

# DRINKING PATTERNS AND BEHAVIOR OF AUSTRALIAN DESERT BIRDS IN RELATION TO THEIR ECOLOGY AND ABUNDANCE

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Aridity is the dominant climatic feature of the Australian continent, and desert conditions exist over almost half of the total land area. The extreme physical characteristics of such an environment, high air temperatures, intense solar radiation, and scarcity of surface water, combine to pose a severe challenge to animal life. Birds are primarily diurnal and, unlike most small desert mammals, generally do not utilize the shelter afforded by underground burrows. In hot weather they must therefore reconcile the antagonistic demands of evaporative cooling and maintenance of water balance.

Investigations of how Australian birds live successfully in desert areas have barely started. The success of many species must be intimately linked with their capacities for locating and utilizing surface water. To obtain information on this, we undertook field studies of the drinking habits of birds in the arid interior of Australia. Our findings are summarized in this report.

## METHODS

The majority of our observations were made between January 1966, and April 1968, but a few records dating as far back as 1959 have been included. Most of the data were gathered from 20 systematic dawn-to-dusk watches of "water holes." At each of these natural or artificial sources of water (fig. 1), an observer recorded the numbers and kinds of birds drinking in each 30-min period throughout the day, beginning approximately one hour before sunrise and continuing until about one hour after sunset. In order to list more accurately all the species in the area, most

of these watches were supplemented on a separate day by observations on the birds to be found within a 2-3 mile radius of the particular water hole. The hourly shade and "black bulb" temperatures, and the relative humidity at approximately 4-hour intervals were also recorded.

Data were obtained over a wide temperature range at every season of the year and in all major desert vegetation zones. Localities where watches were made are shown in figure 2. All lie inside the 15-inch isohyet. Water samples were taken for 10 of the localities and later analyzed in the laboratory for various cations by flame photometry or titrametric procedures.

A rough estimate of the relative abundance of desert birds was obtained through 10 censuses situated at widely spaced localities (fig. 2). Counts were taken in all arid habitats and were confined to the warmer, drier parts of the year when surface water was limited to scattered water holes.

The classification of avian families in this report follows that of Serenty and Whittell (1962) with the following exceptions: *Sphenostoma* is placed in the Timaliidae; Maluridae and Ephthianuridae are included with the Sylviidae; *Rhipidura* and *Seisura* are included with the Muscicapidae; and *Neositta* is placed in the Neositidae.

## RESULTS AND DISCUSSION

### DRINKING HABITS OF SPECIES

*Frequency of Drinking.* A summary of the 20 dawn-to-dusk watches is given in table 1. Although the distance to the next nearest source of water was often known precisely, only an estimate could be made in a few areas. All observations except those for watch number 1 were at localities where livestock was present, and thus watering places were never more than 5 miles apart (except at locality M, where data were obtained at a time of year when moist food was available and temperatures were mild). The distribution of

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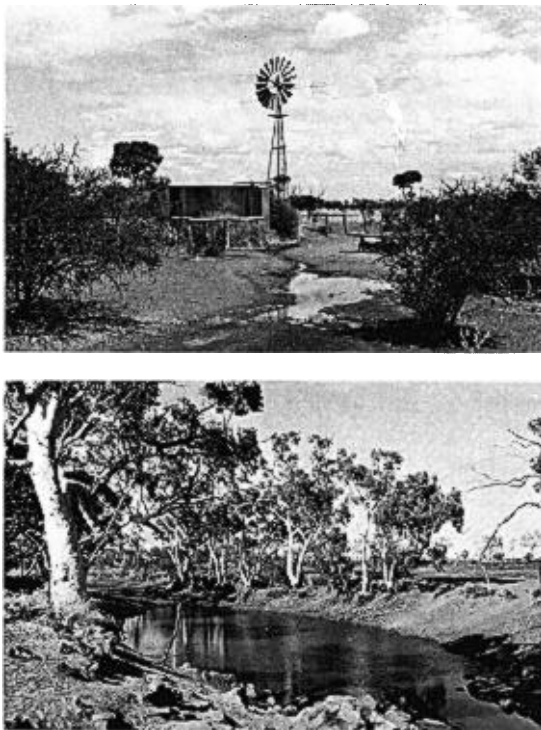


FIGURE 1. Desert water holes. A. (top) Artificial sources of water, usually from a windmill, are found today every 3–5 miles in much of the dry interior because of the development of the land for livestock use. B. (bottom) River gums border a natural water hole in a stream bed near Wiluna, Western Australia. The water in such pools remains potable for birds many months after the last rainfall.

water holes in our study areas was quite uniform, in contrast to the situation in unsettled regions of the Australian interior where surface water is very scarce and irregularly distributed.

Birds listed in table 1 as not drinking are those which were recorded within a 2–3-mile radius of the water hole (except as indicated by parentheses), but which were not seen visiting water. Surveys of birds present in the vicinity were made within 1 or 2 days of the water hole watch. Figures almost certainly underestimate to some extent the total variety of nondrinking species inhabiting an area, because of the difficulty in finding all the birds present. On the other hand, highly mobile species such as hawks, cockatoos, woodswallows, and crows which did not drink at the water hole under observation may easily have done so at another nearby water source. Nocturnal species have been excluded, except for the Spotted Nightjar and Southern Stone-curlew which were seen drinking at dusk, as have shore and water birds with the exception of the Banded Plover, Masked Plover, and Australian Pratincole.

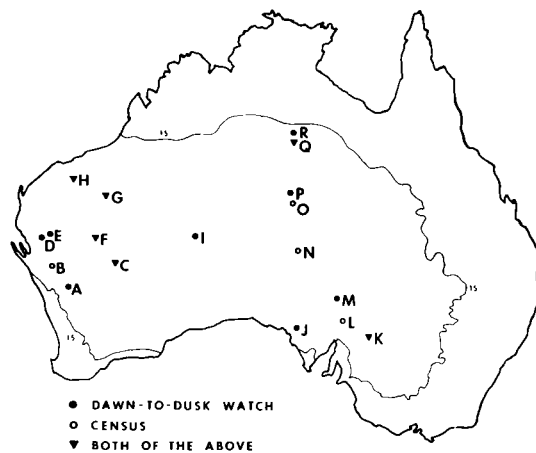


FIGURE 2. Map of Australia showing localities where studies were made, and the 15-inch isohyet. Localities are: Western Australia—A, Thundelarra Station; B, Billabalong Station; C, Wanjarri Station; D, Towrana Station; E, Dairy Creek Station; F, Doolgunna Station; G, Ethel Creek Station; H, Coolawanyah Station; I, 20 mi. E of Warburton Mission; South Australia—J, Middle Tanks Station; K, Mutooroo Station; L, Moralana Station; M, Witchelina Station; N, Lambina Station; Northern Territory—O, Todd River Station; P, 44 mi. N of Alice Springs; Q, Phillips Creek; R, Banka Banka Station.

The total visits by birds to water during a particular watch are a reflection of many factors, including the variety of birds present, local abundance, distance to the next drinking water, temperature, and physical characteristics of the water hole. Total visits include repeated visits by given individuals, and in many cases they therefore undoubtedly overestimate the actual size of the population of a given species drinking. On only one occasion (watch number 2) when an individual Crow could be recognized by a missing rectrix, was it possible to determine how many times a particular individual drank during the day. On this date, the group of four or five Crows, of which the "marked" individual was a member, visited water four times between 10:00 and 15:00, and on every visit but one (when only one bird drank before the group flew off), all the members of the group drank once or twice before leaving the water hole. Thus it may be that individuals of some species which are dependent on water regularly drink a minimum of three or four times on a hot day. Willoughby and Cade (1967) recorded the same two Laughing Doves (*Stigmatopelia senegalensis*) and an individual Pale-winged Starling (*Onychognathus naboroupp*) drinking two or three and three times a day, respectively, in the Namib Desert of South West Africa (when the maximum temperatures were 34.5° C or

TABLE 1. Summary of dawn-to-dusk watches.

Watch no.	Date <sup>a</sup>	Local.	Temp. (°C)		% Rel. hum.		Next water (m <sup>2</sup> )	No. of species <sup>b</sup>			Total visits to water
			Min.	Max.	Min.	Max.		+	-	% drinking <sup>c</sup>	
1	26/2/65	I		39.0			20	25	(10)		6,070
2	1/3/66	A(1) <sup>d</sup>	23.0	46.5	20	32	4	17	15	53	1,010
3	20/9/66	C(1)	2.0	19.0			5	8	28	22	340
4	22/9/66	C(2)	6.5	25.5			2	7	16	30	430
5	1/12/66	E	20.0	34.0			4	9			2,590
6	5/12/66	D	15.0	36.0			3	14	(6)		2,770
7	6/12/66	A(1)	21.0	38.5			4	14	18	44	352
8	8/12/66	A(2)	22.0	38.0			3	10	13	43	540
9	28/2/67	F	21.0	31.5	31	49	3	15	23	39	870
10	7/3/67	G(2)	23.5	34.0	22	44	1.5	10	27	27	1,200
11	8/3/67	G(1)	19.5	31.5	20	49	4?	10	18	36	1,940
12	18/3/67	H	20.5	34.0	20	41	0.5	11	28	28	3,930
13	25/6/67	A(1)	10.5	25.0	22	47	4?	4	38	10	41
14	28/8/67	J	1.5	20.0	34	90	15	9	39	19	280
15	13/9/67	R	13.0	32.5			4	5	7	42	970
16	17/9/67	Q	12.5	32.0	23	38	0.5	18	37	33	1,130
17	21/9/67	P	3.5	23.0	18	51	3	12	(12)		66,970
18	8/10/67	M	15.5	33.5	17	42	4	12	(5)		810
19	1/11/67	K	8.5	33.5	18	46	2	15	17	47	1,940
20	28/11/67	A(3)	14.0	29.5			4	9	(13)		1,550

<sup>a</sup> Dates are recorded in the order of day, month, and year.

<sup>b</sup> The "plus" column indicates the number of species that drank; the "minus" column, the number of species that did not drink. Species not drinking were recorded within a 2-3-mile radius of the water hole except where indicated by parentheses, in which case they were recorded only in the immediate vicinity of the water hole.

<sup>c</sup> Number of species drinking divided by the total number of species.

<sup>d</sup> Subscripts denote different water holes at a particular locality.

less). On the other hand, it is possible that individuals of some species which regularly visit water drink only once every 2 or 3 days, even in hot weather. Unfortunately, we had no marked birds and therefore could not know how often a particular individual drank.

Appendix I lists a total of 127 species which were found in the 10 census areas and on the 20 dawn-to-dusk water hole watches. Information was obtained on the drinking habits of 118 of these species (nine birds having been recorded from a census but not a water hole watch). Sixty-nine species (58%) drank on at least one occasion, but 49 species which were present in the vicinity of water were never seen to drink. Forty-two of the 69 species visiting water were recorded drinking on only 5 days or less. The total number of days on which these 42 birds were seen drinking is shown by the number in parentheses following the species name in Appendix I. Sixteen species were observed to drink on only one day.

In Appendix I, three categories are set up for maximum daily temperature: below 25°, 25°-35°, and above 35° C. Columns with figures indicating the number of days a particular species drank or did not drink, respectively, are presented for each thermal category. All figures are from the 20 dawn-to-dusk watches.

A species is placed in one of four "drinking habit" categories on the basis of the frequency with which it visited water at various temperatures. The 49 species never seen drinking are placed in class "N" (Appendix I) and are considered to be completely independent of drinking water in their distribution throughout the arid portions of Australia. However, it is unlikely that very many species never drink, and this classification is a tentative one until more data are obtained. The Ground Cuckoo-shrike, which was often in the vicinity of water but not seen to drink, has been recorded by White (1915) as drinking at sundown in the desert of South Australia. Perhaps its failure to drink in this study is linked with our lack of opportunities for observing it at ambient temperatures above 35° C. Cameron (1938) records the "buzzard" (*Hamirostra melanosternon?*) as drinking in the dry interior of Queensland, although it was not observed to do so in any of our study areas.

If a species drank on half or fewer of the days having maximum daily temperatures of 25° C or above, it is classified as a facultative drinker (symbol "O"), which sometimes drinks when it has the opportunity but which is probably not dependent on water under most conditions. A species is classified "S" (a summer



FIGURE 3. Photographs from watch number 17 in the Northern Territory. A. (top) Thousands of Budgerygahs and Cockatiels circling over the water hole shortly after sunrise prior to drinking. Both species prefer wide, open water holes from which to drink. B. Dried droppings of Zebra Finches form a white carpet under small trees (*Acacia*?) where thousands of in-

dividuals of this species sat daily while waiting to drink. C. Cockatiels normally spend only 4–6 sec drinking at the edge of a water hole before taking flight again. D. (bottom) Budgerygahs are unique in their habit of alighting in the middle of a shallow pool or puddle to drink. Individuals apparently drink only once a day.

drinker) if it was recorded drinking on more than half of the days on which the temperature exceeded 25° C. It is classified as “Y” if it showed this incidence of drinking above 25° C and also drank more than 50% of the time at cooler temperatures. Birds in both of the latter categories rely on free water during the warmer parts of the year and its availability appears to be a critical factor in their distribution. A total of 47 species (40% of the birds for which data were obtained) are placed in this group of water-dependent species. Some species, such as the Australian Bustard, Masked Wood-swallow, Pied Butcherbird, and Australian Magpie, appear intermediate between the water-dependent and water-independent groups, as defined here.

The only study comparable to ours of which we are aware is Willoughby and Cade’s (1967) in the Namib Desert of southwestern Africa. They divided the drinking habits of 77 species (excluding those birds whose drinking habits are listed with a question mark) into three classes. By arbitrarily assigning the 48 species listed as “seldom” drinking plus half of the

12 “occasional” drinkers to the water-independent category, and the 17 “regular” drinkers plus the other six of those drinking occasionally to the water-dependent group, a rough comparison of drinking habits of xerophilous birds in Australia and southwest Africa can be made. The results show that 54 of 77 species, or 70% of birds in the Namib Desert are water independent, compared with the 60% calculated for Australia. Because of differences in temperature, size of study area, and number of systematic water hole observations, this 10% difference may well not be significant. Indeed, the two regions appear rather similar in regard to the proportion of xerophilous birds, at the species level, which are capable of surviving without drinking.

*Maximum Numbers Drinking.* The maximum number of visits by a species in a single day to a particular water hole is shown in Appendix I. In addition to being a rough index to water dependence, these totals strongly reflect local abundance. Representatives of seven species drank more than 1000 times in a day: Little Corella (on watch num-

TABLE 2. Occurrence of drinking in families.

Family	No. species in drinking classes <sup>a</sup>				% species dependent on water <sup>b</sup>
	Y	S	O	N	
Dromaiidae	0	1	0	0	100
Accipitridae	0	0	5	7	0
Falconidae	0	0	1	5	0
Turnicidae	0	0	0	1	(0)
Gruidae	0	0	0	1	(0)
Otididae	0	0	1	0	(0)
Charadriidae	0	0	0	2	(0)
Burhinidae	0	0	1	0	(0)
Glareolidae	0	1	0	0	(100)
Columbidae	3	3	0	0	100
Psittacidae	5	8	0	0	100
Cuculidae	0	0	0	3	0
Caprimulgidae	0	0	1	0	(0)
Alcedinidae	0	0	0	3	0
Meropidae	0	0	0	1	0
Alaudidae	0	0	0	1	(0)
Hirundinidae	0	3	0	0	100
Motacillidae	0	0	1	0	0
Campephgidae	0	0	2	1	0
Timaliidae	0	0	1	3	0
Sylviidae	0	2	1	11	14
Muscicapidae	0	0	3	1	0
Pachycephalidae	0	0	1	2	0
Neosittidae	0	0	0	1	(0)
Climacteridae	0	0	0	1	(0)
Dicaeidae	0	0	0	3	0
Meliphagidae	2	8	0	0	100
Estrildidae	1	1	0	0	100
Grallinidae	0	2	0	0	100
Artamidae	0	1	2	2	20
Cracticidae	0	2	2	0	50
Ptilonorhynchidae	0	1	0	0	(100)
Corvidae	0	3	0	0	100
Total	11	36	22	49	

<sup>a</sup> Symbols are the same as in Appendix I.

<sup>b</sup> Number of species in categories Y and S divided by the total number of species in the family; figures in parentheses were calculated using data from fewer than five water hole watches.

ber 11), Galah (on watch number 20), Cockatiel (see notes below), Budgerygah (on watch number 17), White-plumed Honeyeater (on watch number 12), Spiny-cheeked Honeyeater (see notes below), and the Zebra Finch (on watch number 17).

Two days deserve special mention. On 13 February 1964, observations were made for a 2-hr period beginning a half hour after sunrise at a water tank and troughs located 7 miles north of Wiluna, Western Australia (almost midway between localities C and F in fig. 2). The season had been a very dry one, but other drinking water was available at a natural pool in a stream bed 4 miles away. During this 2-hr period, an estimated 1500 to 2000 Spiny-cheeked Honeyeaters drank, flying in from all directions from the surrounding mulga country. These figures are significant in that they probably represent only a single visit by each individual, since just a 2-hr period is involved.

It is not known from how far the birds were coming for water. The maximum shade temperature on this date was about 32° C.

The Crested Pigeon, Bourke Parrot, Budgerygah, and Zebra Finch all drank in larger numbers at watch number 17 (see table 1) than anywhere else, and the total of almost 67,000 visits to drink in a single day at this water hole (a shallow dam) far surpasses that for any other water hole (fig. 3). This figure is of particular interest because the maximum temperature on this date was only 23° C. Significantly, however, there had been very little rain for the past 7 months and seeds, though plentiful, were all very dry, as was the vegetation.

The 47,000 Budgerygahs which were conservatively estimated to have drunk on this date is the highest daily count we have for a single species at a given water hole. Barrett (1945) states that "at least one million budgerigars" were seen drinking at a large water hole in the Northern Territory on one occasion, but it seems likely that this estimate is too high. Two weeks earlier, at the same water hole as for watch number 17, approximately 4500 Cockatiels drank during a 2-hr period in the morning, which is the highest daily figure we recorded for this species. The temperature on the earlier date was actually somewhat lower than for the dawn-to-dusk watch.

*Drinking Frequency Within Families.* Drinking habits of families are compared in table 2. In most families, the xerophilous species appear to be either all dependent on water (Y and S drinkers), or all independent of water (O and N drinkers). Only the four species of Cracticidae seem to be fairly evenly divided between these two major categories. Uniform drinking habits within a family may reflect, in part, similarity of the species in food habits, physiology, or behavior.

Our data indicate that in the Australian desert the Columbidae, Psittacidae, Meliphagidae, and Estrildidae are all highly dependent on free water. In addition, the Dromaiidae, Glareolidae, Hirundinidae, Grallinidae, Ptilonorhynchidae, and Corvidae appear to have a strong need for free water during the warmer parts of the year. According to Immelmann (1965), all Australian estrildids are restricted to the vicinity of water, and Irwin (1956) and Willoughby and Cade (1967) found the same to be true in African members of the family. The dependence on drinking water of desert-inhabiting pigeons and doves is well known. Chisholm (1958) mentions 20,000 Flock Pigeons watering daily at a tank in western Queensland and refers to the observation, by

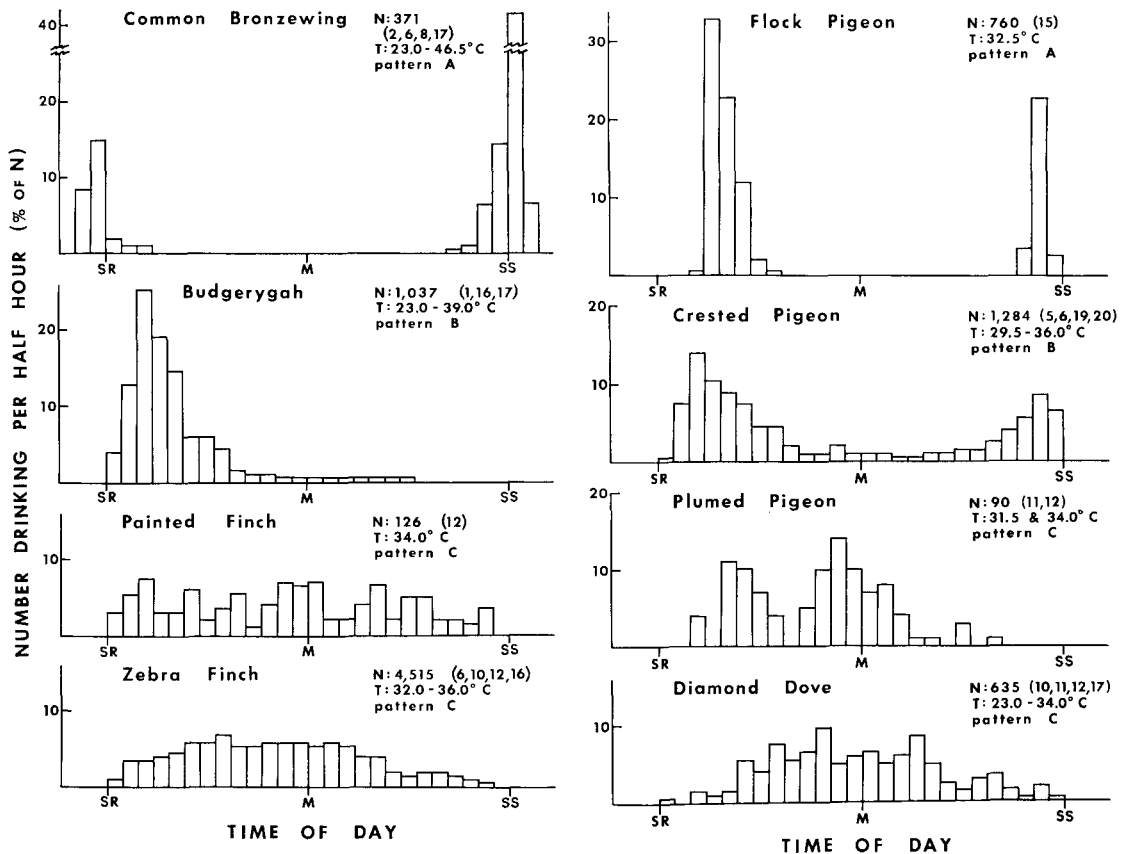


FIGURE 4. Daily patterns of drinking. N, total number of birds drinking; T, maximum daily temperature(s); SR, sunrise; M, midday; SS, sunset; enclosed in parentheses are the dawn-to-dusk watch number(s) from which all or most of the data were obtained. The pattern for the Budgerygah was drawn using only 1% of the total number of individuals drinking (every 30-min period) on watch no. 17.

an explorer in 1865, of 500 Plumed Pigeons coming to drink during a half-hour period at a water hole in the northwest of the continent. The drinking behavior of columbids in arid regions of southern Africa has been recorded by Irwin (1956), Cade (1965b), and Willoughby and Cade (1967), and in North America by Bartholomew and Dawson (1954) and Smyth and Coloumbe (1971). McGilp (1922) reported both the Australian Pratincole and Australian Dotterel (*Peltohyas australis*) drinking at water holes in South Australia, and Cameron (1938) mentions that bowerbirds visited water at any time of day.

It is difficult to gather comprehensive information on drinking habits of nocturnal species, but it is significant that on two occasions Spotted Nightjars were seen skimming the surface of a water hole at dusk, and we believe that birds were drinking rather than foraging for insects. These observations are of particular interest because of the recent findings of Dawson and Fisher (1969) that this species has an excellent capacity for

evaporative cooling under heat stress. In North America, the desert caprimulgid *Chordeiles acutipennis* has been seen drinking at dusk in exactly the same manner (Miller and Stebbins 1964; Smyth and Coloumbe 1971).

*Daily Patterns of Drinking.* Species of desert birds which drink regularly (categories Y and S in Appendix I) vary in characteristic ways concerning the times of day at which they use surface water. These daily drinking patterns are shown for 25 species in figures 4-6. The times of sunrise and sunset have been standardized to 05:30 and 18:30 by expanding or compressing the curve in the middle of the day, where it is relatively flat for all species.

On the basis of the 25 species analyzed, three general patterns have been set up: Pattern A—drinking is confined to two relatively short periods during the day, one in the early morning and one in the late afternoon, with the afternoon peak slightly to considerably lower than the morning peak (with one exception) and with no drinking at all during the middle of the day; Pattern B—similar to pattern A

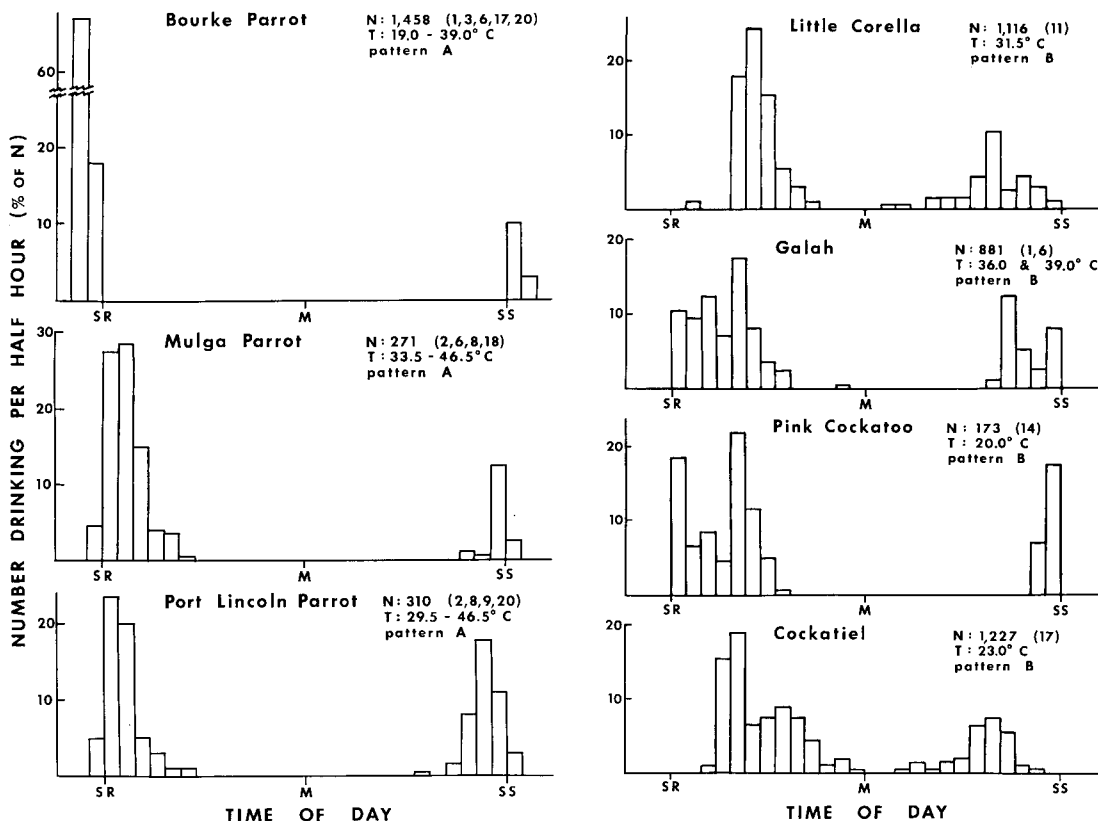


FIGURE 5. Daily patterns of drinking. See figure 4 for explanation.

but the two periods of drinking activity are longer and there is often a small amount of drinking between the peak periods; Pattern C—drinking takes place more or less regularly throughout the day with no well-defined peaks of activity, but with a tendency for a slight increase in frequency of visits during the middle of the day.

Even though these drinking patterns grade into one another, all species in figures 4–6 have been assigned a pattern designation. Figure 4 contains typical examples of all three patterns. It should be emphasized that these are patterns for birds which are water-dependent. Occasional drinkers (category O in Appendix I) are considered water-independent, and individuals of these species, on those occasions when they visit water, do so at almost any time of day, thus conforming to Pattern C. In contrast to water-dependent birds with this pattern, however, each individual probably drinks no more than once a day.

A close correspondence exists between the drinking patterns and categories we have established and the ecological patterns of water economy described by Bartholomew and Cade (1963). Pattern C is identical with the pattern typified by the House Finch (*Carpodacus*

*mexicanus*); Patterns A and B are comparable to the ecological pattern exhibited by the Mourning Dove (*Zenaidura macroura*); and species in drinking categories O and N (Appendix I) fit into the pattern exemplified by carnivorous and insectivorous birds.

Many closely related groups of desert birds tend to display the same general drinking pattern. Drinking during the middle of the day is virtually nonexistent within the Psittacidae. Furthermore, three species of *Cacatua* (fig. 5) have almost identical patterns, and three genera of platycercine parrots (fig. 5) all exhibit Pattern A. Meliphagids for which sufficient data were obtained (*Meliphaga*, *Myzantha*, and *Acanthagenys*, fig. 6) display a very sharp peak of drinking activity just after sunrise followed by a decline during the middle of the day, and then a very slight increase in the middle or late afternoon (Pattern B). Members of the families Grallinidae, Artamidae, Cracticidae, Ptilonorhynchidae, and Corvidae, which regularly visit water, do so at any time during the day (Pattern C), as shown by the examples of *Corvus* and *Struthidea* (fig. 6). The Zebra Finch and Painted Finch are the only common estrildids in dry regions (although the Star Finch, *Bathilda ruficauda*, also

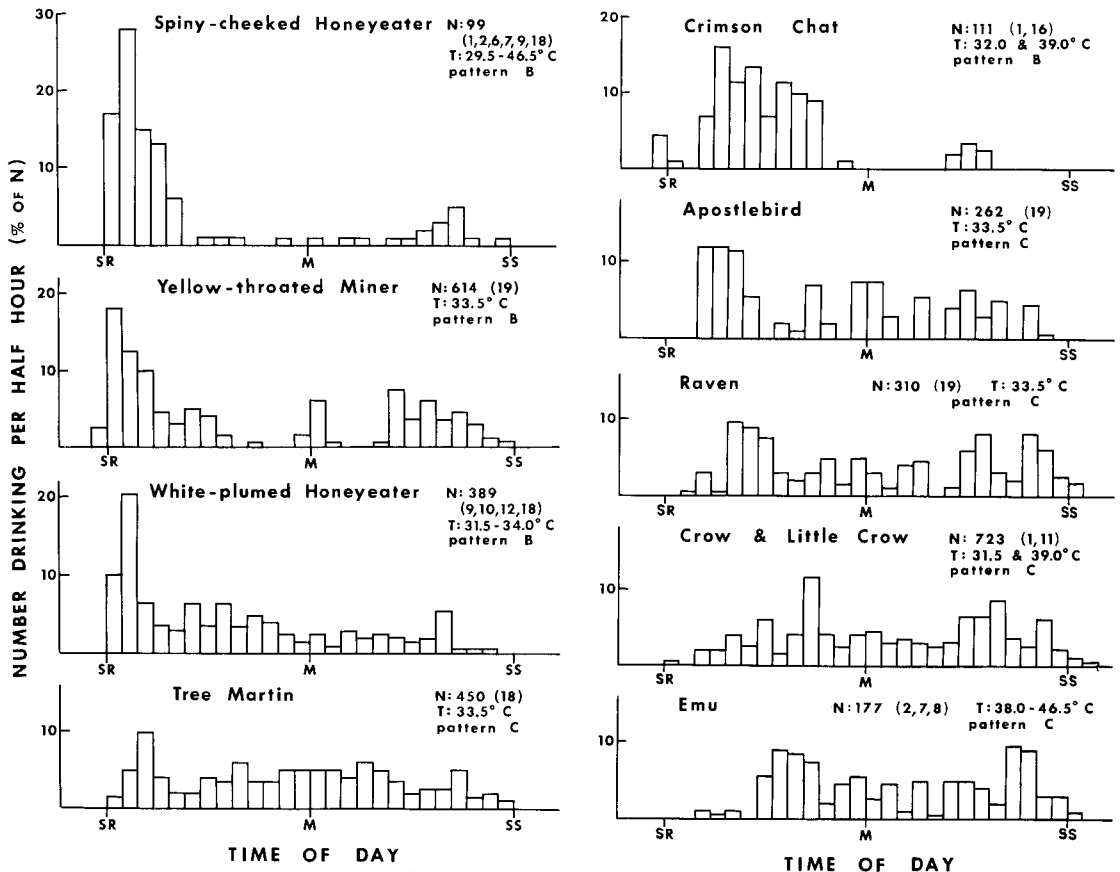


FIGURE 6. Daily patterns of drinking. See figure 4 for explanation. The pattern for the White-plumed Honeyeater was drawn using only 10% of the total number of individuals drinking (every 30-min period) on watch no. 12.

occurs there), and both drink uniformly throughout the day (fig. 4). According to Immelmann (1965), all Australian finches have this pattern except for three species of *Poephila*, which visit water twice a day, once in the morning and once before sunset.

Some birds of close affinity have dissimilar drinking patterns. For example, representatives of five related genera of pigeons—*Phaps*, *Histriophaps*, *Lohophaps*, *Ocyphaps*, and *Geopelia* (Goodwin 1967)—vary strikingly in their daily drinking behavior (fig. 4). The habit of the Common Bronzewing of coming to water in greater numbers in the evening than at any other time of day is well known (Goodwin 1967) and appears unique among Australian desert birds. In this species, half of all visits to water occur after sunset, and no other Australian bird with two well-defined periods of drinking is known to have the later peak higher than the earlier one. Although the pattern for the Plumed Pigeon is based on rather limited data, it is supported by observations of Hyett (1967), who estimated that

a flock of 400 of these birds came to drink at noon at a water hole in the Northern Territory. Intergeneric differences in times of drinking have also been noted among desert columbids in Africa (Irwin 1956; Cade 1965b; Willoughby and Cade 1967).

The Bourke Parrot has the most unusual pattern of all xerophilous birds. All drinking, except for rare visits by one or two individuals, occurs either before sunrise or after sunset, and on most days 85–90% takes place at dawn. Birds start arriving at a water hole an hour prior to sunrise and within only 30 min approximately 80% of the total population drinks (assuming that all birds drink in the morning). Only a very small percentage drink again in the evening after sundown, the actual number varying directly with temperature.

The number of times an individual drinks during the day reflects not only physiological need for water but also the amount of water that can be taken in during a single visit to water. It is noteworthy that all species with Pattern A, and many with Pattern B, are psit-



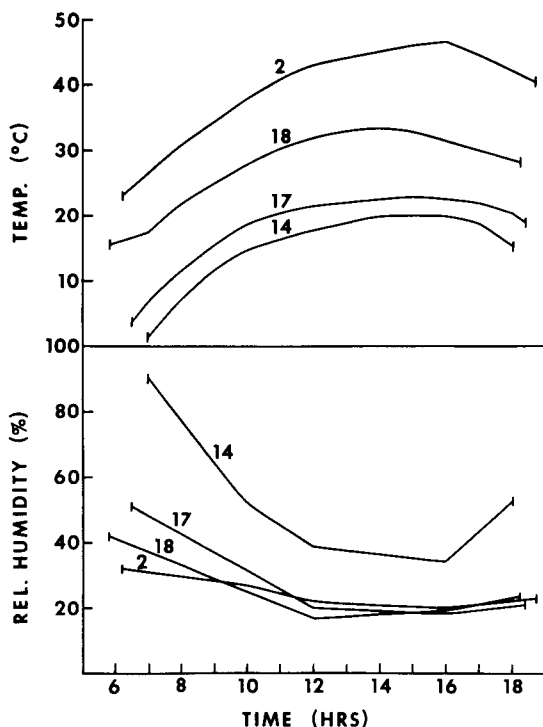


FIGURE 7. Daily patterns of shade temperature and relative humidity from sunrise to sunset on cloudless days. Numbers refer to dawn-to-dusk watches.

tacids or columbids, birds which possess a crop and thus have a relatively large water storage capacity. Most of them are also rather large in size. These factors are probably of primary importance in enabling them to visit water only once or twice a day. Finches also have a well-developed crop, but their small body size, and consequent high weight-specific evaporative water loss, places them at a disadvantage in an arid environment and probably largely accounts for their more frequent visits to water.

Although many selective pressures must have influenced the evolution of drinking patterns, avoidance of high daytime temperatures and intense solar radiation may well have been among the most important considerations in determining the present drinking patterns of many xerophilous species. Temperature regulation becomes a critical factor for survival on very hot days, and restriction of drinking to short early morning or late afternoon periods would be advantageous in that a bird traveling to water at these times would not have to contend with the high ambient temperatures and intense solar radiation characterizing the middle of the day (figs. 7 and 8). A bird such as the Mulga Parrot, which sits quietly in a bush during the middle

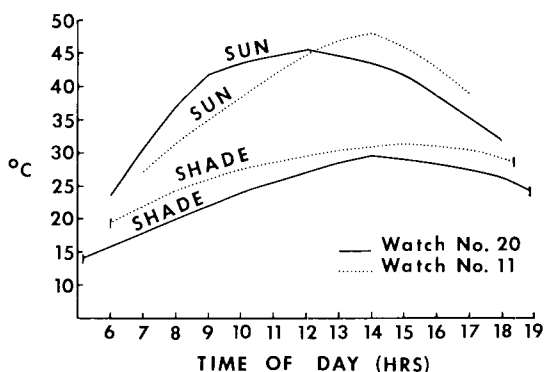


FIGURE 8. Relation between shade temperature and temperature in the sun (measured with a "black bulb" thermometer about 1 m above the ground). Small vertical lines indicate sunrise and sunset.

of a hot day, probably incurs a relatively smaller heat load than a species such as the Zebra Finch, which must continually expose itself to the sun by making repeated trips to and from water (see fig. 8).

The limiting of drinking to the cooler parts of the day is particularly important for species such as the Bourke Parrot and Common Bronzewing, which fly relatively long distances to water and in so doing must generate a considerable amount of heat. Their unusual times of drinking enable these two species to avoid not only the hottest period of the day but also diurnal predators, as noted by Goodwin (1967), who suggests that the dawn drinking of the Bourke Parrot and watering at dusk of the Common Bronzewing might be adjustments on the part of these species serving to minimize congestion at shared water holes.

An important feature of the drinking behavior of all birds with Patterns A or B is that the two daily periods of drinking usually differ markedly in the total visits to water. If a single individual drinks only once in the morning, and no more than once in the afternoon, as is likely, then the explanation for the difference in peak heights must be that a greater number of birds drink in one half of the day than in the other half. This poses a question as to whether some individuals drink twice during the day while others drink only once, or whether all individuals drink just once daily. For the latter to be true, there would have to be two subpopulations, one consisting of morning drinkers and the other of afternoon drinkers. A more plausible explanation is that on a particular day most (if not all) individuals drink once in the morning and then some of these also drink once again in the

afternoon (with the reverse being true for the Common Bronzewing, of course).

Birds that confine 70% or more of their drinking to a single 2-hr period each day include the Common Bronzewing (fig. 4), Flock Pigeon (fig. 4), Mulga Parrot (fig. 5), Bluebonnet Parrot (not figured), Bourke Parrot (fig. 5), Budgerygah (fig. 4), and Spiny-cheeked Honeyeater (fig. 6). In each of these birds it would appear that 70% or more of all individuals are capable of satisfying their water needs with a single daily visit to water, (or possibly a single visit only once every 2 or 3 days). The morning period of drinking is spread out over several hours in the Budgerygah, and an afternoon peak apparently is lacking, which is truly remarkable for a seed-eating species of its size. This is consistent with Cade and Dybas' (1962) conclusion that the special abilities of this species to withstand dehydration and conserve water have freed it from the necessity of drinking more than once or twice a day.

It appears paradoxical that the Zebra Finch is one of the most abundant and widespread birds in the arid parts of Australia, since its drinking habits reveal it to be highly dependent on water, despite its ability to survive for long periods at moderate temperatures in the laboratory with little or no water (Cade et al. 1965; Calder 1964). Individuals apparently remain near a water hole and drink at least several times a day under normal summer conditions. In view of the significant advantages associated with restriction of drinking to the cooler parts of the day in a hot environment, the Zebra Finch must have a strong physiological need for water. This probably arises primarily from its relatively small size and granivorous diet. Its present distribution and abundance are probably significantly associated with the increased availability of water from artificial sources, which has resulted from the establishment and expansion of the pastoral industry in Australia within the last century and a half. The Zebra Finch seems well adapted to exploit such a development because of its unusually high reproductive potential and nomadic habits, which allow it to take advantage of good seasons (Marshall and Serventy 1958; Frith and Tilt 1959; Farner and Serventy 1960). Such adaptations probably play a significant role in the success of many desert species and occur in other Australian birds as well as the Zebra Finch (see particularly Keast 1959; Immelmann 1963).

*Drinking Habits Related To Temperature.* Since birds avoid overheating in hot weather in part by evaporative cooling, it is not sur-

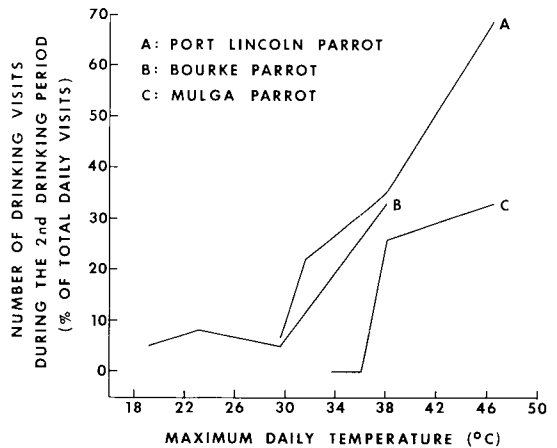


FIGURE 9. Number of afternoon trips to drink of three species of platycercine parrots, all with drinking Pattern A, at various ambient temperatures.

prising that frequency of drinking increases with ambient temperature. Daily variation in temperature is shown in figures 7 and 8 for the period from sunrise to sunset. Even though the daily maxima vary by as much as 26° C, the patterns for each day are very similar, the lowest reading being at sunrise and the highest occurring from 2–4 hr after midday. The range of temperatures shown in table 1 is a good approximation of the annual variation found in many arid localities in Australia. However, hotter (and colder) temperatures sometimes occur, and a prolonged heat wave like that recorded by Finlayson (1932) occasionally prevails over a wide area. During the summer months, days are typically clear and relative humidities during the afternoon are low (fig. 7; table 1), although tropical thunderstorms sometimes extend well inland.

A dawn-to-dusk watch was made at three different times of the year at locality A(1) (table 1). In June, the maximum temperature was 25° C and 41 instances of drinking were recorded. In contrast, 352 trips to drink were recorded in December and 1010 trips in March when the maximum temperatures were 38.5° and 46.5° C, respectively. Several factors, including the availability of succulent food, probably influenced the drinking activity of birds on these dates, but the main influence appears to have been exerted by temperature.

All species with Pattern A (except the Common Bronzewing) have a higher proportion of individuals drinking in the afternoon on hot days than on cooler ones. This is illustrated in figure 9 for three parrots. Presumably, a higher percentage of birds drink a second time in hot weather. It is somewhat surprising that

TABLE 3. Water samples.

Sample no.	Watch no.	Local. <sup>a</sup>	Date taken	Source	Birds drinking	Ion concentration (mEq)			
						Na <sup>+</sup>	Mg <sup>++</sup>	K <sup>+</sup>	Ca <sup>++</sup>
1		B	23/11/66	river pool	No?	174.0	53.3	3.93	9.2
2		B	25/11/66	bore	Yes	10.8	4.0	0.24	3.2
3		(E)	29/11/66	river pool	Yes	18.9	4.3	1.35	2.6
4		(E)	30/11/66	river pool	Yes	81.0	11.3	2.64	6.2
5	6	D	6/12/66	bore	Yes	15.3	2.8	1.35	2.6
6	2,7,13	A	26/6/67	well	Yes	48.0	4.8	1.20	1.0
7	14	J	28/8/67	rain catchment	Yes	20.0	3.9	0.55	2.0
8	15	R	13/9/67	bore	Yes	32.5	2.6	0.85	3.2
9	16	Q	17/9/67	river pool	Yes	1.8	0.0	0.90	0.3
10		(Q)	19/9/67	river pool	Yes	2.0	0.6	0.60	1.2
11	17	P	21/9/67	shallow dam	Yes	0.2	0.0	0.35	0.2
12	18	M	8/10/67	bore	Yes	109.5	35.0	0.85	19.5
13	19	K	1/11/67	well	Yes	139.0	11.0	1.05	6.0
14	12	H	?/9/67	well	Yes	12.0	7.5	0.85	2.2
15	20	A	29/12/67	bore	Yes	45.5	10.5	0.95	2.0

<sup>a</sup> Parentheses indicate nearest locality when not exact.

the second peak was higher than the first for the Port Lincoln Parrot on watch number 2 (when the maximum temperature was 46.5°). Although it might be argued that all individuals in the vicinity of the water hole did not drink during the morning period, it seems more likely, due to the fact the temperature had been above 40° C for over 7 hours (fig. 7), that some individuals drank more than once in the hour and a half before sunset.

It is significant that the highest daily drinking totals for the Magpie-lark, Grey Currawong, Pied Butcherbird, and Australian Magpie are all from watch number 2 when the maximum temperature was 46.5° C, the hottest level at which we made observations. Mulga Parrots did not drink at all at locality C(1) on 20 September 1966, when the maximum temperature was only 19° C (table 1). However, a total of 25 birds drank in a 2-hr period shortly after sunrise at this same water hole on 26 March 1967, when the maximum temperature was 35° C. Furthermore, at this same site on the earlier date just three Galahs visited water out of 40 counted in the near vicinity, and only a single Port Lincoln Parrot drank out of at least 15 present in the immediate area. Data in Appendix I for the Australian Pipit, Willy Wagtail, Yellow-throated Miner, Magpie-lark, and the two species of crows (included together) are additional evidence that birds make more trips to water in hot weather than at moderate temperatures.

Birds which appear never to drink, even on very hot days, include the White-browed Babbler; Whiteface, Chestnut-tailed, and Yellow-tailed Thornbills; Redthroat, Banded Blue, and Variegated Wrens; Western Shrike-thrush; Crested Bellbird; and Mistletoebird (see Appendix I). On watch number 2 (table 1), the

shade temperature was above 44° C for 4 hr, yet at least four species of small insect-eaters—the Red-capped Robin, Whiteface, Chestnut-tailed Thornbill, and *Malurus* sp.—were in the immediate vicinity of water but not drinking.

At the other end of the temperature range, some species regularly drink on days when the maximum temperature is below 25° C. On these cooler days, the temperature at the time drinking occurs is often below 10° C, and sometimes even below 5° C. The Common Bronzewing, Pink Cockatoo, Galah, and Bourke Parrot have all been observed drinking at temperatures under 5° C, and the Diamond Dove, Crested Pigeon, Cockatiel, Port Lincoln Parrot, Budgerygah, Red Wattlebird, Zebra Finch, and Crow have each been recorded visiting water on at least one morning when the temperature was below 10° C.

*Drinking Habits Related To Water Quality.* Although the thermal characteristics of the various seasons are fairly predictable in the arid parts of Australia, rainfall is erratic, coming at almost any time of the year. However, the summer months (Dec.–Mar.) tend to be wetter in the northern half of the interior, and most of the rain falls during the winter months (June–Sept.) in the southern half. The time and extent of the last rainfall in a given locality determines not only how much food and surface water is available but also the quality of water, because evaporation tends to concentrate the electrolytes present.

In order to determine the potability of water from natural and artificial sources, 15 water samples were collected from widely scattered localities and the concentration of sodium, potassium, magnesium, and calcium determined. Results are shown in table 3. The five samples obtained from river pools are of pri-

mary interest. The other samples consisted mainly of underground water pumped to the surface by a windmill.

Sample number 1, which came from a river pool in the Murchison River, has the highest concentration of sodium, magnesium, and potassium, and the second highest concentration of calcium. This water was slightly salty to the taste, and the total concentration of major cations exceeds slightly that of the plasma (see Sturkie 1965), unlike any of the other samples. At the time the water was collected, approximately 2 months had elapsed since the last rain in the area, and less than 3 inches of rain had fallen in the last 7 months. Several hours were spent during the late afternoon and early morning in the vicinity of this pool, but no birds were actually seen drinking, though such species as the Crested Pigeon, Galah, and Port Lincoln Parrot were present in the area. Other pools within 2 miles, where the water was fresher (according to the station manager), probably obviated any need for use of this brackish water.

Samples number 3 and 4 both came from pools along the Wooramel River. The pool from which the latter was obtained was only about 5 m<sup>2</sup> in area, and no more than 12 cm deep. Birds were drinking commonly from both pools. About one inch of rain had fallen in the last 5 months, the most recent precipitation being 2 months prior to the time the water sample was taken, and only 4 inches of rain had fallen all year.

Sample number 9 was taken from a large pool in Phillips Creek and sample number 10 from a rather small pool in Tennant Creek, both from areas in the Northern Territory which had received no rain for 6 months. The two samples proved to have very low concentrations of all four ions.

In addition to the above analyses, 17 water samples were taken at varying times of the year from natural water holes on Thundelarra Station and in the Warburton Range (localities A and I, respectively, in fig. 2). These were analyzed for sodium and potassium ions. In only one sample was the concentration of sodium greater than 40 mEq/l or the concentration of potassium greater than 5 mEq/l.

Our examinations of naturally occurring water suggest that the water in most river and creek pools, including "rock holes", usually remains potable for at least 6 months following the last period of rainfall, and very probably for a much longer time.

*Drinking Habits Related To Diet.* Since different kinds of foods contain varying amounts of preformed water, it is not surprising that a

TABLE 4. Drinking habits correlated with food habits.<sup>a</sup>

	No. species						Total species	% dependent on water
	Water-dependent			Water-independent				
	Y	S	Total	O	N	Total		
In	0	9	9	14	29	43	52	17
Ca	0	1	1	7	15	22	23	4
Gr	9	12	21	0	1	1	22	95
Ne	2	8	10	0	0	0	10	100
Om	0	6	6	1	3	4	10	60
Fr	0	0	0	0	1	1	1	0
Total	11	36	47	22	49	71	118	40

<sup>a</sup> Symbols are the same as in Appendix I.

very close correlation exists between the diet and drinking habits of a species, as shown by table 4, which gives the relationship between the four drinking habit categories and six food habit classes of Appendix I. The food habits of many Australian birds are not well known, and the classification presented here is a general one based on our own studies and field observations, supplemented by data of Lea and Gray (1935-36).

We have distinguished six categories of birds: (1) granivorous; (2) insectivorous; (3) nectarivorous; (4) carnivorous; (5) omnivorous; and (6) frugivorous. Birds placed in a specific category are not necessarily confined to the items indicated, since all species probably occasionally vary their diet as certain foods become available or unavailable seasonally. For example, the Port Lincoln Parrot is primarily a seed-eater, but it feeds largely on the flower buds and green fruits of eucalypts whenever they are available. Such seasonal changes in food habits almost certainly exert a primary influence on drinking habits. Modifications in drinking habits associated with dietary changes have been reported for the Red-faced Mousebird (*Colius indicus*) and Pale-winged Starling in the Namib Desert of South West Africa (Cade and Greenwald 1966), and for the Black-throated Sparrow (*Amphispiza bilineata*) in arid parts of southern California (Smyth and Bartholomew 1966).

Of the many items eaten by birds, dry seeds contain the least amount of moisture, usually about 8-12% by weight, and therefore granivorous desert birds tend to be particularly dependent on surface water. Of 11 species which drink throughout the year, nine are seed-eaters, and all but one of 22 birds classed as granivorous in our study are water-dependent (Appendix I). Neither the drinking habits nor the food habits of this single exception, the

Little Quail, are well known, and we recorded it in the vicinity of a water hole watch on only two occasions, both when the maximum temperature was between 25° and 35° C. It may be that the Little Quail is largely insectivorous (though its relatively heavy beak argues against this) or, more likely, is nocturnal in its time of drinking (like the Southern Stone-curlew). Probably all Australian xerophilic seed-eaters are dependent on drinking water during at least part of the year, as are most if not all of their African or North American counterparts thus far studied (Cade 1965a; Smyth and Bartholomew 1966; Willoughby and Cade 1967; Willoughby 1968; Smyth and Colombe 1971).

The meliphagids, most of which apparently feed on nectar whenever it is available, are just as striking in their dependence on free water in the arid portions of Australia. The 10 species for which data were obtained drank regularly throughout the warmer parts of the year, and two species, the White-plumed Honeyeater and Red Wattlebird, also visited water in cool weather. The White-plumed Honeyeater and Spiny-checked Honeyeater each, on one occasion, made more than 1500 trips to drink in a single day, and the Yellow-throated Miner visited water 614 times on watch number 19. The reason for the water dependence of this group is not clear. Although it is tempting to postulate that their thirst is related to diet, which is the most obvious feature all members share, yet nectar is often unavailable in the desert. It is probable that some species exist almost entirely on insects for much of the year. A more likely explanation for the drinking habits of meliphagids may be their high level of activity. Honeyeaters are very pugnacious and chase each other almost continually while feeding. Some species, particularly the White-plumed Honeyeater, reduce activity only slightly during the middle of the day. Such behavior results in a relatively large amount of heat production and perhaps may account in part for their need to drink.

In view of our findings regarding the Meliphagidae, it is somewhat surprising that in Africa no members of the Nectarinidae were reported drinking by Irwin (1956) in semi-arid areas of Bechuanaland, and Willoughby and Cade (1967) recorded *Cinnyris fuscus*, the single sunbird present in the Namib Desert, to be merely an occasional visitor to water. Furthermore, the desert-inhabiting Costa Hummingbird (*Calypte costae*) in North America appears to be only an infrequent drinker (Miller and Stebbins 1964; Johnson

et al. 1948), but detailed observations at water holes are lacking. The determination of why Australian meliphagids need to drink, and how intake of nectar affects water balance in birds, awaits further study.

Insectivorous species comprise 61 of the 127 species listed in Appendix I, or slightly under half of all the birds encountered in the present study. Of the 52 insect-eaters for which a classification of drinking habits has been made, only nine (17%) are water-dependent. These are the Australian Pratincole, Welcome Swallow, Tree Martin, Fairy Martin, Crimson Chat, Orange Chat, Magpie-lark, Apostle-bird, and White-browed Wood-swallow. The Masked Wood-swallow, although classed as an occasional drinker, also may belong in this group. In view of the fact that the great majority of insectivorous species appear never or only very rarely to visit water (see Cameron 1938; Irwin 1956; Miller and Stebbins 1964; Willoughby and Cade 1967; Smyth and Colombe 1971), it is worthwhile to consider why the above species do not conform to what is apparently a general rule.

The three swallows (Hirundinidae) and two wood-swallows (Artamidae) are all very strong fliers and spend a great deal of time on the wing, either foraging or, in the case of the artamids, soaring high in the sky. Such behavior involves production of considerable heat (see for example Tucker 1968) and exposure to radiation. At high ambient temperatures, heat gained by these means must be lost primarily via evaporative cooling, and this factor may largely account for the need to drink in these species, as has been suggested by Bartholomew and Cade (1963). However, Miller and Stebbins (1964) point out that in birds with aerial habits, such as swallows, heat is also lost by convection and, further, air temperatures well above ground are less than near the surface. The need to drink is widespread in aerial insectivores, however, and both swifts and swallows have been observed to drink, on the wing, in Africa (Irwin 1956; Willoughby and Cade 1967) and in North America (Miller and Stebbins 1964).

Australian Pratincoles, though very powerful fliers, forage mostly on the ground (Bailey 1935), and therefore do not seem to fit in the same category as swallows. A possible reason this species was drinking in large numbers on the Barkly Tableland is that nesting may have been underway at this time (as indicated by gonad size in several specimens examined). Thus, the birds may have had a need for water because of the extra energy demands associated with breeding.

It is more difficult to postulate possible factors responsible for the drinking behavior of the two chats. Although we recorded only a single individual of the Orange Chat drinking on just one occasion (the only time we came across the species in a study area), Aiston (1923) observed Orange Chats drinking in large numbers from shallow water holes in a creek bed near the South Australia-Queensland border in January when the birds were nesting. In the present study, both species of *Epthianura* were always observed to drink whenever they were present in the vicinity of a dawn-to-dusk watch; indeed, 99 trips to water were recorded for the Crimson Chat on watch number 1. We therefore feel that the classifying of these birds as water-dependent is not merely the result of insufficient observation. Both species are highly nomadic and are rarely if ever recorded very far from water in hot weather. It does not appear that the nature of their diet is a likely explanation for the drinking behavior of the chats. Although they occasionally supplement their diet with seeds (Lea and Gray 1935-36), so do quite a few other predominantly insectivorous species which are independent of surface water (e.g., the Singing Bushlark, Crested Bellbird, Wedgebill, quail-thrushes, Whiteface, Red-throat, and Striated Grass-wren). However, it is intriguing that both species are often found around the margins of salt flats where much of the vegetation, such as *Atriplex*, is relatively high in electrolytes.

The Magpie-lark and Apostlebird, although nominally insectivorous (as is the Australian Magpie), may not be very different in food habits from the Grey Currawong and the three species of *Corvus*, here considered omnivorous, or even the two carnivorous butcherbirds (*Cracticus*). It is not apparent why some members of this group should be water-dependent. In Africa *Corvus albus* is an occasional visitor to water but not *Corvus capensis* (Willoughby and Cade 1967), and in North America the two corvids, *Aphelocoma coerulescens* and *Gymnorhinus cyanocephalus*, are frequent drinkers (Miller and Stebbins 1964).

The Spotted Bowerbird drank throughout the day on watch number 9, but why this species should need to drink is not clear, although at some seasons its diet may consist principally of dry seeds. On the other hand, it readily eats berries and other fruit when available, and in this respect is similar to the Red-eyed Bulbul (*Pycnonotus nigricans*), Pale White-eye (*Zosterops pallidus*), and several species of starlings in Africa, all of

which are frequent drinkers at certain times of the year (Irwin 1956; Willoughby and Cade 1967). It is not known in what way, if any, diet underlies the requirement of these species for drinking. The only predominantly frugivorous bird in the arid parts of Australia, the Mistletoebird, was never seen drinking (even though it was present near water when the temperature was as high as 39° C on watch number 1), and in North America the Phainopepla (*Phainopepla nitens*) survives in desert areas, generally without drinking, on a diet of fruit and insects (Miller and Stebbins 1964; Smyth and Coloumbe 1971).

The 23 species classed as carnivorous (Appendix I) obtain relatively large amounts of water from their food, and like insectivores they are therefore relatively well equipped to cope with life in an arid environment, due to the relatively high moisture content of their food and the fact that uric acid excretion is a good way to get rid of large quantities of nitrogen without a large expenditure of water. This is reflected in their drinking habits, and only one species, the Grey Butcherbird, is classed as water dependent.

Probably all birds of prey occasionally take advantage of an opportunity to drink, particularly in hot weather, but under the conditions of heat stress normally encountered in the desert they are not dependent on surface water. Hawks and eagles have the added advantage, like swallows and wood-swallows, of being able to ride thermal currents up to relatively great heights where, as a result of adiabatic cooling, temperatures are lower than near the ground.

Hensley (1954) has reported on the breeding bird populations in the Sonoran Desert, both in Arizona (his study) and in California (censuses by Hutchinson and Hutchinson). A total of 42 species are listed. On the basis of information on food habits contained primarily in Bent (1923-68), these birds have been assigned to the six food habit classes previously established. The 107 species tabulated by Willoughby and Cade (1967) have also been placed in these same food habit categories on the basis of information presented by Roberts (1957). A comparison of the food habits of desert avifaunas in Australia, Africa, and North America, at the species level, is presented in table 5. The remarkable similarity between the three continents indicates that the relative availability of various foods is similar in many arid environments (see also Gullion 1960).

*Drinking and Food Habits Related to Relative Abundance.* Surface water and trees (usually river gums, *Eucalyptus camaldul-*

TABLE 5. Food habits of desert birds.

	Food habits (% of total species) <sup>a</sup>						Total no. of species
	In	Gr	Ca	Om	Ne	Fr	
Australia	48	17	18	8	8	1	127 <sup>b</sup>
Africa	41	25	18	9	1	6	107 <sup>c</sup>
N. America	48	26	17	2	5	2	42 <sup>d</sup>

<sup>a</sup> Symbols are the same as in Appendix I.

<sup>b</sup> This study.

<sup>c</sup> Willoughby and Cade (1967).

<sup>d</sup> Hensley (1954).

*ensis*) were present at each of the ten localities where birds were censused (see fig. 2), and thus the environments are those within which the greatest variety and abundance of desert birds would be expected. Our census areas differed from undeveloped regions of the Australian interior by having a relatively uniform distribution of water. Each count was conducted over a period of 2 to 3 days. A water hole was watched and birds coming to drink were counted for approximately 2 hr at various intervals during the day. These 2-hr periods of observation coincided with known peaks of drinking activity (see figs. 4-6). Data could be taken directly from a dawn-to-dusk watch in six of the ten censuses. In addition, an observer spent about 20 hr counting birds while walking at random through the study area, as far as 3 miles from the water hole.

In order not to bias results in favor of birds which were coming to the water hole to drink, it was necessary to make some assumptions based on the known distribution of water holes and the drinking habits of the species involved. It was assumed that if a water hole were watched for 2 hr during the peak drinking period of a species dependent on water (category Y or S in Appendix I), that probably most or even all of the population resident nearer to this drinking site than to any other, was counted. Any errors in this assumption are probably on the conservative side and would result in the total population being underestimated, because it is unlikely that a particular individual drank more than once during the relatively short period of observation. Although it was not known precisely from what distance birds were coming to drink, it was estimated that in most localities the population drinking was from an area of approximately 20 square miles, since, on the average, half the distance to adjacent water holes (usually water tanks) was about 2.5 miles. Therefore, in calculating relative abundance of water-dependent species, the number of individuals counted in a 2-hr period was divided by 20 to arrive at a rough approximation of density per square mile for each species. An average

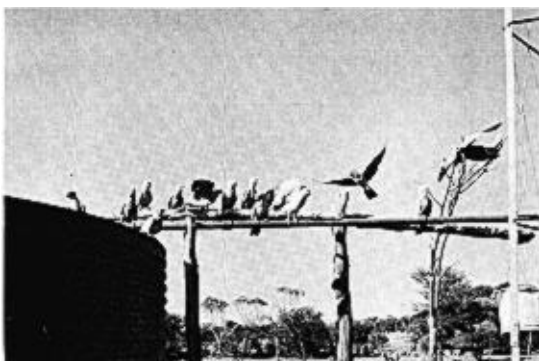


FIGURE 10. The Galah, although needing to drink once or twice daily during much of the year, is the most abundant avian species in arid areas throughout the interior of the continent, wherever water is available, and is a familiar sight around almost every water tank.

density for each species was obtained by dividing the total individual count from all 10 censuses by  $10 \times 20$  square miles.

In calculating relative abundance of species independent of water (categories O and N in Appendix I), it was estimated that in 20 hr of walking, all birds within an area of about 3 square miles were counted. This estimate was based on an average walking speed of 2 miles per hour and the assumption that the birds counted represented the total population in a strip approximately 200 feet either side of the path of the observer. The individual count for a water-independent species was thus divided by three (instead of 20), and the total count from all censuses was divided by 30 (rather than 200) in arriving at an average density per square mile.

Although our figures are very crude estimates of actual population densities, their calculation enables us to assign species to one of four relative abundance categories (Appendix I), and to make some worthwhile comparisons of abundance with drinking and food habits. The eight species classed as abundant (A) are, in order of abundance: Galah (fig. 10), Zebra Finch, White-plumed Honey-eater, Little Corella, Masked Wood-swallow, Budgerygah, Black-faced Wood-swallow, and Crested Pigeon. Significantly, the four commonest xerophilous birds (in areas where water is available) are water-dependent, and only the Black-faced Wood-swallow, of the eight most abundant species, appears to be completely independent of water.

In addition to the above eight species, 14 or 15 others had an average density exceeding two birds per square mile. In order of abundance these are: Australian Bee-eater

TABLE 6. Drinking habits correlated with relative abundance.<sup>a</sup>

	No. of water dependent species			No. of water independent species			Total
	Y	S	Total	O	N	Total	
A	5	1	6	2	0	2	8
C	2	6	8	8	7	15	23
U	2	8	10	7	18	25	35
R	2	21	23	5	24	29	52
Total species	11	36	47	22	49	71	118
Average density <sup>b</sup>	62.47	25.82	88.29	33.77	29.43	63.20	151.49
% of total pop.	41	17	58	22	20	42	100

<sup>a</sup> Symbols are the same as in Appendix I.

<sup>b</sup> Number of individuals per square mile.

(a migrant), Yellow-throated Miner, Willy Wagtail, Diamond Dove, Crow and/or Little Crow, Tree Martin, Australian Pipit, White-winged Triller (a migrant), White-browed Babbler, Black-faced Cuckoo-shrike, Chestnut-tailed Thornbill, Nankeen Kestrel, Grey-crowned Babbler, and Bourke Parrot. Only six of these species are water-dependent.

The most widespread birds in the desert are ten species which were found in nine or all ten of the census areas: Nankeen Kestrel, Crested Pigeon, Galah, Black-faced Cuckoo-shrike, Willy Wagtail, White-plumed Honeyeater, Yellow-throated Miner, Zebra Finch, Magpie-lark, and Black-faced Wood-swallow (Appendix I). Only four of these do not require free water in warm weather.

Five species are both widespread and abundant—the Crested Pigeon, Galah, White-plumed Honeyeater, Zebra Finch, and Black-faced Wood-swallow—and in a sense these can be considered the most successful Australian xerophilous birds, at least in regions where both water and eucalypts are present. The only member of this group which can evidently remain in water balance during the summer without drinking is the Black-faced Wood-swallow. It is also the only insectivorous species, the remaining birds listed with it being either seed-eating or nectar-feeding.

Drinking habits are compared with relative abundance in table 6. Although only 47 species (40%) of the 118 listed are in drinking categories Y and S, yet 58% of all individuals fall in this, the water-dependent, group. Furthermore, 41% of all individuals belong to the 11 species which drink throughout the year. Within the areas of this study, the majority of the avifauna is clearly dependent on drinking water. In localities where water is available, species which regularly drink are more abundant than those which drink only occasionally or not at all. There is no a priori reason why this should be true, and their success in an

arid environment, it appears, is a consequence more of food habits than any particular adjustments to the scarcity of water.

Perhaps some birds drink merely because water is available and not because it is crucial to their maintenance of water balance. However, drinking at isolated water holes in arid regions has several disadvantages: (1) a greater risk of predation; (2) a larger expenditure of energy and water in travelling to and from a drinking site; and (3) a loss in foraging efficiency because of the general depletion of food in the immediate environs of water. These considerations would presumably serve to reduce or eliminate all nonessential drinking. The drinking we have observed, therefore, appears to be a manifestation of physiological need, not capriciousness.

Relative abundance of the various birds and food habits are listed in table 7, both at the species level and the individual level. Granivorous forms, although comprising only 17% of the total species, make up 44% of all individuals, and are thus the most abundant avian group in the desert. Five of the ten most numerous birds are granivorous in their food habits. The most logical explanation for this fact is that seeds as a source of food are more dependable from season to season and year to year than are other food items, and are in greater supply. Because many granivorous species, such as cockatoos and pigeons, are relatively large in body size, the total biomass of seed-eating birds must be very much greater than that of insect-eaters, the majority of which are very small.

In terms of total individuals, 61 insectivorous species rank next to the seed-eaters in order of abundance, constituting 38% of the whole avifauna. All other groups, including nectar-feeders, together make up less than 20% of the population, reflecting the general unavailability in the Australian desert of dietary items other than seeds and insects.



TABLE 7. Food habits and relative abundance.<sup>a</sup>

	In	Ca	Cr	Ne	Om	Fr	Total	%
Number of species								
A	2	0	5	1	0	0	8	6
C	14	3	3	1	2	0	23	18
U	19	5	8	0	3	1	36	28
R	26	15	6	8	5	0	60	47
Total	61	23	22	10	10	1	127	100
%	48	18	17	8	8	1	100	
Average density <sup>b</sup>								
A	10.80	0.00	54.25	8.86	0.00	0.00	73.91	48
C	32.91	5.17	7.18	3.46	3.03	0.00	51.75	34
U	11.31	3.00	4.75	0.00	1.52	0.93	21.51	14
R	2.74	1.24	0.31	0.48	0.59	0.00	5.36	4
Total	57.76	9.41	66.49	12.80	5.14	0.93	152.53 <sup>c</sup>	100
%	38	6	44	8	3	1	100	

<sup>a</sup> Symbols are the same as in Appendix I.

<sup>b</sup> Number of individuals per square mile.

<sup>c</sup> This figure differs slightly from the average total density in table 6 because an additional 9 species are included (see Appendix I).

Few data are available for comparison with avifaunas in other arid regions of the world, but in the study by Hensley (1954), it is noteworthy that the commonest bird in desert washes, by a wide margin, was the White-winged Dove (*Zenaida asiatica*), a granivorous species. Also, in an arid canyon the four most numerous birds, again by a significant amount, were the Gambel Quail (*Lophortyx gambelii*), White-winged Dove, Mourning Dove, and House Finch, all principally seed-eating species. In two other studies of a North American desert, Dixon (1959) and Raitt and Maze (1968) reported on breeding bird densities within small census areas in the Chihuahuan Desert. Of the ten most common species, five were seed-eating, and the most abundant bird was the Black-throated Sparrow, a species which is granivorous for at least several months of the year (see Smyth and Bartholomew 1966).

Although all observations in the present study were made in regions where drinking water was always present, extensive areas still exist in the vast arid interior of the Australian continent which are virtually undeveloped and devoid of water, particularly in the Great Sandy, Gibson, and Great Victoria Deserts. The birdlife encountered on a transect of about 350 miles during a 7-day trip by vehicle across the Great Victoria Desert in late August has been described by Ford and Sedgwick (1967). Temperatures, though not specified, were probably cool to moderate at this time of year, the Austral winter.

It is of interest that not a single seed-eating bird is included among 15 species mentioned

as being particularly numerous, although the Mulga Parrot was very widespread and on one occasion a flock of 40 Port Lincoln Parrots was discovered feeding at a spot where seeds were present on some low green bushes. Crested Pigeons and Diamond Doves were not recorded at all, Budgerygahs and Cockatiels just once, Galahs only twice, and Zebra Finches were seen in small numbers at merely two localities. The Crested Bellbird, White-browed Babbler, Singing Honeyeater, and Black-faced Wood-swallow apparently were the most common species. The fact that meliphagids in general were frequently encountered, particularly in the myall and mallee belts where the vegetation was relatively green, is further evidence that this group is somewhat less dependent on surface water than are seed-eaters.

We postulate that during the summer months when relatively high temperatures are prevalent in the Great Victoria Desert, and in other predominantly waterless regions as well, the only species present would be those which are listed as water independent in Appendix I, except at the few sites where permanent water holes exist. Because water has been made readily and permanently available through the activities of man, birds on the Australian continent today are without doubt far more widespread and abundant in many parts of the arid interior than they were prior to the advent of the pastoral industry.

*Behavior Associated With Drinking.* The birds we observed utilized one of two primary methods of ingesting water. The first involves immersing the beak in water and keeping it there for the entire period of drinking. In

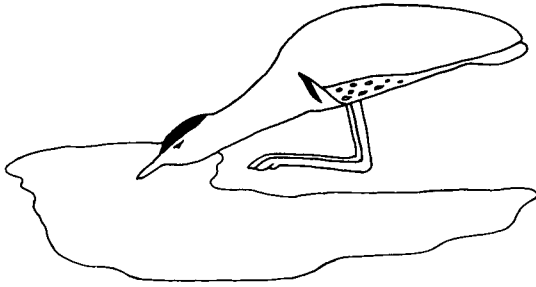


FIGURE 11. Posture sometimes assumed by the Australian Bustard when drinking, with both tarsometatarsi on the ground. Drawn from a photograph.

this method the water is evidently forced into the esophagus or crop by means of a pumping action in the gular area, or perhaps by tongue movement. This method has sometimes been referred to as "sucking," a term we regard as inappropriate. It is employed by all pigeons and doves, but by relatively few other birds. (It has been pointed out by Cade et al. 1966, that sandgrouse, additional representatives of the order Columbiformes, do not drink in this manner.)

The only species observed by us to take in water in this fashion, apart from columbids, were the Australian Bustard, Budgerygah, Star Finch, Gouldian Finch (*Chloebia gouldiae*), Long-tailed Finch (*Poephila acuticauda*), and Zebra Finch. According to Immelmann (1965), a total of eight Australian finches have this method of drinking. He points out that these birds are better able to obtain the last drop of water from a limited source, and furthermore that a minimum amount of time is spent at the water's edge, which would be advantageous in avoiding predators. Consequently, there are strong selective pressures favoring this manner of water intake in an arid environment, and it is somewhat surprising that so few desert birds seem to have evolved such a system. The bustard, in addition to being one of the few species which is able to drink with a pumping action, is unusual in that it sometimes "kneels" to drink, as shown in figure 11, with all of the tarsometatarsus resting on the ground. To our knowledge the only other bird which occasionally assumes such a posture when drinking is the Emu.

The second method of drinking, which is used by the vast majority of birds, with some variation, involves dipping the beak into water and scooping or "sipping" briefly, then raising the head and tilting it slightly backward, allowing the water to run down the throat. Honeyeaters, although usually drinking in this manner, sometimes hang vertically up-

side down and stretch their neck to reach the surface of a pool beneath them with the tip of their beak. They then drink while in this position without raising their head, apparently by use of their protrusible brush-tipped tongue. It may be that this method is similar to the way in which the Zebra Finch drinks.

Almost all birds approach water warily, even those such as the Emu and birds of prey which, it would seem, have no natural predators. In the case of these species, it may be that this behavior is very recent, or even learned in a lifetime, as a response to the presence of man. Platycercine parrots (in general) and the Diamond Dove are among the most cautious birds in the vicinity of a water hole. Individuals approach water very silently and sometimes sit quietly in a tree or bush for a period of 40 or 50 min before finally flying down to drink. The Bourke Parrot, which arrives at a water hole in semi-darkness, alights on the ground 25–40 meters away and then walks or runs in short bursts up to the edge to drink. Common Bronzewings also approach water in much the same manner. Flock Pigeons fly to a drinking site low above the ground from all directions, and then circle several times before alighting at the water's edge (as has been noted by Schmidt 1967).

Birds which have a habit of circling high over a water hole before settling down to drink are the Budgerygah, Cockatiel, and Masked and White-browed Wood-swallows, the latter two frequently occurring in mixed nomadic flocks. All are very timid in the vicinity of water and sometimes fly up again from a pool immediately after alighting, before any birds have drunk. Budgerygahs are unique in that they spend no more than 2–4 seconds drinking, and often alight in the middle of a pool where they apparently float briefly before taking wing again (see fig. 3D), a trait also observed by Schmidt (1967). All these species, if alarmed, will occasionally sit in a tree (often a dead one) near the water hole prior to drinking. Wood-swallows seem to prefer natural water sources to artificial ones.

The only important predators at desert water holes in the interior of Australia are two species of accipiters and four kinds of falcons: the Australian Goshawk, Collared Sparrowhawk, Peregrine Falcon, Black Falcon, Little Falcon, and Grey Falcon. Of these, only three are widespread and relatively common—the goshawk, sparrowhawk, and Little Falcon—the other three falcons are very local and uncommon. It is not surprising that

falcons and accipiters were most numerous around those water holes, watches number 1 and 17, where birds were drinking in the largest numbers.

Because of the alteration of large parts of arid Australia with the introduction of artificial sources of water, it is possible that the selection pressure of predation is less than it was in the dry interior prior to development, when water holes were more scarce and probably more intensively utilized. However, many of the present behavior patterns of birds at watering sites have almost certainly evolved largely in response to diurnal avian predators. Birds are most vulnerable to predation during the periods spent drinking or traveling to and from water, and thus predation would seem to be one of the primary selective pressures tending to restrict all but essential drinking in desert birds.

### SUMMARY

In the Australian desert 71 (60%) of 118 species studied are independent of water, either never observed to drink or visiting water 50% of the time or less on days when the maximum temperature was 25° C or higher. However, the majority of all individuals inhabiting regions where water is available are dependent on water, and its availability is a critical factor in their distribution. These birds have characteristic times of day when drinking occurs. Avoidance of high daytime temperatures and intense solar radiation may have been among the most important selective forces in the evolution of these daily drinking times.

Granivorous species are the most dependent on water, but they are also the most abundant avian group in the arid parts of Australia in localities where surface water is available. Seeds, it appears, are the most dependable and readily available food item. Meliphagids also have a strong physiological need to drink, and

it is suggested that this may in part be a result of their high level of activity. Carnivorous and insectivorous birds, however, are largely independent of water, and many small insect-eaters appear never to drink. A direct correlation is apparent between frequency of drinking and ambient temperature, almost all species that drink visit water more often on hot days than on cooler ones. Diurnal avian predators were probably one of the principal selective pressures in the evolution of present day behavior patterns of birds which regularly drink at water holes.

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### APPENDIX I. Drinking habits, food habits, and abundance of Australian desert birds.

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C-35°C		above 35°C						
	+	-	+	-	+	-					
Emu											
<i>Dromaius novaehollandiae</i>	1	1	1	0	5	0	S	116	Om	5	R
Black-shouldered Kite											
<i>Elanus notatus</i>			0	2			N		Ca	2	R

APPENDIX I. *Continued.*

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C–35°C		above 35°C						
	+	–	+	–	+	–					
Letter-winged Kite <i>Elanus scriptus</i>			0	1			N		Ca	0	R
Black Kite <i>Milvus migrans</i> (1)*			1	1			O	5	Ca	4	U
Square-tailed Kite <i>Lophoictinia isura</i>			0	1			N		Ca	2	R
Black-breasted Buzzard <i>Hamirostra melanosternon</i>	0	1	0	1			N		Ca	1	R
Whistling Eagle <i>Haliastur sphenurus</i> (1)	1	0	0	5			O	1	Ca	6	U
Australian Goshawk <i>Accipiter fasciatus</i> (3)	0	1	0	4	0*	1	O	1	Ca	4	R
Collared Sparrowhawk <i>Accipiter cirrocephalus</i> (3)	0	1	0	2	0*	3	O	1	Ca	4	R
Little Eagle <i>Hieraaetus morphnoides</i> (1)	0	1	0	4	1	0	O	1	Ca	5	R
Wedge-tailed Eagle <i>Aquila audax</i>	0	2	0	4			N		Ca	6	U
Spotted Harrier <i>Circus assimilis</i>					0	2	N		Ca	1	R
Swamp Harrier <i>Circus approximans</i>							N		Ca	2	R
Grey Falcon <i>Falco hypoleucos</i>					0	1	N		Ca	0	R
Black Falcon <i>Falco subniger</i>	0	1	0	2			N		Ca	1	R
Brown Falcon <i>Falco berigora</i> (2)	1	3	0	6	1	0	O	6	Ca	7	C
Peregrine Falcon <i>Falco peregrinus</i>	0	1			0	1	N		Ca	0	R
Little Falcon <i>Falco longipennis</i>	0	2	0	2	0	2	N		Ca	4	R
Nankeen Kestrel <i>Falco cenchroides</i>	0	2	0	10	0	2	N		Ca	10	C
Little Quail <i>Turnix velox</i>			0	2			N		Gr	2	R
Brolga <i>Grus rubicundus</i>			0	1			N		Om	1	R
Australian Bustard <i>Eupodotis australis</i>			0	1	1	0	O	3	Om	2	U
Masked Plover <i>Lobibyx miles</i>	0	1	0	1			N		Om	2	U
Banded Plover <i>Zonifer tricolor</i>	0	1	0	1			N		Om	2	R
Southern Stone-curlew <i>Burhinus magnirostris</i> (1)			0	1	1	0	O	1	In	2	R

APPENDIX I. *Continued.*

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C–35°C		above 35°C						
	+	–	+	–	+	–					
Australian Pratincole <i>Stiltia isabella</i> (1)			1	0			S	201	In	0	R
Peaceful Dove <i>Geopelia striata</i>			2	0			S	150	Gr	2	R
Diamond Dove <i>Geopelia cuneata</i>	1	0	6	0	1	0	Y	211	Gr	6	C
Common Bronzewing <i>Phaps chalcoptera</i>	4	0	2*	0	5*	0	Y	134	Gr	4	U
Crested Pigeon <i>Ocyphaps lophotes</i>	4	0	10*	0	5*	0	Y	543	Gr	10	A
Plumed Pigeon <i>Lophophaps plumifera</i>			3*	0			S	83	Gr	3	U
Flock Pigeon <i>Histriophaps histrionica</i> (4)			1*	0			S	760	Gr	1	R
Red-tailed Black Cockatoo <i>Calyptorhynchus banksii</i> (2)			*				S	20	Gr	2	U
Pink Cockatoo <i>Cacatua leadbeateri</i> (5)	1	0	*		*		Y	112	Gr	1	R
Little Corella <i>Cacatua sanguinea</i>			4*	0	*		S	1,125	Gr	5	A
Galah <i>Cacatua roseicapilla</i>	4*	0	10*	0	5*	0	Y	1,065	Gr	10	A
Cockatiel <i>Leptolophus hollandicus</i>	1*	0	2*	0	1	0	Y	4,500	Gr	5	U
Port Lincoln Parrot <i>Barnardius zonarius</i>	2	2	8*	0	2*	0	S	129	Gr	7	C
Ringneck Parrot <i>Barnardius barnardi</i>			1	0	*		S	8	Gr	2	U
Red-backed Parrot <i>Psephotus haematotus</i> (1)			*				S	5	Gr	1	R
Mulga Parrot <i>Psephotus varius</i>	1	1	5*	0	3*	0	S	200	Gr	6	U
Blue Bonnet Parrot <i>Psephotus haematogaster</i>			1*	0	*		S	175	Gr	1	U
Elegant Parrot <i>Neophema elegans</i> (2)			*		*		S	15	Gr	1	R
Bourke Parrot <i>Neophema bourkii</i>	2	0	2*	0	3*	0	Y	800	Gr	3	C
Budgerygah <i>Melopsittacus undulatus</i>	1*	0	3*	0	1	0	Y	47,000	Gr	4	A
Pallid Cuckoo <i>Cuculus pallidus</i>	0	1	0	2			N		In	3	R
Black-eared Cuckoo <i>Chrysococcyx osculans</i>	0	2	0	1			N		In	1	R
Horsfield Bronze Cuckoo <i>Chrysococcyx basalis</i>	0	2	0	3			N		In	3	U

APPENDIX I. *Continued.*

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C–35°C		above 35°C						
	+	–	+	–	+	–					
Spotted Nightjar <i>Eurostodopus guttatus</i> (2)	0	1	1	0	0*	1	O	5	In	2	R
Blue-winged Kookaburra <i>Dacelo leachii</i>			0	1			N		Ca	0	R
Red-backed Kingfisher <i>Halcyon pyrrhopygia</i>			0	3			N		Ca	4	U
Sacred Kingfisher <i>Halcyon sancta</i>			0	2			N		Ca	4	U
Australian Bee-eater <i>Merops ornatus</i>			0	5	0	1	N		In	8	C
Singing Bushlark <i>Mirafra javanica</i>			0	2			N		In	2	U
White-backed Swallow <i>Cheramoeca leucosternum</i>									In	3	R
Welcome Swallow <i>Hirundo neoxena</i> (3)	0	1	2	0	1	1	S	3	In	5	R
Tree Martin <i>Petrochelidon nigricans</i>	0	1	5	0	1*	0	S	450	In	7	C
Fairy Martin <i>Petrochelidon ariel</i> (2)			1	0	1	0	S	5	In	1	R
Australian Pipit <i>Anthus novaeseelandiae</i> (2)	0	2	0	7	2	0	O	46	In	7	C
Ground Cuckoo-shrike <i>Pteropodocys maxima</i>	0	2	0	5			N		In	7	U
Black-faced Cuckoo-shrike <i>Coracina novaehollandiae</i> (2)	0	3	0	8	1*	2	O	18	In	10	C
White-winged Triller <i>Lalage suerri</i> (2)			1	2	*		O	51	In	4	C
Wedgebill <i>Sphenostoma cristatum</i>			0	1			N		In	4	U
Chestnut-breasted Quail-thrush <i>Cinclosoma castaneothorax</i>	0	1			0	1	N		In	1	U
Grey-crowned Babbler <i>Pomatostomus temporalis</i> (2)			0	2	*		O	12	In	5	C
White-browed Babbler <i>Pomatostomus superciliosus</i>	0	1	0	2	0	2	N		In	4	C
Chestnut-crowned Babbler <i>Pomatostomus ruficeps</i>									In	1	R
White-fronted Chat <i>Ephthianura albifrons</i>									In	1	U
Crimson Chat <i>Ephthianura tricolor</i> (3)			1	0	1*	0	S	99	In	4	R
Orange Chat <i>Ephthianura aurifrons</i> (1)					1	0	S	1	In	0	R
Western Warbler <i>Gerygone fusca</i>									In	1	R
Weebill <i>Smicromnis brevirostris</i> (1)	0	3	0	3	*	1	O	4	In	7	U

APPENDIX I. *Continued.*

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C–35°C		above 35°C						
	+	–	+	–	+	–					
Whiteface <i>Aphelocephala leucopsis</i>	0	2	0	3	0	2	N		In	6	C
Brown Thornbill <i>Acanthiza pusilla</i>									In	1	R
Robust Thornbill <i>Acanthiza robustirostris</i>					0	2	N		In	2	R
Chestnut-tailed Thornbill <i>Acanthiza uropygialis</i>	0	4	0	3	0	4	N		In	5	C
Yellow-tailed Thornbill <i>Acanthiza chrysorrhoa</i>	0	2	0	2	0	1	N		In	4	U
Redthroat <i>Pyrholaemus brunneus</i>	0	1			0	2	N		In	1	R
Banded Blue Wren <i>Malurus splendens</i>	0	1			0	3	N		In	1	R
Turquoise Wren <i>Malurus callainus</i>	0	1					N		In	1	R
Blue-and-white Wren <i>Malurus leucopterus</i>			0	2			N		In	4	U
Variiegated Wren <i>Malurus lamberti</i>	0	1	0	3	0	1	N		In	6	C
Rufous-crowned Emu-wren <i>Stipiturus ruficeps</i>									In	1	R
Striated Grass-wren <i>Amytornis striatus</i>									In	1	R
Brown Songlark <i>Cinclorhamphus cruralis</i>			0	2			N		In	2	U
Rufous Songlark <i>Cinclorhamphus mathewsi</i>			0	3			N		In	4	U
Willy Wagtail <i>Rhipidura leucophrys</i> (5)	0	4	1	6	3*	1	O	5	In	10	C
Brown Flycatcher <i>Microeca leucophaea</i>	0	1	0	1			N		In	1	R
Red-capped Robin <i>Petroica goodenovii</i> (1)	0	3	0	3	1	4	O	2	In	5	U
Hooded Robin <i>Petroica cucullata</i> (1)	0	3	0	3	1	0	O	2	In	4	U
Rufous Whistler <i>Pachycephala rufiventris</i> (1)	0	4	0	5	0*	2	O	1	In	6	U
Western Shrike-thrush <i>Colluricincla rufiventris</i>	0	3	0	3	0	1	N		In	7	U
Crested Bellbird <i>Oreocia gutturalis</i>	0	4	0	4	0	3	N		In	6	U
Black-capped Sitella <i>Neositta pileata</i>	0	1	0	1			N		In	1	R
Black-tailed Tree-creeper <i>Climacteris melanura</i>			0	1			N		In	1	R

APPENDIX I. *Continued.*

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C-35°C		above 35°C						
	+	-	+	-	+	-					
White-browed Tree-creeper <i>Climacteris affinis</i>								In	1	R	
Mistletoebird <i>Dicaeum hirundinaceum</i>	0	1	0	3	0	1	N	Fr	5	U	
Red-tipped Pardalote <i>Pardalotus substriatus</i>	0	2	0	3			N	In	5	C	
Red-browed Pardalote <i>Pardalotus rubricatus</i>			0	3			N	In	4	U	
Brown Honeyeater <i>Lichmera indistincta</i> (3)					*		S	15	Ne	3	R
Grey Honeyeater <i>Lacustroica whitei</i>								In	1	R	
Pied Honeyeater <i>Certhionyx variegatus</i> (2)			*		1	0	S	60	Ne	0	R
Black Honeyeater <i>Myzomela nigra</i> (1)					1	0	S	1	Ne	0	R
Singing Honeyeater <i>Meliphaga virescens</i>	0	1	2	1	2	2	S	16	Ne	7	R
Yellow-fronted Honeyeater <i>Meliphaga plumula</i> (2)			1	0	*		S	7	Ne	0	R
White-plumed Honeyeater <i>Meliphaga penicillata</i>	1	0	7*	0			Y	1,558	Ne	9	A
White-fronted Honeyeater <i>Phylidonyris albifrons</i> (2)	0	2			1	0	S	1	Ne	1	R
Yellow-throated Miner <i>Myzantha flavigula</i>	1	3	5*	4	2	0	S	614	Ne	10	C
Spiny-cheeked Honeyeater <i>Acanthagenys rufogularis</i>	0	4	2*	0	4	0	S	1,750	Ne	8	R
Red Wattlebird <i>Anthochaera carunculata</i> (2)	1	0	1	0			Y	18	Ne	0	R
Painted Finch <i>Zonaeginthus pictus</i>			2	0	*		S	126	Gr	2	U
Zebra Finch <i>Taeniopygia castanotis</i>	2*	0	8*	0	3*	0	Y	17,750	Gr	9	A
Magpie-lark <i>Grallina cyanoleuca</i>	0	3	3	4	3*	0	S	25	In	10	C
Apostlebird <i>Struthidea cinerea</i> (1)			1	0			S	262	In	1	U
White-breasted Wood-swallow <i>Artamus leucorhynchus</i>			0	2			N		In	2	U
Masked Wood-swallow <i>Artamus personatus</i> (5)			1*	2	1	0	O	250	In	6	A
White-browed Wood-swallow <i>Artamus superciliosus</i> (5)			1	0	1	0	S	10	In	1	R
Black-faced Wood-swallow <i>Artamus cinereus</i> (1)	0	1	0	5	*		O	1	In	9	A



APPENDIX I. *Continued.*

Species	Days recorded on dawn-dusk watches <sup>a</sup>						Drinking habits <sup>b</sup>	Maximum visits/day to drink <sup>c</sup>	Food habits <sup>d</sup>	Distribution <sup>e</sup>	Relative abundance <sup>f</sup>
	below 25°C		25°C–35°C		above 35°C						
	+	–	+	–	+	–					
Little Wood-swallow											
<i>Artamus minor</i>					0	1	N		In	1	R
Grey Currawong											
<i>Strepera versicolor</i> (2)	0	3			2	0	S	12	Om	1	R
Pied Butcherbird											
<i>Cracticus nigrogularis</i> (3)	0	2	0*	6	2	1	O	16	Ca	7	C
Grey Butcherbird											
<i>Cracticus torquatus</i> (4)	0	2	1	1	3	0	S	6	Ca	4	R
Australian Magpie											
<i>Gymnorhina tibicen</i>	1	1	2	4	2	2	O	18	In	7	C
Spotted Bowerbird											
<i>Chlamydera maculata</i> (1)	0	1	1	0			S	13	Om	2	R
Raven											
<i>Corvus coronoides</i> (1)	0	1	1	0			S	310	Om	1	U
Crow											
<i>Corvus ceciliae</i>	1	2	7*	3	5*	0	S	589	Om	8	C
Little Crow											
<i>Corvus bennetti</i>							S		Om		C

<sup>a</sup> The “plus” column indicates the number of days the species drank; the “minus” column the number of days it did not drink; temperatures are maximum daily temperature; an asterisk indicates there are additional drinking records (not from a dawn-to-dusk watch).

<sup>b</sup> Y: year around drinker; S: summer drinker; O: occasional drinker; N: no drinking records; categories are based on drinking frequencies at different temperatures (see text).

<sup>c</sup> Figures in italics are from a dawn-to-dusk watch; others are from a water hole watch of shorter duration.

<sup>d</sup> Gr: granivorous; In: insectivorous; Ne: nectarivorous; Ca: carnivorous; Om: omnivorous; Fr: frugivorous.

<sup>e</sup> Figures are the number of censuses out of 10 in which the species was present.

<sup>f</sup> A: abundant (above 4.00 individuals per square mile); C: common (1.01–4.00 ind. per sq. mi.); U: uncommon (.21–1.00 ind. per sq. mi.); R: rare (.01–.20 ind. per sq. mi.).

<sup>g</sup> A number in parentheses following the species name indicates the total number of days the species was recorded drinking; shown only for birds which drank once but no more than five times.

LITERATURE CITED

AISTON, G. 1923. Notes on birds seen on a recent trip up the Diamantina River near the Queensland border. *Emu* 23:65–66.

BAILEY, R. F. 1935. Field notes on the Australian pratincole. *Emu* 35:1–10.

BARRETT, C. L. 1945. *Australian Bird Life*. Oxford Univ. Press, Melbourne.

BARTHOLOMEW, G. A., AND W. R. DAWSON. 1954. Body temperature and water requirements in the mourning dove, *Zenaidura macroura marginella*. *Ecology* 35:181–187.

BARTHOLOMEW, G. A., AND T. J. CADE. 1963. The water economy of land birds. *Auk* 80:504–539.

BENT, A. C. 1923–68. Life histories of North American birds. U.S. Nat. Mus. Bull. (various nos.).

CADE, T. J. 1965a. Survival of the scaly-feathered finch *Sporopipes squamifrons* without drinking water. *The Ostrich* 36:131–132.

CADE, T. J. 1965b. Relations between raptors and columbiform birds at a desert water hole. *Wilson Bull.* 77:340–345.

CADE, T. J., AND J. A. DYBAS. 1962. Water economy of the budgerygah. *Auk* 79:345–364.

CADE, T. J., C. A. TOBIN, AND A. GOLD. 1965. Water economy and metabolism of two estrildine finches. *Physiol. Zoöl.* 38:9–33.

CADE, T. J., E. J. WILLOUGHBY, AND G. L. MACLEAN. 1966. Drinking behavior of sandgrouse in the Namib and Kalahari deserts, Africa. *Auk* 83:124–126.

CADE, T. J., AND L. I. GREENWALD. 1966. Drinking behavior of mousebirds in the Namib Desert, southern Africa. *Auk* 83:126–128.

CALDER, W. A. 1964. Gaseous metabolism and water relations of the zebra finch, *Taeniopygia castanotis*. *Physiol. Zoöl.* 37:400–413.

CAMERON, A. C. 1938. Birds drinking in the dry interior. *Emu* 38:336–337.

CHISHOLM, A. H. 1958. *Bird wonders of Australia*. Mich. State Press, East Lansing.

DAWSON, W. R., AND C. D. FISHER. 1969. Responses to temperature by the spotted nightjar (*Eurostopodus guttatus*). *Condor* 71:49–53.

DIXON, K. L. 1959. Ecological and distributional relations of desert scrub birds of western Texas. *Condor* 61:397–409.

FARNER, D. S., AND D. L. SERVENTY. 1960. The timing of reproduction in birds in the arid regions of Australia. *Anat. Rec.* 137:354.

FINLAYSON, H. H. 1932. Heat in the interior of South Australia and in central Australia. *S. Aust. Ornithol.* 11:158–163.

FORD, J., AND E. H. SEDGWICK. 1967. Bird distribu-

- tion in the Nullarbor Plain and Great Victoria Desert region, Western Australia. *Emu* 67: 99-124.
- FRITH, H. J., AND R. A. TILT. 1959. Breeding of the zebra finch in the Murrumbidgee irrigation area, New South Wales. *Emu* 59:289-295.
- GULLION, W. 1960. The migratory status of some western desert birds. *Auk* 77:94-95.
- GOODWIN, D. 1967. Australian pigeons: their affinities and status. *Emu* 66:319-336.
- HENSLEY, M. M. 1954. Ecological relations of the breeding bird population of the desert biome in Arizona. *Ecol. Monogr.* 24:185-207.
- HYETT, J. 1967. Flocking of spinifex pigeon. *Emu* 67:132.
- IMMELMANN, K. 1963. Tierische Jahresperiodik in ökologischer Sicht. *Zool. Jahrb. Syst.* 91:91-200.
- IMMELMANN, K. 1965. Australian finches. Angus and Robertson, Sydney.
- IRWIN, M. P. S. 1956. Notes on the drinking habits of birds in semi desertic Bechuanaland. *Bull. British Ornithol. Club.* 76:99-101.
- JOHNSON, D. H., D. B. MONROE, AND A. H. MILLER. 1948. Vertebrate animals of the Providence Mountains area of California. *Univ. Calif. Pub. Zool.* 48:221-376.
- KEAST, A. 1959. Australian birds: their zoogeography and adaptations to an arid continent. Chapt. 6 in A. Keast [ed.] *Biogeography and ecology in Australia*. W. Junk, The Hague.
- LEA, A. M., AND J. T. GRAY. 1935-36. The food of Australian birds. *Emu* 34:275-292; 35:63-98, 145-189, 251-280, 335-347.
- MARSHALL, A. J., AND D. L. SERVENTY. 1958. The internal rhythm of reproduction in xerophilous birds under conditions of illumination and darkness. *J. Exp. Biol.* 35:666-670.
- MCCILP, J. N. 1922. The drinking habits of *Peltohyas australis*. *S. Aust. Ornithol.* 6:155-156.
- MILLER, A. H., AND R. C. STEBBINS. 1964. The lives of desert animals in Joshua Tree National Monument. Univ. of California Press, Berkeley.
- RAITT, R. J., AND R. L. MAZE. 1968. Densities and species composition of breeding birds of a creosote-bush community in southern New Mexico. *Condor* 70:193-205.
- ROBERTS, A. 1957. Birds of South Africa. Rev. ed. Cape Times Ltd., Cape Town.
- SCHMIDT, P. J. 1967. Notes on two North Australian bird species. *Emu* 66:368.
- SERVENTY, D. L., AND H. M. WHITTELL. 1962. Birds of Western Australia. Third ed. Paterson Brokensha Pty. Ltd., Perth.
- SMYTH, M., AND G. A. BARTHOLOMEW. 1966. The water economy of the Black-throated Sparrow and Rock Wren. *Condor* 68:447-458.
- SMYTH, M. AND H. N. COULOMBE. 1971. Notes on the use of Desert Springs by birds in California. *Condor* 73:240-243.
- STURKIE, P. D. 1965. Avian physiology. Second ed. Cornell Univ. Press, Ithaca.
- TUCKER, V. A. 1968. Respiratory exchange and evaporative water loss in the flying budgerigar. *J. Exp. Biol.* 48:67-87.
- WHITE, S. A. 1915. Scientific notes on an expedition into the north-western regions of South Australia: Aves. *Trans., Proc., Rep. Roy. Soc. S. Aust.* 39:740-759.
- WILLOUGHBY, E. J. 1968. Water economy of the Stark's lark and grey-backed finch-lark from the Namib Desert of South West Africa. *Comp. Biochem. Physiol.* 27:723-745.
- WILLOUGHBY, E. J., AND T. J. CADE. 1967. Drinking habits of birds in the central Namib Desert of South West Africa. *Sci. Papers Namib Desert Res. Sta.* no. 31.

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