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BEHAVIOR AND ACTIVITY CYCLES OF GAMBEL'S QUAIL AND RAPTORIAL BIRDS AT A SONORAN DESERT WATERHOLE

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A field study designed to observe the behavior and activity cycles of animals attendant at a Sonoran Desert waterhole was conducted during January 1969. The rationale for the choice of waterholes as study areas is discussed elsewhere (Beck and Tuttle 1972). The activity of a winter flock of Gambel's Quail (Lophortyx gambelii) and of raptorial birds was monitored. Among the raptors seen in the waterhole area, those positively identified were Marsh Hawks (Circus cyaneus), Sparrow Hawks (Falco sparverius), Red-tailed Hawks (Buteo jamaicensis), Harris' Hawks (Parabutea unicinctus), and Bald Eagles (Haliaeetus leucocephalus). The daily cycle of quail presence at the waterhole differed systematically from that of raptors and it appears that the presence of raptors at the waterhole was associated with the absence of quail.

METHODS

The observations were made at Jose Juan Tank in the Cabeza Prieta Game Range, southern Arizona (about 32° 5' N, 113° 6' W). Jose Juan is the only perennial source of standing water within 8 km in the Game Range although small temporary accumulations of rain may occur. Additionally, there are drinking troughs provided for cattle about 1.5 km away in the fenced Organ Pipe Cactus National Monument.

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The tank is roughly rectangular in shape, measuring, at the top of the banks, about 73 m on the N-S axis and about 56 m on the E-W axis. The tank has been artificially deepened and an earthen dike has been erected on the north end. Water accumulates from rainfall run-off. The tank was only partially filled at the time of the study, leaving a surrounding apron about 10 m wide sloping gently upward from the water to the top of the banks.

Jose Juan Tank is ringed by honey mesquite trees (*Prosopis juliflora*) which grow on top of the banks. Microphyll flatland desert, populated primarily by creosote bush (*Larrea tridentata*), surrounds the tank for at least 3 km in all directions.

The observations were made from a blind built on top and at the mid-point of the west bank about 10 m from the water's edge. Usually three, but never less than two, observers began work at about 06:00 and ended about 18:30. The study encompassed 258 hr and 45 min of observation on 21 days (30 December 1968-5 January 1969, 13-25 January 1969, and 29 January 1969).

Average daily shade temperature in the blind ranged from 41.8° F (5.4° C) before sunrise to 65.5° F (18.6° C) at about 14:30. The lowest temperature recorded during the study was 28° F (-2.2° C) and the highest, 76° F (24.4° C). Light to moderate rainfall was recorded on 13, 14, 17, and 21 January; no measurement was made at the site but 0.7 inches (1.78 cm) of rain fell during the study period at the headquarters of the Organ Pipe Cactus National Monument, about 32 km away. During the study, sunrise occurred, on the average, at 07:45 and sunset, at 17:45. There was sufficient light for detailed observation from about 06:55 to about 18:30.

Movement to and from the blind was as limited as possible and was always to the rear (west) of the blind so as to interfere minimally with faunal activity. When a vehicle was present during the day, it was parked inconspicuously some distance from the waterhole. The group camped about 10 km away and other people were observed near the study area only twice.

Binoculars $(7 \times 35, 8 \times 40)$, pens, notebooks,

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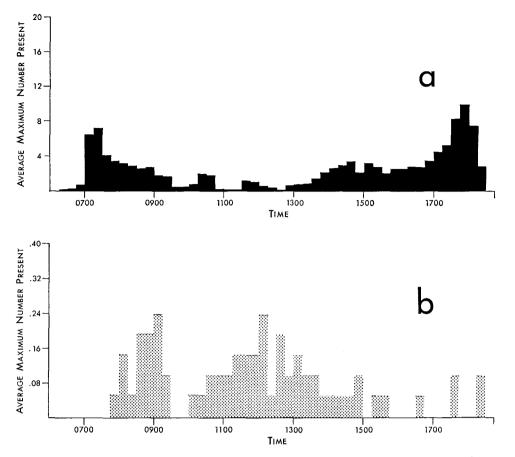


FIGURE 1. Average daily distribution of Gambel's Quail presence (a) and raptor presence (b). The negative correlation between the two functions is significant indicating that quail and raptors differ in the timing of their use of waterhole resources.

watches, tape recorders, thermometers, and standard field guides were used in observation and recording.

Positive identification of a species was defined as independent agreement by at least two members of the team, with no contrary identification by the third. If there was identification by less than two team members or was disagreement, the identification was recorded as tentative. There was never disagreement as to identification of quail or as to whether a bird was a raptor; lack of positive identification of the raptors was due to poor light, dense vegetation, or briefness of the observation.

When an animal was sighted, it was identified and observation of qualitative and quantitative aspects of behavior was begun. Entrance time (defined as when the subject was first sighted) and exit time (defined as when the subject could no longer be seen as it left the waterhole area) were recorded. Additionally, if the animal drank, times of onset and cessation of drinking were noted.

Computation of ordinate values of the daily cycles of presence shown in figures 1a and 1b was based on the largest number of quail or raptors observed at one time during a 15-min interval. The choice of 15 min as an interval duration was based on convenience and accurate representation of timing of bird activity. All of the animals counted need not have been present throughout the 15-min interval and the same animal was recounted if observed in successive intervals. This leads to a slight overestimate of the actual number of individuals present. However, the quail flock was frequently observed at the top of the banks of the waterhole and individuals moved quickly in and out of sight in the vegetation. If one quail entered as another exited, there would be no increase in the total number recorded as present although one individual "substituted" for another in the total count. This tends to underestimate the total number actually present and, in all, the counts can be considered to be quite accurate expressions of quail and raptor presence.

RESULTS

Quail. Figure 1a shows the average daily distribution of presence of Gambel's Quail during the study. These data were derived by averaging the overall total of the largest number observed during each 15min interval over the 21 days of the study. There are two clear crepuscular peaks although the dawn peak ends gradually, reaching a low point at about 11:00 and the dusk peak builds gradually, beginning at about 13:00. This function is essentially isomorphic with that reported by Elder (1956) for Gambel's Quail utilizing waterholes in Tucson Mountain Park, about 170 km E of Jose Juan. This similarity is notable because Elder's study was conducted during the summer when mean daily temperatures were considerably higher and rainfall lower than in the present study. Further, the quail observed by Elder appeared not in winter flocks but in mated pairs, some with immature young, and they did not roost at the waterhole.

In the morning the quail in the present study typically were found roosting in several honey mesquite trees on the west side of the waterhole near the blind. Between 06:45 and 07:00, the quail began to descend quickly from the trees to the waterhole apron. The flock then spread out over the apron, but there was a definite and repeated clockwise rotation of the flock as a whole around the waterhole apron. During this time the quail fed intensively, largely on mesquite seeds and pods. Many quail drank during the morning but since few of the quail were individually identified, no quantification of individual drinking frequency and duration was possible. The gradual decline in the dawn peak seen in figure 1a is a result of averaging; there is considerable variability about these means and a gradual decrease in numbers from 07:00 to 11:00 on a given day was seen only a few times. Ouail were seen infrequently between 11:00 and 13:00. Vocalizations were often heard during this time, indicating that the quail were on the desert floor in the vicinity of the waterhole even though they were not visible. After 13:00, the quail began to return to the waterhole, feeding, drinking, and moving generally in a clockwise direction as in the morning. Again, there is considerable variability about the means for the period between 13:00 and 18:00 shown in figure 1a, and a gradual buildup resembling the overall average was seen on only a few individual days. As dusk approached, the flock spread out around the apron and interindividual distance increased. Many quail drank between 17:45 and 18:15. At about 18:15, the quail began moving toward the roosting trees. Some flew directly over the water but most walked, taking the shortest route around the circumference of the apron, i.e., the clockwise rotation pattern ended. By 18:20, all had reached the roosting trees. The flock was found in the same trees when the observers entered the blind before dawn on the next morning. Occasionally, a few individuals spent the night in trees at the northeast or southeast corner of the waterhole. The largest number of quail seen at one time was 43 and, as this count was replicated on another day, it is taken as a good estimate of the total number in the flock and is consistent with Gorsuch's estimate (1934) of from "thirty to several hundred" as the size of winter flocks of this species.

Midway in the study, there was a sharp decline in the number of quail seen at the waterhole. Those quail which were present on the last 11 days of the study used a greater number of roosting trees, departed from the waterhole area earlier in the morning, and returned later in the evening. During this period, no quail was seen between 08:00 and 13:15 and vocalizations were heard only infrequently. No quail was observed on 4 of the last 5 days of the study.

Raptors. Figure 1b summarizes the daily presence of raptorial birds during the study. These data were derived by averaging the overall total of the largest number observed during each 15-min interval over the 21 days of the study. Thirty-seven raptor entries were recorded ranging from brief "fly-bys" lasting only a few seconds to prolonged bathing, drinking, preening, and resting sessions, the longest of which lasted 104 min. The overall distribution of raptor presence is bimodal, with peaks at 09:00 and 12:00.

Of the raptors sighted, only Marsh Hawks were observed to drink at the waterhole. A male was seen to drink on three occasions and a female drank twice (it could not be determined definitely if the same individual was involved more than once). In all cases, the animals' feet were submerged in the water and in three cases the tail and breast plumage were also partially submerged during drinking. Once, a male drank during rain. Bathing was also observed in conjunction with two of the drinking bouts by males.

Preening was observed in trees opposite the blind on a total of seven occasions: four times by male Marsh Hawks; once by a female Marsh Hawk; once by a Harris' Hawk whose sex could not be determined; and once by an unidentified raptor. One male Marsh Hawk defecated during a preening bout; the fecal material did not land in the water.

Midway in the study, there was a sharp increase in the number of raptors seen at the waterhole. Twenty-nine of the 37 raptor sightings were recorded on the last 12 days of the study. During this period, raptors were observed earlier in the morning and later in the evening than they had been during the first half of the study.

Quail/raptor interactions. Comparison of figures 1a and 1b reveals an inverse relationship between the average daily distributions of quail and raptor presence during the study. A Spearman Rank Correlation comparing the average number of quail and raptors present during each set of corresponding 15-min intervals yields a coefficient of -0.41 (utilizing the correction for ties). Relating this coefficient to the Student's t distribution, the inverse relationship is found to be significant (t = 3.08, df = 47, P < 0.01, one-tailed). On the average, quail tend to be present at the waterhole at those times of the day when raptors are not and vice versa.

There were two predatory attacks by raptors on quail during the study. A raptor, tentatively identified as a Red-tailed Hawk, flew suddenly into the area one morning (10:07) and swooped low over the apron on the east side of the waterhole. Eleven quail had just drunk and were walking toward the trees as the hawk entered. They ran to the trees, vocalizing loudly, and all escaped. The hawk flew out of the area without slowing; the interaction lasted 3 sec. One evening (18:17), a Sparrow Hawk flew quickly from the northwest to the southeast corner of the waterhole about 6 m above the water. Twelve quail, settling into their roosting trees, and one desert cottontail rabbit (Sylvilagus auduboni) were present. Eight minutes later, a Sparrow Hawk flew from the southeast corner close in pursuit of a quail which was flying toward the roosting trees on the west side of the waterhole. The hawk flew with feet and talons extended, there was much vocalization by the flock. and the pursued quail escaped into the roosting trees. Two desert cottontails were present during this interaction which lasted about 5 sec. These were the only attacks on quail observed during the study. On three occasions quail ran or walked quickly to the trees when raptors were present, on six they showed no discernable response to the presence of raptors, and during the other 26 raptor sightings they were absent. Bent (1932) and Gorsuch (1934) report that quail cocks frequently stand as "sentinel" for a feeding flock of Gambel's Quail. No such behavior was noted in the present study either in the absence or presence of raptors or other potential predators.

A reconnaissance was made of the study area on the day following termination of the study. Fresh quail remains (chiefly feathers) were found in and beneath a tree on the northeast corner of the waterhole apron. That these remains were found up in the tree as well as on the ground indicates that the quail was probably taken by a raptorial bird. Quail remains were also found in the bottom of a wash on the east side of the area.

Other interactions involving predators. Quail and coyote (Canis latrans) were present simultaneously on 15 occasions, but coyotes were not seen to attack quail and no detectable response to coyotes by quail was ever observed. Quail were seen to feed undisturbed within 5 m of coyotes. Gorsuch (1934) reports no quail remains in a small sample of coyote stomachs and confirms the present observation that the proximity of coyote has little effect on quail activity. Of other potential quail predators which are known to occur in the study locale, only one badger (Taxidea taxa) was seen. Sumner (1935a,b) concludes that neither coyotes nor badgers are significant predators on California Quail (Lophortyx californicus).

Three desert cottontail rabbits were seen simultaneously with raptors but were not seen to be attacked. However, at 10:00 one morning a cottontail ran across the south apron of the waterhole 3 min after a male Marsh Hawk had exited. Hawks had been in the area since 07:45. Since no other cottontail was observed during the study between 07:45 and 17:15, it is hypothesized that this individual had hidden during the hawks' presence and then had run to its den when they left.

DISCUSSION

The data presented indicate that Gambel's Quail differ from raptors in the timing of their use of the waterhole area. The inverse correlation between average daily quail and raptor presence is not evidence for a causal relationship but the most plausible explanation involves predatory dynamics.

First, many raptors are known to prey on quail. On the basis of stomach contents and remains found in nests, Cooper's Hawks (Accipter cooperii), Sharpshinned Hawks (Accipter striatus), Swainson's Hawks (Buteo swainsoni), Marsh Hawks, and Sparrow Hawks are known to prey on quail and other gallinaceous birds (e.g., Bent 1937; Fisher 1893; Gorsuch 1934). All of these are among those raptor species positively or tentatively identified at the waterhole and include those involved in predatory attacks on quail during the study. Sumner (1935a,b) concludes that predation on California Quail by Cooper's and Sharpshinned Hawks is significant but feels that the importance of predation by Marsh and Red-tailed Hawks is minimal.

Second, several other obvious factors which might control the observed phenomena do not appear to have been operative. For example, higher midday temperatures could have controlled the daily exodus of quail from the waterhole, but there appears to be little difference between the waterhole area and the desert floor to which they move in regard to environmental features which may aid in thermoregulation (with the exception of the water itself). Fisher et al. (1972), in a survey of birds using Australian desert waterholes, find some species drink primarily in early morning and late afternoon. They conclude

that such a pattern is determined mainly by avoidance of high midday temperatures and of intense solar radiation and do not mention predation in this regard. However, they conclude that the evolution of the topography of drinking behavior has been determined primarily by minimizing vulnerability to avian predators. If raptor predation influences the topography of drinking behavior, it must also influence the temporal pattern of drinking. Additionally, the temperature exceeded 70° F (21.1° C) on only 6 of 21 days in the present study, while in Elder's study (1956) the temperature exceeded 90° F (32.2° C) on 172 of 184 days; yet the temporal pattern of quail drinking was unchanged. Another possibility for the quail pattern is that they are seeking insects which might be maximally active at midday but insect activity is minimal during January in this area. Also, Gorsuch (1934) notes that 99% of the diet of Gambel's Quail in January consists of plant matter. The exploitation of other plant food sources is also possible but, if this is the case, their maximal utilization at midday is puzzling. Additionally, Gorsuch (1934), who followed Gambel's Quail through their daily routine, and Sumner (1935a), who did likewise for California Quail, report that feeding of any type is minimal during this time. They observed that quail mainly engage in maintenance activities and rest at midday and the waterhole area affords ample sheltered resting places.

A third line of evidence comes from the distribution of daily presence of desert cottontail rabbits, highly preferred raptor prey. Like the quail, but to an even greater degree, they were seen at dawn and dusk when raptors are not usually present.

It appears that the timing of utilization of the resources of the waterhole by the flock of Gambel's Quail and by raptors overlapped minimally, thus reducing the probability of quail encountering avian predators. Many authors, e.g., Cade (1965); Fisher et al. (1972); and Miller and Stebbins (1964), have suggested that the topography of drinking patterns have evolved to minimize capture by diurnal birds of prey. It appears that, at least for Gambel's Quail, the temporal pattern of drinking may have been similarly influenced. The confirmation of this conclusion as well as discovery of the precise dynamics and proximate stimuli operative in the behavior await controlled experimentation.

It might be noted that observation concentrated solely on quail or on raptors would probably not have yielded quantitative support for the relationship reported above and underscores the importance of studying the behavior of a cross section of the faunal assemblage of an area rather than a single target species.

SUMMARY

The daily cycle of presence of a winter flock of Gambel's Quail at a desert waterhole in Arizona was found to be crepuscular. Raptors, on the other hand, were seen at the waterhole nearer the middle of the day. We hypothesize that this inverse temporal usage of the waterhole area by quail and raptors is based on predatory dynamics.

We thank the citizens of the United States for their foresight in establishing and preserving the Organ Pipe Cactus National Monument and the Cabeza Prieta Game Range where we lived and worked during our study. Claude Lard of the Fish and Wildlife Service and Superintendent of the Game Range, Matt Ryan of the National Park Service and Superintendent of the Monument and the Monument Staff, Jim Carrico, Dick Cunningham, Ed Abby, Wilton Hoy and Jack Mann offered invaluable support and hospitality for which we are most grateful. Millicent Ficken read the manuscript and offered valuable criticism and suggestions. Dolores Fisera typed the manuscript.

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THE CAYENNE TERN IN BRAZIL

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The wide distribution of the Cayenne Tern (Thalasseus eurygnathus = Sterna eurygnatha = S. sandvicensis eurygnatha) has been shown by several authors to be on the Caribbean and Atlantic coasts of South America from the southern Caribbean Islands (12° N) and Trinidad along the coasts of Colombia, Venezuela, Surinam, Brazil, and Uruguay south to Argentina as far as Puerto Deseado (48° S, Santa Cruz Prov.). Junge and Voous 1955; Voous 1957, 1963, 1968; Phelps and Phelps 1958, 1959; Escalante 1959, 1962, 1970a,b; ffrench and Collins 1965; Sick and Leao 1965; Zapata 1965; Olrog 1967; Haverschmidt 1968; Korschenewski 1969; and Daciuk 1972). Breeding colonies were reported in four different areas: Netherland Antilles (Junge and Voous 1955; Voous 1957, 1963; Ansingh et al. 1960); near Cabo Frío, Brazil, 23° S (Sick and Leao 1965); Golfo San José, 43° S (Daciuk 1972); Punta Tombo, 44° S (Korschenewski 1969); and Punta de los Pájaros, in Argentina, 44°55' S (Zapata 1965). Phelps and Phelps (1958, 1959) and ffrench and Collins (1965) mentioned isolated breeding pairs with eggs, and chicks on islands off Venezuela and on Trinidad. Voous (1968) and Escalante (1970:89-94; 1970:171-177) concluded that the Argentinian and Uruguayan birds differ from the Antillean ones, principally in possessing longer bills, and probably represent a distinct population. Most of the samples studied were ob167. As republished by Dover Publications, Inc. 1961.

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tained from well-defined areas (Netherland Antilles, 12° N; Uruguay, 35° S; Argentina, 43° S) but the Brazilian sample (Voous 1968) was not suitable for comparative purposes. Most of the specimens of this sample are in the British Museum (Junge and Voous 1955), and represent a composite assemblage obtained from localities between Bahia (12° S) and Santa Catharina (27° S), an area 2000 km in extent and with a 15° difference in latitude. According to Voous (1968), "the Brazilian birds show the largest coefficient of variation (7.7, exposed culmen)." This might be ascribed to geographical variation and the possible occurrence of northern and southern migrants. Therefore, the status of the Brazilian birds could not be clearly settled. This paper attempts to (1) analyze the characteristics of an adequate sample of specimens (adults) obtained from a well-defined latitudinal area within the Brazilian Atlantic coast, where breeding terneries have been recorded, and (2)to compare the data with those from southern and northern South America. Accordingly, the data considered are those obtained by the author from 10 adult specimens (nuptial and nesting plumages, etc.) in the collections of the Museu de Zoologia da Universidade de São Paulo (six skins) and Museu Nacional da Universidade de Río de Janeiro (four skins). These specimens were collected at Rio de Janeiro (Guanabara) and from Santos to Iguapé (São Paulo) localities at almost the same latitude. This is in the neighborhood of Ilha dos Papagahios (23° S) near Cabo Frío, where Sick and Leao (1965) showed the existence of a breeding colony on 12 July 1963. According to Sick (unpubl. data), the tern is a permanent resident in the area, but there is no clear idea about the variation in numbers throughout the year.