

## Surface water dependency among Kalahari Desert birds

The availability of free-standing water sources is a key determinant of animal and plant community structure in arid environments, and an understanding of the extent to which particular species depend on drinking water is vital for modelling the effects of climate change on desert avifauna. We investigated interspecific variation in dependence on artificial water sources among birds in the Kalahari Desert, South Africa, by 1) observations at waterholes and 2) tracing spatial water-use patterns during summer using isotopically-labelled water and blood sampling. More than 50 % of the avian community (primarily insectivores and omnivores) were not observed to drink. The majority (53%) of species drinking at waterholes were granivorous, and most visited waterholes daily. Blood samples revealed that only 11 of 42 species (again, mostly granivores) showed evidence of drinking at a waterhole labelled with deuterium, with between 2.2 and 92.9 % of individual birds' body water pools originating from the labelled waterhole. These findings illustrate how two methods employed in this study provide different but complementary data on the relative importance of a water source for an avian community. Although our results suggest that most species are independent of drinking, drinking patterns on the hottest days during our study period suggest that free-standing water might become more important for some of the non-drinking species under hotter climatic conditions.

1 **Surface water dependency among Kalahari Desert birds**

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**21 Abstract**

22 The availability of free-standing water sources is a key determinant of animal and plant  
23 community structure in arid environments, and an understanding of the extent to which  
24 particular species depend on drinking water is vital for modelling the effects of climate change  
25 on desert avifauna. We investigated interspecific variation in dependence on artificial water  
26 sources among birds in the Kalahari Desert, South Africa, by 1) observations at waterholes and  
27 2) tracing spatial water-use patterns during summer using isotopically-labelled water and blood  
28 sampling. More than 50 % of the avian community (primarily insectivores and omnivores)  
29 were not observed to drink. The majority (53%) of species drinking at waterholes were  
30 granivorous, and most visited waterholes daily. Blood samples revealed that only 11 of 42  
31 species (again, mostly granivores) showed evidence of drinking at a waterhole labelled with  
32 deuterium, with between 2.2 and 92.9 % of individual birds' body water pools originating from  
33 the labelled waterhole. These findings illustrate how two methods employed in this study  
34 provide different but complementary data on the relative importance of a water source for an  
35 avian community. Although our results suggest that most species are independent of drinking,  
36 drinking patterns on the hottest days during our study period suggest that free-standing water  
37 might become more important for some of the non-drinking species under hotter climatic  
38 conditions.

39 **Keywords:** water balance, evaporative water loss, stable isotopes, drinking behaviours,  
40 metabolic water, preformed water, surface water

41

**42 Introduction**

43 Small animals have limited capacities to store body water and consequently need to regulate  
44 water intake over time scales of minutes to hours, particularly in hot, arid terrestrial  
45 environments where high environmental temperatures and high vapor pressure deficits result

46 in rapid evaporative water loss (Hill et al., 2004). Daily water demands are particularly high in  
47 small endotherms, such as birds, because of their high mass-specific metabolic and evaporative  
48 water loss (EWL) rates (Williams and Tieleman, 2005, Wolf, 2000); for example, in small  
49 desert birds daily water fluxes may exceed 50% of body mass (Webster and Weathers, 2000).

50 Birds can obtain water through metabolic water (i.e., oxidative water), drinking,  
51 and/or water rich food sources (i.e., preformed water) (Bartholomew and Cade, 1963,  
52 MacMillen, 1990). Reliance on surface water sources is generally related to dietary needs of  
53 avian species (MacMillen, 1990). Although metabolic water production can sometimes offset  
54 sources of water loss at  $T_{\text{air}s}$  below 25 °C, birds need to supplement intake by drinking  
55 surface water or eating water rich foods at higher  $T_{\text{air}s}$  when rates of EWL exceed rates of  
56 metabolic water production (MacMillen, 1990, Williams, 1999, MacMillen and Baudinette,  
57 1993, Williams, 2001). Species relying on food with low water content (e.g., dry seeds)  
58 generally need to drink daily in hot, arid habitats. Moreover, daily drinkers must sometimes  
59 allocate time to visit water sources that are distant from their foraging grounds and nesting  
60 sites. During daily trips to water, birds potentially incur costs related to metabolic heat  
61 production while flying (Hudson and Bernstein, 1981, Aulie, 1971, Torre-Bueno, 1978,  
62 Engel et al., 2006), and increased water requirements because EWL is elevated when flying  
63 during hot weather (Torre-Bueno, 1978, Hudson and Bernstein, 1981, Tucker, 1968). An  
64 additional cost is related to predation risk, which is often very high around isolated water  
65 sources on account of greater concentrations of predators (Cade, 1965, Fisher et al., 1972,  
66 Rosenstock et al., 1999). The spatial distribution of species that rely on drinking water daily  
67 will, therefore, be tied to the availability of free-standing water sources.

68 Birds that feed on diets with high water content (e.g. carnivores, insectivores and  
69 frugivores) can obtain most, if not all, of their required water intake while foraging (Wolf et  
70 al., 2002, Wolf and Martinez del Rio, 2000). By being independent of surface water, species

71 can therefore utilize habitats where surface water is unavailable (e.g. sandy deserts).  
72 However, one potential disadvantage of this mode of water acquisition is that foraging  
73 efficiency could greatly affect hydration state. If these birds experience reduced foraging  
74 efficiency on hot days, they are likely to face hydration bottlenecks when evaporative water  
75 loss demands exceed water intake (du Plessis et al., 2012, Smit and McKechnie, 2015, Wolf  
76 and Walsberg, 1996b, Wolf and Walsberg, 1996a). Several studies of arid-zone passerines  
77 have revealed that during hot weather individuals do not maintain body mass, despite  
78 maintaining foraging efforts during hot periods of the day, and the authors linked these  
79 patterns to high water efflux rates and increased evaporative cooling demands (du Plessis et  
80 al., 2012, Smit and McKechnie, 2015).

81 In many arid environments natural fresh water sources are scarce and unpredictable,  
82 and the availability of water-rich foods such as fruits and insects is generally low and/or  
83 restricted to only short seasons (Wolf and Martinez del Rio, 2000, Wolf and Martinez del Rio,  
84 2003). Artificial water sources are often provided by conservation managers or livestock  
85 farmers for large mammals, and may represent the only drinking water sources in many areas.  
86 Although artificial water sources may be beneficial to terrestrial organisms, including birds  
87 (McKechnie et al., 2012) and large mammals (Hayward and Hayward, 2012) under hot  
88 conditions, it has been shown that the presence of these artificial sources can greatly contribute  
89 to habitat degradation (Dean and Macdonald, 1994, Jeltsch et al., 1997, Landman et al., 2012).  
90 An improved understanding of the dependence of terrestrial communities on free-standing  
91 water sources, and how this changes under hot conditions, is needed to facilitate conservation  
92 management decisions about the availability of artificial water sources. For example, Kearney  
93 et al. (2016) modelled thermal heat load and EWL rates in the endangered Night Parrot  
94 (*Pezoporus occidentalis*) showing that reliance on drinking surface water will increase under  
95 climate warming scenarios.

96 In this study we investigated interspecific variation in drinking dependence in an arid-  
97 zone bird community. We predicted that species relying on diets with low water content  
98 (granivores) are more reliant on free-standing water sources compared to insectivores,  
99 frugivores and nectarivores. This prediction was tested using both direct observations of birds  
100 at waterholes, and identifying which birds use a specific water source via an isotopic labelling  
101 approach. We propose that these two methods provide complementary insights into drinking  
102 dependence. We also predicted that birds increase their dependency on free-standing water  
103 during hot and/or dry weather.

104

## 105 **Methods and materials**

### 106 *Study site*

107 We examined interspecific variation in drinking dependence within a Kalahari Desert bird  
108 community at Tswalu Kalahari Reserve (TKR; ~1100 m a.s.l. S 27° 19', E 22° 25'), Northern  
109 Cape Province, South Africa during the austral summers of 2009/2010 and 2011/2012. TKR  
110 consists of approximately 100,000 ha of semi-arid Kalahari savanna on vegetated red sand  
111 dunes. Mean annual rainfall over a 30-year period at TKR was  $295 \pm 172$  mm (coefficient of  
112 variation, CV = 58.3%) (unpublished data, Tswalu Kalahari Reserve). With the exception of  
113 seasonal dams at the foothills of the Koranna Mountain range (1400-1600 m a.s.l., forming the  
114 eastern border of TKR), and a few isolated calcareous pans, no natural surface water occurs in  
115 the dune habitat (even during the rainy season). Artificial waterholes have been established  
116 throughout the reserve (generally more than 4 km apart), primarily to supply drinking water to  
117 large ungulates.

118 We assessed drinking dependence using two methods: first, by monitoring drinking  
119 patterns at four artificial waterholes directly, and second, by investigating the importance of a

120 specific free-standing water body by enriching a waterhole with a stable isotope label and then  
121 sampling body water of the bird community at distances of 0–2.5 km from the labelled water  
122 source. Many previous studies have investigated the potential benefits of artificial water  
123 developments to desert avian communities (Brien et al., 2006, Broyles, 1995, Lynn et al., 2006,  
124 Lynn et al., 2008, Simpson et al., 2011, Smyth and Coulombe, 1971, Williams and Koenig,  
125 1980). However, whereas direct observations provide qualitative data on which species drink  
126 and their drinking frequency, isotopic data provide quantitative insights into the importance of  
127 a water source to individuals' body water pools [see Hyde (2011)].

128

#### 129 *Weather data*

130 Weather data were obtained using a portable weather station (Vantage Pro2, Davis Instruments,  
131 Hayward, CA), set 2 m above the ground at a central location in the study site. This weather  
132 station has an aspirator fan to ensure air movement over the temperature and humidity sensors.  
133 We checked the factory calibration of the weather station against a mercury thermometer  
134 (resolution 0.1 °C, accuracy traceable to the South African Bureau of Standards) at a range of  
135 temperatures (5 to 50 °C).

136

#### 137 *Observations of drinking patterns*

138 Avian drinking patterns were assessed using video cameras (Sony Handycam, DCR-SR45E,  
139 Sony Corporation, Tokyo, Japan) to record behaviour continuously from sunrise to sunset  
140 during mid-summer (November to December 2009), at four waterholes in TKR. All four  
141 waterholes were in the dunes, each > 3 km away from its nearest neighbour and artificially  
142 maintained by boreholes. All waterholes were fully exposed to the sun and the nearest  
143 vegetation was > 5 m away. We placed video cameras in rain- and baboon-proof steel boxes

144 next to waterholes or in nearby trees. Video cameras were positioned to cover the maximum  
145 area over the waterhole to ensure birds would be visible when drinking at any edge of the water.  
146 Recordings commenced between dawn and sunrise, i.e. 5h00 and 6h00 (UTC + 02h00),  
147 respectively (variation due to the 45-min travel time between the first and fourth cameras). The  
148 cameras were set to record continuously throughout the day, and in most cases batteries lasted  
149 until sunset. We downloaded video footage and recharged batteries on days following  
150 recordings and therefore video recordings were repeated on alternate days. We obtained video  
151 recordings over a total of 9, 13, 13 and 16 days at the four waterholes, respectively (~ 660 hours  
152 of video recordings). We subsequently viewed play-backs of each waterhole's recording at 30-  
153 minute intervals for 10 minutes (i.e. two 10 minute periods per hour per waterhole). We  
154 recorded species and estimated the number of individuals utilising the waterhole during each  
155 10-minute period. If it was obvious that a particular individual utilised the waterhole more than  
156 once during a 10-minute period (for instance, when the bird is disturbed from the first drinking  
157 attempt) it was counted as a single event. We compared avian species composition at waterhole  
158 and drinking events obtained from sub-sampled video footage (18 x 10 minute intervals) to  
159 continuous observations (video or manual) at one waterhole for an entire day, and found that  
160 only two species (generally rare species) were missed during interval counts compared to a full  
161 day of observation. We determined the relative abundance of avian species at the study site at  
162 different around the waterholes to better quantify species visitation rates to waterholes relative  
163 to the background avian community (see supplementary materials, Table S1).

#### 164 *Water resource use inferred from stable isotope label*

165 Water resource use by organisms can be assessed using stable hydrogen isotopes, especially if  
166 the hydrogen or oxygen isotope ratio of a prominent water sources is enriched above natural  
167 levels (McKechnie, 2004, McKechnie et al., 2004). The presence of enriched isotope ratios in  
168 the body water pool of an individual is used to infer the percentage of an animal's body water



169 pool derived from a particular water source, thereby giving a quantitative estimate of  
170 dependence on a free-standing water source (McCluney and Sabo, 2010).

171 We assessed the use of one waterhole by an avian community during 1) a wet (23  
172 February to 6 March 2011) and 2) a dry period in summer (21 October to 3 November 2011),  
173 following Hyde (2011) by enriching the stable hydrogen isotope ratio ( $\delta^2\text{H}$ ) of a relatively  
174 isolated waterhole (> 5 km from nearest neighbouring water source). The waterhole system  
175 consisted of a shallow (~20 cm depth) waterhole with a diameter of 3 m, with water supplied  
176 by a ~ 22,800-L reservoir (diameter = 4.3 m, depth = 1.57 m). Although large mammals  
177 frequently made use of the water source, we estimated that the reservoir took more than 4  
178 weeks to run completely dry. We therefore emptied the reservoir to approximately 14,000 L (1  
179 m deep) and closed the main inlet to prevent the labelled water from being diluted by inflow.  
180 We then added 585 mL of 99.99 ‰ deuterium oxide to the reservoir, estimated to enrich the  
181 waterhole by 200-300 ‰<sub>VSMOW</sub> (Vienna Standard Mean Ocean Water) above background  
182 levels, and stirred the water for at least two minutes. We then emptied the waterhole, before  
183 allowing labelled water from the reservoir to fill the waterhole. We collected water samples  
184 before the experimental enrichment and subsequently every 1-2 days for two weeks after  
185 enrichment.

186 During February 2011 (wet season) we enriched the  $\delta^2\text{H}$  levels in Donderkamp  
187 waterhole from -41.7 ‰<sub>VSMOW</sub> to 264 ‰<sub>VSMOW</sub> (average of values obtained over 14 days after  
188 enrichment, range = 243–286 ‰<sub>VSMOW</sub>). During October 2011 (dry season) we enriched the  $\delta$   
189  $^2\text{H}$  levels in Donderkamp waterhole from -31.7 ‰<sub>VSMOW</sub> to 238 ‰<sub>VSMOW</sub> (average of values  
190 obtained over 14 days after enrichment, range = 227–247 ‰<sub>VSMOW</sub>).

191 We collected blood samples from birds trapped 1) within 2 km of a non-enriched  
192 waterhole and 2) within 2.4 km of the enriched waterhole. We used mistnets (10 per trapping

193 site) and spring traps baited with tenebrionid larvae to trap birds. Trapping sites around the  
194 enriched waterhole were selected along a radius from the waterhole in a direction devoid of  
195 waterholes/surface water sources for at least 6 km. We selected trapping sites starting at the  
196 first shrubs and trees from waterhole (10 m) at intervals of ~500 m to a distance of 2 km (non-  
197 enriched waterhole) or 2.4 km (enriched). The latter site was the furthest we could trap from  
198 the enriched waterhole without being nearer to neighbouring waterholes. We spent at least one  
199 day at each trapping site and carried out 132 trapping hours (80 during February and 52 during  
200 October 2011), trapping a total of 333 birds (196 and 137 in February and October,  
201 respectively). We trapped birds during the morning, from 06h00 (sunrise) until about 11h00,  
202 and in the afternoon (depending on temperature) from 15h00 till 19h00 (sunset). We obtained  
203 blood from each bird shortly after capture, or held trapped birds in cotton bags suspended in  
204 full shade until they could be processed. No birds were held for longer than 3 hours.

205 We obtained blood samples (10-150 $\mu$ l) by brachial venipuncture, using a sterile 27-  
206 gauge hypodermic needle and heparinised microcapillary tubes. We transferred each blood  
207 sample immediately to a 150- $\mu$ l micropipette and flame-sealed both ends of the pipette  
208 (Speakman 1997). We stored the blood samples at a temperature of 2-5 °C in a domestic  
209 refrigerator prior to further analyses. We separated pure water from the blood samples by  
210 cryogenic vacuum distillation, and measured  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  of the water samples obtained from  
211 bird blood and waterholes, using a PAL autosampler and DLT-100 liquid water isotope  
212 analyser (Los Gatos Research, Mountain View, CA, USA). Samples were bracketed with  
213 standards spanning the ranges of -79 to 978 ‰<sub>VSMOW</sub> ( $\delta^2\text{H}$ ) and -11.54 to 260.82 ‰<sub>VSMOW</sub> ( $\delta$   
214  $^{18}\text{O}$ ). A minimum of ten 1- $\mu$ L replicates were analyzed per sample or standard, and values for  
215 the first five replicates were typically discarded in order to avoid isotopic memory effects. All  
216 experimental procedures were approved by the University of Pretoria's Animal Use and Care

217 Committee (clearance #EC058-09), permits for animal sample collection were obtained from  
218 Department of Environment and Nature Conservation (permit #FAUNA 721/2010).

219

220 *Data analyses*

221 *Observations*

222 We performed chi-square tests to establish if the presence (% days observed drinking) at  
223 waterholes of different feeding guilds were representative of their relative abundance (%  
224 reporting rate). We further investigated the temperature-dependence of drinking behaviour by  
225 performing simple regression analyses of the number of drinking events of the 16 species most  
226 frequently observed drinking between 12:00 and 19:00 (i.e. hottest part of day and subsequent  
227 day-light hours) as a function of daily maximum air temperature ( $T_{\text{air}}$ ) (supplementary material).  
228 To establish whether daily temperature could affect drinking patterns, especially in infrequent  
229 drinkers, we also averaged the maximum  $T_{\text{air}}$ , linked to each drinking event (hereafter referred  
230 to as Max  $T_{\text{drink}}$ ) for each species. We then fitted a simple linear regression to investigate the  
231 relationship between Max  $T_{\text{drink}}$  and the percentage of days each respective species was  
232 observed drinking.

233

234 *Stable isotopes*

235  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  of body water of organisms at the community level vary collinearly—depending  
236 on the organisms' prime water source (McCluney and Sabo, 2010). We used this relationship  
237 to establish a predictive equation of  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values within the bird community—thereby  
238 incorporating physiological and natural variation of body water isotopes at a local scale. A two  
239 endpoint mixing model (Gannes et al., 1997) was used to estimate the proportion of an

240 individual's body water pool derived from an artificial water source enriched with  $\delta^2\text{H}$ .  
241 Artificially enriched  $\delta^2\text{H}$  levels in a water source will result in  $\delta^2\text{H}$  ratios falling significantly  
242 away from the local physiological line (i.e. the baseline  $\delta^2\text{H}$  versus  $\delta^{18}\text{O}$  relationship).

243 We obtained isotope ratios from a total of 302 birds representing 42 species over the  
244 two sampling periods. Of these we obtained 55 samples (18 species) at distances of 0 and 2km  
245 around two non-enriched waterholes. The remaining 247 samples were obtained within a 2.4  
246 km radius of the enriched waterhole (process described above).

247 We established two baseline regression lines of  $\delta^2\text{H}$  as a function of  $\delta^{18}\text{O}$  for the TKR avian  
248 community trapped around the non-enriched waterhole for the wet summer and dry summer,  
249 respectively; we also included values from resident species that were never observed to drink  
250 from waterholes at TKR as this improved the fit of the linear regression model. The intercepts  
251 of the baseline regression for the wet summer season was lower ( $\delta^2\text{H} = 3.48\delta^{18}\text{O} + 16.31$ ,  $r^2 =$   
252  $0.81$ ) and in the dry summer season ( $\delta^2\text{H} = 2.69\delta^{18}\text{O} + 24.35$ ,  $r^2 = 0.64$ ). We subsequently used  
253 residual  $\delta^2\text{H}$  values falling above of the 95 % prediction intervals of the respective baseline as  
254 evidence that individuals obtained water from the enriched waterhole; these were significantly  
255 different from the expected  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  relationship along the natural physiological line. For  
256 each season we determined the proportion of each individual's body water derived from the  
257 enriched source (hereafter referred to as P%) using  $\delta^2\text{H}$  residuals from the baseline predicted  
258 values for a given  $\delta^{18}\text{O}$  value. P% was calculated using the following equation,

259 
$$\text{P\%} = [\delta^2\text{H}_{\text{bird}} - \delta^2\text{H}_{\text{baseline}}] / [\delta^2\text{H}_{\text{spike}} - \delta^2\text{H}_{\text{baseline}}]$$

260 where  $\delta^{2}\text{H}_{\text{spike}}$  is the  $\delta^{2}\text{H}$  value of the enriched source,  $\delta^{2}\text{H}_{\text{baseline}}$  is the expected  $\delta^{2}\text{H}$  value of  
261 the sample based on the regression of  $\delta^{18}\text{O}$  and  $\delta^{2}\text{H}$  around the non-enriched source, and  $\delta$   
262  $^{2}\text{H}_{\text{bird}}$  represents the measured  $\delta^{2}\text{H}$  value for the bird sample.

263 We used regression analyses to test and the relationship between drinking frequency  
264 and P%, including only species that were observed drinking and sampled more than three times  
265 during the study. Values are presented as means  $\pm$  SD, unless otherwise stated. We obtained  
266 representative samples to test for seasonal changes in P% for Namaqua Dove (*Oena capensis*)  
267 and Scaly-feathered Weaver (*Sporopipes squamifrons*) only. We used a paired t-test and  
268 Kolmogorov-Smirnov test in R (R Core Team, 2012) to establish if P% was different between  
269 seasons in Scaly-feathered Weavers and Namaqua Doves, respectively; significant  
270 heteroscedasticity existed in the seasonal data for the latter species.

271

## 272 **Results**

### 273 *Weather during study periods*

274 Mean daily maximum  $T_{\text{air}}$  on the days for which we obtained video recordings was 32.1 °C,  
275 ranging from 26.4 °C to 37.4 °C (two days > 35 °C). Mean daily maximum  $T_{\text{air}}$  during the  
276 stable isotope study was  $32.7 \pm 2.7$  °C (25–35 °C) during the wet season and  $30.6 \pm 4.2$  °C  
277 (26–37 °C) during the dry season, respectively.

278

### 279 *Drinking patterns - observational data*

280 We recorded 76 species during the study (Supplementary material Table S1). The avian  
281 community at TKR was dominated by insectivores (49.3 % of species) and granivores

282 (32.8 %); birds of prey, omnivores, frugivores and nectarivores represented 10.4, 10.4, 9.0 and  
283 1.5 %, respectively (Fig. 1). We observed a total of 36 species drinking at the waterholes  
284 (Supplementary material Table S1). The drinking frequencies of the respective foraging guilds  
285 were significantly different from those expected based on their relative abundances. Whereas  
286 granivores, frugivores and omnivores were significantly over-represented ( $\chi^2_{1,15} = 385.9$ ,  $p <$   
287  $0.001$ ,  $\chi^2_{1,3} = 173.6$ ,  $p < 0.001$ ,  $\chi^2_{1,2} = 84.8$ ,  $p < 0.001$ , respectively), insectivores were  
288 significantly under-represented at the waterholes ( $\chi^2_{1,4} = 95.4$ ,  $p < 0.001$ ) (Fig. 1).

289 The majority of species observed drinking at the waterholes showed a bimodal drinking  
290 pattern, with drinking events concentrated during early morning (between 6h00 and 10h00)  
291 and late afternoon to evening (16h00 to 19h00) and birds avoiding waterholes during midday  
292 (Supplementary material Figure S1). Drinking during the warmest part of the day (12h00 to  
293 18h00) was not significantly related to maximum daily air temperature in any of the species  
294 during the study (Supplementary material Figure S2), and these patterns were similar when  
295 species were pooled within dietary groups (i.e. no significance).

296 Mean maximum daily temperature of drinking events ( $\text{Max } T_{\text{drink}}$ ) was significantly  
297 related to the overall frequency of drinking events ( $r^2 = 0.47$ ,  $F_{1,31} = 27.39$ ,  $p < 0.001$ ) (Fig.  
298 2A).  $\text{Max } T_{\text{drink}}$  values were similar to the average daily maximum  $T_{\text{air}}$  during the study (31.7  
299 °C) in species that drank frequently (e.g. doves), whereas species that drank infrequently had  
300 a higher  $\text{Max } T_{\text{drink}}$  because they drank on the hottest days (Fig. 2A). Drinking events were  
301 most temperature dependent in insectivorous compared with granivorous and frugivorous  
302 species (Fig. 2B), whereas omnivorous species showed more variable temperature dependence  
303 (Fig. 2B).

304

305 *Drinking inferred from isotopically labelled water sources*

306 The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values of the two non-enriched water sources were  $-47.2\text{‰}_{\text{VSMOW}}$  and -  
307  $7.6\text{‰}_{\text{VSMOW}}$  respectively (large reservoir), and  $-24.0\text{‰}_{\text{VSMOW}}$  and  $-0.9\text{‰}_{\text{VSMOW}}$  respectively  
308 (small shallow waterhole). These values fall below the local meteoric water line (LMWL)  
309 established by Schachtschneider & February (2013) for the Kalahari region, which is typical  
310 for rain water that undergoes some evaporation during the transition in the vadose zone before  
311 assimilation in to the groundwater. The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values obtained from birds sampled near  
312 these non-enriched waterholes show a clear distinction between the drinking behaviour of  
313 granivores and the other guilds (Fig. 3A). Water  $\delta^2\text{H}$  vs.  $\delta^{18}\text{O}$  relationship for granivores  
314 follows the gradient of the LMWL while the gradient for the other guilds differs from the  
315 LMWL. The  $\delta^2\text{H}$  vs.  $\delta^{18}\text{O}$  gradient is determined by the kinetics of water precipitation and  
316 evaporation, and it is clear that the water regime of the granivores is linked to precipitation,  
317 while the other guilds are linked to evaporated water. The granivore guild has a wide range of  
318 water isotope values that are consistent with the groundwater signal, implying that they are  
319 making use of water provisioning stations (that are recharged from groundwater), and almost  
320 certainly using more than one provisioning point. In contrast, the distribution of water isotope  
321 values for the remaining guilds is indicative of evaporative processes taking place before the  
322 water is assimilated when feeding on invertebrate, animal and plant matter. The evaporative  
323 processes take place during plant water uptake, and the assimilation of water into fruit or  
324 through trophic transfer to insects that are also dependent on the plants for their water.

325 Although many of the granivore data points plot at the intersection between the LMWL  
326 and the evaporative line of the other guilds, this does not affect our interpretation. As annual  
327 rainfall is low, and intermittent, and the substrate is predominantly Kalahari sand, there are no

328 standing water bodies and the only water source in the region is groundwater. The fact that the  
329 granivores plot at the intersection of the evaporative line and the LMWL is indicative of their  
330 direct dependence on the groundwater via the provisioning waterholes. The remainder of the  
331 birds are obtaining water from the same groundwater source, but through vegetation and  
332 invertebrates that evaporate the water through their respective vital processes. Insectivores  
333 have the highest  $\delta^{18}\text{O}$  values because there are two trophic intermediaries (vegetation and  
334 insects), and since neither of these intermediaries are affected by the enrichment of the water  
335 provisioning troughs, it is not surprising that insectivores show no enrichment when trapped  
336 around the enriched waterhole (Fig 3B).

337         Only 11 of 42 species showed clear evidence of the the enriched water source in their  
338 body water pools (Supplementary material Table S1). The  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  ratios for all  
339 insectivores, carnivores, and frugivores fell within the 95 % prediction intervals of the isotopic  
340 baseline, which we interpret as indicating that these species did not use the labelled water  
341 source (Fig. 3B). Granivores and, to a lesser extent omnivores, were the only guilds where  $\delta$   
342  $^2\text{H}$  and  $\delta^{18}\text{O}$  values fell above the LMWL, indicating use of the enriched water source (Fig.  
343 3B).

344         The percentage of body water derived from the enriched source varied between seasons  
345 (Table 1); these seasonal differences were significant in Scaly-feather Weavers ( $t_{1,6} = 2.45$ ,  $p$   
346  $< 0.05$ ) and Namaqua Doves (Kruskal-Wallis  $\chi^2_{1,10} = 7.5$ ,  $p < 0.01$ ). During the wet season six  
347 species used the enriched waterhole, compared to nine during the dry season (Table 1).

348         Namaqua Doves and Violet-eared Waxbills (*Uraeginthus granatinus*) showed enriched  
349 P% values at most trapping sites, up to 2 km away from the enriched waterhole (Fig. 4). A  
350 number of the irregularly drinking species (Fig. 4; Supplementary material Table S2) trapped



351 within 100 m of the enriched waterhole obtained on average a slightly greater proportion of  
352 their body water pool from the source. Although a number of samples were obtained from  
353 insectivores within 100 m of the waterhole, none of these individuals used the waterhole  
354 (Supplementary material Table S2).

355 We found a weak correlation between drinking frequency and P% in species ( $r^2 = 0.35$ ,  
356  $F_{1,7} = 3.84$ ,  $p = 0.091$ ); species that drank infrequently tended to have low P% but species that  
357 drank frequently showed more variable P% (Fig. 5).

358

## 359 Discussion

360 Our data, obtained using two complementary approaches, reveal that most species at our study  
361 site are largely independent of drinking free-standing water. Whereas our observations of avian  
362 drinking patterns provide ecologically relevant insights into drinking behaviours (such as  
363 timing of drinking, individual numbers, and temperature-dependence of drinking events), our  
364 stable isotope approach provides quantitative estimates of the importance of a specific  
365 waterhole for the water balance of birds in the surrounding area. Both techniques revealed that  
366 avian granivores are dependent on surface water—in some cases > 90% of their body water  
367 pools was derived from the enriched source. In contrast, insectivores and most omnivores did  
368 not rely on surface water, except on very hot days when a few species visited waterholes. These  
369 data corroborate previous findings based on observational data that relatively few species  
370 inhabiting the arid regions of Africa and Australia are dependent on drinking water  
371 (Willoughby and Cade 1967, Fisher et al. 1972). Together, these findings allowed us to  
372 quantify avian community-level surface water dependency in the Kalahari Desert. Empirical  
373 data on species' surface water dependency could improve mathematical models of water  
374 balance under hot conditions as the source and quantity of water gains can be included as a  
375 quantitative parameter. Moreover, we suggest that data on community-level surface water

376 dependency should be used to inform ecosystem management practices, such as  
377 provision/removal of artificial waterholes in conservation areas.

378 Both the approaches we used here revealed that granivores represent the guild with the  
379 greatest dependence on drinking water. A few individuals of some granivorous species in our  
380 study, including Namaqua Doves (*Oena capensis*), Laughing Doves (*Spilopelia senegalensis*)  
381 and Yellow Canaries (*Crithagra flaviventris*), did not drink from the labelled waterhold based  
382 on their  $\delta^2\text{H}$  values (Fig. 3A). However, these individuals typically had  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values  
383 close to that of the non-enriched water-holes, suggesting they drank from non-enriched water  
384 sources at TKR. Our isotopic assessment on the surface water source is based on enrichment  
385 of a single waterhole. Therefore, we may have underestimated surface water dependency, as  
386 some of the regular drinking species almost certainly visit more than one waterhole thus  
387 diluting P% as we measured it here. Enriching more than one waterhole with  $\delta^2\text{H}$  was not  
388 feasible in our study, because 1) our aim was to establish the minimum distance travelled by  
389 individual birds to the enriched source, and 2) replicating the trapping and blood sampling of  
390 birds around more waterholes, simultaneously, was not logistically feasible. Granivores  
391 drinking from non-enriched waterholes also explains the weak correlation between drinking  
392 frequency (estimated through observations) and dependence on free-standing water source  
393 (quantified from P%). However, some of the regularly drinking omnivores and frugivores  
394 species (such as mousebirds), incorporate water rich foods (insects and fruits) in their diets that  
395 explain their low P% values.

396 In contrast, insectivores were greatly under-represented at waterholes, despite this  
397 group dominating the avian community at TKR. A few insectivore species drank occasionally  
398 (on days when Max  $T_{\text{air}}$  was above average) in small numbers, but the events were too  
399 infrequent to statistically quantify the temperature-dependence of their drinking behaviour. It

400 is noteworthy that many of these occasional drinkers are very common in the Kalahari Desert  
401 community (for example, Ant-eating Chat, *Myrmecocichla formicivora*, and Common Fiscal,  
402 *Lanius collaris*); supplementary material Table S1) and the low drinking frequency suggest  
403 that only individuals occupying territories or home ranges around the waterhole drank on hot  
404 days. Our blood isotope data corroborate our observational data that the common insectivorous  
405 species are largely independent of surface water. Nevertheless, the occasional drinking patterns  
406 suggest that some of these individuals do make use of free-standing water under hot conditions  
407 when EWL demands likely represent a greater component of their daily water budget (Smit  
408 and McKechnie, 2015).

409 Our findings that none of the granivores studied here show a greater frequency of  
410 drinking on hot days is surprising. Although we had a limited number of hot days during the  
411 study, we argue that the mean maximum  $T_{\text{air}}$  was high enough for birds to experience operative  
412 temperatures [a measure of the thermal environment experienced by an organism (Bakken,  
413 1992)] well above 40°C when exposed to direct solar radiation and/or perched on exposed  
414 ground (Wolf and Walsberg, 1996b). Williams and Koenig (1980) also found limited evidence  
415 for temperature-dependency of drinking events in a temperate woodland avian community  
416 (California, North America) over a range of  $T_{\text{air}}$  similar to that in our study. In contrast, Fisher  
417 *et al.* (1972) studied avian drinking behaviour in the deserts of Australia at higher  $T_{\text{air}}$  maxima  
418 (up to 46°C) and showed that many species (including granivores) significantly increased  
419 drinking events with  $T_{\text{air}}$ . The authors of these studies argued that the presence of a crop might  
420 play a role in frequency of drinking events per day. For example, doves and other granivores  
421 could potentially take in large amounts of water during a single visit to a water source, because  
422 repeated trips to water sources might be costly in terms of energy and water expenditure, and  
423 predation risk (Williams and Koenig 1980). Previous studies have investigated water intake in  
424 the laboratory as function the duration of single drinking event and extrapolated these to

425 individuals in the field (Smyth and Coulombe 1971). However these efforts will be limited to  
426 individuals that can be identified easily in the field (e.g. colour ringed, tagged or dyed), and  
427 detailed laboratory calibrations for each drinking species.

428

#### 429 *Ecological implications of drinking*

430 The distribution of water isotope values presented in Figure 3A provides evidence for tightly  
431 constrained ecological functioning of the Kalahari Desert that is linked to groundwater. The  
432 frugivore and insectivore avian guilds are effectively sampling three trophic levels in the  
433 Kalahari ecosystem (plants, insects, birds) and the fact that their water isotope values all fall  
434 on a consistent evaporative line in the isotope biplot is clear evidence that each trophic level  
435 depend on the same water source. Without water provisioning stations, this water source would  
436 normally be groundwater and its availability to birds would be facilitated through the trophic  
437 cascade, in perennial plants such as trees. The prevalence of granivores in the sample is  
438 therefore likely an artefact of water provisioning by humans.

439 Previous studies in semi-arid and arid ecosystems of North America, using behavioural  
440 observations have revealed a greater reliance on surface water sources by avifauna (Williams  
441 and Koenig, 1980, Lynn et al., 2006) compared to the case in southern Africa's Kalahari and  
442 Namib Deserts and Fynbos biome (this study; (Willoughby and Cade, 1967, Lee et al., 2017).  
443 Drinking patterns in the Australian arid zone (Fisher et al., 1972) also suggest that  
444 comparatively few species (mostly granivores) rely on permanent free-standing water. These  
445 intriguing patterns suggest that African and Australian avifauna have been under greater  
446 selection to become independent of drinking water.

447 Our observations provided us with an overview of the timing of drinking for individual  
448 species and feeding guilds. Consistent with the temporal patterns shown in previous studies,  
449 our data revealed a continuum of drinking times throughout the day, with bimodal or uni-modal

450 patterns most common. Although the functional significance of these patterns is not completely  
451 understood, it has been argued that variation in temporal water demands and predation risks  
452 could play a role (Fisher et al., 1972). We suspect relaxed predation risk is a key factor;  
453 densities of raptors around waterholes at TKR are far lower than typically observed elsewhere  
454 in the Kalahari Desert (B. Smit and A.E. McKechnie, personal observations). We anticipate  
455 that temporal drinking patterns will more directly influenced by predation risk elsewhere, most  
456 notably in the Kgalagadi Transfrontier Park, where the density of species such as Lanner  
457 Falcons, Pale Chanting Goshawks and Gabar Goshawks are far higher than at TKR.

458         Spatial patterns of dependence on surface water sources are of particular interest as  
459 these could structure animal communities when water sources are isolated in the landscape.  
460 Our isotopic labelling approach revealed that a number of granivores travelled in excess of 2  
461 km to the enriched source, and that between 35 and 91% of their body water pools were derived  
462 from the experimentally enriched water hole. The water isotope values obtained in the baseline  
463 study indicates that they use multiple waterholes, and so their travelling distance is probably  
464 much greater than 2 km, and the calculated contribution of provisioned water to the body water  
465 pools is a minimum estimate. Small, granivorous species (e.g. Violet-eared Waxbill) are likely  
466 to be most strongly tied to water availability, and likely face the strongest trade-offs between  
467 elevated rates of EWL *versus* water gain when flying to water sources during hot weather.  
468 Future research could determine if an increase in the density of water points have a positive  
469 effect on water balance of small drinking dependent species, as well as species that rely more  
470 on water during hot weather, and address questions surrounding how water balance is affected  
471 by trade-offs between surface water availability and predation risk.

472         Natural variation in stable isotope ratios has been widely employed to quantify the  
473 importance of a given resource at a landscape scale. For example, this technique has been used  
474 to show dependence of White-winged Doves (*Zenaida asiatica*) on saguaro fruit as a water

475 source during summer in the Sonoran Desert (Wolf and Martinez del Rio 2000). Moreover,  
476 this method has also revealed how White-winged Doves obtain both water and nutrients from  
477 these fruits, whereas Mourning doves (*Zenaida macroura*) obtain mainly nutrients, but not  
478 water (Wolf *et al.* 2002). We are aware of only one previous study (Hyde, 2011) using the  
479 technique of artificially enriching a water source to investigate drinking dependency in an avian  
480 community. The stable isotope approach we adopted here allowed us to demonstrate that  
481 physiological dependence on the enriched water source was greater during the dry summer  
482 season, compared to the wet summer season for at least two species. These patterns were also  
483 reflected in greater number of individuals drinking (i.e., the proportion of birds with enriched  
484 levels) during the dry summer in both the above species and Sociable Weavers (*Philetairus*  
485 *socius*). These patterns suggest that some species relied more on free-standing water during dry  
486 periods when the availability of water rich foods are lower.

487

## 488 **Conclusion**

489 Our study illustrates how two methods can be used to obtain complementary data on surface  
490 water dependency in a desert bird community. Information on the importance of surface water  
491 as a daily requirement, or as a limiting resource on hot days, will be important for developing  
492 water and energy balance models and time-activity budget models for specific species. For  
493 example, knowledge of whether species need to obtain their water through their food and by  
494 foraging, from metabolic water, or from drinking, will be important in understanding how  
495 much time and energy an individual needs to spend to avoid dehydration on hot days. Our  
496 findings that a greater number of species start visiting waterholes on hot days, echo predictions  
497 that more species will rely on surface water, particularly artificial sources under future climate  
498 warming scenarios (McKechnie *et al.*, 2012). Providing artificial water has been a contentious  
499 and highly debated issue, particularly when larger mammals degrade habitat around waterhole

500 (Hayward and Hayward, 2012, Landman et al., 2012). With these landscape-level changes we  
501 might expect increasing conflicts between provisioning of free-standing water to meet  
502 increasing evaporative cooling demands, and habitat protection where ecosystem function and  
503 microclimate availability are key objectives in semi-arid/ arid environments. Water  
504 provisioning as a global change conservation effort needs to be carefully evaluated and  
505 implemented.

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518

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 625 and implications for microsite selection. *Ecology*, **77**: 2228-2236.  
 626

627 Tables:

628 Table 1. Percentage of the body water pool (P%) derived from the enriched waterhole in bird  
 629 species during a wet- (February 2011) and dry (October 2011) period in summer at Tswalu  
 630 Kalahari Reserve. Values in bold text indicate significant differences ( $p < 0.05$ ) in P%  
 631 between seasons (see text for statistics).

<b>Mean P% <math>\pm</math> SD (# enriched/total):</b>		
<b>Species</b>	Wet season (Feb 2011)	Dry season (Oct 2011)
Black-faced Waxbill <i>Estrilda erythronotos</i>		29.2 (1/1)
Cape Sparrow <i>Passer melanurus</i>		40.5 (2)
Cape Turtle-Dove <i>Streptopelia capicola</i>	57.7 (1/1)	
Golden-breasted Bunting <i>Emberiza flaviventris</i>		49.8 (1/1)
Southern Masked-Weaver <i>Ploceus velatus</i>	7.72 (1/6)	NA (0/3)
Namaqua Dove <i>Oena capensis</i>	<b>30.6<math>\pm</math>21.7 (5/7)</b>	<b>78.7<math>\pm</math>10.5 (6/6)</b>
Scaly-feathered Finch <i>Sporopipes squamifrons</i>	<b>3.95<math>\pm</math>2.47 (4/29)</b>	<b>8.60<math>\pm</math>2.69 (4/19)</b>
Sociable Weaver <i>Philetairus socius</i>	4.59 (1/19)	16.7 $\pm$ 7.57 (6/17)
Violet-eared Waxbill <i>Uraeginthus granatinus</i>		32.8 $\pm$ 17.0 (9/12)
White-browed Sparrow-Weaver <i>Plocepasser mahali</i>	5.15 (1/11)	92.9 (1/14)
Yellow Canary <i>Crithagra flaviventris</i>		63.4 (1/4)

632

633

634 Figure legends:

635 Figure 1: The total number of species present (grey bars) and number of species observed

636 drinking (black bars) for six dietary guilds in the avian community at Tswalu Kalahari

637 Reserve during the summer (November to December 2009).

638

639 Figure 2: A) Species that drink less frequently visited water on hotter days compared to more

640 frequent drinkers. The mean maximum daily temperature ( $\text{Max } T_{\text{drink}}$ ) linked to each drinking

641 event for each species decreased as a function of drinking frequency (% of days observed

642 drinking) during summer (November to December 2009) at Tswalu Kalahari Reserve (TKR).

643 The trendline (solid line) represents the significant negative relationship with 95% prediction

644 intervals represented by the dashed lines (PI). B) Whereas insectivores visited water on the

645 hottest days of the study, frugivores and granivores visited water on cooler days. Omnivores

646 and carnivores varied most in their temperature-dependency of visiting water holes. In this

647 panel mean  $\text{Max } T_{\text{drink}} \pm 95\%$  confidence interval (CI) is displayed as a function of dietary

648 guild. In both panels the solid and dashed red line represents mean and 95% CI of maximum

649 daily air temperature ( $\text{Max } T_{\text{air}}$ ), respectively, over the study period at TKR.

650

651 Figure 3: A)  $\delta^2\text{H}$  and  $\delta^{18}\text{O}$  values of birds sampled around two non-enriched water sources in

652 Tswalu Kalahari Reserve (October 2011). B)  $\delta^2\text{H}$  as a function of  $\delta^{18}\text{O}$  of birds sampled within

653 2km of an enriched waterhole in Tswalu Kalahari Reserve (during February and October 2011).

654 In both panels, the dashed trendlines represent the local meteoric water line (LMWL)

655 established by Schachtschneider & February (2013) for the Kalahari region. The solid

656 trendlines represent a linear regression model ( $\delta^2\text{H} = 2.9 \delta^{18}\text{O} + 22.5$ ; pooled for wet and dry

657 season for sake of clarity) fitted to  $\delta^2\text{H}$  as a function of  $\delta^{18}\text{O}$  from the samples obtained from

658 non-users with 95 % prediction intervals around the model are indicated by the small dotted  
659 lines. Data points falling above the upper 95 % prediction interval indicate that individuals  
660 used the enriched waterhole. The blue circles represent mean  $\delta^{18}\text{O}$  and  $\delta^2\text{H}$  values for the  
661 enriched waterhole during the wet and dry seasons.

662

663 Figure 4: Mean proportion of body water derived from the enriched water source as a function  
664 of approximate distance (categories A-F) away from the water hole in six species at Tswalu  
665 Kalahari Reserve (A < 100m, B < 500m, C < 1000m, D < 1500m, E < 2000m, F < 2500m).

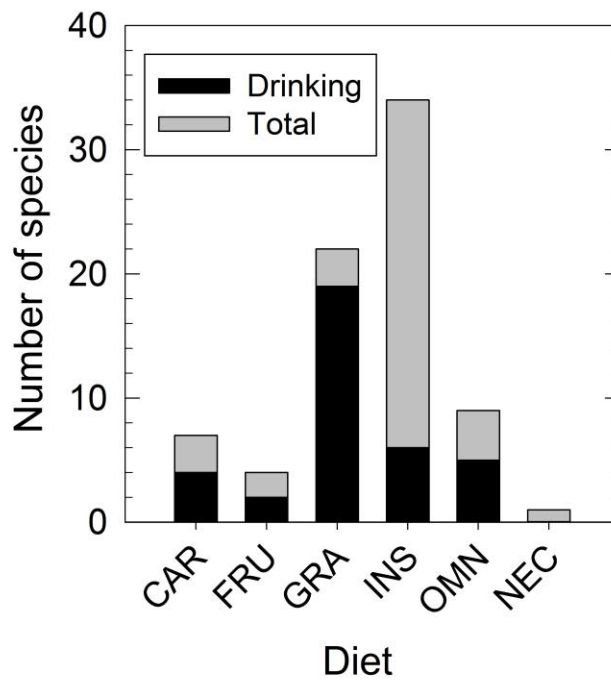
666

667 Figure 5: Mean proportion of body water pool derived (P%) from the enriched waterhole as a  
668 function drinking frequency (i.e. % of days observed drinking) in species observed drinking  
669 during summer at Tswalu Kalahari Reserve ( $r^2 = 0.35$ ,  $F_{1,7} = 3.84$ ,  $p = 0.091$ ).

670

671

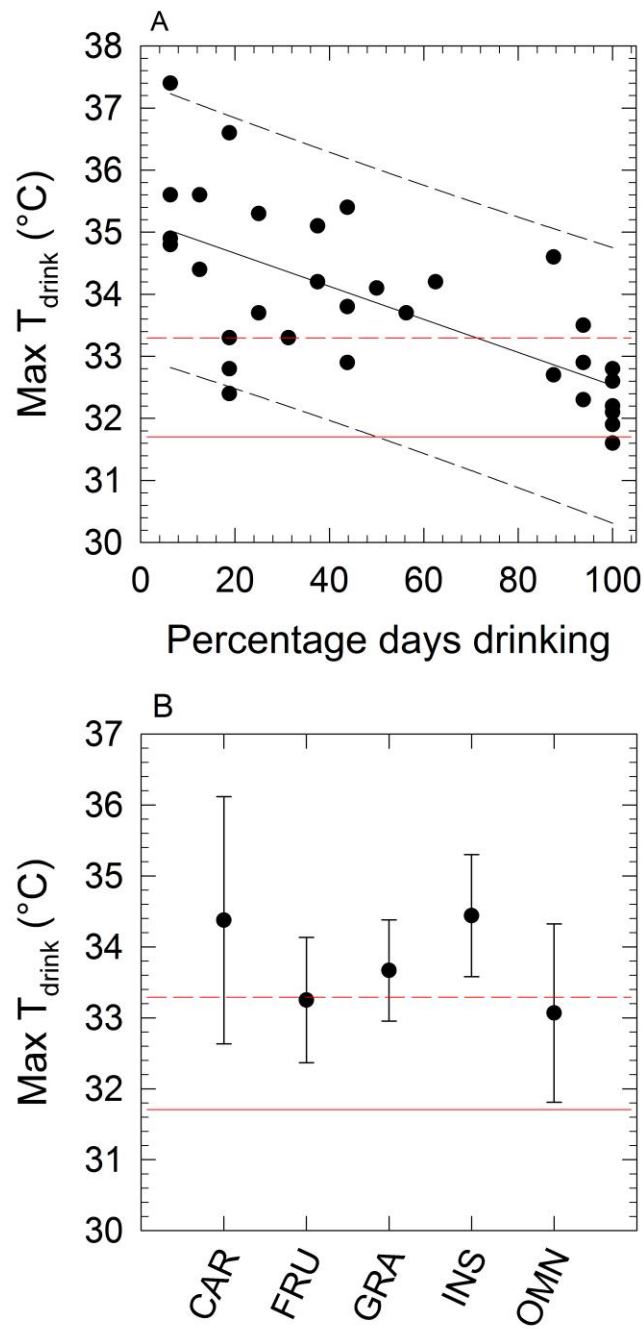
672

673 **Figures:**

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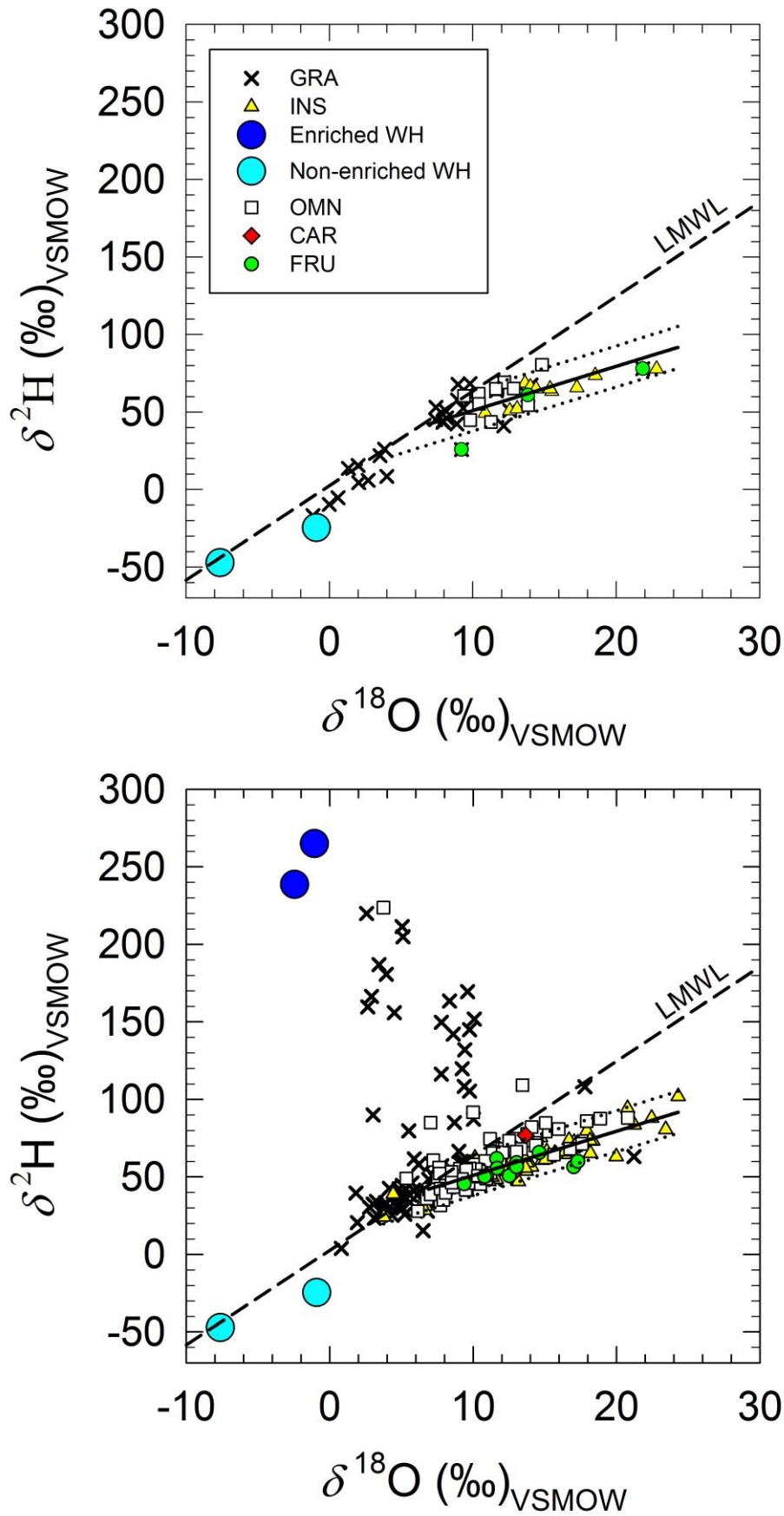
675 **Figure 1.**

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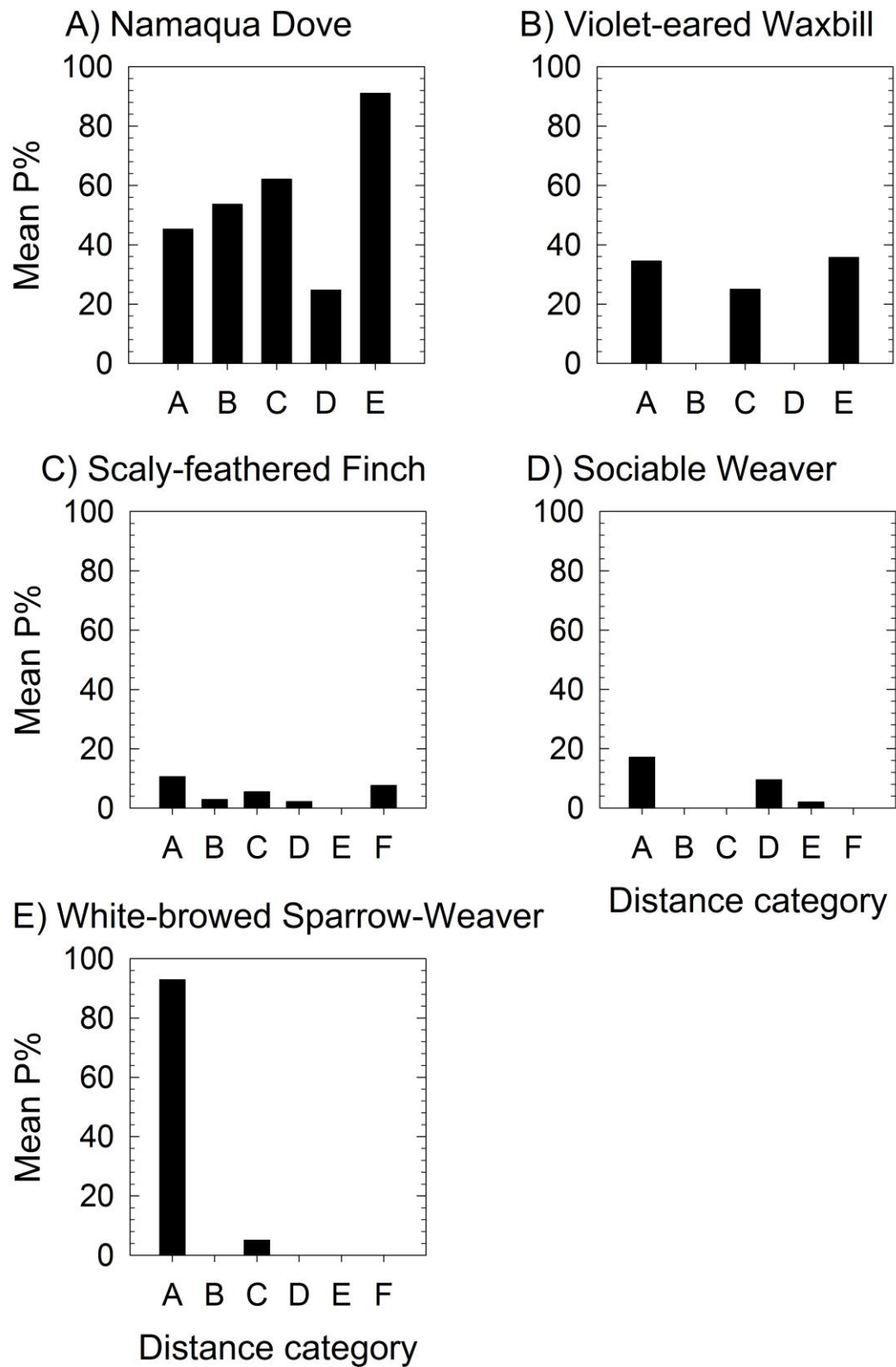
678 Figure 2



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680 Figure 3

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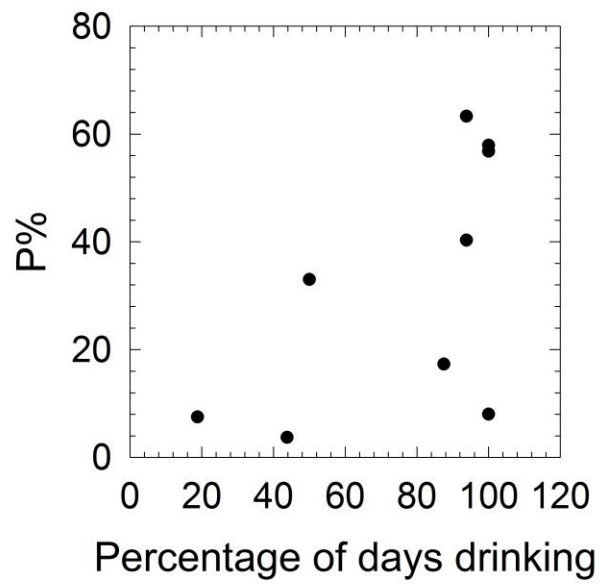


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683 Figure 4



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686 Figure 5

- 687 Additional files:
- 688 Supplementary material: Additional description of methodology and results, including Table
- 689 S1-2 and Figure S1-2.