertaining to large female *Uta* between M and August, 1973, during which time she laid seven clutches of eggs. Table 4 gives the distribut of clutch frequency for 30 females observed throughout the 1973 season. Individual schedule egg-laying varied, although the interval between clutches was usually about two weeks. ensuing descriptions are of what we considered to be typical schedules. Older females laid t first clutches around 17 April. The second clutch was not produced until about a month later, subsequent clutches were laid at two-week intervals. All of the eight old females under observa laid clutches on about 17 April, 15 May, and 1 July. Seven of them laid eggs on 15 June an

TABLE 5. Estimated egg production by *Uta stansburiana* in Rock Valley, Nevada, during 1973.

| Dates | Young females (< 12 months) Schedule A | Schedule B | Percentage of population reproductive | Old females (> 12 months) | Percentag populat reproduc |
|---|---|---|---|---|---|
| April 17 | – | – | – | 5.35 | 100.0 |
| April 24 | 1.23 | – | 31.8 | – | – |
| May 1 | – | 2.89 | 68.2 | – | – |
| May 15 | 4.05 | 4.05 | 95.4 | 5.03 | 100.0 |
| June 1 | – | – | – | 2.75 | 75.0 |
| June 5 | 3.50 | 3.50 | 100.0 | – | – |
| June 15 | – | – | – | 3.21 | 87.5 |
| June 25 | 3.34 | 3.34 | 95.4 | – | – |
| July 1 | – | – | – | 2.62 | 100.0 |
| July 10 | 2.27 | 2.27 | 81.8 | – | – |
| July 15 | – | – | – | 2.29 | 87.5 |
| July 23 | – | 1.52 | 54.5 | – | – |
| July 30 | 0.76 | – | 27.3 | 1.31 | 50.0 |
| August 6 | – | 0.51 | 18.2 | – | – |

July. Six laid eggs on 1 June, and four on 30 July. Two schedules of egg-laying could be discer among younger females (Table 5). Some laid eggs as early as 24 April, but others did not a first clutch until 1 May. Both groups laid clutches around mid-May, in early June, in June, and around 10 July. A few females laid another clutch on or about 23 July and anothe early August, but most laid their final clutch at the end of July. Of the 22 young females ur observation, only seven laid eggs as early as 24 April. The others first laid eggs on 1 May. Percentages of females producing clutches between 15 May and 10 July ranged from 81.8 (10 July) to 100 (5 June). About 27% of the young females observed laid eggs on 30 July, and only 4 (18%) laid clutches as late as 8 August. Table 5 summarizes schedules of egg production by female *Uta* during 1973. The production values were derived by multiplying the monthly mean clutch sizes (Table 1) by the proportion of the sampled population laying clutches on the various dates (Table 4).

It is now possible to estimate the net reproductive rate ($R_0$) associated with the remarkable fecundity observed in 1973 (Table 6). As pointed out previously, the survival rates are based on those given by Turner et al. (1970), but the age-specific fertilities are drawn from the 1973 data given in Table 5. The starting value in the $l_x$ column represents the survivors of a cohort of 1,000 females born during the summer, with 24.5% survival to 1 March of the ensuing year. The $m_x$ values represent potential daughters only, and are 50% of the estimates in Table 5. $R_0$ is estimated as 2,336/1,000, or 2.34—appreciably greater than the estimate for 1966 (1.65).

The 1973 estimate of $R_0$ was based on survival rates measured in 1966 and its reliability can, of course, be questioned on these grounds. We are, nonetheless, impressed by the remarkable egg production observed in 1973 and feel obliged to question our earlier description of the 1966 data as representing" . . .a population increase close to the maximum possible. . ." (Turner et al., 1970: 510). The deposition of seven clutches of eggs may not be the maximum ever observed among seasonally breeding lizards, but it is a remarkable effort. Up to five clutches have been reported for *Callisaurus draconoides* (Fitch, 1970: 29), *Holbrookia texana* (Johnson, 1960), *Mabuya maculilabris* and *Panaspis nimbaensis* (Barbault, 1973). Six clutches may be laid by *Urosaurus ornatus* (Fitch, 1970: 62) and *Takydromus tachydromoides* (Telford, 1969). It is important to remember that these maximum frequencies may be only rarely expressed among species occupying variable environments, and that modal egg production is less. We also reemphasize that, in terms of influencing year-to-year changes in the densities of desert lizards, annual variations in clutch frequency are more important than variations in mean clutch size (Turner, Lannom, et al., 1969; Turner, Medica, et al., 1969; Turner et al., 1970; Turner, Medica, and Smith, 1973, 1974).

TABLE 6. Estimating the net reproductive rate ($R_0$) of *Uta stansburiana* in Rock Valley, Nevada, in 1973.

| Age, x (months) | $l_x$ | $m_x$ | $l_x m_x$ |
|---|---|---|---|
| 9.8 | 200.0 | 0.614 | 122.8 |
| 10.3 | 190.0 | 1.449 | 275.3 |
| 10.5 | 188.0 | 2.027 | 381.1 |
| 11.1 | 178.0 | 1.750 | 311.5 |
| 11.8 | 165.0 | 1.670 | 275.6 |
| 12.3 | 158.0 | 1.137 | 179.6 |
| 12.8 | 150.0 | 0.771 | 115.7 |
| 13.0 | 147.0 | 0.379 | 55.7 |
| 13.2 | 143.0 | 0.253 | 36.2 |
| 21.6 | 53.0 | 2.675 | 141.8 |
| 22.5 | 45.0 | 2.515 | 113.2 |
| 23.0 | 42.0 | 1.376 | 57.8 |
| 23.5 | 38.0 | 1.606 | 61.0 |
| 24.0 | 35.0 | 1.310 | 45.9 |
| 24.5 | 32.5 | 1.146 | 37.2 |
| 25.0 | 29.5 | 0.655 | 19.3 |
| 33.6 | 8.2 | 2.675 | 21.9 |
| 34.5 | 7.6 | 2.515 | 19.1 |
| 35.0 | 7.2 | 1.376 | 9.9 |
| 35.5 | 6.8 | 1.606 | 10.9 |
| 36.0 | 6.5 | 1.310 | 8.5 |
| 36.5 | 6.2 | 1.146 | 7.1 |
| 37.0 | 5.9 | 0.655 | 3.9 |
| 45.6 | 2.4 | 2.675 | 6.4 |
| 46.5 | 2.3 | 2.515 | 5.8 |
| 47.0 | 2.2 | 1.376 | 3.0 |
| 47.5 | 2.1 | 1.606 | 3.4 |
| 48.0 | 2.0 | 1.310 | 2.6 |
| 48.5 | 1.9 | 1.146 | 2.2 |
| 49.0 | 1.8 | 0.655 | 1.2 |
| | | | 2335.6 |

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