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Accepted for publication 21 August 1970.

NOTES ON THE USE OF DESERT SPRINGS BY BIRDS IN CALIFORNIA

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We now know a good deal about the temperature regulation and water economy of desert birds in the laboratory, but to properly interpret this knowledge we need to know more about the behavior and physiology of the birds in the wild. Bartholomew and Cade (1963) have summarized much of the scattered information about desert birds' drinking habits, and detailed observations have also been published by Heim de Balzac (1936), Miller and Stebbins (1964), and Willoughby and Cade (1967). Our own observations, reported below, confirm and extend those of Miller and Stebbins on the birds of the southern California deserts.

Most of our observations were made at and around Upper Carrizo Spring, on the eastern edge of the San Jacinto Mountains, Riverside County, California. The habitat is Lower Sonoran, with creosote bush (*Larrea tridentata*), *Yucca mohavensis*, *Agave deserti*, *Opuntia* spp., and Ocotillo (*Fouquieria splendens*) on the slopes and flats, and mesquite (*Prosopis chilensis*), screwbean (*P. pubescens*), catclaw (*Acacia greggii*), and desert willow (*Chilopsis linearis*) in the creeks. Upper Carrizo Spring is one of three springs within about six miles along Carrizo Creek; there is also permanent water in Deep Canyon, about three miles away. Because of its altitude (about 750 m), the area is considerably cooler than is the Coachella Valley below, and the temperature did not exceed 40°C while we were there, though undoubtedly on occasions it does.

Between 1 August 1964 and 30 July 1965 we spent more than 150 hr watching at Upper Carrizo Spring, including six all-day watches in the summer and fall; we also spent many hours looking for and watching birds in the surrounding hills. We were watching especially for Black-throated Sparrows (*Amphispiza bilineata*), and our results for this species have already been published (Smyth and Bartholomew 1966a).

Our incidental observations on other relatively common species resident during the summer are given in table 1. Also in table 1 are a few observations made during a single all-day watch at Cottonwood Spring, Joshua Tree National Monument (see Miller and Stebbins 1964 for a description of this area).

The first group in table 1 contains insectivorous, carnivorous, or fructivorous birds, none of which was seen to drink at air temperatures up to 40°C. The second group contains birds of similar diets which, in contrast, were seen to drink. It is likely that all species in both groups can live without drinking at all, except perhaps at extremely high temperatures; the most likely exceptions to this are the Poor-will and Lesser Nighthawk, which feed on the wing. Further field observations on the drinking habits of these two species are needed.

On the other hand, it is probable that all birds in both groups drink occasionally if water is available, and that the individual species differ only in the temperatures below which they do not bother to drink at all. This temperature must be at least above 40°C for some birds, for at this temperature we have watched Bewick, Rock, and Cañon Wrens all foraging near the water's edge without once trying to drink.

The third group in table 1 consists of birds which, at least for part of the year, are mostly granivorous. All of them drank regularly in the summer, though all but the doves can probably live without drinking when succulent green vegetation or insects are available (Bartholomew and Cade 1963; Smyth and Bartholomew 1966a).

In general, these observations and those of other workers imply that whether desert birds drink or not depends very much on their diet and much less on air temperatures. This might mean that, in colonizing the desert, insectivorous, carnivorous, or fructivorous species are limited more by the desert's food resources, or their inability to exploit them, than by a lack of drinking water.

The study area was also used by migrants, either in passage or as winter residents. The fringillids among them drank frequently, even when edible green vegetation was available; these were the Black-headed Grosbeak (*Pheucticus melanocephalus*), Lazuli Bunting (*Passerina amoena*), Pine Siskin (*Spinus pinus*), Sage Sparrow (*Amphispiza belli*), Oregon Junco (*Junco oreganus*), Chipping Sparrow (*Spizella passerina*), and White-crowned Sparrow (*Zonotrichia leucophrys*). Also, several insectivorous migrants or winter residents were frequently seen to drink; these were the Nashville Warbler (*Vermivora ruficapilla*), Yellow Warbler (*Dendroica petechia*), Wilson Warbler (*Wilsonia pusilla*), and Western Bluebird (*Sialia mexicana*).

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TABLE 1. A summary of the drinking habits of the commoner birds resident around Upper Carrizo Spring in the summer.

Species	Food ^a
Not seen drinking	
Ladder-backed Woodpecker (<i>Dendrocopos scalaris</i>)	I
Ash-throated Flycatcher (<i>Myiarchus cinerascens</i>)	I
Verdin (<i>Auriparus flaviceps</i>)	I
Bewick Wren (<i>Thryomanes bewickii</i>)	I
Cactus Wren (<i>Campylorhynchus brunneicapillum</i>)	I
Cañon Wren (<i>Catherpes mexicanus</i>)	I
Rock Wren (<i>Salpinctes obsoletus</i>)	I
Loggerhead Shrike (<i>Lanius ludovicianus</i>)	I, C
Scott Oriole (<i>Icterus parisorum</i>)	F, I
Seen drinking	
Roadrunner (<i>Geococcyx californianus</i>)	I, C
Poor-will (<i>Phalaenoptilus nuttallii</i>) ^b	I
Lesser Nighthawk (<i>Chordeiles acutipennis</i>) ^b	I
Say Phoebe (<i>Sayornis saya</i>)	I
Mockingbird (<i>Mimus polyglottos</i>) ^b	I, F
Phainopepla (<i>Phainopepla nitens</i>) ^b	F, I
Gray Vireo (<i>Vireo vicinior</i>) ^b	I
Drinks regularly	
Gambel Quail (<i>Lophortyx gambelii</i>)	G, I
Mourning Dove (<i>Zenaidura macroura</i>)	G
White-winged Dove (<i>Zenaida asiatica</i>)	G
House Finch (<i>Carpodacus mexicanus</i>) ^c	G, F
Black-throated Sparrow (<i>Amphispiza bilineata</i>)	G, I

^a C = carnivorous, F = fructivorous, G = granivorous, I = insectivorous. Taken from Miller and Stebbins (1964).

^b This species, though resident around Upper Carrizo Spring, was seen to drink only at Cottonwood Spring.

^c Resident in spring and early summer, but later moved away from the vicinity.

METHOD OF DRINKING

Birds are very wary at waterholes, and they seem very reluctant to lower their heads to drink. At Upper Carrizo Spring this was especially true of Mourning Doves. Doves drink by continuously sucking and swallowing, "like a horse" (Levi 1945), unlike most other birds, which dip their beaks into the water and then tip their heads back for the water to trickle down their throats. So when a Mourning Dove finally commits itself to drinking, its head may remain continuously down for up to at least 20 sec, during which time it drinks at an average of nearly three gulps per sec. Gambel Quail, by contrast, take much longer to drink, and we have seen them spend up to three minutes drinking (if uninterrupted), dipping and tipping on the average once every 3-5 sec. The same contrast can also be seen in table 2 by comparing the times spent drinking by caged Mourning Doves and Black-throated Sparrows.

Cade (1965) has suggested that the way doves drink is an obvious advantage against aerial predators; this way, they spend less time drinking. But doves

TABLE 2. Drinking rates of three Mourning Doves and three Black-throated Sparrows in the laboratory at temperatures of 20-24°C and 40-50 per cent relative humidity.

	Mean	Min.	Max.
Mourning Doves ^a			
Sec spent at water	11.7	4.3	25.4
No. draughts	4	1	8
ml drunk/draught	1.03	0.39	5.40
ml drunk/sec spent at water	0.35	0.20	0.63
Body weight (g)	112.4		
Black-throated Sparrows ^a			
Drinking time (sec)	42.0	26.0	62.0
No. dips	10	6	16
ml drunk/dip	0.05	0.04	0.07
ml drunk/sec spent at water	0.006	0.003	0.014
Body weight (g)	13.5		

^a Mourning Doves each measured twice; Black-throated Sparrows each measured once only.

also keep their heads down for longer continuous intervals than do other birds, and it could be argued that they are so very wary in approaching water because their way of drinking makes them especially vulnerable.

TIME OF DRINKING

Very few birds of any species drank early in the morning. Usually there were more birds drinking in the middle of the morning than at any other time of day. Figure 1 shows the distribution of visits of Mourning Doves to Cottonwood Spring one day, together with air temperature. Unfortunately the birds were disturbed occasionally by visitors, but the pattern is clear; few doves drank early in the morning, and more drank at mid-morning than at any other time.

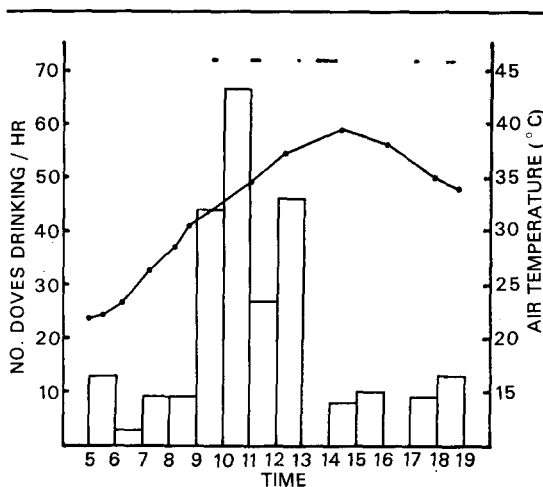


FIGURE 1. The number of Mourning Doves drinking per hour (bars) at Cottonwood Spring, Joshua Tree National Monument, on 31 July 1965, and air temperature in the shade (graphed line). The horizontal lines at the top indicate when visitors to the Spring disturbed the birds.

This is consistent with the statements of Cowan (1952) and Schmid (1965) that Mourning Doves first feed, then drink, and it is a pattern which seems to be widespread among desert birds (Cade et al. 1966; Smyth and Bartholomew 1966a; Willoughby and Cade 1967).

Cowan and Schmid both found that Mourning Doves drink again in the late afternoon; our data do not show this, perhaps because of the disturbances.

A METHOD FOR MEASURING WATER CONSUMPTION IN THE FIELD

The amount of water that birds drink in the field could be roughly estimated if one knew the average number of visits made to water per day, the average number of draughts taken per visit, and the average amount of water drunk per draught. We have measured the latter for three Mourning Doves and three Black-throated Sparrows in the laboratory. The birds were kept under the conditions described by Smyth and Bartholomew (1966a, b); drinking water was removed for 24 hr before the measurements were made, and tap water was then given in L-shaped drinking tubes. The birds were watched through one-way glass, and the number of draughts, the time spent drinking, and the amount drunk were recorded for each bird as it slaked its thirst. The results are given in table 2.

Unfortunately we both left California before we could get adequate data to calculate daily consumption from these calibrations, but, given color-banded birds and careful observation, it should not be difficult to get sufficient data to relate drinking to ambient temperature in the field.

BATHING

Bathing, sitting, or standing in the water would allow heat to be lost by conduction, and by evaporation when the bird leaves the water. Yet few desert birds bathe in water even in the heat of the day. The only species we saw bathing were the Yellow Warbler and the Nashville Warbler, both at Upper Carrizo Spring. These of course are not desert species at all, and King and Farner's (1964) statement that "the tendency for birds to bathe under conditions of high ambient temperature is a matter of common observation" probably applies mostly to birds of more temperate climates or to desert birds at very high ambient temperatures. Bathing in isolated desert waterholes would carry the same dangers as drinking, namely an increased vulnerability to predators, and many of the desert birds that do not bathe in water regularly bathe in dust.

OSMOTIC CONCENTRATION OF DESERT WATERS

The usefulness of water to a bird depends on how brackish it is. We therefore measured the osmolality and chloride concentration of water from six California desert springs and from one stream in a more mesic area (Placerita Creek). The results are given in table 3. The osmotic and chloride concentrations of most of the springs were relatively low, but in one spring the osmotic concentration was almost as high as that of the blood of a bird. But birds can produce urine hyperosmotic to their blood, so all these springs should have been useful to them.

The ratio of chloride concentration to total osmotic concentration is a useful index to the proportion of the osmotic concentration accounted for by chlorides. In these waters, this ratio was between 0.05 and 0.25. The ratio for seawater is about 0.45.

TABLE 3. Osmolality and chloride concentrations of some southern California springs.

Locality	mOsmol/liter*	mEq/liter*
Willow Springs, Granite Mts., San Bernardino Co., 6 March 1965	12.8	3.1
Upper Carrizo Spring, Riverside Co., 20 March 1965	27.6	3.9
30 July 1965	33.4	5.3
Cottonwood Spring, Joshua Tree National Monument, Riverside Co., 16 September 1966	17.1	2.2
Budweiser Spring, Granite Mts., San Bernardino Co., 7 March 1965	42.4	9.0
Upper Warm Spring, Saline Valley, Inyo Co., 12 April 1965 (pond)	33.8	3.2
Same locality and date (seepage used by feral burros)	329.0	24.7
Indian Spring, Saline Valley, Inyo Co., 12 April 1965	181.0	24.6
Placerita Creek, Los Angeles Co., 20 April 1965	15.0	0.8

* All figures are the means of five readings.

SUMMARY

At two desert waterholes in Riverside County, California, several species of resident birds were not seen to drink at air temperatures up to 40°C. These were all insectivorous, carnivorous, or fructivorous. Some insectivorous, carnivorous, or fructivorous birds did drink occasionally. All granivorous birds drank regularly.

Mourning Doves, which drink by sucking, must lower their heads for longer intervals than other birds; this perhaps makes them vulnerable to predators and explains their great wariness at water.

Most birds, if they drink, do so first at mid-morning, probably after they have fed.

A method for estimating water consumption in the field is outlined.

Very few if any desert birds normally bathe in water.

The osmotic concentration of water from several desert springs was low, but water from one spring was nearly isosmotic with birds' blood.

ACKNOWLEDGMENTS

These observations were made with the help of a grant from the National Science Foundation, GB-966, to G. A. Bartholomew. We are grateful for discussion with Bartholomew and with L. Tevis of the Philip L. Boyd Desert Research Center.

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Accepted for publication 21 September 1970.

AN AGE DIFFERENTIAL OF MIGRANTS IN COASTAL CALIFORNIA

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While the age distribution and species composition of North American avian breeding populations is reasonably well known, comparable information is generally not available on migrating populations. Capture data taken at the Point Reyes Bird Observatory on the coast at Bolinas, 23 km NW of San Francisco, and at other stations in California have provided information on the composition, seasonal timing, and relative abundance of various species of land bird migrants.

The data presented below concern the fall migration of three nocturnally migrating passerine species, the Warbling Vireo (*Vireo gilvus*), the Wilson's Warbler (*Wilsonia pusilla*), and the Western Flycatcher (*Empidonax difficilis*). I wish to emphasize one fact: the abnormally high percentage of young found along the coast in fall migration. I feel that a majority of these young birds are not adapted for successful migration. A study of these individuals might reveal the relative importance of the various adaptations for migration, and thus the causes of mortality during this critical period.

These species have been chosen for analysis because of their abundance during both migration and breeding at Point Reyes, and because their wintering grounds are in the tropics. This latter fact ensures that the birds captured are long distance migrants, and are thus subjected to the maximal selection induced by migration. On the mainland the birds analyzed in this study were captured entirely by mist nets, while on the Farallon Islands, 25 km W of the Observatory, a Heligoland trap was also used. Age was determined by the extent of skull ossification and by plumage characteristics, criteria felt to be accurate in more than 95 per cent of individuals examined.

THE WARBLING VIREO AT POINT REYES

A brief summary of the annual cycle of the Warbling Vireo in the Point Reyes area, is reasonably represent-

ative of all three species and will give perspective to the following data. The summer residents at Point Reyes generally arrive during March (fig. 1A), and by April are nesting. Migrants breeding farther north pass through in peak numbers during the latter part of April and the first part of May (fig. 1B). This late influx is synchronous with the arrival of this species on the Farallon Islands (fig. 1C), where there is no breeding population. The majority of Point Reyes adults leave during July and early August, and may be in full migration (but see below). At this time there is an increase in young birds (fig. 1B), probably representing dispersal of locally produced young.

The evidence available indicates that fall migration begins after 1 August and continues through October, and this period was used in calculations. The first fall migrants of this species were recorded on 6 August at San Diego (Alan and Jean Craig, pers. comm.) at the extreme southern limit of breeding of the subspecies *V. g. swainsonii*. The species was first noted on the Farallon Islands on 29 August.

AGE RATIO OF MIGRANTS

During the fall migration period described, virtually all Warbling Vireos captured are young (table 1). The adult:young ratio is 1:19, far too high for the normal age distribution of 1:1 to 1:4 (expected on the basis of normal clutch size and survival of young). Similarly, captures of the Wilson's Warbler and Western Flycatcher show even higher age ratios during the fall migration (1:28 and 1:26). These disproportionate ratios indicate either that the adults in all three species produced between 38 and 56 young per pair, or that an additional factor(s) is influencing the occurrence of these species on the coast of central California. Note that the age ratio of all three species is even more disproportionate on the Farallon Islands than on the adjacent mainland, the difference being significant at the 0.05 level. This very high proportion of young in fall migration is found in all species of nocturnal passerine migrants in this area (Ralph, unpubl. data), and can thus be considered a general phenomenon, although the specific causes may vary in each species.

HYPOTHESES ADVANCED TO EXPLAIN AGE DIFFERENTIAL

The great preponderance of young of nocturnal migrants in coastal situations has long been recognized

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