WATER DEPENDENCE OF BIRDS IN A TEMPERATE OAK WOODLAND

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ABSTRACT.—Observations from June to September 1977 at a spring in central coastal California showed that 24 of 45 species of birds found within a 1.6-km diameter area used the spring as a source of free water. Color-banded individuals of several species drank more than once a day. A significant seasonal variation in the number of drinking visits per hour was found for all species combined. Only the Brown Towhee showed a conspicuous diurnal drinking pattern, however. Temperature on a particular day was not correlated with number of species visiting the spring, the total number of visits by all birds to the spring, or the number of visits by five of the six species considered to be water dependent.

Granivory was significantly, positively correlated with water dependence. Permanent residents were more regular drinkers than summer residents, but this was a secondary effect resulting from the high proportion of granivory among permanent residents. The habitat surrounding the water hole, species abundance, and human disturbance at the spring all showed possible influence on our measures of water dependence. These findings suggest that surface water may be an important determinant of species distribution and community organization in mesic as well as desert environments. *Received 25 June 1979, accepted 30 October 1979.*

WATERING points are of critical importance to many species of birds in the deserts of Africa, Australia, and North America (Bartholomew and Cade 1963, Willoughby and Cade 1967, Fisher et al. 1972). The importance of water sources in seasonally stressful environments, however, has been little studied. Our work was undertaken to determine the importance of free water to birds in the coastal mountains of central California. This area has a Mediterranean climate with less than 2% of the average annual precipitation falling in June through September (Bradford 1974), when many of the streams and pools evaporate and vegetation becomes very dry.

STUDY AREA

Hastings Reservation, an 800-ha preserve, lies at the northern end of the Santa Lucia Mountains in Monterey County, California, 39 km southeast of the mouth of the Carmel River. The broad-sclerophyll vegetation and physical conditions of the region have been described by Cooper (1922), Shreve (1927a, b), Linsdale (1943), White (1966), and Griffin (1974).

Arnold Spring is tapped for the water supply of the Reservation. A box 1.0 × 0.5 m has been built nearby with a float valve to which water is piped to provide surface water to wildlife. The elevation of the spring is 762 m. Surrounding vegetation is mixed evergreen forest; oaks (*Quercus agrifolia, Q. kelloggii,* some *Q. lobata*) and madrone (*Arbutus menziesii*) are the dominant tree species, and there is a diverse understory of *Rhus, Rhamnus, Ribes,* and other shrubs. This complex is described by Griffin (1974) as the oak-madrone phase of mixed evergreen forest.

On either side of the spring, vegetation grades into foothill woodland and chaparral. The foothill woodland is a deciduous oak community on warm, dry upland slopes, particularly of southern exposure (Griffin 1971, 1973; White 1966). The chaparral is dominated by chamise (*Adenostoma fasciculatum*) and occurs on steep south-facing slopes.

The nearest surface water sources to the spring were three water holes 0.5 km away and 270 m lower in elevation in a creek bed, each containing no more than 10 l of water. Additional sources within 3 km of the spring included 2 other creek bed water holes 1 km away, 2 water troughs 2.4 km away, and several leaky faucets and garden pools 2.9 km away. In addition, there may have been water available in holes in trees, which are known sources of drinking water for some bird species on the reservation including Brown Towhees[1] (J. Davis, pers. comm.) and Acorn Woodpeckers.

[1] Scientific names are given in Table 1.

The mean annual precipitation at Reservation headquarters, 2.9 km from the spring, is 513 mm (n = 39, SD = 178 mm), with a high of 1,051 mm in 1940–41 and a low of 261 mm in 1975–76 since records were first kept in 1938–39. The 1976–77 season was also very dry, with only 302 mm of rainfall. While the creeks do not usually start flowing until at least December (Davis 1973), between 1975 and 1977 they did not flow at all. Two or more consecutive yr of below average rainfall are not uncommon, however, occurring 5 times in the last 50 yr with up to 5 consecutive yr falling below the mean (1946–47 to 1950–51). Although the drought from 1975 to 1977 may have accentuated the stress of the dry season in the summer of 1977, the lack of water availability during the summer months is an annual occurrence.

During the study period the lowest temperature was 3.3°C and the highest 38.5°C, with a mean range of 21°C per day. Average daily maxima and minima from 1939 to 1968 were: June, 26.3° maximum, 7.9° minimum; July, 30.8°, 10.3°; August, 30.4°, 10.7°; September, 29.3°, 8.8°. Extreme maxima (1939–1974) were 44° for July and 43° for June, August, and September. Extreme minima for the same years were −1° for July and −2° for June, August, and September.

METHODS

Between 15 June and 18 September 1977 we watched the spring for a total of 162 h on 26 days. During watches, each visit of a bird to drink and the time of the visit was recorded. The presence of nondrinking birds was noted as well. A cabin 7.5 m from the spring served as a blind. Five watches were from dawn to dusk, while most of the others were in the morning only. Watches fell into four categories: half and whole day watches on which birds were banded during the watch and half and whole day watches uninterrupted by banding. The number of drinking visits per hour for each species in these categories was significantly correlated (Kendall's coefficient of concordance, $\chi^2 = 55.7$, df = 3, $P < 0.001$). Thus, data from all watches were combined.

Birds were mist-netted in four nets between 1 and 15 m from the spring. Some species were color-banded for individual recognition. Two Glenhaven four-celled sparrow traps were set on watches in June and early July, but their use was suspended after disturbance by ground squirrels.

A 1.6-km census was made on 11 mornings along a dirt road that passes the spring in order to provide an index of the abundance of each species in the area and to record species that were present but did not drink at the spring. Temperature was recorded at 0.5-h intervals. On days when temperature was not taken at the cabin, the maximum and minimum values from Reservation headquarters (2.9 km from the spring) were used.

Nonparametric statistical procedures (two-tailed whenever applicable) were used, and tests yielding a probability of ≤ 0.05 were considered significant.

Water dependence was measured for each species in the following ways:

(A) Drinking visits per hour: (Total number of times an individual of the species drank) ÷ (total number of hours watched)
(B) Fisher water-dependence categories (Fisher et al. 1972): (1) never drank; (2) occasional drinker—drank on half or fewer of the days with a maximum temperature of 25°C or above; (3) summer drinker—drank on more than half of the days with a maximum temperature of 25°C or above; (4) water dependent—drank on more than half of the days with a maximum temperature of 25°C or above and also drank on more than half of the days at lower temperatures.
(C) Proportion of days an individual of the species was recorded drinking.
(D) Number of individuals of the species banded.

We use "water dependent" to indicate persistent and regular use of water by individuals of a species (i.e. FWD categories 3 or 4) without further information about whether such use is physiologically necessary.

The following variables were considered in determining what factors influenced our measures of water dependence:

(A) Diet. Each species was rated separately for granivory (G) and insectivory (I) on a scale of 1 to 3. Dietary information was obtained from Beal (1907–1912), Bent (1932–1968), Gutiérrez (1977), and Martin et al. (1951): (1) <20% G or I; (2) 20 to 50% G or I; (3) >50% G or I.
(B) Abundance of the species on censuses, determined by dividing the total number of each species seen on censuses by the number of censuses.
(C) Whether the species was a permanent resident, summer resident, winter resident, or migrant at Hastings.
(D) Body weight. Weights are from Grinnell et al. (1930) when available and otherwise from specimens in the Museum of Vertebrate Zoology.

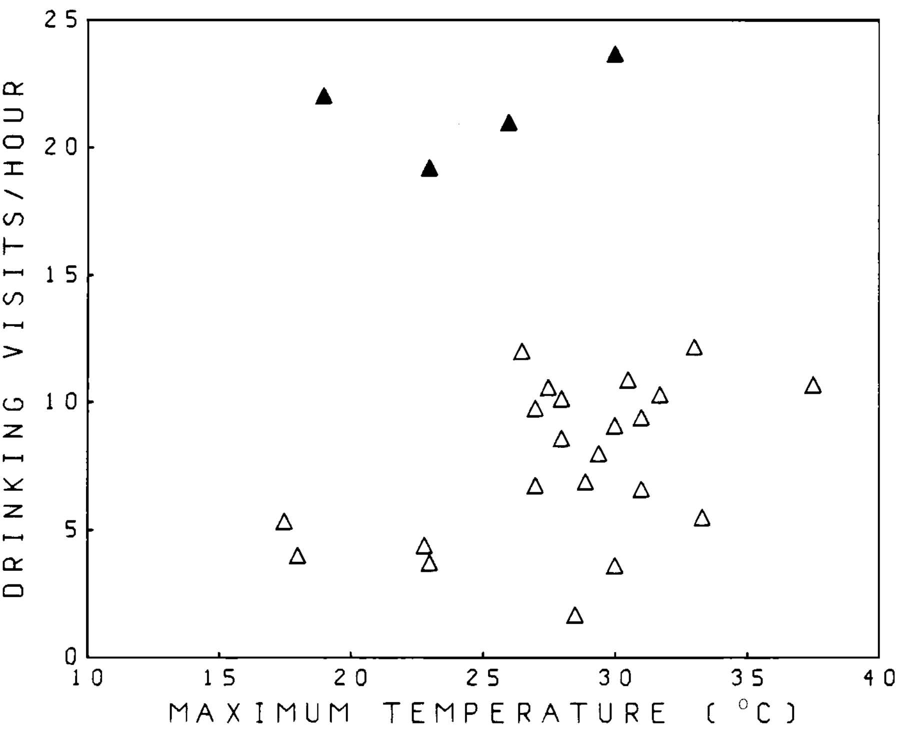

Fig. 1. Relationship between maximum temperature and total drinking visits per hour made for 26 days between 15 June and 18 September 1977 at the Arnold Spring, Hastings Reservation. The solid triangles are the four late season watches, 12 August to 18 September.

Results

Forty-five species of birds were observed during the study (Table 1). Twenty-one (47%) never drank, while 24 (53%) drank on at least one occasion. Of the 24 species that drank, 13 did so on less than 25% of the watches, and 5 were seen drinking on only one watch. Measured by Fisher water-dependence categories, 18 (40%) of the species were occasional drinkers and 6 (13%) were water dependent. A total of 246 birds of 25 species were banded.

All four measures of water dependence were highly correlated (smallest Spearman rank correlation between pairs, $r = 0.75$, $P < 0.001$). Thus, drinking visits per hour (DVH) and Fisher water-dependence categories (FWD) were chosen as the measures of water dependence in the following analyses according to whether a discrete or continuous variable was appropriate.

Factors influencing species drinking patterns.—Figure 1 plots maximum temperature on each of the 26 days against the total DVH observed for that day. The correlation for all data is positive but not significant (Spearman rank correlation, $r = 0.11$, $P > 0.10$). Even when late season watches (when significantly more birds came to the spring) are eliminated (solid triangles in Fig. 1), the correlation is still nonsignificant ($r = 0.37$, $P > 0.05$). Individually, only one of the six water-dependent or summer-drinker species (FWD categories 3 and 4, Table 1), the Black-headed Grosbeak, showed a significant temperature dependence in drinking pattern

TABLE 1. Measures of water dependence and possible influencing factors.

Species	Measures: Drinking visits per hour[b]	Measures: Fisher water-dependence category[b]	Influencing factors: Abundance on census[c]	Influencing factors: Mean weight (g)	Diet[a]: Granivorous	Diet[a]: Insectivorous	Resident status[d]
Turkey Vulture (*Cathartes aura*)	0	1	0	1,570	1	1	PR
Cooper's Hawk (*Accipiter cooperii*)	0	1	0	327	1	1	PR
Red-tailed Hawk (*Buteo jamaicensis*)	0	1	0.36	1,038	1	1	PR
Band-tailed Pigeon (*Columba fasciata*)	0	1	5.00	390	3	1	WR
Mourning Dove (*Zenaida macroura*)	0	1	0.45	117	3	1	PR
Hairy Woodpecker (*Dendrocopus villosus*)	0	1	0	65	1	3	PR
Downy Woodpecker (*Dendrocopus pubescens*)	0	1	0	26	1	3	PR
Ash-throated Flycatcher (*Myiarchus cinerascens*)	0	1	0.27	27	1	3	SR
Western Flycatcher (*Empidonax difficilis*)	0	1	0.09	11	1	3	SR
Western Wood Pewee (*Contopus sordidulus*)	0	1	0.64	14	1	3	SR
Olive-sided Flycatcher (*Nuttallornis borealis*)	0	1	0.09	31	1	3	SR
Violet-green Swallow (*Tachycineta thalassina*)	0	1	1.36	13	1	3	SR
Common Bushtit (*Psaltriparus minimus*)	0	1	6.73	6	1	3	PR
House Wren (*Troglodytes aedon*)	0	1	0.36	10	1	3	SR
Bewick's Wren (*Thryomanes bewickii*)	0	1	1.55	10	1	3	PR
Western Bluebird (*Sialia mexicana*)	0	1	0.09	28	1	3	PR
Solitary Vireo (*Vireo solitarius*)	0	1	0.27	14	1	3	SR
Hutton's Vireo (*Vireo huttoni*)	0	1	0.27	11	1	3	PR
Warbling Vireo (*Vireo gilvus*)	0	1	0.82	12	1	3	SR
Hermit Warbler (*Dendroica occidentalis*)	0	1	0	10	1	3	M
Northern Oriole (*Icterus galbula*)	0	1	0.18	29	1	3	SR
White-breasted Nuthatch (*Sitta carolinensis*)	0.01	2	0.45	18	1	3	PR
California Thrasher (*Toxostoma redivivum*)	0.01	2	0	98	2	3	PR
Robin (*Turdus migratorius*)	0.01	2	0	91	1	2	PR
Wilson's Warbler (*Wilsonia pusilla*)	0.01	2	0.09	17	1	3	M
Purple Finch (*Carpodacus purpureus*)	0.01	2	4.00	23	3	1	PR
Chipping Sparrow (*Spizella passerina*)	0.02	2	0.27	13	3	2	SR
Common Flicker (*Colaptes auratus*)	0.02	2	0.55	147	1	3	PR
Nuttall's Woodpecker (*Dendrocopus nuttallii*)	0.02	2	1.09	37	1	3	PR
Orange-crowned Warbler (*Vermivora celata*)	0.05	2	0.09	8	1	3	SR
Anna's Hummingbird (*Calypte anna*)	0.06	2	0.18	5	1	2	PR
Black-throated Gray Warbler (*Dendroica nigrescens*)	0.06	2	0.27	8	1	3	SR
Plain Titmouse (*Parus inornatus*)	0.11	2	2.64	16	2	2	PR
Acorn Woodpecker (*Melanerpes formicivorus*)	0.13	2	2.36	78	3	2	PR
Western Tanager (*Piranga ludoviciana*)	0.16	2	0	29	1	3	M
Wrentit (*Chamaea fasciata*)	0.21	2	1.64	15	1	3	PR

TABLE 1. Continued.

Species	Measures: Drinking visits per hour[b]	Measures: Fisher water-dependence category[b]	Influencing factors: Abundance on census[c]	Influencing factors: Mean weight (g)	Influencing factors: Diet[a] Granivorous	Influencing factors: Diet[a] Insectivorous	Influencing factors: Resident status[d]
Black-headed Grosbeak (*Pheuticus melanocephalus*)	0.23	3	0.73	41	1	3	SR
Mountain Quail (*Oreortyx pictus*)	0.25	2	0.18	254	3	1	PR
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	0.31	3	3.73	41	3	2	PR
California Quail (*Lophortyx californicus*)	0.38	2	10.45	180	3	1	PR
Scrub Jay (*Aphelocoma coerulescens*)	0.52	2	2.82	86	3	2	PR
Lesser Goldfinch (*Spinus psaltria*)	1.01	4	0.64	9	3	1	PR
Steller's Jay (*Cyanocitta stelleri*)	2.51	4	1.27	108	3	2	PR
Dark-eyed Junco (*Junco hyemalis*)	2.70	4	0.91	18	3	1	PR
Brown Towhee (*Pipilo fuscus*)	3.62	4	4.55	56	3	1	PR

[a] 1 = <20% granivorous or insectivorous; 2 = 20% to 50% granivorous or insectivorous; 3 = >50% granivorous or insectivorous.
[b] See text.
[c] (Total number of birds of that species seen on census) ÷ (total census days).
[d] PR = permanent resident; SR = summer resident; M = migrant only; WR = winter resident.

TABLE 2. Relation of migratory status to water dependence.[a]

Fisher water-dependence category	Permanent resident (n = 27)	Summer resident (n = 14)	Winter resident (n = 1)	Migrant (n = 3)
1 Never drank	9 (33%)	10 (71%)	1 (100%)	1 (33%)
2 Occasional drinker	13 (48%)	3 (21%)	0	2 (67%)
3 Summer drinker	1 (4%)	1 (7%)	0	0
4 Water dependent	4 (15%)	0	0	0

[a] Difference between permanent and summer residents (combining FWD categories 3 and 4) not significant (χ^2 = 5.39, df = 2, P < 0.05).

(r = 0.53, P < 0.01). There was no significant correlation between the number of species drinking on a day and the maximum temperature (r = 0.20, P > 0.05).

Table 2 presents a cross-tabulation of Fisher water-dependence categories and the season of residency for each species. Comparison of permanent residents and summer residents indicates no overall significant difference in water dependence (χ^2 = 5.39, df = 2, P > 0.05). When measured by drinking visits per hour, permanent residents were significantly more water dependent than summer residents (Mann-Whitney U test, z = 2.21, P < 0.05). This effect, however, appears to be primarily an indirect result of a high degree of granivory among permanent residents (41% of permanent residents but only 7% of summer residents were more than 50% granivorous). A two-way analysis of variance using granivory (categories 1 to 3) and residency (permanent or summer) as predictors of drinking visits per hour indicates that, while the effect of diet on DVH controlling for residency is significant (F = 6.56; df = 2,36; P < 0.01), the effect of being a permanent or summer resident, controlling for diet, is not significant (F = 0.229; df = 1,36; P > 0.60).

Table 3 examines the relationship between the measures of water dependence and the three remaining factors examined (diet, abundance on censuses, and body weight). There was a strong significant correlation between granivory and water dependence. Abundance on censuses correlated to a lesser extent, weight was uncorrelated, and insectivory was negatively correlated with water dependence.

Seasonal drinking patterns.—A conspicuous increase in the number of birds drinking was observed beginning on 12 August (Fig. 1, solid triangles). Although there was no banding on three of the four late-season watches, a fact that obscures the comparison, the number of birds coming in late August and September was significantly greater than the number that came on days on which we did not band in June (Mann-Whitney U test, z = 3.31, P < 0.01). There was no significant difference in the number of species drinking in these two periods (Mann-Whitney U test,

TABLE 3. Correlations among water-dependence measures and factors possibly influencing water dependence.[a]

Measures of water dependence	Drinking visits per hour	Fisher water-dependence categories	Number of birds banded	Number of days drank
Diet				
Granivory	0.59***	0.54***	0.45**	0.60***
Insectivory	−0.38**	−0.34*	−0.23	−0.39**
Relative abundance on census	0.38*	0.32*	0.56***	0.43**
Weight	0.10	0.06	−0.10	0.13

[a] Spearman rank correlation, * = P < 0.05, ** = P < 0.01, *** = P < 0.001; others not significant.

TABLE 4. Marked individuals that drank more than once a day.

Species	Maximum number of times per day	Dates
Steller's Jay	6	1 September
Lesser Goldfinch	6	23 July (5× on 30 July)
Black-throated Gray Warbler	6	30 July (4× on 5 August)
Dark-eyed Junco	6	1 September (5× on 1, 18 September)
Brown Towhee	4	5 August, 1 September
Acorn Woodpecker	3	5 August, 1 September
Wrentit	3	18 September
Scrub Jay	3	1 September
Wilson Warbler	3	18 September
Rufous-sided Towhee	2	17 July
Chipping Sparrow	2	16 July

$z = 1.78$, $P > 0.05$). This increase in drinking frequency coincided with a diminished amount of free surface water and green vegetation late in the season. The added physiological stress as a result of birds molting at this time may also have contributed to this increase (see below).

Individual drinking patterns.—Individuals of 11 species were observed to drink more than once in a day (Table 4), and individual birds of four species drank at least six times in one day. Individuals of other species were either not identifiable or did not drink more than once a day. In three cases, the sample size of marked birds was sufficient to determine how frequently individuals drank: 1.9 times per day for Brown Towhees ($n = 60$ birds), 3.3 times per day for Dark-eyed Juncos ($n = 13$), and 3.5 times per day for Steller's Jays ($n = 8$). This was calculated by taking the average number of drinking visits made by marked individuals on the two full-day watches without banding. Dark-eyed Juncos and Brown Towhees were the most regular visitors to the spring. Seven of the former and five of the latter species were seen more than 50% of the days after banding; one marked individual of each species was seen every day after it had been banded.

Daily drinking patterns.—Brown Towhees showed a conspicuous diurnal drinking pattern such as that reported for many parrots and pigeons in Africa and Australia (Cameron 1938, Fisher et al. 1972) Most Brown Towhees drank in the morning (0700–1059) or the evening (1500–1859), with a considerably smaller number drinking in midday ($\chi^2 = 36.4$, df = 2, $P < 0.001$). A daily drinking pattern was not found in any of the other species observed.

Evidence of overlapping home ranges.—Although Brown Towhees are permanently territorial (Quaintance 1937, 1938; Bent 1968; Tvrdik 1977), 69 individuals were banded at the spring. Of these, 37 (54%) were adults, 19 (28%) were young of the year, and 13 (19%) were of unknown age. Thus, assuming that all adults were paired and territorial, at least 19 pairs were using the spring. Brown Towhee territory size varies from approximately 0.9 ha to over 2.3 ha (Bent 1968). Thus these birds came from an area at least 17–44 ha in size, counting the minimum and maximum areas for 19 territorial pairs. Given the addition of birds of unknown age who may have been adults and the unbanded birds visiting the spring (an estimated 28 on 5 August, calculated by dividing the number of drinking visits by unbanded birds by the mean number of drinking visits by color-banded birds on that day), it is likely that birds were coming to drink from a far wider area. Brown Towhees banded at the spring were seen as far as 0.3 km away, but the hilly terrain made it difficult to find many banded individuals. One individual, a female, originally banded 2.5 km away, was recaptured twice at the spring and subsequently recaptured in December 1978 near its original banding locality, suggesting the possibility that birds drinking at the spring may have been drawn from a far wider area than our data conclusively show.

Members of 8 of the 9 groups of color-banded Acorn Woodpeckers known to live within a 0.8-km radius of the spring were identified at the spring, as were 2 previously unbanded birds from outside this area. The spring is the only area on Hastings Reservation where group home ranges consistently overlap (MacRoberts and MacRoberts 1976, Koenig pers. obs.). The Wrentit is a third territorial species (Erickson 1938) whose home ranges overlapped at the spring. Four adults, 2 young of the year, and 3 birds of unknown age were banded; thus the spring area was shared by at least 2 pairs.

Other evidence of water dependence.—As expected, some species were recorded on the censuses but not at the spring. Surprisingly, eight species recorded at the spring were not recorded on the censuses. In all but one case this can be accounted for by the scarcity of the species in that area and the greater number of hours spent watching the spring than on censuses. Western Tanagers, however, were seen on all but one of 11 watches from 17 July through 1 September, drank on 6 consecutive watches from 22 July through 12 August, and 11 birds were banded (8th in abundance of species banded). This concentration of Western Tanagers in the vicinity of the spring may be an indication of water dependence. Surface water may be important to these birds on migration, despite the high water content of their insectivorous and frugivorous diet.

DISCUSSION

FACTORS AFFECTING WATER DEPENDENCE AND DRINKING PATTERNS

Influence of diet.—Granivory is closely correlated with water dependence. Of the 21 species that never drank at the Arnold Spring, only two (Mourning Dove and Band-tailed Pigeon) were primarily granivorous (Table 1), and these most likely used other sources of free water (see below). Of the 24 species that did drink, the eight species with the highest number of drinking visits per hour were all over 50% granivorous. Additionally, five of the six species that drank on more than half the watches were granivorous. A few granivorous species were only occasional drinkers (FWD category 2), but three of these (Mountain and California quail and Scrub Jay) were in the top eight species in DVH and can reasonably be considered water dependent on that basis. In total, 11 of 13 granivorous species drank (84.6%), and 4 (30.8%) were water dependent by FWD.

Although insectivory is negatively correlated with water dependence, 10 (38.5%) of 26 insectivorous species (>50% of diet) drank at the spring, and one (3.8%), the Black-headed Grosbeak, is a summer drinker by FWD. Another insectivorous species, the Western Tanager, may also be water dependent, at least on migration, as suggested by its localization at the spring. Several other insectivorous species may also be water dependent during migration. A Black-throated Gray Warbler, for example, drank six times on 30 July, after which it was not seen again, and a different individual drank four times on 5 August (Table 4).

Influence of physiology.—Habitat preference alone does not explain differences in water consumption between closely related species. Both Brown Towhees (Davis 1957) and Scrub Jays live in exposed habitats demanding greater heat tolerance than the forest and understory habitats of the Steller's Jay and Rufous-sided Towhee. Forest-dwelling Steller's Jays, however, drink more regularly than Scrub Jays, and sun-dwelling Brown Towhees are more regular drinkers than Rufous-sided Towhees. Laboratory studies are necessary to determine the physiological adaptations of each species to withstand exposure to heat and sun.

Changes in the metabolic needs of birds due to reproduction or molt may also affect their water dependence on a seasonal basis. We observed an increase in the frequency of drinking visits late in the season; this presumably coincided with the period of maximum molt and may in part have been the result of this factor.

Influence of habitat.—The habitat surrounding the spring clearly affected the extent to which several species drank there. Mourning Doves and Band-tailed Pigeons, species known from other studies to be water dependent (Cowan 1952, Smith 1968), were present in the area but did not drink at the spring (Table 1). This is probably because water holes in more desirable habitats were available within an individual's home range. Mourning Doves have been observed on the Reservation drinking regularly at water holes in creek beds and at water troughs in oak savannah habitat near Reservation headquarters. Cowan (1952) observed that Mourning Doves preferred shallow edges of ponds and streams devoid of vegetation where grit was available. Smith (1968) observed that Band-tailed Pigeons prefer mineral springs, at least during the early fall and winter. Both Mourning Doves and Band-tailed Pigeons are known to fly many kilometers daily and would find stock ponds, springs, and creek bed pools not covered by the scope of our investigations.

Some species, however, came to the spring even though it was not surrounded by their preferred habitat. Both Acorn Woodpeckers and Wrentits, for example, were regularly present at the spring, even though neither species lives in the immediate vicinity.

Influence of abundance.—Abundance of a species may have affected our calculation of water dependence in several cases. For example, a California Thrasher drank only once and thus was considered only an occasional drinker (Table 1). This species was never seen on a census, however, and was clearly quite rare in the area. If thrashers had been more common, we suspect that we would have observed them drinking more frequently, and thus our assessment of their water dependence would have risen accordingly. In general, the more abundant a species, the more frequently individuals of that species were seen drinking (Table 3). Thus differences in abundance may exaggerate the differences in calculated water dependence among species.

Influence of human disturbance.—Our activities at the spring may have affected drinking by both the quails and the Acorn Woodpecker. These species spent a long time approaching the spring and were often disturbed by banding. California Quail are known to be water dependent in the summer and early autumn (Sumner 1935: 316, Leopold 1977: 54) and thus might have been expected to drink more frequently. Other less obvious differences in wariness of certain species may have affected how often they came to drink during watches.

Influence of body weight.—Because of the inverse relation between body weight and evaporative water loss, small birds need relatively more water than large birds (Bartholomew and Dawson 1953, Bartholomew and Cade 1963). It is difficult, however, to translate this relationship to a field situation, as drinking visits per hour is not a measure of the amount of water consumed. In this study, we found no correlation between weight and our measures of water dependence (Table 3).

Influence of temperature.—Laboratory studies have generally shown an increase in water consumption with increasing temperature (Dawson 1954, Bartholomew and Dawson 1954, Bartholomew and Cade 1956). Only in the highly drought-adapted Budgerigar (*Melopsittacus undulatus*) has water consumption not been reported to increase at higher temperatures (Cade and Dybas 1962). However, our data indicate only how often birds drank, not how much water was consumed.

We found a positive but nonsignificant correlation between maximum temperature and drinking visits per hour for all species combined (Fig. 1). There was also a positive but nonsignificant correlation between the number of species that drank during a watch and the maximum temperature on that watch. Of the six species that were either water dependent or summer drinkers by FWD (Black-headed Grosbeak, Rufous-sided Towhee, Lesser Goldfinch, Steller's Jay, Brown Towhee, and Dark-eyed Junco), only one species, the Black-headed Grosbeak, showed a significant correlation between drinking visits per hour and maximum temperature. The Black-headed Grosbeak was also the only water-dependent species that never drank on days when the maximum temperature was below 25°C.

If individuals are able to compensate for higher temperatures by drinking more on each visit, this would in part explain the lack of a significant correlation between maximum temperature and DVH among the species of the study (with the exception of the Black-headed Grosbeak). This finding, however, contrasts with that of Fisher et al. (1972), who reported that frequency of drinking increased with ambient temperature for several species in the Australian deserts.

In order to clarify the amount of water consumption by birds under field conditions, Smyth and Coulombe (1971) suggested calculating water consumption in the laboratory by recording the number of drinking visits, the time spent drinking, and the amount taken in each visit for individual birds. By comparing such observations to field studies of color-banded birds, it may be possible to refine the measures of water dependence used here by estimating the amount of water consumed by individuals of each species.

Influence of season.—From 12 August until the end of the study, there was a significant jump in the number of drinking visits per hour (Fig. 1). This increase suggests that the seasonal effects of the lengthening dry season may be a dominant influence on water dependence in this area.

Influence of drought.—The drought of 1975–77 may have resulted in a greater concentration of birds at the Arnold Spring than usual, as many other water sources available in normal years had dried up. Additionally, birds may have depended on free surface water for a longer than normal length of time because a smaller amount of green vegetation was available, and this subnormal amount dried up earlier than usual. The water stress of the dry season, however, is an annual occurrence independent of the rainfall of the prior winter. Therefore, we believe that the observations we report here are representative of the water needs of the species in this area.

CONCLUSION

These findings suggest that free surface water may be an important resource for a wide variety of species in mesic areas that experience seasonal droughts. Marked individuals moved at least as much as 0.8 km (possibly as far as 2.5 km) in order to gain access to the spring. These data, therefore, suggest that the local distribution of some of the species considered here may be limited by the availability and distribution of water sources. Through its effects on species distributions, the community organization may be influenced by water availability. These effects may be significant in any environment that undergoes regular or occasional periods of water stress.

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