

OBSERVATIONS ON THE BREEDING ADAPTATIONS OF THE ROADRUNNER

ROBERT D. OHMART¹

Department of Zoology
University of California
Davis, California 95616

The Roadrunner (*Geococcyx californianus*) is a diurnal ground-dwelling cuckoo, which is a permanent resident in the arid and semiarid regions of southwestern North America. Some features of its physiology are known (Calder and Bentley 1967; Calder and Schmidt-Nielsen 1967; Calder and Schmidt-Nielsen 1968; Calder 1968). However, the presence of a salt-secreting nasal gland (Ohmart 1972) and studies on the efficiency in body water turnover in birds under simulated desert conditions (Ohmart et al. 1970) indicated that detailed field information was needed to integrate physiological and ecological findings in an attempt to better understand the Roadrunner's success in its hot, dry environment.

MATERIALS AND METHODS

All field observations were conducted in an area 7 miles S and 7 miles E of Tucson, Arizona. General information on nest site and height (23 nests) was recorded during the spring and summer of 1968, with intensive field investigations from April through September of 1969. A total of 269 hours of nest observations (using a 30× spotting scope) were made on four nests (herein referred to as A, B, C, D) from blinds situated 15–20 m away. Initially the birds seemed shy, but after 4–5 hr a pair appeared disturbed only when the observer was outside the blind.

Black-bulb readings were noted hourly, or whenever one of the parents came into or left the nest. The black-bulb consisted of a metal commode float painted with black total solar absorption paint. A thermometer inserted through a rubber stopper was positioned so that the mercury-filled bulb was in the center of the float. The system was suspended nest high beside the blind and fully exposed to solar radiation.

Core temperature readings of a nestling were obtained with a telemetry unit produced by Sensory Systems Laboratory of Tucson, Arizona. The unit was positioned below the nest, with the recording lead passing through the center of the nest to the dorsum of the nestling. The sensor was implanted in the right side of the peritoneal cavity and sutured in place. Sensor placement was checked each afternoon when both parents were away from the nest. The unit was calibrated to the nearest 0.1°C.

A member of each pair was marked with orange dye on small areas of the brooding bird. At night a brooding parent could be approached and daubed

with a dye-saturated cotton ball affixed to the end of a stick. Scratch marks on the mandibles allowed positive identification of two of the undyed partners. Three marked birds, along with mates of two, were collected and sexed to determine roles in feeding and brooding.

Weights of nestlings were obtained in the field on a triple beam balance; notes on plumage development were recorded simultaneously. Ten young of known age were preserved in alcohol to document various stages of development.

RESULTS

BREEDING SEASON AND NESTING

The Roadrunner has a bimodal nesting pattern in the Tucson area—mid-April to mid-June, and late July to mid-September. Extreme heat and aridity in late June and early July, followed by rains in late July, separate the breeding periods.

I could not determine whether individual adults would have successfully reared clutches in both seasons, since spring nests were not allowed to reach termination. Eight pairs which had nested in the spring were not followed again during the summer, either because members of the pair had been collected or because of the time required to locate nests. The summer period involved three pairs, which renested after the spring season, and two pairs of unknown spring status.

Cholla cactus (*Opuntia* spp.) is the most common nest site in the Tucson area. Of 23 nests observed (7 prior to 1969), 12 were in staghorn cholla (*O. versicolor*), 6 in jumping cholla (*O. fulgida*), 3 in desert hackberry (*Celtis pallida*), and 2 in palo verde (*Cercidium floridum*). Mean nest height for 16 nests was 130 cm (range 40–245 cm). All 16 nests were constructed in such a way that bands of shade crossed the nest during the extreme heat of the day.

Clutch size, for seven nests where each egg was marked the morning it was laid, ranged from two to seven with a mean of 4.6. Two clutches of four eggs were completed on 16 and 22 May. A clutch of two, completed on 12 June, was the last active nest to be found before the onset of the July rains. Shortly after the summer rains in July, the female

¹ Present address: Department of Zoology, Arizona State University, Tempe, Arizona 85281.

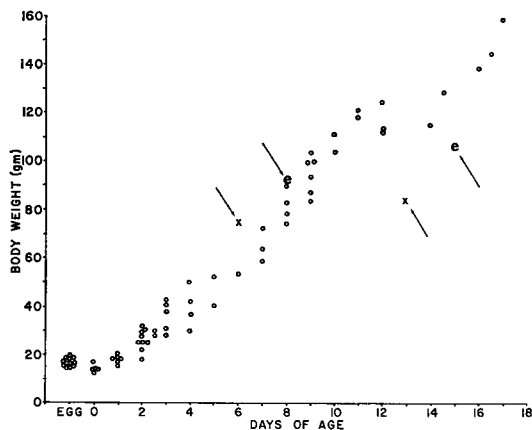


FIGURE 1. The relationship between body weight and age in days in nestling Roadrunners. The letters *x* and *e* denote body weights of two young in nest D (fig. 3) in June (see text for full discussion).

that laid this clutch presumably constructed another nest 10 m away and laid a clutch of six. After the July rains, four complete clutches contained four, six, six, and seven eggs ($\bar{x} = 5.7$), respectively.

Timing of egg deposition was determined directly in seven nests and indirectly by egg hatch sequence in four others. In seven of the nests, one egg was deposited each day, and in three other nests, one egg was deposited every other day. The eggs of a two-egg clutch were laid three days apart in mid-June. The incubation period for these clutches was 17–18 days.

NESTLING WEIGHT INCREASE AND PLUMAGE DEVELOPMENT

The weight increase curve in figure 1 is based on weights of 31 young of known age, a number of which were weighed two or more times. The mean weight at hatching was 14.2 g. By fledging time the mean weight had increased approximately elevenfold; however, this was only 50% of adult weight. The age at fledging was variable; two young fledged at 17 days, six at 18, and two at 19 days.

Rates of weight increase for nestling Roadrunners were calculated from Brody's equation (1945:508) and are presented in table 1. Rapid weight increase occurred until day 4 after which there was a general leveling off. After the first few days, weight increase ranged from 10–22% except between days 12–14 when the paucity of nestling weights yielded values below the mean.

Nestling weight and clutch size showed some seasonal changes. The two young designated *x* and *e* in figure 1 were nest mates

TABLE 1. Instantaneous percentage growth rates (*K*) in nestling Roadrunners near Tucson, Arizona.

Age (days)	<i>K</i> (%/day)
0–1	30.0
1–2	26.6
2–3	39.2
3–4	30.1
4–5	9.5
5–6	14.5
6–7	14.2
7–8	20.4
8–9	22.6
9–10	15.1
10–11	12.1
11–12	11.3
12–13	–15.7
13–14	–8.9
14–15	14.9
15–16	8.8
16–17	11.3

from nest D. Their weights at age 6 and 8 days agree closely with the general weight curve, but body weights at 12.5 and 14.5 days show a decline from the expected. The younger was approximately 32% less, while the oldest deviated 12%. These two were nestlings during June when a female, approximately 1500 m to the northeast, laid a complete clutch of *only* two eggs. Both clutch size and nestling weights were reduced as the hot, dry season approached.

The weight values for Roadrunners in figure 1 were fitted to the appropriate weight increase equation discussed by Ricklefs (1967, 1968). The von Bertalanffy equation yielded the best fit. The asymptote was estimated at 300 g, *K* (weight increase) was determined to be 0.0134, and t_{10-90} (time span in that segment of the asymptote between 10–90%) was 40.5 days.

The naked nestling has been described as a "featherless, greasy, black" creature (Bent, 1940). The only areas that are not black are the pink interramal region and the blue-gray feet.

The hair-like white down is sparse and occurs only in the pterygiae. Between days 1–2, the central rectrices and their upper coverts are visible as developing pins. By days 2–3, early pins can be seen in the dorsopelvic and femoral tracts, and the remiges and their upper greater coverts appear. At 3–4 days, the central pair of rectrices are 6–7 mm; pairs 2–5 are progressively shorter with 5 about 1 mm. Between days 5–6, the central rectrices are 12–13 mm, and the tips of pairs 1 and 2 are beginning to rupture. Pin tips are visible from the lores posterior along the capital area

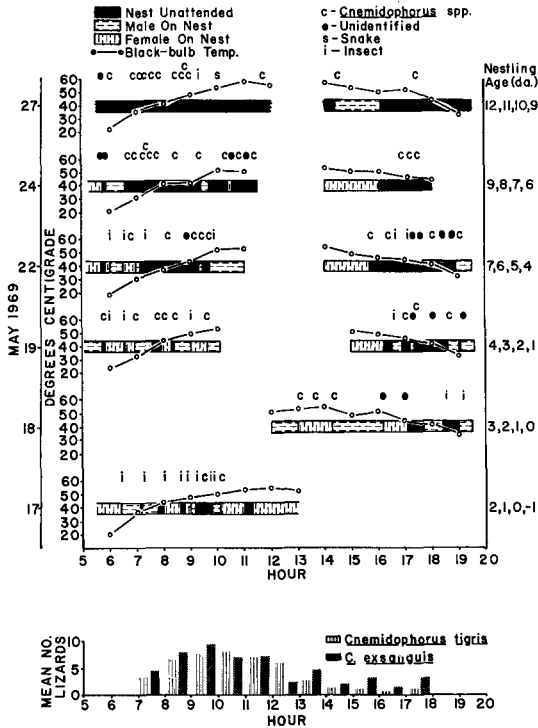


FIGURE 2. Upper graph represents nest C and shows the correlation between age of youngest nestling and adult Roadrunners' freedom from nesting duties so that predator-prey activities can be synchronized. Food items fed to nestlings, black-bulb temperatures, and parent activities at the nest are included. Lower graph shows activity pattern of two species of *Cnemidophorus* lizards in southern Arizona (Echternacht 1967).

to the posterior portion of the cervical region. The pins of the dorsopelvic and femoral tract are 2-3 mm long and the humeral and sternal regions are beginning to show pin tips. The secondary marginal and upper middle primary coverts 6-10 also show as pin tips. Pins of the abdominal region, under rectrix coverts, and alula are about 0.5 mm. At 7-8 days, the central pair of rectrices are 25 mm and all rectrices and their respective upper coverts are ruptured, except for pair 5. The pins from the lores to the posterior cervical region range from 0.5-2.0 mm. Early brushes are scattered through the dorsopelvic and femoral tracts. The longer proximal remiges and their coverts are beginning to rupture. Pin tips are beginning to show ventrally and anteroventrally to the eye, in the auricular and malar regions. Pins are still present in the interramal, submalar, cervical, sternal, and abdominal regions, whereas the alula and under rectrix pins have ruptured. Between 9-10 days, the central rectrices are about 41 mm. The brushes of the capital, cervical, femoral, sec-

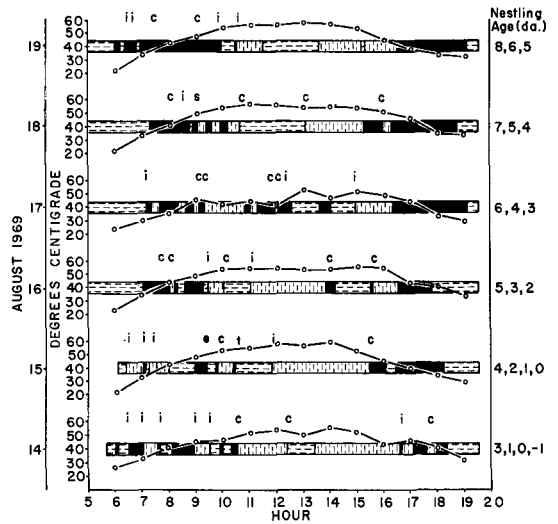


FIGURE 3. Nest B showing similar correlations as figure 2.

ondary marginal coverts, dorsopelvic, and femoral regions give the nestling a sparse feather covering dorsally. Early brushes are beginning to show in the ventral cervical, sternal, and abdominal regions. The pins of the interramal and submalar regions are just rupturing, but pins of the malar, loreal, ocular, and auricular regions are not yet ruptured. The alular and coverts are showing as early brushes. By day 15, the central rectrices are about 77 mm and all pins have ruptured except those of the loreal, ocular, and auricular regions. At fledging (18 days), the pins of the above regions are just beginning to rupture, and the central rectrices are about 114 mm.

CARE AND BODY TEMPERATURE OF THE YOUNG

Throughout the daylight hours both parents tended the young (figs. 2, 3, 4). At dusk, all observations revealed the male going to sleep on the nest, and frequent nightly checks verified that he remained on the nest. Each of three brooding birds marked at night was a male. The female usually relieved the male shortly after daybreak. As temperatures rose

TABLE 2. Tabulation of total number of feedings and lizards fed by each Roadrunner pair member for three nests.

Nest	Text figure	Total items		Lizards		Hr nest observed
		♂	♀	♂	♀	
A	2	55	32	34	16	50.5
C	4	23	24	15	9	87.3
D	3	27	44	10	17	100.0

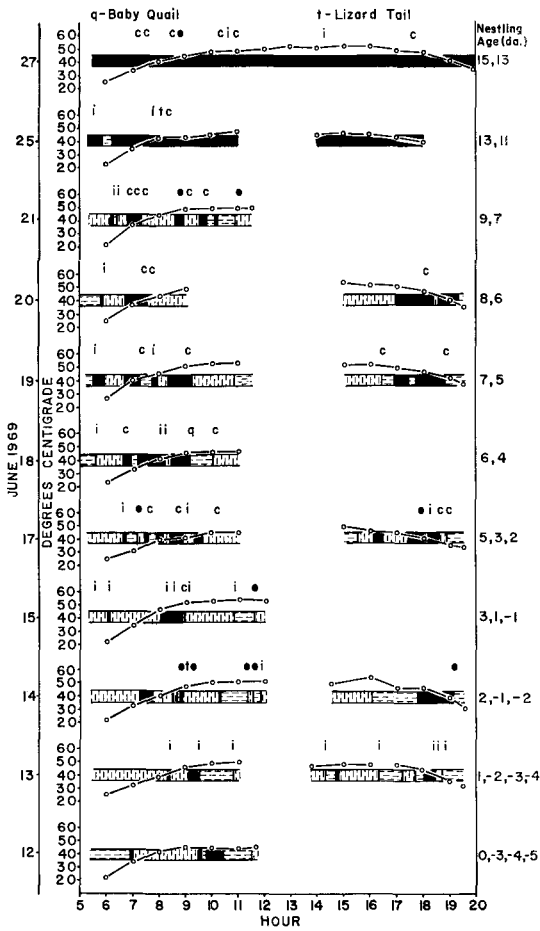


FIGURE 4. Nest D showing similar correlations as figures 2 and 3. This nest contained the two nestlings designated by the letters *x* and *e* in figure 1.

during mid- to late morning, the adults took turns shading the young, with wings slightly spread and drooped and the breast lowered to where it sometimes rested on the rim of the nest. When shading, the adults were usually

positioned with the tail into the breeze, thereby funneling air down and over the young. It could not be determined if the adult deliberately used its tail for shading. Generally, the tail was held horizontally or obliquely, but occasionally it was directed over the back, casting shade on the adult's body.

A pattern of parental absence emerged as the youngest nestling reached 4-5 days of age (figs. 2, 3, 4). By this time, body size had tripled, yielding a more favorable surface-mass ratio for prevention of heat loss (table 1), and the capabilities of heat dissipation were present (Lowe and Hinds 1969). By the time the still featherless nestling was 6 days old, the inattentive periods were extensive and corresponded with the activity period of the whiptailed lizards (*Cnemidophorus* spp.) (figs. 2 and 4), the food item most frequently offered to nestling Roadrunners. Figure 3 shows some deviation from this pattern of nest absence on 20 and 21 June, when, for unknown reasons, the female spent much time on the nest.

Both adults provided food items for developing nestlings, although the feeding effort was quite variable between pair members (table 2). Newly hatched young were typically fed insects (figs. 2, 3, 4), but whiptailed lizards comprised the greatest number of identified food items (113) fed to nestlings in 269 hr of nest observations (table 3). In conjunction with each food item offered, there appeared to be a regurgitation of additional material from the parent to the nestling. This possible regurgitation was observed in all feeding until the time the nestlings were about 14 days old. Composition and quantity of the regurgitated material were not determined, but on two occasions the material was

TABLE 3. Food items consumed by nestling Roadrunners near Tucson, Arizona.

Nest Fig.	Vertebrate Material							Arthropods				Total	No. young	Hr of nest observation
	<i>Cnemidophorus</i>	<i>Callisaurus</i>	<i>Uta</i>	Lizards (sp.)	Miscellaneous	Insects (sp.)	Grasshoppers	Cicadas	Unidentified					
A 2	50 (58) ^a	0	0	0	1 (1)	13 (15)	8 (9)	0	15 (17)	87	4	50.5		
B -	16 (35)	0	0	0	1 (2)	4 (9)	0	0	25 (54)	46	2	31.0		
C 3	20 (43)	1 (2)	1 (2)	3 (6)	2 (4)	15 (32)	4 (9)	1 (2)	0	47	3	87.3		
D 4	27 (38)	0	0	0	3 (4)	1 (1)	16 (23)	13 (18)	11 (16)	71	2	100.0		
Total	113 (46)	1 (0)	1 (0)	3 (1)	7 (3)	33 (13)	28 (11)	14 (6)	51 (20)	251	11	268.8		
						50%						30%		

^a Parenthetical values are percentages of total items fed at that particular nest except for those in the total line and these are percentages of the total.

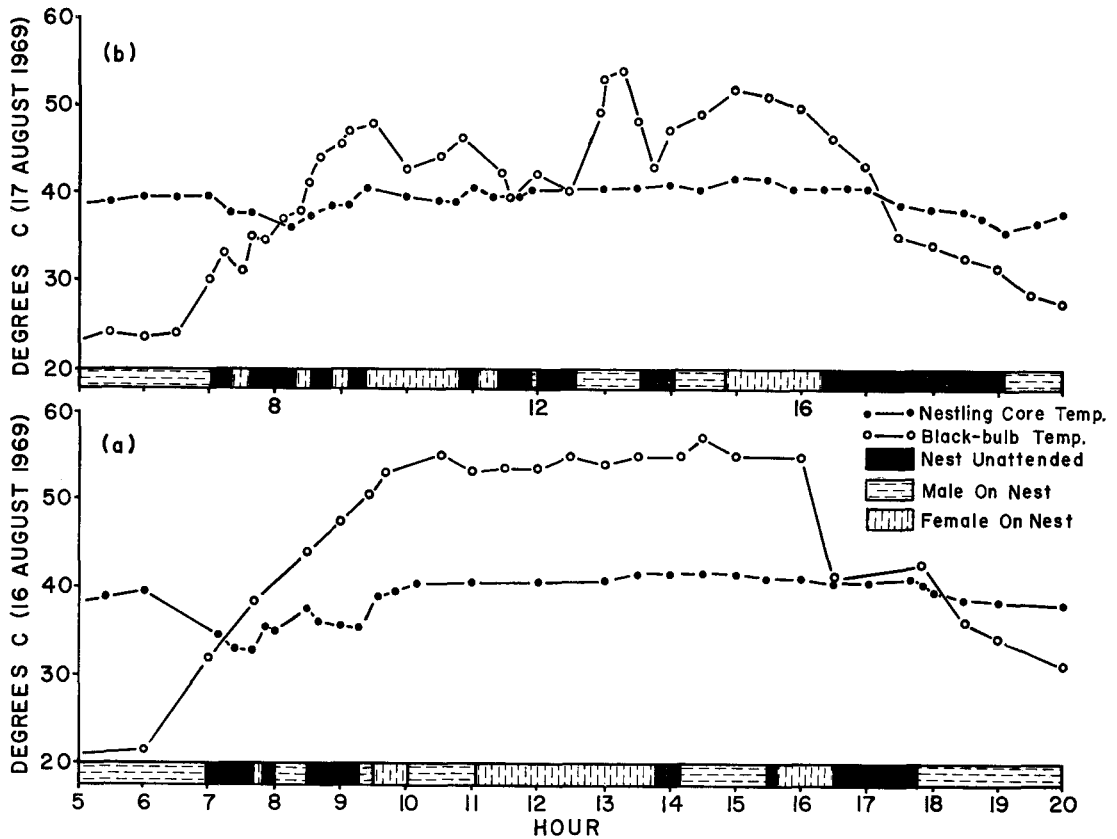


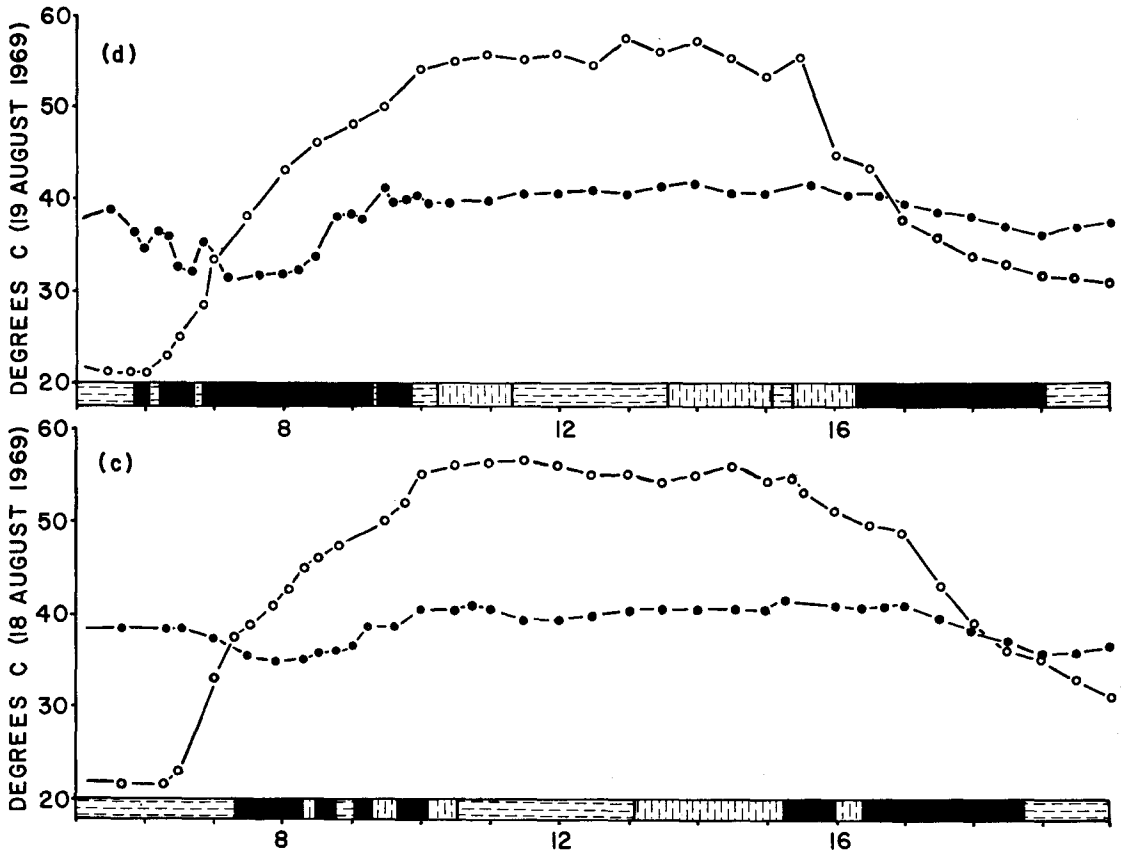
FIGURE 5. a-d shows black-bulb temperatures, body temperatures of the youngest nestling, and nest inattentance periods by the adults. The nestling (from nest C, fig. 2) is 2 days old in a and 5 days old in d. Note in graph d the nest absence span of the adults and the ability of the 5-day-old nestling to limit its heat load.

observed to be a clear, slightly viscous liquid. The parent would present an insect or lizard positioned anteriorly in the mandibles; the young would grasp the food item and mandibles of the adult, first to consume any regurgitated fluid and finally the food item. During the transfer, the hyoid of the parent could occasionally be seen moving, but for the most part the flow appeared to be gravitational. The unions between the parents and young when the presumed regurgitation was taking place ranged from 25-195 sec. After feeding, or when a parent returned to the nest without food, the adult would consume small food particles, ants, or fecal sacs in the nest.

Frequently, an adult would prod and move the young about with its mandibles. Occasionally, one of the adults would grasp a nestling by the synsacral region and roughly move the squealing, struggling nestling. In two instances, the youngest nestling, which was possibly lethargic, was picked up by the head and consumed. In nest D, the first hatched young from a clutch of four eggs was

carried away from the nest on 11 June and presumably eaten. The final egg hatched on 16 June, and at 06:01 on 17 June, I recorded "Unmarked (♀) bird came in and fed something small, regurgitating for 55 seconds, and then consumed a fecal sac. It picked over the young and the smallest nestling which was lethargic (he didn't beg when pecked) was thereupon eaten." At 08:02 on 18 August, the male from nest C consumed the youngest of four nestlings. Whether the young had failed to beg is not known.

The youngest of three nestlings in nest C had a telemetry unit implant to obtain body temperatures (T_b). Its two siblings were 1 and 3 days older. The T_b of the monitored nestling from age 1-5 days ranged from 32-42.3°C (fig. 5a-d). On the first 3 days (fig. 5a-c), the adults' initial morning departures and subsequent returns were similarly timed, although the period of adult attendance at the nest varied in length. On the fourth day (fig. 5d), there was a broadening of the absence span. The reduction in brooding and shading



time freed the adults to hunt lizards, whereupon thermoregulation was left solely to the black, naked young.

Gular flutter was observed in the temperature-monitored nestling at 16:30 on 17 August (age 3 days). It may have begun earlier, but the young were almost completely hidden by the rim of the nest; notes on the young were obtained only when the nest was visited briefly in the afternoons during the parents' absence.

The ability of the nestling to dissipate a continuing heat load was observed on 19 August at 08:40 (age 5 days). The nestling's T_b had been rising rapidly and, in the absence of the parents, it began dissipating heat and maintaining a stable T_b . At 09:17, the male visited the nest briefly and the nestling's T_b increased. The male left and the young again reduced its T_b .

Temperature readings were taken every 2 hours throughout the night. Shortly after dark, the nestling's T_b dropped to between 38.2 and 38.5°C and remained there until about 05:30. The brooding male and the two nonmonitored young were taken from the nest at 03:00 on 20 August and cloacal T_b 's were found to be 38.5°C.

DISCUSSION

The Roadrunner is a relatively large (300 g), essentially flightless, diurnal carnivore endemic to a region of very low primary productivity in North America. Other avian carnivores in the desert are either smaller, nocturnal, or possess excellent powers of flight. Because of the unique niche occupied by the Roadrunner, it is not surprising that, during the evolution of the species, selection has resulted in a number of highly specialized adaptations. Of the problems confronting the Roadrunner in the unpredictable desert environment, that which appears to be the most vital is providing an adequate amount of food for its developing nestlings.

Evolution of a bimodal nesting season directly correlated with higher lizard and insect densities has resolved part of the problem. In the Sonoran Desert this adaptation appears to be common among avian species which feed animal material to their young. It occurs in the Brown Towhee (*Pipilo fuscus*) (Ohmart, pers. observ.), the Rufous-winged Sparrow (*Aimophila carpalis*) (Ohmart 1969), and the Curve-billed Thrasher (*Toxostoma curvirostre*) (E. L. Smith, pers. comm.). In contrast, the totally granivorous Mourning

Dove (*Zenaidura macroura*) has a continuous breeding season from January–October, and some of the earlier hatched young may even breed later that same season (Irby and Blankenship 1966). Lack's (1954, 1968) hypothesis that avian breeding seasons have evolved in direct relationship to the period when food is most abundant for the young has received support from a number of avian studies, and appears directly applicable to the Roadrunner.

Evidence in this study strongly suggests that clutch size in the Roadrunner is regulated by food supply. The increase in mean clutch size from the spring to the summer breeding periods supports this assumption since the Sonoran Desert typically is much more productive following the summer rains than in the spring after a normal winter. Under deteriorated habitat conditions (before the onset of the summer rains), a complete clutch of *only two* was laid, and two young in a nearby nest were well below the normal body weight. The female which had laid the clutch of two presumably built another nest after the summer rains and produced a clutch of six. Bendire (1878) proposed such regulation of clutch size in the Roadrunner, but collected the spring nests shortly after incubation began and probably disrupted the normal egg-laying sequence. Sutton (1940, 1967) reported clutch size variability of 2–12 eggs which is highly unusual in birds. He suggested that possibly two or more females might be involved in the largest clutches. I have no data which refutes this assumption, but I strongly suspect that the large clutches are laid by only one female. It would be advantageous to lay as many eggs as food supply would allow, so long as egg quality was not sacrificed for quantity. During periods of high arthropod and whiptailed lizard densities, the maximum clutch size might be set by the number of eggs the adults could adequately incubate. These questions can be resolved only with clutch size data from marked pairs combined with food indices from the marked birds' territory. The latter would be necessary because habitat diversity between adjacent pairs is frequently dramatic.

Efficiency in feeding the nestlings is increased by the adults' procurement of large food items, e.g., *Cnemidophorus* lizards. A sample of 33 collected in June and July showed the mean weight of the preferred food item to be 7.6 g (range 2.4–15.1 g). The underfed nestlings of June (fig. 3), whose diet consisted of a greater proportion of in-

sects to lizards than the other three broods studied, substantiate this. Insects were adequate to provide the energy required for maintenance and growth until the young were 6 and 8 days old; but shortly after that, body weight did not increase normally, apparently because of the inability of the adults to meet the food demands of the young. The importance of selection of large food items for feeding nestlings has been demonstrated in Starlings (*Sturnus vulgaris*) (Kluijver 1933; Dunnet 1955), the Great Tit (*Parus major*) (Tinbergen 1949), the Kingfisher (*Alcedo atthis*) (Swanberg 1952) and the Long-billed Marsh Wren (*Telmatodytes palustris*) (Verner 1965). The preponderance of lizards in the diet of the young Roadrunner has also been referred to in other studies. Finley and Finley (1915:164) state, "Again came a lizard—and again—and again—there was no use counting. The larder was full of lizards and nothing else." Interestingly enough, the intensive study of food habits by Bryant (1916) in which stomach contents of 84 Roadrunners were examined, 16 during their breeding season, showed that less than 4% of the adult diet consisted of lizards; better than 80% was invertebrates. The larger food items (primarily lizards) are fed to the young, and smaller items are consumed by the adults.

It is important that the adult Roadrunners be free of nest activities to hunt when lizards are most active and obtainable. Studies of the genus *Cnemidophorus* show only one period of high activity, which occurs from about 07:00 until about 13:00 (Milstead 1957; Laughlin 1958; Echternacht 1967; Medina 1967; Pianka 1970). By having a more favorable surface-mass ratio for heat conservation, black skin for solar brooding, gular flutter and bands of shade to limit the heat load, and efficient salt-secreting nasal glands to counterbalance evaporative water loss, the young at 4–5 days of age require very little parental care during the lizard activity period. As the ambient temperature rises, the lizards reduce their activity, and the Roadrunners share the duty of shading the young, the greatest portion of the daily ration to the young already having been provided (figs. 2, 3, 4).

Staghorn cholla appears to be the favored nest site because it allows direct sunlight to the nest while simultaneously providing some bands of shade. It also provides a densely branched support for the platform of sticks, and possibly the spines act as a deterrent to predators. Direct sunlight appears to be the most important, for the young are black-

skinned, allowing for solar brooding. They are not maladapted as Lowe and Hinds (1969) suggested when they stated that the Roadrunner appears to be a "forest evolved species, preadapted for life in open arid and semiarid environments, that has a severe legacy for desert inhabitation—a strikingly black skin at hatching that is carried through the first critical weeks of life of the juvenile that sits on a relatively exposed platform nest."

Lack (1947) has suggested that asynchronous hatching might allow an immediate method for adjusting food supply since the younger siblings would be quickly removed through starvation. However, in a few clutches reported in the Roadrunner (Coues 1903; Finley and Finley 1915; Sutton 1922) where there were *large* age differences between siblings (about 18 days), the problem of providing food for the young would be aggravated by asynchronous hatching. While a narrow period of asynchrony would be advantageous, an extended age difference among nestlings would aggravate the problem of providing food for the young. Food demands would be set by the older nestlings, whereas adult attention to the nest would be controlled by the youngest nestlings. Unfortunately, we have no knowledge of the fate of these seemingly unusual nests. In all the nests that I have observed, 7 days was the greatest disparity between the first and last egg; Bendire (1878) examined 20 nests and his data are essentially in agreement with my findings.

Asynchronous hatching not only distributes the food demands of the young over a broad period; it also provides a mechanism, which in the event of a diminishing food supply, brings about removal of the youngest sibling competitors. In the desert, the food supply is frequently erratic and productivity can be reduced rapidly and drastically by hot, dry winds. Should the food supply wane during the incubation period, the brood size of Roadrunners can be regulated by the adults' eating the young. Interestingly enough, brood reduction has been reported for another Sonoran Desert species, the Curve-billed Thrasher (*Toxostoma curvirostre*) (Ricklefs 1965). However, the thrashers take a less active role than Roadrunners; reduction of their broods occurs by the starvation of nestlings. The Lesser Roadrunner (*Geococcyx velox*), a more tropical species, apparently does not lay clutches of such variable size and appears not to have evolved asynchronous hatching (Miller 1932).

Some insight can be gained into the evolution of reproduction rates and development of young in Roadrunners by examining the strength of selective forces. The apparent lack of strong predation pressure has allowed the evolution of asynchronous hatching, a long nestling period, and a slow development rate in the young. The weight increase fit to the von Bertalanffy equation is significant in that of the 105 species examined by Ricklefs (1968) the growth of only 3 was best described by the von Bertalanffy equation. This equation described rapid weight increase the first few days and then slowing of weight increase with the inflection point occurring when approximately 30% of the asymptote was attained. The three species best described by the von Bertalanffy equation were either sea birds or large terrestrial birds (3–4 kg) which are relatively free from predation. At the inflection point, the young Roadrunners are 9–10 days old, obtaining their first feather covering and probably beginning to maintain a stable body temperature. At 7 days, the naked young require little diurnal protection, but are still brooded at night. Asynchronous hatching is diametrically opposed to a short nestling period and could only have evolved if predation pressures were low. Asynchronous hatching allows a broader distribution of nestling food demands, and this apparently has been important in the evolution of the reproductive scheme in Roadrunners. The paucity of diurnal prey species has forced the Roadrunner to specialize in single, large food items (lizards) which are carried one at a time to the nest. The necessity of both pair members being free to hunt whiptailed lizards during the single activity period of the lizards is obvious. When possible, a long nestling period appears to be more advantageous in birds; Lack (1948, 1954) and Nice (1957) have presented evidence which indicates that the length of the nestling period is positively correlated with nestling success.

While this paper deals with the evolution of breeding adaptations in Roadrunners, it should also be pointed out that specialized adaptations have evolved for existence during the lean winter months when other large avian carnivores, hawks and owls, have migrated to more productive regions. Physiological information on the capability of the Roadrunner to enter hypothermy spontaneously and then to use low intensity solar energy, instead of biochemical stores, to increase and maintain its T_b , suggests strong selective

forces operating for energy conservation (Ohmart and Lasiewski 1971). The reduction in arthropod and lizard densities and the increase in the diet of vegetable material (Bryant 1916) would make energy conservation necessary during the cold season (Sutton 1967; Geluso 1970). Roadrunners, in an apparently permanent pair bond, live on their territory year around and may defend it during the winter months to insure an adequate food supply for the adults themselves. The Lesser Roadrunner does not possess dorsal cutaneous melanization (Udvardy, pers. comm.); this trait would be necessary for it to achieve the degree of solar absorption observed in the Roadrunner (Ohmart and Lasiewski 1971).

The Roadrunner possesses a number of adaptations which are unique to the genus. It differs from the congeneric Lesser Roadrunner in possessing dorsal cutaneous melanization in the adult, asynchronous hatching, a highly variable clutch size, and a greater body weight. Possession of a salt-secreting nasal gland and the ability to go into hypothermia may also be unique to this species.

Asynchronous hatching appears to be present only in the north temperate members of the family, and may have evolved in response to lower food availability and/or an erratic food supply. Cutaneous melanization in nestlings appears to be common to all species in the family.

SUMMARY

General observations of 23 Roadrunner nests and 269 hr of observations of 4 specific nests reveal that both the young and adults possess many specialized adaptations for breeding in the southern Arizona desert. Placement of the platform nests is primarily in round-stemmed cholla cactus, allowing direct sunlight while simultaneously providing scattered bands of shade. Nesting periods coincide with greatest food abundance and clutch size appears to be related to food supply during the egg-laying period. Incubation begins with the laying of the first egg, yielding young of different ages in the nest. Whiptailed lizards are the primary food items offered to the nestlings and these lizards have a single activity pattern which begins about 07:00 and terminates about 13:00. It is of utmost importance that both adult Roadrunners be free from brooding or shading the young to hunt lizards during the lizards' short period of activity as the growing nestlings require increasingly larger quantities of food. The food demands of

nestlings in a clutch begin to reach their maximum as the youngest nestling is about 7-8 days old. At age 4-5 days, the black-skinned young has grown large enough so that the parents can leave it unattended in the early morning hours (06:30-08:00) without it undergoing a severe body temperature drop. The black young then begins to absorb solar radiation and increases its body temperature (08:00-09:30). Gular flutter and alignment in the bands of shade are used to limit the heat load. The water lost in gular fluttering and cutaneous evaporation is then counterbalanced by the excretion of salts by the salt-secreting nasal gland and by the adults' possible regurgitation of a clear liquid to the nestling at each feeding. These physiological and behavioral interrelationships allow complete synchrony of predator-prey activities. The young are shaded by the adults in the early afternoon hours. Should the food supply diminish during the nestling period, the youngest nestlings are consumed by the adults.

ACKNOWLEDGMENTS

I thank W. J. Hamilton III, O. W. Johnson, J. B. Leigh, R. J. Raitt, Jr., G. M. Sutton, D. W. Tinkle, and S. M. Woodward for their comments and help during the preparation of the manuscript. I am particularly indebted to Susan M. Woodward for her invaluable help and patience in collecting nest observation data. Her comments and criticism during the study were most helpful. The help and cooperation of Mr. and Mrs. S. W. (Buck and Sally) Fletcher is deeply appreciated. The work was conducted while I was supported by PHS training grant ES 00101-03.

This paper is dedicated to the memory of Padre (Loye H.) Miller in gratitude for his encouragement during the study, and for his friendship.

LITERATURE CITED

- BENDIRE, C. 1878. Breeding habits of *Geococcyx californianus*. Bull. Natl. Ornithol. Club 3:39.
- BENT, A. C. 1940. Life histories of North American cuckoos, goat suckers, hummingbirds, and their allies. U.S. Natl. Mus. Bull. 176:36-51.
- BRODY, S. 1945. Bioenergetics and growth. Reprinted 1964. Hafner, New York.
- BRYANT, H. C. 1916. Habits and food of the Roadrunner in California. Univ. Calif. Publ. Zool. 17:21-50.
- CALDER, W. A. 1968. The diurnal activity of the Roadrunner, *Geococcyx californianus*. Condor 70:84-85.
- CALDER, W. A., AND P. J. BENTLEY. 1967. Urine concentrations of two carnivorous birds, the White Pelican and Roadrunner. Comp Biochem. Physiol. 22:607-609.
- CALDER, W. A., AND K. SCHMIDT-NIELSEN. 1967. Temperature regulation and evaporation in the Pigeon and the Roadrunner. Amer. J. Physiol. 213:883-889.
- CALDER, W. A., AND K. SCHMIDT-NIELSEN. 1968.

- Panting and blood carbon dioxide in birds. *Amer. J. Physiol.* 215:477-482.
- COUES, E. 1903. Key to North American birds. Fifth ed. Dana Estes Co., Boston.
- DUNNET, C. M. 1955. The breeding of the Starling *Sturnus vulgaris* in relation to its food supply. *Ibis* 97:619-662.
- ECHTERNACHT, A. C. 1967. Ecological relationships of two species of the lizard genus *Cnemidophorus* in the Santa Rita Mountains of Arizona. *Amer. Midland Nat.* 78:448-459.
- FINLEY, W. L., AND I. FINLEY. 1915. With the Arizona road-runners. *Bird-Lore* 17:159-165.
- GELUSO, K. N. 1970. Feeding behavior of a Roadrunner in winter. *Bull. Oklahoma Ornithol. Soc.* 4:32.
- IRBY, H. D., AND L. H. BLANKENSHIP. 1966. Breeding behavior of immature Mourning Doves. *J. Wildl. Mgmt.* 30:598-604.
- KLUJVER, H. N. 1933. Bijdrage tot de biologie en de ecologie von den Spreeuw (*Sturnus vulgaris vulgaris* L.). gedurende zijn voortplanting stijd. *Versl. Plziekt. Dienst. Wageningen* 69.
- LACK, D. F. 1947. The significance of clutch-size. *Ibis* 89:302-357.
- LACK, D. F. 1948. Natural selection and family size in the Starling. *Evolution* 2:95-110.
- LACK, D. F. 1954. The natural regulation of animal numbers. Oxford Univ. Press.
- LACK, D. F. 1968. Population studies of birds. Oxford Univ. Press.
- LAUGHLIN, H. E. 1958. Interrelationships between two sympatric species of Racerunner lizards, genus *Cnemidophorus*. Master's thesis, Univ. Texas, Austin.
- LOWE, C. H., AND D. S. HINDS. 1969. Thermoregulation in desert populations of Roadrunners and Doves, p. 113. In C. C. Hoff and M. L. Riedesel [eds.] *Physiological systems in semiarid environments*. Univ. New Mexico Press, Albuquerque.
- MEDICA, P. A. 1967. Food habits, habitat preference, reproduction, and diurnal activity in four sympatric species of whiptail lizards (*Cnemidophorus*) in south central New Mexico. *Bull. So. Calif. Acad. Sci.* 66:251-276.
- MILLER, A. H. 1932. Observations on some breeding birds of El Salvador, Central America. *Condor* 34:13-14.
- MILSTEAD, W. W. 1957. Observations on the natural history of four species of whiptail lizard, *Cnemidophorus* (Sauria, Teiidae), in Trans-Pecos, Texas. *Southwestern Nat.* 2:105-121.
- NICE, M. M. 1957. Nesting success in altricial birds. *Auk* 74:305-321.
- OEHMART, R. D. 1969. Physiological and ethological adaptations of the Rufous-winged Sparrow (*Aimophila carpalis*) to a desert environment. Ph.D. dissertation, Univ. Arizona, Tucson.
- OEHMART, R. D. 1972. Salt-secreting nasal gland and its ecological significance in the Roadrunner. *Comp. Biochem. Physiol.* 43a:311-316.
- OEHMART, R. D., T. E. CHAPMAN, AND L. Z. MCFARLAND. 1970. Water turnover in Roadrunners under different environmental conditions. *Auk* 87:787-793.
- OEHMART, R. D., AND R. C. LASIEWSKI. 1971. Roadrunners: Energy conservation by hypothermia and absorption of sunlight. *Science* 172:67-69.
- PIANKA, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:703-720.
- RICKLEFS, R. F. 1965. Brood reduction in the Curve-billed Thrasher. *Condor* 67:505-510.
- RICKLEFS, R. F. 1967. A graphical method of fitting equations to growth curves. *Ecology* 48:978-983.
- RICKLEFS, R. F. 1968. Patterns of growth in birds. *Ibis* 110:419-451.
- SUTTON, G. M. 1922. Notes on the Roadrunner at Fort Worth, Texas. *Wilson Bull.* 34:3-22.
- SUTTON, G. M. 1967. Oklahoma birds: their ecology and distribution, with comments on the avifauna of the Southern Great Plains. Univ. Oklahoma Press, Norman.
- SWANBERG, P. O. 1952. Observationer rörande ett por kungsfiskares (*Alcedo atthis*) matning och ruvning av ungarna, bodningsteknik, m. m. *Vår Fågelvärld* 11:49-66.
- TINBERGEN, L. 1949. Bosvogels en insecten. *Ned. Boschbouw-Tijds.* No. 4.
- VERNER, J. 1965. Breeding biology of the Long-billed Marsh Wren. *Condor* 67:6-30.

Accepted for publication 4 October 1972.