Accepted: 7 August 2017
DOI: 10.1111/aje.12484

SHORT COMMUNICATION

WILEY African Journal of Ecology

Factors affecting the foraging distance and duration of a colonial bird, the sociable weaver, in a semi-arid environment

Kyle John Lloyd[1] | Res Altwegg[2,3] | Claire Doutrelant[1,4] | Rita Covas[1,5]

[1]Department of Biological Sciences, Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch, South Africa
[2]Department of Statistical Sciences, Statistics in Ecology, Environment and Conservation, University of Cape Town, Rondebosch, South
[3]African Climate and Development Initiative, University of Cape Town, Rondebosch, South Africa
[4]CEFE-CNRS, University of Montpellier, Montpellier, France
[5]Research Centre in Biodiversity and Genetic Resources, CIBIO-InBio, Vairão, Portugal

Correspondence
Kyle John Lloyd
Email: kyle.john.lloyd@gmail.com

Funding information
South African National Science Foundation; University of Cape Town

1 | INTRODUCTION

Coloniality has clear foraging benefits such as reducing the probability of being predated, enhancing the probability of finding food and allowing for easier estimation of habitat quality (Danchin & Wagner, 1997). However, living in a colony can also have potential foraging-related costs, because all of the birds in the colony are conspecifics with similar food requirements (Wittenberger & Hunt, 1985). Individuals living in larger colonies may deplete local resources and have to travel farther and for a longer duration in search of food than those living in smaller colonies (Brown & Brown, 1996). We examined this idea for the sociable weaver (*Philetairus socius*), a facultative colonial cooperative breeder that builds large communal nests (Maclean, 1973a). An effect of colony size might be expected because previous studies have found that fewer eggs and nestlings successfully hatch and fledge in large colonies (Altwegg, Doutrelant, Anderson, Spottiswoode, & Covas, 2014), which may be due to the high levels of intraspecific competition for resources (Covas, du Plessis, & Doutrelant, 2008). Foraging farther away from the colony for longer periods of time may also reduce adult survival by increasing the chances of being seen and caught by a predator, as a greater distance needs to be covered to reach the safety of the colony. The hypothesis that larger colonies forage farther and for a longer time than smaller colonies was investigated by tracking the foraging paths of flocks from eight colonies of varying sizes. In this study, we also tested the effects of covariables known to affect the foraging behaviour of birds, namely landscape structure and weather (du Plessis, Martin, Hockey, Cunningham, & Ridley, 2012; Turcotte & Desrochers, 2003). In addition, the foraging behaviour of sociable weavers in a more mesic region (431 mm/year) of the Kalahari is described for the first time (see Maclean, 1973b for arid regions, 226 mm/year).

2 | MATERIALS AND METHODS

2.1 | Study area & species

The study took place at Benfontein Nature Reserve, South Africa (28°53′S, 24°89′E), situated in the southern Kalahari. The landscape consists of a continuous herbaceous layer of *Stipagrostis* grasses and a discontinuous arborescent layer of *Vachellia erioloba* (Rutherford et al., 2006). During the study period, there were 22 sociable weaver colonies distributed over an area of 15 km^2. Sociable weavers forage primarily on insects and seeds, the proportions of which vary seasonally (Maclean, 1973b). The birds forage in flocks on the ground, mainly during early morning and late afternoon (Maclean, 1973b).

2.2 | Tracking foraging paths

Eight colonies of varying sizes (18–116 birds, average of 51 ± *SD*. 35 birds) were selected and followed before the start of the breeding season (before eggs were laid) from mid-September to mid-October 2015. Flocks were followed when the birds left their colony just after sunrise, so that the colony identity of the flock was known. The flock was then followed from a distance that did not disturb the birds' behaviour (~50 m). No apparent alarm calls or movements provoked by the observer were observed during tracking. However, we are aware that unobservable responses to disturbance may be displayed, such as less efficient foraging, and that this may be more prevalent in larger flocks that have a higher probability of detecting the observer. The GPS coordinates were recorded at the centre of each feeding station as the foraging trajectory of the flock was followed. A feeding station qualified as the area that the flock flew to and landed in. The flock was followed until it returned directly to the colony. This was performed twice for each colony, with the start and end time of each foraging bout recorded. No further replicates could be collected as there was a sudden peak in insect abundance, which altered foraging behaviour.

Several social (colony size) and environmental (tree density, mean, minimum and maximum temperature and relative humidity) variables were measured to explain foraging distance and duration. Annual capture data for 2015 were used to determine colony size (see Covas et al., 2008). Most of the feeding stations were underneath tree canopies, and we therefore examined whether tree density affected foraging distance and duration. Tree density was estimated by counting the number of trees in a 500 m radius (the average farthest distance travelled by all flocks) around each colony on Google Earth (Google Earth, 2015). All weather data were collected from the weather station at the Kimberley airport (~12 km away). Temperature and humidity data were recorded at 5-min intervals, and the mean temperature and relative humidity were calculated for the duration of each tracking session. The minimum and maximum temperatures of each tracking session were also recorded.

2.3 | Statistical analysis

The influence of social and environmental variables on foraging distance and duration was estimated using linear mixed effects models. The foraging distance of each colony was measured as the sum of distances between feeding stations. The sum distance and time travelled followed a normal distribution. A correlation analysis was conducted to determine whether there was collinearity among explanatory variables and between foraging distance and duration (Zuur, Ieno, & Elphick, 2010). Colony identity was treated as a random effect to account for variation in foraging distance and duration among colonies that was not explained by the explanatory variables. Thus, each model was fitted with one of the explanatory variables and colony identity. The models were fitted by maximum likelihood, and Akaike's information criterion (AIC_c) was used to determine which combination of explanatory variables best explained foraging distance and duration (Akaike, 1973). A constant model, containing only the random colony identity effect, was included to determine whether any of the models with fixed effects was better supported than the one only accounting for colony differences. The statistical analysis was performed using R, v.3.2.1 (R Core Team, 2016; function *lmer* in package *lme4*, Bates, Maechler, Bolker, & Walker, 2015).

3 | RESULTS AND DISCUSSION

3.1 | Foraging behaviour

Observations made whilst tracking revealed that sociable weavers became active shortly after sunrise (average of 33 min ± *SD*. 20 min after sunrise). The first signs of activity involved much chattering, with some individuals flying in and out of different nest chambers and others foraging on the ground for several minutes before returning to a nest chamber. In some cases, several individual birds flew to the branches of the colony tree or trees surrounding the colony, where they called to the rest of the colony. At some point, a large group of birds flew together to a nearby tree and started to forage on the ground underneath the tree canopy (subcanopy). The initial group was followed shortly afterwards by more groups of birds. Flocks were seen feeding more often on the ground in the subcanopy than on the ground between tree canopies (intercanopy). This qualitative finding was based on the observations made whilst flocks were tracked and could not be quantified. In some cases, the flock was led by one or two birds to the next feeding station and the transition was accompanied by a distinct call (made only when flying) from most of the birds in the flock (see Supporting Information). The flock often landed on one side of the subcanopy and foraged on the ground to the opposite side of the subcanopy before moving to the next tree. Flocks rarely split or joined other flocks whilst foraging. When the flock had finished feeding, most birds flew back to the colony and then proceeded to perform other activities individually or in small groups, such as foraging and nest building.

During our observations, the flocks were always accompanied by one or more forked-tailed drongos (*Dicrurus adsimilis*). When the sociable weavers were feeding, the drongos perched on the lower branches above the flock. From this vantage point, the drongos sometimes chased the sociable weavers away from their food. The

TABLE 1 Summary of the AIC_c-based model selection for factors explaining the foraging distance (m) of eight sociable weaver colonies (*N* = 8, two replicates of each) on Benfontein Reserve, South Africa

	Model	ΔAIC_c	w_i	*K*	logLik
1	Colony size	3.09	0.085	4	237.58
2	Tree density (trees per km^2)	0	0.40	4	234.50
3	Mean temperature (°C)	3.55	0.068	4	238.04
4	Minimum temperature (°C)	3.99	0.054	4	238.49
5	Maximum temperature (°C)	2.75	0.10	4	237.25
6	Relative humidity (%)	4.16	0.050	4	238.66
7	Max temp × rel. humidity	2.29	0.13	6	232.78
8	Constant	2.44	0.12	3	238.94

ΔAIC_c, the model AIC_c minus the smallest AIC_c; w_i, akaike weight; *K*, number of parameters; logLik, maximized log likelihood.

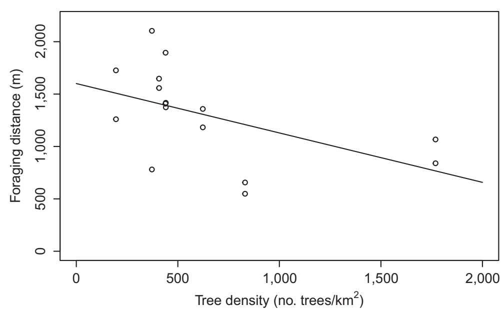

FIGURE 1 The observed (points) and predicted linear relationship between the foraging distance (m) and tree density (no. trees/km^2) of eight sociable weaver colonies on Benfontein Reserve, South Africa (Model 2, Table 1, *N* = 8, two replicates of each): log(foraging distance) = 1600.47−0.47 × tree density

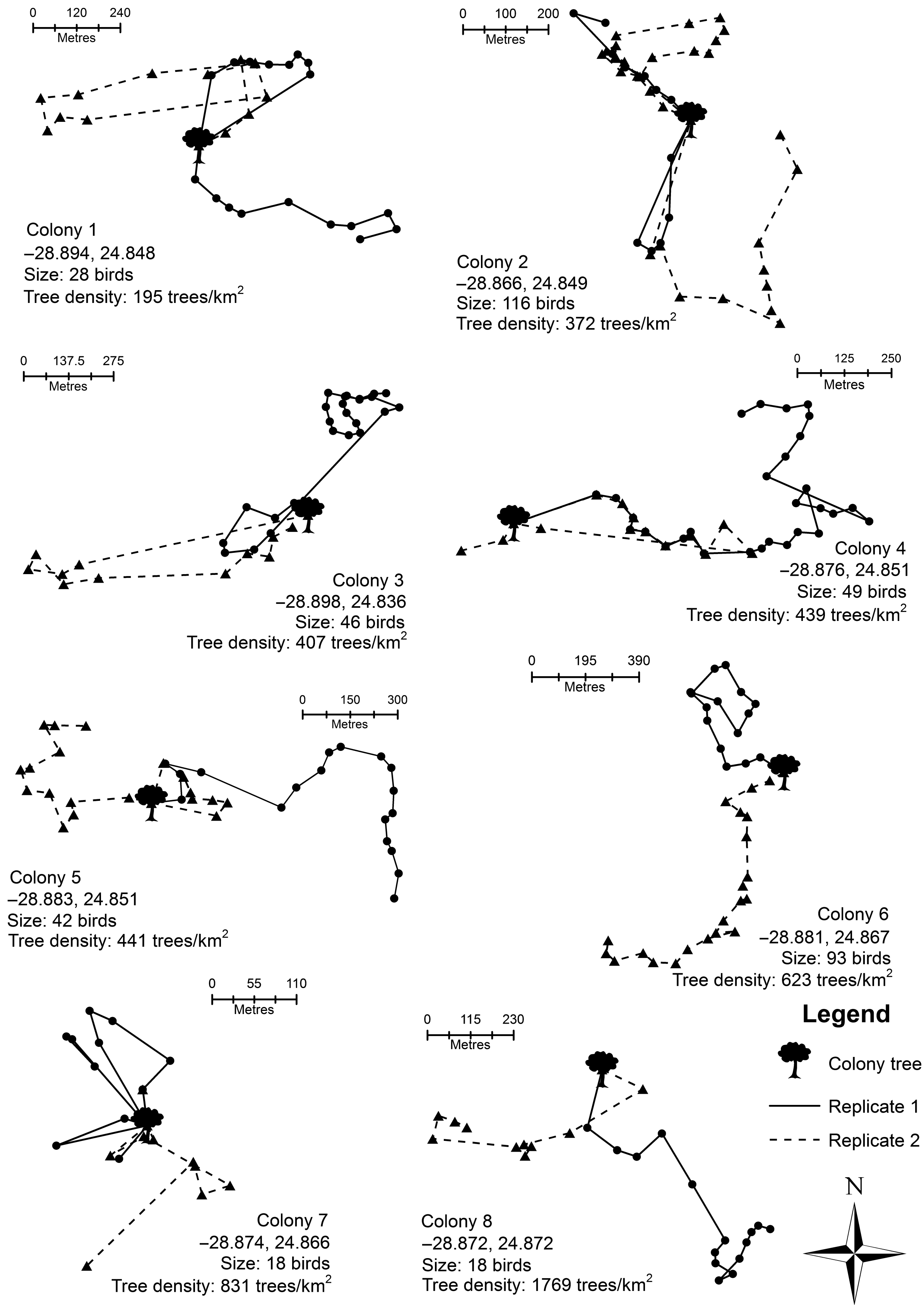

FIGURE 2 The foraging trajectories of eight sociable weaver colonies (N = 8, two replicates of each) on Benfontein Reserve, South Africa, before the 2015 breeding season. Lines show the path taken during a foraging bout and points indicate feeding stations (replicate 1 [●] & replicate 2 [▲]). The GPS co-ordinates of the colonies are expressed as decimal degrees

drongos also served as sentries as they were seen and heard giving alarm calls when gabar goshawks (*Micronisus gabar*) attacked flocks on three separate occasions. Drongos also gave alarm calls when no predators were nearby and then stole food left by the escaping weavers.

3.2 | Foraging distance

We found no evidence for foraging distance to be related to colony size (Model 1 was less well supported by the data than the constant Model 8, Table 1). Rather, it was tree density and weather conditions (maximum temperature and humidity) that best explained variation in foraging distance (Models 2 and 7, Table 1). The best supported model (Model 2) suggested a negative relationship between foraging distance and tree density (Figure 1). Sociable weaver flocks preferred to feed under the subcanopy of a tree rather than in the intercanopy. This might be because birds can sift through the soil of the subcanopy more easily, because the soil is less compact as a result of grass exclusion and the activity of animals that take refuge from the heat of the day (Scholes & Archer, 1997). In addition, the search effort of the birds is reduced in the subcanopy, because the subcanopy microhabitat attracts a diversity of animal dispersed plants and insects (Scholes & Archer, 1997). The tree itself also provides the birds with shade and a quick escape from the ground should they feel threatened (K.J.L., pers. obs). Therefore, it was not surprising to find that flocks foraging in areas with a high tree density had shorter foraging distances than flocks foraging in areas with a low tree density. The greater distance between trees (or feeding stations) in areas with a low tree density would mean that flocks would need to travel greater distances in order to feed at enough feeding stations before returning to the colony nest (Figure 2).

The second best model included an interactive effect of maximum temperature and humidity on foraging distance (Model 7, Table 1). Similarly, the best supported model for explaining the variation in foraging duration included maximum temperature (Model 5, although this was not much better than the constant Model 8, Table 2). In both cases, foraging distance and duration increased with increasing maximum temperature (Figures 3 & 4). This is likely to be related to the availability of insects, the main prey item of sociable weavers (Maclean, 1973b). Insects are poikilothermic meaning that they cannot maintain a constant body temperature independent of environmental fluctuations (Gullan & Cranston, 2010). Therefore, insects may be more available during warmer mornings as they are basking and able to fly. With increased insect availability during warmer mornings, sociable weavers may visit more feeding stations (trees) and/or spend a longer time foraging at each feeding station than during cooler mornings. Optimal foraging theory would predict that the flock would maximize food intake with the increased insect availability at each feeding station (Pyke, Pulliam, & Charnov, 1977). An assumption of the model is that as a predator depletes food in a patch, the capture rate decreases with time spent searching (because there is less food) until the predator leaves at a critical point (Krebs, Ryan, & Charnov, 1974). Therefore, a higher insect availability would take the flock longer to reach the critical point for departure. As both tree density and maximum temperature were

TABLE 2 Summary of the AIC_c-based model selection for factors explaining the foraging duration (min) of seven sociable weaver colonies ($N = 7$, two replicates of each) on Benfontein Reserve, South Africa

	Model	ΔAIC_c	w_i	K	logLik
1	Colony size	0.050	0.21	4	103.81
2	Tree density (trees per km^2)	10.16	0	4	113.91
3	Mean temperature (°C)	0.43	0.17	4	104.19
4	Minimum temperature (°C)	0.61	0.16	4	104.37
5	Maximum temperature (°C)	0	0.22	4	103.76
6	Relative humidity (%)	3.72	0.034	4	107.48
7	Max temp × rel. humidity	6.81	0.0072	6	106.56
8	Constant	0.19	0.20	3	105.94

ΔAIC_c, the model AIC_c minus the smallest AIC_c; w_i, akaike weight; K, number of parameters; logLik, maximized log likelihood.

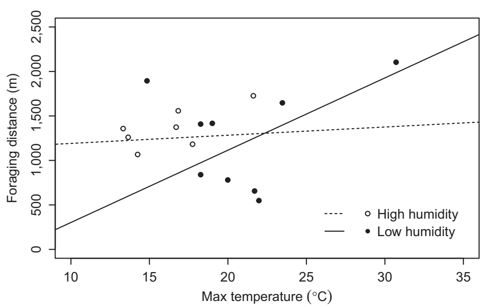

FIGURE 3 The observed (points) and predicted linear relationship between the foraging distance (m), maximum temperature (°C, max temp.) and relative humidity (%) of eight sociable weaver colonies on Benfontein Reserve, South Africa (Model 7, Table 1, $N = 8$, two replicates of each): log(foraging distance) = −1471.24 + 131.68 × max temp. + 38.86 × rel. humidity−1.86 × (max temp. × rel. humidity). The lines show predictions for high and low humidity conditions using the upper quartile (66.4%) and lower quartile (25.2%) of the relative humidity recorded during tracking, respectively. Points were categorized as being either above (○) or below (●) the average relative humidity recorded (48.0%)

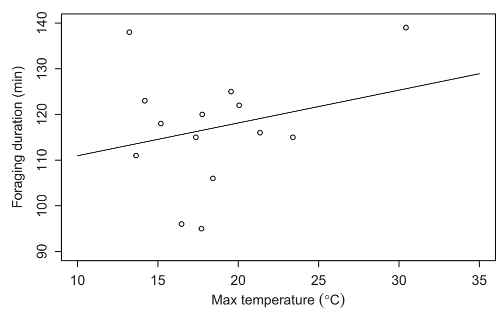

FIGURE 4 The observed (points) and predicted linear relationship between the foraging duration (min) and maximum temperature (°C, max temp.) of seven sociable weaver colonies on Benfontein Reserve, South Africa (Model 5, Table 2, $N = 7$, two replicates of each):log(foraging duration) = 103.78 + 0.72 × max temp

found to best explain foraging distance and duration, respectively, the results of this study suggest that local environment conditions play a more important role in determining the foraging behaviour of sociable weavers than colony size. The importance of environmental conditions on sociable weaver foraging duration is supported by the initial descriptions of Maclean (1973b), although extreme daily temperatures appeared to be the most influential determinant.

Flocks forage as a unit and thus the majority of the birds in a flock travel the same distance and duration from the nest during a morning foraging bout. Therefore, if intraspecific competition was present, the study would only be able to detect the effects of it at the colony level, not the individual level. However, it is possible that the effect of colony size on foraging behaviour may appear at different stages of the sociable weaver life cycle. For example, foraging distances and duration may be greater during the breeding season when weavers fly back and forth from the colony to feed nestlings as well as themselves (Maclean, 1973c). Future studies need to be conducted to improve our understanding by recording the foraging distance and duration of more colonies across a range of spatial and temporal scales. Recording the time spent at each feeding station may also provide insights on intraspecific competition and assumptions made about optimal foraging theory.

ACKNOWLEDGEMENTS

We thank the University of Cape Town (PPI grant to KJL) and the South African National Research Foundation (RA and KJL) for funding. The NRF accepts no liability for opinions, findings and conclusions or recommendations expressed in this publication.

ORCID

Kyle John Lloyd http://orcid.org/0000-0001-8668-1449
Res Altwegg http://orcid.org/0000-0002-4083-6561

REFERENCES

Akaike, H. (1973). Information theory and an extension of the maximum likelihood principle. In B. N. Petrov & F. Caski (Eds.), *Proceedings of the Second International Symposium on Information Theory* (pp. 267–281). Budapest: Akademiai Kiado.

Altwegg, R., Doutrelant, C., Anderson, M. D., Spottiswoode, C. N., & Covas, R. (2014). Climate, social factors and research disturbance influence population dynamics in a declining sociable weaver metapopulation. *Oecologia*, *174*, 413–425.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48.

Brown, C. R., & Brown, M. B. (Eds.) (1996). Social foraging 2. In *Coloniality in the Cliff Swallow* (pp. 275–320). Chicago: The University of Chicago Press.

Covas, R., du Plessis, M. A., & Doutrelant, C. (2008). Helpers in colonial cooperatively breeding sociable weavers *Philetairus socius* contribute to buffer the effects of adverse breeding conditions. *Behavioral Ecology and Sociobiology*, *63*, 103–112.

Danchin, E., & Wagner, R. H. (1997). The evolution of coloniality: The emergence of new perspectives. *Trends in Ecology & Evolution*, *12*, 342–347.

Google Earth. (2015). *Benfontein nature reserve, South Africa, 28°53'S, 24°89'E*. Pretoria, South Africa: AfriGIS. Retrieved from http://www.earth.google.com/

Gullan, P. J., & Cranston, P. S. (Eds.) (2010). Chapter 4: Sensory systems and behaviour, thermoregulation. In *The insects: An outline of entomology* (p. 102). 4th edn. Oxford: Wiley-Blackwell.

Krebs, J. R., Ryan, J. C., & Charnov, E. L. (1974). Hunting by expectation or optimal foraging? A study of patch us by chickadees. *Animal Behavior*, *22*, 953–964.

Maclean, G. L. (1973a). The sociable weaver, part 2: Nest architecture and social organization. *Ostrich*, *44*, 191–218.

Maclean, G. L. (1973b). The sociable weaver, part 5: Food, feeding and general behaviour. *Ostrich*, *44*, 254–261.

Maclean, G. L. (1973c). The sociable weaver, part 3: Breeding biology and moult. *Ostrich*, *44*, 219–240.

du Plessis, K. L., Martin, R. O., Hockey, P. A., Cunningham, S. J., & Ridley, A. R. (2012). The costs of keeping cool in a warming world: Implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology*, *18*, 3063–3070.

Pyke, G. H., Pulliam, H. R., & Charnov, E. L. (1977). Optimal foraging: A selective review of theory and tests. *The Quarterly Review of Biology*, *52*, 137–154.

R Core Team (2016). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. URL https://www.R-project.org/.

Rutherford, M. C., Mucina, L., Lötter, M.C., Bredenkamp, G.J., Smit, J.H.L., Scott-Shaw, C.R., … Powrie, L. W. (2006). Savanna biome. In L. Mucina & M. C. Rutherford (Ed.), *The vegetation of South Africa, Lesotho and Swaziland, Strelitzia 19* (pp. 438–539). Pretoria: South African National Biodiversity Institute.

Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, *28*, 545–570.

Turcotte, Y., & Desrochers, A. (2003). Landscape-dependent response to predation risk by forest birds. *Oikos*, *100*, 614–618.

Wittenberger, J. F., & Hunt, G. L. (1985). The adaptive significance of coloniality in birds. In D. S. Farner & J. R. King (Eds.), *Avian biology, volume 8* (pp. 1–78). San Diego: Academic Press.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, *1*, 3–14.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Lloyd KJ, Altwegg R, Doutrelant C, Covas R. Factors affecting the foraging distance and duration of a colonial bird, the sociable weaver, in a semi-arid environment. *Afr J Ecol*. 2018;56:659–663. https://doi.org/10.1111/aje.12484