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Life History of a Successful Colonizer: the Mediterranean Gecko, *Hemidactylus turcicus*, in Southern Texas

KYLE W. SELCER

A southern Texas population of the introduced lizard *Hemidactylus turcicus*, was examined for life history characteristics of a colonizer. Density estimates were high, ranging from 544–2210 lizards per ha. The population was early maturing (8.6 months) with low fecundity (1–3 clutches of two eggs/yr) and high survivorship for a small lizard (55% annual turnover, three or more year life-span). Survivorship was similar between adults and juveniles, but small juveniles (<30 mm) had significantly lower survivorship than large juveniles (30–43 mm). The Mediterranean gecko's success in southern Texas appears to result from low predation pressure, little interspecific competition and a life history which maximizes survival at all ages. This gecko's ability to disperse may be enhanced by its calcareous shelled eggs serving as propagules of new colonies.

LEWONTIN (1965) suggested that colonizing species should have a life history which maximizes reproductive output through early maturity and high fecundity. However, because the costs of early maturity and high fecundity are levied against somatic growth and longevity, colonizers would be expected to have small bodies and short life-spans as well (Hairston et al., 1970; MacArthur and Wilson, 1967; Pianka, 1970).

The purpose of this study was to determine the life history of a colonizing lizard, the Mediterranean gecko (*Hemidactylus turcicus*) in a population from southern Texas. The Mediterranean gecko was introduced to the United States less than a century ago, but has become well established throughout the Gulf coastal states (Conant, 1975). The first report of *H. turcicus* in Texas was from Brownsville (Conant, 1955). Davis (1974) reported that the gecko's range in Texas consisted of many well established populations found south of a line from Del Rio through San Antonio to Austin and Houston, Texas. However, the gecko has continued to expand its range farther north to include Fort Worth (Gary Ferguson, pers. com.) and west to include Big Bend National Park (Easterla, 1978) and El Paso (Jerry Johnson, pers. com.). Recent reports from Georgia and Alabama indicate that *H. turcicus* continues to colonize elsewhere as well (Bechtel, 1983; Dundee, 1984).

Despite the broad range of *H. turcicus* in the United States, little is known of the life history of this gecko. Rose and Barbour (1968) studied a New Orleans population and provided information on habitat and activity, movement, food and feeding habits and reproduction. Other reports on the ecology of *H. turcicus* in the United States are largely anecdotal.

MATERIALS AND METHODS

A population of *H. turcicus* was studied from May 1981 through Aug. 1982 on the campus of Pan American University at Edinburg, Hidalgo County, Texas. The area has a subtropical climate with long hot summers and short mild winters. The temperature often exceeds 38 C in summer and rarely drops below 0 C in winter.

Man-made structures served as the primary study areas. Mark-recapture techniques were utilized on two study areas: a large brick building and four portable metal buildings. The brick building was irregular in shape, measuring 6 m in height and having a perimeter of 120.7 m for a total surface area of 724 m^2. The metal buildings measured 4 m in height, 20 m in length and 11 m in width for a total surface area of 248 m^2 each (992 m^2 total). The distance between metal buildings ranged from 4–6 m. Buildings were divided into 6.1 m sections with chalk lines that served as reference points for measuring locations.

Surveys of the study areas were conducted in all months except Jan. and March. Each study area was surveyed by walking around the build-

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ing until the entire surface was covered. Surveys were conducted at all hours from dusk to dawn, but were concentrated from 2200–0200 h.

Lizards were captured by hand and permanently marked by toe-clipping (Tinkle, 1967). Upon each capture, the following data were recorded: date, time of day, location, body weight to 0.1 g using a Pesola spring scale, snout–vent length (SVL) in mm, sex and reproductive condition of females. Sex was determined by examining individuals for the presence or absence of pre-anal pores, which are found only in males. Sex of juveniles could not be determined in the field. Reproductive condition of females was determined by "candling" individuals using a flashlight. Oviductal eggs and larger yolked follicles (>4 mm) can be seen through the body wall due to the lack of a black peritoneum in this species. Lizards were processed at the site of capture and no individual was held captive for more than 30 min.

Biweekly collections of lizards were made from buildings not used in the mark-recapture study. An attempt was made to collect 15 adults of each sex on each sampling date. Lizards were collected by hand, placed in plastic bags and frozen until processed. Upon processing, body weight was taken in mg on a Mettler P 163 balance, SVL and tail length were measured to the nearest mm and sex was determined. Lizards were necropsied and reproductive condition was noted. In females, the number of yolked follicles (>10 mg), oviductal eggs and corpora lutea were recorded. Yolked follicles and oviductal eggs were removed and weighed in mg. In males, the right testis was removed and weighed in mg. Sperm smears were prepared by crushing a section of ductus deferens on a slide. Slides were then checked for the presence of spermatozoa.

Most information on reproductive parameters came from the biweekly collections. Males were considered reproductively active if they contained sperm in the ductus deferens. Females were considered reproductively active if they contained yolked follicles or oviductal eggs. Clutch size was determined from counts of yolked follicles, oviductal eggs and corpora lutea. Yolked follicles and oviductal eggs found simultaneously in the same individual was taken as evidence of multiple clutches. There were insufficient recaptures of reproductively active females to determine clutch frequency directly. Therefore, clutch frequency was determined indirectly as the length of the reproductive season divided by the length of time required to produce a clutch.

Information on sex ratios was also obtained from the biweekly collections. χ^2-tests were used to determine if the observed sex ratios differed significantly from 1:1.

Growth rates were determined for lizards on the mark-recapture areas which were captured on two or more occasions at least 30 d apart. Growth rate for an individual was estimated as the change in SVL between captures divided by the time span separating the capture dates.

Minimum size at sexual maturity was determined from the smallest individual of each sex which was reproductively active. Age at sexual maturity was estimated from measurements of lizards marked as juveniles and later recaptured as adults. A growth line was drawn for each individual with months on the abcissa and SVL on the ordinate. A horizontal line was drawn at the minimum size at sexual maturity (44 mm). The date that sexual maturity was achieved was estimated as the day corresponding to the point of intersection of the growth line and the minimum size at sexual maturity line. Date at hatching was extrapolated for each individual using the mean size at hatching (24 mm) and the growth rate for hatchlings (6 mm/month). Given the date at sexual maturity and the date at hatching, the age at sexual maturity was calculated.

Population size was estimated from mark-recapture data using a weighted Lincoln-Peterson method (Begon, 1979) and a minimum numbers method. Minimum number estimates were calculated as the number of lizards known to be alive at each survey date. Density was estimated as the population size divided by the surface area of the study area.

Throughout the study, notes were taken on activity, behavior, nesting, potential predators and potential competitors. Statistical methods not otherwise specified are those of Sokal and Rohlf (1981). Means, where given, are accompanied by ± 2 standard errors. Probabilities of less than 0.05 were considered significant.

Results

Sex ratios and reproduction.—Table 1 shows the number of males and females collected in each sample. In no sample did the ratio of males to females differ from 1:1, nor did the total num-

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TABLE 1. PERCENTAGES OF REPRODUCTIVELY ACTIVE MALE AND FEMALE *Hemidactylus turcicus* AMONG SAMPLES.

	Male		Female	
Sample	N	% Reproductive	N	% Reproductive
1981				
15 June	8	—	3	66
1 July	8	88	8	63
15 July	15	100	14	100
1 Aug.	21	95	13	77
15 Aug.	12	75	12	50
1 Sept.	20	95	17	24
15 Sept.	15	27	19	0
1 Oct.	24	21	25	0
15 Oct.	11	0	25	0
1 Nov.	13	7	18	0
15 Dec.	13	23	7	0
1982				
1 Feb.	13	62	7	0
1 April	22	100	9	44
15 April	14	93	20	45
1 May	14	100	11	91
15 May	19	100	17	65
1 June	19	100	13	92
15 June	18	100	19	95
1 July	18	100	18	94

ber of males and females taken differ from a 1:1 sex ratio.

Of 323 females collected in 22 samples (Table 1), the earliest a reproductively active female was taken was April 1 and the latest was Sept. 1. This suggests a potential reproductive season of 154 d. However, only samples from May 1 through Aug. 15 contained over 50% reproductively active lizards; thus, the reproductive season for most females probably extended no more than 107 d.

The first female with oviductal eggs was taken on May 15. Four lizards in the May sample contained corpora lutea, indicating recent oviposition. Given that reproduction began about April 1 and that lizards with oviductal eggs and corpora lutea were first found on May 15, it appears that clutch production required about 45 d. One female in the mark-recapture study contained oviductal eggs on two occasions 40 d apart. These data suggest that there is time for approx. three clutches of eggs per season.

Three lines of evidence suggest that multiple clutches are produced: 1) eight females contained oviductal eggs and small yolked follicles

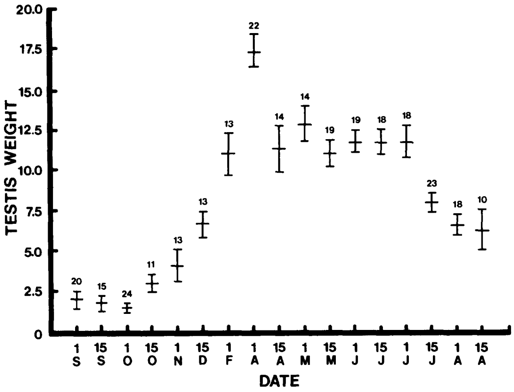

Fig. 1. Comparison of mean testis mass among samples of *Hemidactylus turcicus*. Horizontal lines represent means, vertical lines represent ±1 SE. Numbers are sample sizes.

(10–74 mg) simultaneously; 2) six lizards contained corpora lutea and small yolked follicles simultaneously; and 3) two females from the mark-recapture study were reproductively active at two widely separated times in one year.

One hundred sixty of 323 females necropsied contained yolked follicles or oviductal eggs. All but five of these developed exactly two follicles per clutch, one in each ovary. One individual contained two medium yolked follicles (75–150 mg) in the left ovary and a small yolked follicle in the right ovary. Two females contained two medium yolked follicles in the right ovary and unyolked follicles in the left ovary. Two individuals held one oviductal egg and two corpora lutea.

Relative clutch mass was determined as clutch mass divided by the total mass of the lizard (Vitt and Congdon, 1978; Vitt and Price, 1982). Relative clutch mass for 33 *H. turcicus* averaged 0.156 ± 0.038 (range = 0.106–0.268).

A total of 348 males was taken in 22 samples from June 15, 1981 to Aug. 15, 1982 (Table 1). Reproductively active males were taken in all samples except Oct. 15. High percentages of reproductively active males (>75%) were found from April 1 to Sept. 1, the same period in which reproductively active females were taken.

Mean testis mass was high from April until late July. In Aug., testis mass began to decrease (Fig. 1). Mean testis mass decreased steadily from Aug. 15 through Oct. 1, then increased steadily until it peaked on April 1. Sperm remained in the ductus deferens after the onset of testicular regression as evidenced by the lag between the

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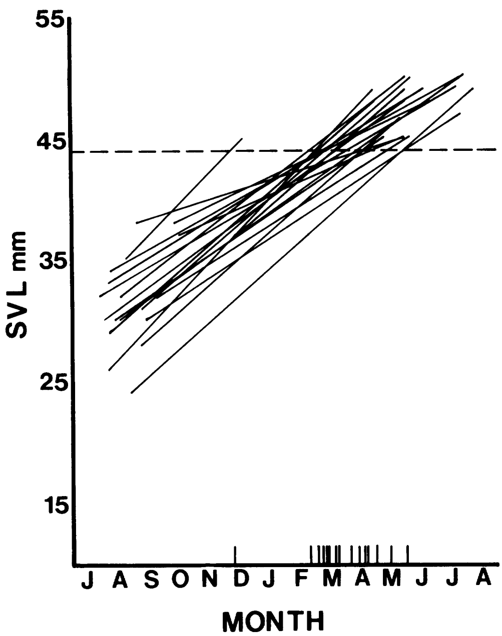

Fig. 2. Date at sexual maturity for 20 *Hemidactylus turcicus* marked as juveniles and recaptured as adults. Solid lines represent growth lines, dashed line marks the minimum size at sexual maturity. Short lines at the bottom mark the date at sexual maturity.

date that testis weights began to decline and the date the percentage of reproductively active males decreased.

Growth, age at maturity and size.—Growth rates of 93 individuals ranged from 0–10.9 mm/month ($\bar{x} = 1.49 \pm 1.76$ mm/month). There was no significant difference in growth rate of males and females ($t = 0.28$, 77 df, $P > 0.05$). Growth rate was inversely related to SVL ($r = -0.60$, 91 df, $P < 0.001$) indicating that growth slowed as lizards grew. Growth slowed during the colder months, but did not cease altogether.

The smallest female containing yolked follicles or oviductal eggs measured 43 mm SVL. Only one of three females which measured 43 mm SVL during the reproductive season was reproductively active; thus, modal size at sexual maturity is 44–45 mm SVL. The smallest male containing sperm in the ductus deferens was 44 mm SVL. Only two 44 mm males were collected during the reproductive season and both were reproductively active. Males appear to reach sexual maturity at a size similar to that of females.

The age at maturity for 20 known-age lizards ranged from 5.9–10.9 months ($\bar{x} = 8.6 \pm 1.22$ months). Two individuals reached mature size in winter. However, the majority of lizards reached mature size in spring about nine months after hatching the previous summer (Fig. 2). Five females marked as juveniles in 1981 were reproductively active in 1982.

Table 2. Percentage of Lizards Comprising Four Size Groups Among Months.

Month	20–29 mm	30–39 mm	40–49 mm	50–59 mm	N
1981					
May	0	0	35	65	26
June	2	0	62	36	47
July	38	9	16	37	32
Aug.	43	22	11	24	91
Sept.	38	37	8	17	60
Oct.	19	47	28	6	36
Nov.	25	0	75	0	4
Dec.	30	40	25	5	43
1982					
April	0	6	66	28	32
May	0	14	50	36	90
June	0	4	42	54	69
July	17	5	21	57	42
Aug.	22	12	33	33	9

Table 2 shows the relative frequencies among months of lizards comprising four size categories. In April, most lizards were 40–60 mm SVL. Major increases in the percentage of hatchlings (20–30 mm SVL) occurred in July of each year, although hatchlings were recorded as early as June 2. The proportion of large (and presumably older) adult lizards (>50 mm SVL) declined as the percentage of hatchlings and subadults increased in Aug. and Sept. By Oct., only a small percentage of the active population measured over 50 mm SVL.

Recaptures, survivorship, density, and movement.—A total of 387 lizards was marked on the two study areas. Total captures equalled 606 for a mean of 1.6 captures per individual. Thirty-five percent of the lizards marked were recaptured at least once. The greatest number of captures for an individual was seven.

Survivorship was estimated as the percentage of lizards marked in 1981 which were recaptured in 1982. Although this method is not accurate for overall survivorship, it is adequate for comparisons of subsets of the population. A

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TABLE 3. DENSITIES (LIZARDS/HA) OF *Hemidactylus turcicus* FROM LINCOLN-PETERSON AND MINIMUM NUMBERS ESTIMATES FOR THE BRICK BUILDING AND THE METAL BUILDINGS.

	Brick building	Metal buildings
Lincoln-Peterson 1981	1326	685
Lincoln-Peterson 1982	2210	1310
Minimum numbers (high)	786	544

total of 21.5% of the lizards marked in 1981 were recaptured in 1982. Survival of adult females was not significantly different from that of adult males (G = 2.258, 1 df, $P > 0.05$). Survival was similar between adults and juveniles (G = 1.89, 1 df, $P > 0.05$) but was significantly lower for small juveniles (20–30 mm SVL) than for large juveniles (30–43 mm SVL) (G = 9.724, 1 df, $P < 0.05$). Thus, mortality is highest shortly after hatching.

Lincoln-Peterson estimates of population size varied considerably between study areas and between years. Population estimates for the metal buildings were 67.8 (95% C.I. = 45–136) for 1981 and 129.9 (95% C.I. = 103–177) for 1982. Population estimates for the brick building were 96.0 (95% C.I. = 72–134) for 1981 and 160 (95% C.I. = 103–286) for 1982. Minimum number estimates were considerably lower than Lincoln-Peterson estimates. Minimum number estimates were 52 for the metal buildings and 54 for the brick building. Density estimates are shown in Table 3. Density estimates ranged from 544–2210 lizards/ha depending on the method, year and study area.

Movement between metal buildings was infrequent even though the distance between buildings was only 4–6 m. Of 72 lizards which were captured at least twice on the metal buildings, only two moved between buildings. One was a juvenile, the other a small male. Both lizards shifted to adjacent buildings and were less than 6 m from their original capture points.

Nesting behavior.—A number of nests of *H. turcicus* were discovered in attics, sheds, garages and between wallboards of houses. Nests were often located in boxes of old papers, in drawers of cabinets and in piles of old clothing. Egg number within a nest ranged from 2–20 and eggs within a nest were in all stages of development, as evidenced by their color (eggs of *H. turcicus* change from white to pink to blue as they develop). Nest sites were apparently reused year after year. Old egg shells frequently formed a thick layer beneath newly deposited eggs. Eggs in nests were often covered with debris consisting of dirt, paper shreds or old egg shells.

DISCUSSION

The Mediterranean gecko is abundant in the Lower Rio Grande Valley of Texas. Densities found in this study exceed those of any sympatric lizard species and rival those of North America's most abundant squamates (Turner, 1977). The high densities of *H. turcicus* reported here may not be unusual for this species as evidenced by surveys I conducted along the coast of the Gulf of Mexico. I collected 25 or more *H. turcicus* in roughly 2 h surveys of each of the following cities: Corpus Christi and Galveston, Texas; New Orleans, Louisiana; Gainesville, Tampa, Miami and Key West, Florida. The time required to collect 25 geckos in Edinburg was also 2 h, suggesting that gecko abundance in coastal cities may be as great as in Edinburg. Additionally, Rose and Barbour (1968) marked 265 *H. turcicus* on two five story buildings during a 20 month study in New Orleans, Louisiana. These data suggest that *H. turcicus* may commonly occur in populations of high density. High densities coupled with rapid dispersal (Davis, 1974) indicate that this gecko is a successful colonizer.

Discussions of life history often focus on the parameters of age at maturity, age specific fecundity and age specific survivorship. *H. turcicus* reaches mature size the spring following hatching, at about nine months of age. The Edinburg population can thus be considered early maturing. Mediterranean geckos have low fecundity. The fixed clutch size of two eggs, coupled with a clutch frequency of 1–3 clutches per season results in an annual fecundity of only 2–6 eggs. Mediterranean geckos have a relatively long life-span for a small lizard. Analysis of growth rates of *H. turcicus* revealed that individuals of 50 mm SVL are approx. 2 yr old. In the early summer, prior to the emergence of hatchlings, adults 50 mm SVL and over comprise about one-third of the population. Twenty-two percent of the individuals marked at 50 mm SVL and over were recaptured the following year. This indicates that Mediterranean geckos may commonly live 3 yr or longer.

All members of the subfamily Gekkoninae produce clutches of exactly two eggs (Bustard,

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1968). These geckos have low fecundity unless they can produce many clutches in a season. Data on *H. turcicus* indicate that they produce few clutches per season and have low fecundity. Information on clutch frequency of other geckos is sparse. Bustard (1971) suggested that *Oedura ocellata* may produce two clutches per season; however, there was no direct evidence of multiple clutches. Thus, clutch frequency for this gecko is as low as, or lower than, that of *H. turcicus.*

Some lizards other than geckos have fixed clutch sizes. The most well known of these are the anoles, which produce one egg per clutch. However, at least one species of anole (*Anolis carolinensis*) produces clutches very frequently and has an annual fecundity considerably higher than that of *H. turcicus* (Andrews, 1985).

Many iguanid lizards show an increase in clutch size and therefore fecundity, with increasing body size. Mediterranean geckos cannot vary clutch size; thus, variations in fecundity are due solely to differences in clutch frequency. I found no evidence to suggest that larger lizards produced more clutches than smaller lizards. Also, egg size showed no relationship to female body size. It appears that fecundity is low for all ages of *H. turcicus.* However, the low age specific fecundity of this gecko may be in part countered by high survivorship. Total fecundity of a gecko which survived three breeding seasons would be 6–18 eggs, similar to that of a species having high fecundity with a one year life-span (e.g., *Holbrookia propinqua*: Selcer and Judd, 1982).

A wide array of survival mechanisms are employed by Mediterranean geckos from the egg to the adult. Eggs of *H. turcicus* are calcareous-shelled, as are eggs of all members of the subfamily Gekkoninae (Bustard, 1968). Calcareous-shelled eggs of geckos do not desiccate as rapidly as do parchment-shelled eggs (Dunson, 1982). Thus, gecko eggs may be deposited in many locations not available to lizards with parchment-shelled eggs, which must be placed in a proper moisture gradient to prevent desiccation. Hatching success may be higher for calcareous-shelled eggs than for parchment-shelled eggs because of the reduction in moisture related problems. Hatching success of 100 eggs I collected in the field was 100%.

Mediterranean geckos utilize several predation escape and avoidance mechanisms, despite the apparently low predation pressures in southern Texas. The lizards are nocturnal, arboreal and cryptically colored. These are traits which reduce encounters with potential predators. When disturbed, Mediterranean geckos use known escape routes to cracks or holes in the walls. Hatchling and juvenile *H. turcicus* have brightly banded tails in contrast to their cryptically colored bodies. Tail wagging was often observed when young lizards were disturbed. Presumably, tail wagging draws a potential predator's attention toward the tail, which is easily autotomized if it is seized.

The factors which account for the abundance of *H. turcicus* are not necessarily those which facilitate dispersal. Davis (1974) demonstrated that the spread of the Mediterranean gecko through Texas followed the major highways leading north from Brownsville. He stated that produce trucks were the most likely agents for dispersal of the gecko. Evidence from the Edinburg population suggests that this is unlikely because geckos do not actively disperse. I calculated ranges of movement using the minimum polygon method (Rose, 1982) for all lizards captured four or more times. Mean range of movement was 0.93 m ($N = 15$, $SD = 1.04$ m), far below the daily movement of most lizards. Also, only two lizards changed buildings even though there was a short distance between buildings. Rose and Barbour (1968) reported that 82% of the *H. turcicus* they recaptured were within 6 m of the initial capture site.

The egg may be the Mediterranean gecko's primary form of dispersal. The calcareous shell would allow eggs to be transported for long periods of time without desiccation. The average incubation time is about 40 d (Rose and Barbour, 1968) thus affording a long period of time the embryo could survive without food or water. Werner (1972) suggested that the calcareous-shelled egg probably evolved in connection with arboreality. The features of this egg which made it advantageous for arboreality (i.e., drought resistance) may have been preadaptive for dispersal.

The case for dispersal of *H. turcicus* by eggs is strengthened by this species nesting habits. The eggs are often located in boxes, which could be transported when people move. The communal nest in these boxes may contain as many as 20 eggs. A box containing a communal nest could thus carry a mini-colony.

The Mediterranean gecko represents an excellent model for study of the evolution of life history characteristics in a colonizing species. Comparative studies of old vs new colonies (in-

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cluding old world colonies) could provide information on the relative importance of various life history characteristics. Data collected in this study suggest that these colonizing geckos combine relatively high adult survivorship with low fecundity but high egg survival. This suite of life history traits allows these geckos to achieve high densities in the absence of intense predation and competition pressures.

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