

A DEMOGRAPHIC ANALYSIS OF FENCED
POPULATIONS OF THE WHIPTAIL LIZARD,
CNEMIDOPHORUS TIGRIS, IN
SOUTHERN NEVADA

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ABSTRACT. Between 1964 and 1967, spring densities of *Cnemidophorus tigris* in four study areas in southern Nevada ranged from 3-8 per acre. Estimated biomass ranged from around 43 to 114 g/acre. The sex ratio was 1:1. Minimal annual survival of adults was 54-60%, and life-spans of at least 7 years are postulated. An undetermined proportion of mature females laid two clutches of eggs in 1965, but the general pattern was one clutch of 2-4 eggs per year. Large females produced more eggs than small ones. Occasionally females 9-10 months of age laid eggs, but sexual maturity normally was attained at about 21 months. By assuming that all mature females laid two egg clutches in 1965 our fecundity estimates could be approximately reconciled with the observed size and age composition of populations in the spring of 1966. Possible compensatory errors in this analysis are discussed.

One of the challenging problems of contemporary ecology is the analysis of ecosystems and the development of mathematical models capable of simulating the trophic transfers of energy and materials and the interactions between species which collectively constitute ecosystem function. This endeavor requires not only an understanding of the processes of primary production, but also the roles of primary and secondary consumers.

The net production and material transfers of a consumer population can be estimated only if one understands the time changes in the structure and size of such populations, *i.e.*, the rates of age-specific mortality and the schedule of recruitment by which the population is sustained.

In another paper we have discussed the demography of *Uta stansburiana* and related annual changes in densities of this species to changes in schedules of female survival and fecundity (Turner *et al.*,

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unpublished). In this paper we describe some of the attributes of fenced populations of the whiptail lizard, *Cnemidophorus tigris*, in southern Nevada as determined by six years of continuing study. We consider not only structural features (age distributions and sex ratios), but also estimate age-specific survival and fertility over a two-year period. Finally, we attempt to explain the population increase observed between 1965 and 1966 in terms of estimated regimes of egg production and survival.

METHODS. The facilities in Rock Valley have been described in detail elsewhere (French 1964, Turner *et al.* 1965, Turner and Lannom 1968). Four circular 20-acre areas, three fenced, have been under continuous observation since 1964. One of the fenced plots (2) is subjected to essentially continuous gamma irradiation from a centrally located Cs¹³⁷ source. French *et al.* (1966) and Turner and Lannom (1968) have discussed the radiation field and tissue doses sustained by animals.

Cnemidophorus were captured by noosing in each of the four areas during 1964, 1965, and 1966. We also worked in one of the fenced control plots (1) during August of 1962 and in 1963. In 1967, we sampled only two fenced areas (2 and 3) and in 1968 we worked again in all three fenced areas. Captured animals were marked by toe-clipping and released after snout-vent lengths and body weights were determined. Age assignments (in months) were made for all newly registered animals. We could distinguish young-of-the-year (in August and September), yearlings (8–10 months old in the spring), and two-year olds (20–22 months) with reasonable certainty. In six cases age assignments of 33 months were made. No new animal was ever assigned a greater age.

In 1965, 1966, and 1967 female *Cnemidophorus* were collected in adjoining portions of Rock Valley. The ovaries of these animals were examined by autopsy. Conventional records of the number of follicles, oviducal eggs and corpora lutea were maintained. Clutch size was inferred from the numbers of these stages counted. Follicles less than 5 mm in diameter were not included in our calculations. Large ovarian follicles and oviducal eggs, or follicles and corpora lutea, were interpreted as evidence of two clutches. However, the absence of mixed stages in ovaries did not exclude the possibility of more than one clutch.

Spring densities were evaluated by two methods. First, we made capture-recapture analyses as suggested by Bailey (1952). Our approach was as follows. Those animals registered in a given year (except young-of-the-year marked in August and September) were considered

the marked cohort (*a*). All individuals registered in the ensuing year (except for one-year olds and young-of-the-year) constituted the second sample (*n*), and recaptures (*r*) were simply those animals originally registered in *a* the previous year. Each pair of consecutive years was analyzed separately, and the capture-recapture history of each individual was assessed independently of events in any but the two years in question. This procedure may seem cumbersome, but we suspect that it is more reliable than capture-recapture analyses based on short-term samples. The period of above-ground activity of adult *Cnemidophorus* in Rock Valley is compressed into a period of about four months (late April to early August). Not all animals are active throughout this period. Females become active later in the season than males. There is thus a dilution effect as the season advances, and not all of the population is active at any one time (see Tanner and Jorgensen 1963).

We also estimated spring density by direct enumeration. In establishing a roster of all animals alive in a given season we considered records from all subsequent seasons. An animal registered in 1964 and 1966 was known to be alive in 1965, etc. Also, an animal newly registered at an estimated age of 20 months was known to have been an unregistered yearling during the previous year. Sex ratios were inferred from these registries. Minimal age-specific survival was estimated from the recoveries of marked animals. Survivorship between t_0 and t_1 was based only on animals registered directly at t_0 . Animals assumed to be alive at t_0 because of subsequent capture were not included in these calculations.

The biomass of the spring standing crop was estimated from the following: 1) the population density, based on capture-recapture estimates, 2) age distribution of the population, inferred from the annual sample, and 3) the mean weight of males and females of known ages.

RESULTS. Estimated spring densities and biomass of *Cnemidophorus* in the four plots are given in Table 1. The 1968 data are reflected in this table only insofar as they contribute to density estimates for previous years. We have not attempted to infer the size of the 1968 populations. Minimum registrations were always less than the corresponding capture-recapture estimates, and we judge that the discrepancies are an approximate measure of our sampling efficiency. In the three fenced areas the minimum registries averaged about 90% of the capture-recapture estimates. Hence, our method of direct enumeration is a reasonable assessment of numbers when 1) the area is fenced, and 2) the registry for a given year is predicated on data available from that year as well as several subsequent years. Minimum registries for the

TABLE 1

Estimated density and biomass of *Cnemidophorus tigris* in four 20-acre areas in Rock Valley, Nevada. Each cell gives, from top to bottom; 1) the minimum number of animals known to be alive during the spring of each year, 2) a capture-recapture estimate of this datum (with standard deviation, and 3) the estimated biomass (g/acre). Plot 4 is not fenced and plot 2 is irradiated

| Year | Areas | | | |
|------|---------|----------|----------|----------|
| | 1 | 2 | 3 | 4 |
| 1963 | 113 | | | |
| | .. | | | |
| 1964 | 77 | 65 | 86 | 95 |
| | 99 (13) | 68 (4) | 105 (12) | 138 (19) |
| | 53 | 49 | 59 | 90 |
| 1965 | 74 | 64 | 81 | 90 |
| | 83 (7) | 65 (2) | 89 (7) | 137 (20) |
| | 43 | 46 | 60 | 78 |
| 1966 | 147 | 107 | 141 | 110 |
| | .. | 130 (14) | 159 (14) | .. |
| | .. | 91 | 114 | .. |
| 1967 | .. | 80 | 137 | .. |
| | .. | 86 (9) | 139 (8) | .. |
| | .. | 60 | 99 | .. |

unfenced plot (4) were only about 68% of the capture-recapture estimates. *Cnemidophorus tigris* is a highly vagile species and the data from the unfenced plot probably reflect some immigration. We consider the data from the three fenced areas to be the most reliable, and we have not used data from the unfenced plot in our analysis of survival.

TABLE 2

Male:female ratios in populations of *Cnemidophorus tigris* studied in Rock Valley, Nevada. Numbers represent all animals known to be alive in the spring of each year

| Year | Areas | | | | Totals |
|------|-------|-------|-------|-------|---------|
| | 1 | 2 | 3 | 4 | |
| 1963 | 53:60 | | | | 53:60 |
| 1964 | 35:42 | 30:35 | 45:41 | 50:45 | 160:163 |
| 1965 | 36:38 | 29:35 | 40:41 | 49:41 | 154:155 |
| 1966 | 77:70 | 51:56 | 67:74 | 58:52 | 253:252 |
| 1967 | | 47:33 | 63:74 | | 110:107 |

Data pertaining to sex ratios are given in Table 2. Males and females are equally abundant. We emphasize that these data reflect all individuals known to be alive at the beginning of the period of spring activity, regardless of when these animals were actually registered. Thus, we are describing the true rather than apparent structure of the population. We recognize that seasonal differences in the activity of males and females produce apparently unbalanced sex ratios at certain times of the year. This effect may be intensified by behavioral differences.

TABLE 3

Estimated age distributions of *Cnemidophorus tigris* populations in Rock Valley, Nevada

| Area | Year | Age, Months | | | | | |
|------|------|-------------|-----------------|-----------------|-----------------|-----------------|-------|
| | | 8-12 | 20-24 | 32-46 | 44-48 | 56-60 | 68-70 |
| 1 | 1964 | 29 | 31 | 16 ¹ | 1 ¹ | .. | .. |
| | 1965 | 31 | 18 | 17 | 8 | .. | .. |
| | 1966 | 100 | 22 | 10 | 9 | 6 | .. |
| 2 | 1964 | 14 | 51 ² | .. | .. | .. | .. |
| | 1965 | 19 | 11 | 34 | .. | .. | .. |
| | 1966 | 61 | 15 | 9 | 22 ² | .. | .. |
| 3 | 1967 | 23 | 38 | 6 | 6 | 7 ² | .. |
| | 1964 | 35 | 46 ² | 5 ² | .. | .. | .. |
| | 1965 | 23 | 31 | 26 | 1 | .. | .. |
| | 1966 | 91 | 16 | 16 | 17 ² | 1 | .. |
| | 1967 | 31 | 75 | 9 | 9 | 12 ² | 1 |

¹ Of the 17 animals 30 months and older in area 1 in 1964, all but one were recaptured individuals marked initially in either 1962 or 1963.

² Includes some older individuals of unknown age.

Estimated age distributions for three areas are given in Table 3. There are uncertainties associated with some of the original age designations. We adopted a conservative position when original designations were made, but six individuals were assumed to be 33 months of age when first registered. These animals, four males (93 mm) and two females (90 and 93 mm), were near maximal size when first marked. Males 21 months of age rarely exceed 90 mm in snout-vent length; females of this age are usually < 88 mm. As our study progressed the uncertainties in the age distributions diminished, and we believe that the 1966 and 1967 data are reasonably accurate. The main deficiency is that the 44-48 month age group in plots 2 and 3 include older individuals. In 1968 we recaptured two individuals judged to be 81 months old.

TABLE 4

Minimal survival (1964-5 and 1965-6) observed among *Cnemidophorus* in Rock Valley, Nevada. Data from three 20-acre fenced areas are combined. Numbers of individuals registered at beginning of each time interval are given in parentheses

| Year | Age intervals, months | | | | | Totals (>8) |
|-----------|-----------------------|-----------|------------|-----------|----------|-------------|
| | 0-8 | 8-20 | 20-32 | 32-44 | 44-56 | |
| 1964-1965 | | 0.53 (36) | 0.57 (121) | 0.25 (12) | | 0.54 (169) |
| 1965-1966 | 0.52 (60) | 0.68 (57) | 0.55 (56) | 0.57 (69) | 0.50 (4) | 0.60 (186) |

Minimal age-specific survival is given in Table 4. Clearly, after the age of 9 months is attained, annual survival is good and may approach or exceed 60%. We have not acquired as much information on survivorship between birth and the age of 8 months because it is difficult to register large numbers of the young during the fall. In addition to the data given in Table 4 (for 1965-66) we have data from other years (1963-64, plot 1; 1966-67, plots 2 and 3). In these years 8 of 26 females and 23 of 64 males marked shortly after hatching survived to the age of at least 8 months. We believe that this minimal survival rate (0.34 for the sexes combined) was significantly inferior to that observed between 1965 and 1966 (0.52). For all years combined, 22 of 53 females (0.42) and 40 of 97 males (0.41) survived until 8 months of age.

TABLE 5

Mean clutch sizes observed among *Cnemidophorus tigris* in Rock Valley, Nevada. Sample sizes are given in parentheses

| Year | Snout-vent length (mm) | |
|-----------------|------------------------|-------------------------------------|
| | 73-89 (9-21 months) | 90* (usually 33 months or older) |
| 1965 | | |
| first clutch | 2.46 (26) | 3.73 (15) |
| second clutch | 2.50 (6) | 3.33 (3) |
| 1966 | 2.56 (9) | 3.25 (8) |
| 1967 | 2.18 (28) | 3.50 (2) |
| unweighted mean | 2.42 | 3.45 |

Mean clutch sizes observed are given in Table 5. Of the 41 females examined in 1965 nine (22%) exhibited evidence of a second clutch, but only one of the 47 reproductive females examined in 1966 and 1967 showed such signs. We do not know the true proportion of females of females laying two clutches but it is certainly clear that two clutches

were much more common in 1965 than in 1966 and 1967. As would be expected, large females laid more eggs than small ones. Some of the larger females exhibited as many as five large yolked follicles in 1965.

We believe that the typical pattern of fecundity is one annual clutch of 2-4 eggs, depending on the size of the female. The 1965 data showed that two clutches are within the physiological capacity of the species, but the events promoting this increased fertility are not surely known. The data in Table 5 suggest that if increases in population size occur, they result from the deposition of multiple clutches rather than increased clutch size. In 1965 four females 73-75 mm in snout-vent length were reproductively active, and some of these may have been only 9 months old. Normally, sexually mature females are 80 mm or longer, and 21 months old. Only two of the reproductively active females examined in 1966 and 1967 were less than 80 mm.

DISCUSSION. What may now be inferred as to the structure and performance of populations of *Cnemidophorus* in southern Nevada? Spring densities in our areas ranged from around 3 to 8 per acre between 1964 and 1967. Biomass varied comparably between 43 and 114 g/acre. Apparently 1964 and 1965 were years of approximate equilibrium, but the enhanced reproduction in 1965 resulted in a distinct increase in spring densities in 1966. The 1965 recruitment also led to 1966 populations in which around 57-68% of the populations were made up of individuals 8-10 months of age.

In another paper we discussed the correlation of egg production by *Uta* with the production of winter annuals, and suggested a causal relationship mediated by the abundance of ground-dwelling arthropods (Hoddenbach and Turner 1968). Sampling data indicated that production of winter annuals in Rock Valley was 0.35 g/m² in 1964, 0.02 g/m² in 1965 and 13.7 g/m² in 1966 (Beatley, unpublished). Rock Valley populations of *Uta* increased about 40% between 1966 and 1967 (Turner *et al.* 1969). Conversely, populations of *Cnemidophorus* increased sharply between 1965 and 1966, but not between 1966 and 1967.

It appears, then, that *Uta* may be responding to factors not strongly related to changes in *Cnemidophorus*. If *Uta* is most sensitive to yearly differences in winter annual production, whiptail lizards may be more closely tied to fluctuations in the growth of perennials, and to the arthropod species associated with these shrubs. The spring of 1965 was unusual phenologically. Although the fall and winter rainfall of 1964-65 failed to promote annual growth and germination, heavy rains in late March and early April of 1965 resulted in scattered germi-

nation of annuals. These plants matured about six weeks later than usual (Beatley 1966). Perhaps more important was the strong flush of perennial growth and fruiting which followed these rains (Beatley 1965). It is possible that the egg production by *Cnemidophorus* observed in 1965 was indirectly supported by the perennial growth occurring at a time when egg development was under way. Whether the late maturation of winter annuals was also implicated we do not know.

A review of estimated densities of four species of *Cnemidophorus* (Table 6) indicates that the eastern *C. sexlineatus* apparently regu-

TABLE 6

Some density estimates for species of *Cnemidophorus* (see also Tinkle 1967)

| Species | Density (per acre) | Locale | Reference |
|--------------------|--------------------|-------------------------|---------------------------|
| <i>sexlineatus</i> | 400-800* | Oklahoma | Carpenter (1959) |
| <i>sexlineatus</i> | 100* | Virginia | Bellis (1964) |
| <i>sexlineatus</i> | 40-72 | Kansas | Fitch (1958) |
| <i>tigris</i> | 7 | Colorado | McCoy (1965) |
| <i>tigris</i> | 12 | Yucca Flat, Nevada | Tanner & Jorgensen (1963) |
| <i>tigris</i> | 18 | Black Gap, Texas (1952) | Milstead (1965) |
| <i>tigris</i> | 74 | Black Gap, Texas (1962) | Milstead (1965) |
| <i>tigris</i> | < 5† | New Mexico | Degenhardt (1966) |
| <i>gularis</i> | 38 | Texas | Milstead (1961) |
| <i>hyperythrus</i> | 24 | California | Bostic (1965) |

* Judged very rough estimates by Tinkle (1967).

† More of an index of relative abundance than a measure of absolute numbers.

larly maintains higher densities than the more western *tigris*. In fact, spring densities of *tigris* of more than 20/acre would be remarkable. We emphasize that the exceedingly high density of *tigris* reported by Milstead (1965) at Black Gap in 1962 was associated with a dramatic 10-year change in the quality of the vegetation, and is not comparable to the earlier density of 18/acre registered at a time when the area was relatively impoverished. Year-to-year changes in density are to be expected, but we judge that more than 2-fold fluctuations of this nature would be unusual. Mechanisms of regulation are at present unknown; *C. tigris* in Rock Valley is not known to figure prominently as prey in any known predator-prey relationship.

The sex ratio is apparently 1:1 in our areas. We stress this point because it is impossible to ascertain this fact by casual sampling. Our collection of reproductive samples always yielded more males than females, and conventional sampling procedures accumulated consider-

ably more records of males—at least early in the season. For example, April-May registrations in the areas between 1963 and 1967 included 378 males and 244 females; during July and August 285 males and 293 females were recorded. The trapping records of Tanner and Jorgensen (1963) indicated a similar experience on Yucca Flat. Only repeated sampling, with a view towards establishing a roster of all different individuals in the population can determine the true sex ratio. With the exception of Fitch (1958) and Bostic (1966), other workers with *Cnemidophorus* have recorded a preponderance of males. Of 100 lizards examined by Tinkle (1959) 62 were males, and he stated that: "Males outnumber females in every month when samples of five or more lizards were available, with the ratios being almost equal in October." McCoy (1965) stated that males outnumber females 6:4 in Colorado, and attributed the difference to somewhat greater mortality in females. If this be true, the situation in his areas differs from that which we have observed in Rock Valley. Bellis (1964) registered 26 males and 18 females of *C. sexlineatus* in Virginia, and this is probably an expression of the problems we have discussed above.

The life-span of *C. tigris* is at least 6 years in Colorado (McCoy 1965) and 7 years in Nevada. We suspect that greater ages may be attained, but such old animals are probably not important in the function of the population. The maximum life-span is similar to that observed by Fitch for *C. sexlineatus* in Kansas. Not surprisingly, irregular age distributions build up, reflecting survival from earlier good and bad years. The relationship between the good reproductive success in 1965 and the 1966 age distribution has already been pointed out. We judge also that 1962 was probably a relatively good year.

The long life-span and complex age distributions of *C. tigris* make it difficult to evaluate age-specific survival. Fitch (1958) estimated about 50% survival per year from his 3-year composite age distribution of *C. sexlineatus*, but we believe that an attempt to infer a vertical life table from an instantaneous age distribution would be fruitless where distinct year-to-year differences in reproductive success occur (as in Nevada). Rather, one must attempt to follow the experience of particular age cohorts over a period of several consecutive years. The Nevada *Cnemidophorus* show very good survival, at least after the age of 8-10 months has been attained. Tanner and Jorgensen (1963) reported a minimal annual adult survival of 59%, which is in good accord with our estimates. The adaptive value of extended life-spans in desert areas where reproduction may be very poor in certain years is clear.

As a general pattern we believe that the Nevada *Cnemidophorus* become sexually mature at the age of 21 months. Thereafter, they

usually lay one clutch of 2–4 eggs a year. We know that departures from this schedule occur, but we cannot yet assess the significance of these variations. We do not believe that the number of females attaining sexual maturity at the age of 9 months is apt to be important, but this issue is not a closed one. Tinkle (1959) originally concluded that *C. tigris marmoratus* in Texas matured at the age of 20 months (as did Milstead 1957). More recently Tinkle (1967: 48) has maintained that *C. t. marmoratus* matures in one year, basing this view on work by Hoddenbach (1965) and Medica (1967). McCoy (1965) reported that *C. t. septentrionalis* in Colorado became sexually active at an age of about 22 months, and this is in accord with our findings.

Of potentially greater importance in Nevada, and more difficult to assess, is the frequency of clutches. McCoy and Hoddenbach (1966) have compared the frequency of clutches laid by *C. tigris* in Texas and Colorado and concluded that whereas only one clutch is laid annually in Colorado, Texas females lay two. The authors might have given more consideration to possible year-to-year departures from these regimes. We believe it likely that many lizard populations exhibit such variations, depending on annual fluctuations in weather and available food.

In the concluding portion of this paper we present a suggested reconciliation of the estimated 1965 reproduction with the change in population size and structure observed between 1965 and 1966. If we consider the capture-recapture estimates of total population size given in Table 1 and the estimated age distributions given in Table 3, we can calculate the numbers of breeding females alive in the three areas in 1965. For example, the expected number of females 20 months of age in plot 1 in 1965 would be $83(1/2)(18/74)$, or ten. We can then estimate the number of young that these females would have produced given the following simplifying assumptions: 1) no females < 20 months of age laid eggs, 2) all females \geq 20 months old in the spring of 1965 laid two clutches of eggs, and 3) there was no egg mortality. These procedures are illustrated in Table 7, in which data from three plots are combined. Finally, we can compare the recruitment suggested by Table 7 with the actual composition of the spring population of 1966 (Table 8). The number of yearlings alive in 1966 was calculated by summing the products of the best estimates of 1966 density (Table 1) and the fractions of the 1966 populations made up of individuals 8–12 months old (Table 3). For example, the expected number of yearlings in area 2 in 1966 would be $130 \times 61/107$, or 74.

Given the assumptions described above, the figures given in Table 8 are consistent. However, this accord must be somewhat fortuitous, and

TABLE 7

A suggested schedule of reproduction by female Cnemidophorus tigris in three 20-acre areas in Rock Valley, Nevada, during 1965

| Age, months | Number of females | Mean clutch size | Number of young hatched* |
|-------------|-------------------|------------------|--------------------------|
| 20 | 33 | 2.46 | 81 |
| | | 2.50 | 83 |
| 32 + | 46 | 3.73 | 172 |
| | | 3.33 | 153 |

* Assuming no egg mortality.

TABLE 8

A comparison of the estimated number of young Cnemidophorus tigris surviving from the summer of 1965 to the spring of 1966 based on (i) the 1965 fecundity data, and (ii) the observed size and age-composition of the 1966 population

| Estimated 1965 hatch (from Table 7) | Minimal survival rate from 0–8 months (from Table 4) | Estimated survivors, spring of 1966 | 8-month old individuals alive in the spring of 1966 (estimated from Tables 1 and 3) |
|-------------------------------------|--|-------------------------------------|---|
| 489 | 0.52 | 254 | 270 |

the result of compensating errors. It is unlikely that all females \geq 20 months of age actually reproduced, and certainly there was some egg mortality. Maslin (1966) reported poor hatching success (0–50%) in the laboratory of eggs of four unisexual species of *Cnemidophorus*, but it is probably inappropriate to compare the bisexual *C. tigris* with unisexual forms. It is also improbable that all females laid two clutches in 1965. These considerations would all tend to reduce the production of young. We suggest that whatever errors have been introduced in this manner have been approximately compensated by underestimates of survival.

Although problems still remain, we have established at least lower limits for some important parameters. Future work should be addressed to 1) a documentation of the degree of year-to-year variability in the reproductive performance of females, and of the factors promoting this variability, and 2) a search for possible evidence of regulatory mechanisms tending to stabilize the abundance of this species in a distinctly variable environment.

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