

1 Burrow depth, carbon dioxide and reproductive success in Sand

2 Martins (*Riparia riparia*)

3

4 Thomas O. Mondain-Monval* and Stuart P. Sharp

5 Lancaster Environment Centre, Lancaster University, Lancaster, LA1 4YQ, UK

6 *Corresponding Author: t.mondain-monval@lancaster.ac.uk

7

8 **Short title:** Breeding costs in sand martins

9

10 **Keywords:** Burrowing, colony, gas exchange, reproductive success, semi-fossorial

11

12 **Summary**

13

14 **Capsule:** Carbon dioxide (CO₂) concentrations in the burrows of sand martins *Riparia*
15 *riparia* increase with depth but have no detectable impact on fledging success.

16 **Aims:** To investigate whether burrow depth and CO₂ concentrations influence reproductive
17 success in sand martins.

18 **Methods:** We monitored two Sand Martin colonies along the River Lune, Lancashire (UK) to
19 investigate the effect of burrow depth on reproductive success. We also measured CO₂ levels
20 in a sample of burrows to test whether burrow depth predicts CO₂ concentration, and to test
21 for a relationship between CO₂ concentration and breeding success.

22 **Results:** Burrow depth was significantly correlated with fledging success, but the correlation
23 was positive in first broods and negative in second broods. The highest CO₂ concentration
24 recorded was 73 650 ppm and the mean concentration across burrows was 31 757 ppm.
25 However, while CO₂ concentrations were positively correlated with burrow depth after
26 controlling for the number and age of nestlings, they were not correlated with reproductive
27 success.

28 **Conclusion:** There are reproductive costs associated with deeper burrows in second broods,
29 but these could not be attributed to CO₂ concentrations despite the exceptionally high levels
30 recorded. This study highlights the need for further investigation into gas exchange and the
31 potential impacts of, or adaptations to, CO₂ accumulation in avian burrows.

32

33 **Introduction**

34 The construction of a burrow to sleep or reproduce in has evolved in many species from
35 a range of vertebrate taxa, chiefly to reduce predation and to buffer against extreme
36 environmental conditions (Cowles & Bogert 1944, Clutton-Brock *et al.* 1999, Randall *et al.*
37 2000, Shenbrot *et al.* 2002, Ke & Lu 2009). Digging a burrow is energetically demanding and
38 many studies have tried to quantify this (Vleck 1979, Lovegrove 1989, Seymour *et al.* 1998,
39 Ebensperger & Bozinovic 2000). It has also been shown that the cost of digging is positively
40 correlated with burrow depth and complexity (Vleck 1979), but this may be offset by the
41 greater protection from outside conditions which these characteristics typically provide
42 (Cowles & Bogert 1944, Shenbrot *et al.* 2002, Ke & Lu 2009).

43 Gas exchange presents another significant physiological challenge to burrowing animals.
44 Models suggest that in burrows with narrow entrances, the main source of air flow is through
45 the soil, potentially leading to a significant accumulation of carbon dioxide (CO₂) and
46 corresponding decrease in oxygen (O₂) concentration (Wilson & Kilgore 1978, Withers
47 1978). The CO₂ concentration of free air is typically around 400 ppm but concentrations over
48 50 000 ppm have been recorded in the burrows of some species and these levels are likely to
49 have severe physiological effects (Boggs *et al.* 1984, Schmidt-Nielsen 1997). The
50 concentration of CO₂ is positively correlated with the metabolising mass of the burrow's
51 occupants due to respiration (White *et al.* 1978, Wickler & Marsh 1981), but even in
52 unoccupied burrows CO₂ concentrations are higher than in free air (Birchard *et al.* 1984),
53 presumably due to soil microbe and root respiration in the substrate. The levels also depend
54 on abiotic factors such as the substrate, season, burrow depth and structure (Wilson &
55 Kilgore 1978, Arieli 1979, Birchard *et al.* 1984), but more work is needed to understand how
56 biotic and abiotic influences interact.

57 Most studies investigating the impact of exposure to high CO₂ concentrations on
58 burrowing animals have addressed physiological responses, specifically how fossorial and
59 semi-fossorial species (i.e. animals which spend all or some of their lives underground,
60 respectively) may be adapted to such conditions. Burrowing birds, for example, have a lower
61 ventilatory response to elevated CO₂ concentrations than non-burrowing species (Boggs &
62 Kilgore 1983; Boggs *et al.* 1984). Comparisons between closely related fossorial and non-
63 fossorial mammals have shown higher skeletal muscle myoglobin concentrations and slower
64 metabolisms in the former (McNab 1966, Lechner 1976). Other research has examined the
65 effects of elevated CO₂ levels on survival in poultry farms, where concentrations are high due
66 to bird densities and low ventilation. In these farms, CO₂ levels greater than 2500 ppm
67 increase the risk of heart disease (Frame *et al.* 1999) and when greater than 4000 ppm can
68 cause chick mortality through lethargy and reduced feeding (Donaldson *et al.* 1995).

69 Despite the implications of this research, very little is known about the potentially
70 adverse effects of CO₂ on the reproductive success of animals which raise their young in
71 burrows. The young of semi-fossorial species may be particularly susceptible because they
72 are exposed to high CO₂ and low O₂ concentrations for extended periods of time, yet may not
73 show the same adaptations to these conditions as fossorial species (Soholt *et al.* 1973). A
74 study of the European Bee-Eater *Merops apiaster* showed that chicks raised in burrows with
75 CO₂ concentrations above 60 000 ppm had noticeably laboured and rapid breathing,
76 averaging about 100 breaths/min compared with 68 breaths/min for chicks exposed to
77 concentrations of 30 000 ppm (White *et al.* 1978). Being exposed to such high concentrations
78 could inhibit development (Scheid 1982) and reduce begging and feeding (Donaldson *et al.*
79 1995). This could be especially problematic in birds, where adults take direct cues from
80 begging chicks when making choices about food distribution and feeding frequency (Kilner
81 & Johnstone 1997, Leonard & Horn 2001). However, only a small number of other studies

82 have measured CO₂ levels in the burrows of wild birds (Birchard *et al.* 1984, Ar &
83 Piontkewitz 1992, Lill & Fell 2007) and the relationship between burrow depth and CO₂
84 accumulation has rarely been investigated.

85 Sand Martins *Riparia riparia* are colonial Afro-Palaearctic migrant birds that nest in
86 burrows excavated into river banks and man-made quarries. They are a Species of European
87 Conservation Concern (BirdLife International 2004), but the underlying causes of within-
88 colony variation in reproductive success are poorly known. Sand Martins arrive in Europe
89 from West Africa in spring and start digging new burrows or renovate pre-existing ones
90 (Szép *et al.* 2003, Turner & Rose 2010). Each burrow has a single entrance and the nest is
91 placed in a small chamber at the far end at a depth varying from 30cm to over 100cm
92 (Heneberg 2003, Turner & Rose 2010). In a comparative study of three burrowing bird
93 species – Sand Martins, Rhinoceros Auklets *Cerorhinca monocerata* and Burrowing Owls
94 *Athene cunicularia* – the burrows of Sand Martins had the highest mean CO₂ concentrations
95 (32 000 ppm), the highest overall CO₂ concentration (67 000 ppm) and the widest range
96 (4000 ppm to 67 000 ppm, Birchard *et al.* 1984). They are therefore an ideal model system
97 for understanding the relationship between burrow depth, CO₂ concentration and
98 reproductive success.

99 Wickler and Marsh (1981) took gas samples from Sand Martin burrows and reported
100 a positive correlation between CO₂ content and burrow depth. Burrow depth is likely to
101 exacerbate CO₂ accumulation because air convection, due to either wind or the movement of
102 occupants, is typically the most important mechanism of gas exchange in animal burrows yet
103 may be restricted at greater depths (White *et al.* 1978, Wilson & Kilgore 1978, Withers 1978,
104 Wickler & Marsh 1981, Birchard *et al.* 1984, Lill & Fell 2007). Another previous study of
105 Sand Martins reported a negative correlation between burrow depth and breeding success, but
106 CO₂ concentrations were not measured (Cruickshank 2013). In our study, we monitored all

107 nesting attempts at two colonies during a single season in order to: (1) investigate how
108 different components of reproductive success vary with burrow depth; (2) test whether
109 burrow depth predicts CO₂ concentration after controlling for other influences; and (3) test
110 whether CO₂ concentration is correlated with breeding success.

111

112 **Materials and methods**

113 STUDY POPULATION AND NEST MONITORING

114 Fieldwork was carried out during the 2015 breeding season at two Sand Martin colonies
115 along the River Lune near Whittington, Lancashire, UK (54°182'N, 2°597'W); these colonies
116 were 250 m apart with no suitable breeding habitat in between. Each colony was divided into
117 approximately equal sections and photographed, and all burrows were then individually
118 labelled on the photographs to create reference maps. Burrows were inspected and their depth
119 measured (in cm) using a Micro CA-100 endoscope (RIDGID, Ohio, USA). Inspections
120 started in mid-April before laying had commenced and ended after the last chicks had fledged
121 on the 2nd September; the first nest containing eggs was found on the 27th April. A maximum
122 of one hour was spent in front of any given colony section in order to limit the amount of
123 time that chicks and eggs were left unattended; birds from neighbouring sections continued to
124 visit their nests during this time.

125 Every burrow in both colonies was inspected once every two to four days until laying
126 commenced, and then left unchecked for at least five days in order to record clutch size on
127 the following visit. Nests were then checked regularly around the time that hatching was due
128 (allowing for a typical incubation period of 14-15 days) and on average once every four days
129 thereafter until the nest failed or fledged. A nest was considered fledged if at least one
130 nestling survived until 16 days old, after which time juveniles leave the nest but may return
131 regularly to their own or neighbouring burrows (Szabó & Szép 2010, Turner & Rose 2010).

132 Most failed nests were found empty and it was therefore impossible to be sure of the cause of
133 death, not least because adults may remove broken eggs or dead chicks to prepare the nest for
134 a second brood. In other cases, dead chicks or their remains were found in burrows but the
135 cause of death could not be determined from visual inspection with the endoscope. Once a
136 nest had failed or fledged, the burrow was checked every three days in order to obtain laying
137 dates for any replacement clutches or second clutches, respectively; these were then
138 monitored in the same way as first breeding attempts. Burrow depth was recorded whenever a
139 new clutch was found because depth sometimes varied between breeding attempts.

140 The following parameters were recorded for every breeding attempt (i.e. where at least
141 one egg was found): lay date, clutch size, hatch date, brood size and fledgling number. Lay
142 date was the date on which the first egg in a clutch was laid and was calculated
143 retrospectively once incomplete clutches were found (assuming one egg was laid per day;
144 Turner & Rose 2010). Clutch size was determined once the number of eggs remained the
145 same on successive visits to a nest which was not subsequently found to have failed at the
146 egg stage. Hatch date was estimated to within a day using the physical attributes of chicks
147 (Fernaz *et al.* 2012). Where hatching was missed by more than six days, hatch date was
148 estimated based on the lay date, an incubation period of 15 days and the modal clutch size for
149 these colonies (5 eggs), assuming one egg was laid per day and incubation started with the
150 penultimate egg (Turner & Rose 2010). Partial brood mortality occurred in a small proportion
151 of nests, so brood size was taken as the maximum number of chicks recorded on any visit
152 prior to fledging. Fledgling number was the brood size recorded on the final visit before
153 fledging (between day 12 and 16 of the nestling period) or zero for nests that failed.

154 A total of 824 nests were monitored throughout the breeding season. All dates were
155 converted to a Julian Date (JD, days since 1st January) for analyses. Active nests were
156 sometimes found late in the season in burrows that had previously been unoccupied; these

157 were considered unlikely to be first breeding attempts, especially as pairs are known to
158 sometimes change burrow between broods (Cowley 1983). Second broods were therefore
159 classified as follows: ‘true’ second broods were first identified as a second breeding attempt
160 in a nest that had previously fledged; the lay date for the earliest known true second brood
161 was 15th June (JD 165) and this was then used as a threshold for determining second broods
162 in other burrows. All eggs laid on or after this date were considered part of a second brood
163 and all those before, a first brood (i.e. including replacement clutches).

164

165 CARBON DIOXIDE CONCENTRATION

166 CO₂ was measured (in ppm) throughout the breeding season using a GM70
167 CARBOCAP probe (Vaisala, Vantaa, Finland) calibrated to 10% CO₂ concentrations. The
168 probe was placed directly alongside the nest at the end of the burrow and left in place until
169 the reading stabilised (approximately five minutes), and the time of day was then recorded.
170 The probe was allowed to return to ambient CO₂ concentrations (measured as 380-450 ppm
171 during each day of the study), before the next sample was taken; 228 samples were taken
172 throughout the season. Many nests were only sampled once ($n = 122$) but repeat
173 measurements were made for those nests which survived long enough ($n = 53$ nests, each
174 sampled twice). Repeat measurements were taken once within the first part of the nestling
175 period (day 1-10) and once within the last nine days before fledging (day 11-20). For burrows
176 in which chicks may have been old enough to fly (age 16-20), all chicks were counted and the
177 CO₂ probe inserted only if all were present. CO₂ concentration was also measured in a sample
178 of unoccupied burrows ($n = 66$) for which depth was measured. Ambient air temperature was
179 obtained to the nearest 0.01°C from TGP-4017 Tinytag data loggers (Gemini, Chichester,
180 UK) placed in trees between the colonies and set to record every 30 minutes throughout the

181 entire breeding season. These were calibrated in a United Kingdom Accreditation Service
182 approved laboratory using 0 and 30°C calibration points.

183

184 STATISTICAL ANALYSES

185 **Burrow Depth and Reproductive Success**

186 The effect of burrow depth on reproductive success, controlling for lay date, brood
187 number (1 or 2) and colony (north or south), was analysed using a mixed modelling
188 approach. Analyses were restricted to those nests for which complete data were available ($n =$
189 768). Collinearity between the explanatory variables was assessed using correlation plots and
190 variance inflation factors (VIFs, following Zuur *et al.* 2009). Lay date and brood number
191 were highly positively correlated ($r > 0.9$) and so only brood number was retained in
192 subsequent analyses. This was partly because retaining lay date would have reduced the
193 sample size by over 100 nests (for which lay date was unknown) but also because variation in
194 breeding success between broods was of greater interest than temporal variation more
195 generally. All other correlations were weak ($r < 0.4$) with small associated VIFs (< 2) and so
196 the remaining explanatory variables were fitted as fixed effects. Any effects of burrow depth
197 may vary between broods, especially if the accumulation of carbon dioxide is an important
198 factor, and so the interaction between burrow depth and brood number was also fitted.
199 Burrow depth was both centred and standardised, and brood number and colony were centred
200 (Schielzeth 2010). Burrow identity was fitted as a random effect in order to account for
201 repeated measures.

202 The distribution of the number of fledglings showed high zero inflation and so a hurdle
203 model was fitted (Zuur *et al.* 2009). The *glmmADMB* package (Fournier *et al.* 2012) in R
204 version 3.2.3 (R Core Team 2015) was used to fit two separate generalised linear mixed
205 effects models (GLMMs). In one, the response variable was a binary indicator of whether or

206 not the nest fledged at least one chick, hereafter ‘fledging success’. In the other, restricted to
207 successful nests, the response variable was the number of chicks fledged, hereafter ‘fledgling
208 number’.

209 For the analysis of fledging success, models were fitted with a binomial error distribution
210 and logit link function. All possible candidate models (excluding those containing the
211 interaction term but not the constituent main effects) were compared using the AIC_c value
212 (the second order Akaike Information Criterion). No candidate models were within 2 AIC_c
213 units of the full model, so the full model was retained after validation using an index plot of
214 residuals and a binned plot of the scaled average residuals against expected values (Collett
215 2002). Models for the analysis of fledgling number were fitted with a truncpoisson error
216 distribution (Zuur *et al.* 2009) and the log link function. All possible candidate models were
217 fitted and ranked by AIC_c using the dredge function in the *MuMIn* package (Bartoń 2015).
218 AIC_c is the Akaike’s Information Criterion corrected for sample size. Models within 2 AIC_c
219 units of the best-fitting model were then averaged (Bartoń 2015). To obtain relative
220 importance values for each explanatory variable, the Akaike weights (the normalised relative
221 likelihoods of each model) were calculated and summed across all models which contained
222 the variable (Bartoń 2015). The best-fitting model was validated by plotting the distribution
223 of the residuals, the residuals versus fitted values and the residuals versus each explanatory
224 variable.

225

226 **Burrow Depth and Carbon Dioxide Concentration**

227 Linear mixed effect models (LMEs) were used to investigate the relationship between
228 burrow depth and CO₂ levels; models were fitted with the *lme4* package (Bates *et al.* 2015).
229 CO₂ concentration was fitted as the response variable and burrow depth, brood number (1 or
230 2), colony (north or south), brood size and chick age (measured in days from hatch date) were

231 fitted as fixed effects (number of samples per age group: age 0-5, n = 55; age 6-10, n = 69;
232 age 11-15, n = 59; age 16+, n = 45); the latter two were included together with their
233 interactions with burrow depth because these factors were considered likely to influence CO₂
234 levels based on previous work (Wickler & Marsh 1981). Time of day (timing of the samples
235 throughout the day: 07.00-10.00, n = 36; 11.00-14.00, n = 54; 15.00-18.00, n = 121; 18.00 or
236 later, n = 17) and ambient air temperature are also likely to affect CO₂ concentrations due to
237 the impact of light levels and temperature on soil microbe respiration (Lloyd & Taylor 1994),
238 and so were included as fixed effects together with their interactions with burrow depth.
239 Burrow identity was included as a random effect in order to control for repeated measures.
240 Continuous variables were centred and standardised before analysis; brood number and
241 colony were centred (Schielzeth 2010). All variables were included in the analyses because
242 correlations between them were weak ($r < 0.3$) and VIFs small (< 2 ; Zuur *et al.* 2009).
243 Models were compared, averaged and validated using the same approach described above. To
244 compare CO₂ concentrations in occupied and unoccupied burrows, the mean level per burrow
245 was analysed using a Mann-Whitney U Test. A linear regression was used to investigate the
246 relationship between unoccupied burrow depth and CO₂ concentration.

247

248 **Carbon Dioxide Concentration and Reproductive Success**

249 GLMMs were used to investigate the relationship between carbon dioxide concentration
250 and fledging success using the *lme4* package (Bates *et al.* 2015). The effect of CO₂ on
251 fledging number was not considered as fledgling number was very strongly correlated with
252 brood size, an important determinant of CO₂ concentration. Due to missing fledging success
253 data, analyses were carried out using a sub-sample of the dataset ($n = 221$ samples from 175
254 nests). Fledging success was fitted as the response variable in a model with a binary error
255 distribution and logit link function. CO₂ concentration, brood number (1 or 2), colony (north

256 or south) and the interaction between CO₂ concentration and brood number were fitted as
257 explanatory variables. The interaction term was included because reproductive costs are
258 likely to differ between broods, and the potential costs associated with CO₂ concentrations
259 may therefore also differ. Burrow identity was included as a random effect to control for
260 repeated measures. CO₂ concentration was centred and standardised before analysis; brood
261 number and colony were centred (Schielzeth 2010). All variables were included in the
262 analyses as correlations between them were weak ($r < 0.4$) and VIFs small (< 2 ; Zuur *et al.*
263 2009). Models were compared, averaged and validated using the same approach described
264 above.

265

266 **Results**

267 BURROW DEPTH AND REPRODUCTIVE SUCCESS

268 Fledging success varied with burrow depth after controlling for differences between the
269 colonies, but this relationship was significantly different between the two broods (Table 1,
270 Table A1, Fig. 1). In first broods, fledging success was significantly higher and positively
271 correlated with burrow depth, but there was a negative correlation between fledging success
272 and burrow depth in second broods (Fig. 1).

273 The best-fitting models of fledgling number contained burrow depth and brood number
274 as fixed effects, but no interaction between them (Table 2, Table A2). Fledgling number
275 differed significantly between broods (Table 2), with the number of chicks fledged in
276 successful nests being higher in first broods than second broods (first brood mean: $2.53 \pm$
277 1.92 sd, second brood mean: 1.67 ± 1.80 sd). Although burrow depth was retained in the best-
278 fitting models, the effect size was very small and unlikely to be biologically meaningful
279 (Table 2).

280

281 BURROW DEPTH AND CARBON DIOXIDE CONCENTRATION

282 The average CO₂ concentration in occupied burrows was 31 757 ppm (\pm 17 152 sd), but
283 ranged from 570 ppm to 73 650 ppm. In the analysis of the factors affecting these levels, all
284 fixed effects and interactions were contained in the model set used for averaging (Table 3,
285 Table A3). Brood number had the largest effect, with CO₂ concentrations significantly lower
286 in nests containing second broods (Table 3, first brood mean: 35 356 ppm \pm 16 905 sd,
287 second brood mean: 24 557 ppm \pm 15 053 sd). Time of day and air temperature were
288 negatively and positively correlated with CO₂, respectively (Table 3). CO₂ concentration was
289 also positively correlated with chick age, brood size and burrow depth (Table 3). The
290 interaction between brood size and burrow depth revealed a more marked effect of depth on
291 CO₂ in smaller broods (Fig. 2), but the effect sizes for all other interactions were extremely
292 small (Table 3).

293 In unoccupied burrows, CO₂ concentration ranged from 350 ppm to 33 180 ppm with a
294 mean of 6700 ppm, significantly lower than in occupied burrows ($W = 27866$, $P < 0.001$).
295 CO₂ concentration in unoccupied burrows was also positively correlated with burrow depth
296 (linear regression: $r = 0.415$, $P < 0.001$).

297

298 CARBON DIOXIDE CONCENTRATION AND REPRODUCTIVE SUCCESS

299 Fledging success was not correlated with burrow CO₂ concentrations. Colony and brood
300 number were retained in the best-fitting model set but effect sizes were low and therefore
301 unlikely to be biologically meaningful (Table 4, Table A4).

302

303 Discussion

304 Burrow depth was positively correlated with fledging success in first broods but
305 negatively correlated in second broods, and there was no correlation with fledgling number in
306 either. A previous study of the same colonies by Cruickshank (2013) reported a negative
307 relationship between burrow depth and fledgling number but the sampling was far less
308 comprehensive and the effect size was small. Here, the results suggest that while the depth of
309 a burrow may impact on whether or not a nest is successful, there is no further effect on the
310 productivity of successful nests. Alternatively, the magnitude of any such effect may be small
311 and difficult to detect, especially in this study as there were relatively few nests that fledged a
312 very small or large number of chicks.

313 The positive correlation between burrow depth and fledging success in first broods is
314 likely due to the greater protection from predators and more stable microclimates that deeper
315 burrows provide (Randall *et al.* 2000, Shenbrot *et al.* 2002, Ke & Lu 2009). The causes of
316 nestling mortality were difficult to identify but environmental conditions may be particularly
317 important earlier in the season when it is colder and wetter. Some studies of other animals
318 have found positive correlations between burrow depth and reproductive success (e.g.
319 Patricia & Passmore 1996, Heg & Rasa 2004), whereas others have found no correlation (e.g.
320 Hampton *et al.* 2009). Further work is needed to understand this interspecific variation.

321 Whatever the mechanism behind the positive relationship between burrow depth and
322 reproductive success in first broods, the benefits of a deeper burrow are apparently
323 outweighed by the associated costs in second broods. Declines in reproductive success
324 throughout the season are not uncommon in birds, for example due to reduced food
325 availability (Crick *et al.* 1993, Møller 2002) or the energetic costs associated with second
326 breeding attempts (Verhulst & Tinbergen 1991). However, this does not explain the negative
327 effect of burrow depth on reproductive success in second broods. It could be that birds using
328 deep burrows for their first brood, in which there was generally higher fledging success, face

329 trade-offs which lead to reduced success in their second. Such trade-offs are difficult to
330 determine because Sand Martins often change burrows between broods (Cowley 1983), but
331 they may be driven by the accumulation of ectoparasites which impose significant costs on
332 nestlings (Szép & Muller 2000). The relationship between parasite load and burrow depth
333 requires further study.

334 CO₂ concentrations in occupied burrows were significantly higher than in unoccupied
335 burrows and, in common with other studies, increased with the age and number of chicks
336 (Wilson & Kilgore 1978, Withers 1978, Wickler and Marsh 1981, Birchard *et al.* 1984). High
337 CO₂ levels can reduce begging and feeding behaviour, leading to lower growth rates and
338 increased mortality through reduced food consumption (Donaldson *et al.* 1995, Frame *et al.*
339 1999). Indeed, it was expected that high CO₂ would be one of the primary drivers of reduced
340 fledging success in deeper burrows. Our findings suggest, however, that it had no influence
341 on fledging success. CO₂ concentration in burrows was positively correlated with ambient air
342 temperature, and warmer temperatures are likely to correspond with a higher abundance of
343 the insects on which Sand Martins feed (Bale *et al.* 2002, Turner & Rose 2010). It could be
344 that this increase in prey abundance offsets any negative effects of elevated CO₂
345 concentration, meaning that chicks remain well fed despite having reduced begging
346 capabilities. Alternatively, the effects of CO₂ concentration on chicks may not have been
347 detected in our study. CO₂ varied significantly throughout the day and those in deeper
348 burrows may be exposed to higher concentrations for longer periods of time; this would not
349 be reflected in our measures of CO₂ concentration. It could also be that Sand Martins are
350 unaffected by high CO₂ levels due to physiological adaptations (Boggs *et al.* 1984), or that
351 there are post-fledging fitness costs such as reduced offspring survival. Investigating these
352 possibilities would increase our understanding of avian behaviour and physiology in
353 burrowing species.

354 The positive correlation between burrow depth and CO₂ concentration was stronger in
355 small broods, perhaps indicating that large broods produce enough CO₂ to mask any effect of
356 depth. This may be because airflow in shallower burrows can reduce CO₂ levels providing
357 that broods are relatively small. It is also possible that a significant proportion of CO₂
358 accumulation is accounted for by bacteria within the burrows; bacteria may be enhanced by
359 large broods producing more faecal matter. This might explain why temperature is highly
360 correlated with CO₂ concentration as soil microbe respiration is greater at higher
361 temperatures (Lloyd & Taylor 1994). The large overall effect size of burrow depth indicates
362 that, even after accounting for other abiotic and biotic factors, it is an important determinant
363 of the gas composition of burrows, as suggested by previous studies (Maclean 1981, Wickler
364 & Marsh 1981). In fact, as far as we are aware, the CO₂ concentrations reported here are the
365 highest found in burrows of any vertebrate species to date, and far greater than those thought
366 to be dangerous for birds in poultry farms (Donaldson *et al.* 1995). This makes the absence of
367 any relationship between CO₂ concentration and reproductive success all the more intriguing.
368

369 **Acknowledgements**

370 We would like to thank the Metcalfe and Whittaker families for granting permission to
371 work on their land. Ian Hartley and Rob Robinson provided useful feedback on an earlier
372 version of the manuscript, and discussions with Peter Wynn regarding gas exchange were
373 extremely helpful. Special thanks to Nick Ostle for helping to support the analysis of carbon
374 dioxide concentrations. This study complies with all current laws in Britain.

375

376 **References**

377 **Ar, A. and Piontkewitz, Y.** 1992. Nest ventilation explains gas composition in the nest-
378 chamber of the European Bee-eater. *Respir. Physiol.* **87**:407-418.

379 **Arieli, R.** 1979. The atmospheric environment of the fossorial mole rat (*Spalax ehrenbergi*):
380 effects of season, soil texture, rain, temperature and activity. *Comp. Biochem. Phys. A*
381 **63**:569-575.

382 **Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K.,**
383 **Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R.,**
384 **Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D.**
385 **and Whittaker, J.B.** 2002. Herbivory in global climate change research: direct effects of
386 rising temperature on insect herbivores. *Global Change Biol.* **8**:1-16.

387 **Bartoń, K.** 2015. MuMIn: multi-model inference. Version 1.15.6.

388 **Bates, D., Maechler, M., Bolker, B. and Walker, S.** 2015. Fitting linear mixed-effects
389 models using lme4. *J. Stat. Soft.* **67**:1-48.

390 **Birchard, G.F., Kilgore Jr, D.L. and Boggs, D.F.** 1984. Respiratory gas concentrations and
391 temperatures within the burrows of three species of burrow-nesting birds. *The Wilson*
392 *Bulletin* **96**:451-456.

393 BirdLife International 2004. *Birds in Europe: Population Estimates, Trends and*
394 *Conservation Status*. Cambridge, UK. BirdLife International.

- 395 **Boggs, D.F. and Kilgore Jr, D.L.** 1983. Ventilatory responses of the burrowing owl and
396 bobwhite to hypercarbia and hypoxia. *J. Comp. Physiol.* **149**:527-533.
- 397 **Boggs, D.F., Kilgore Jr, D.L. and Birchard, G.F.** 1984. Respiratory physiology of
398 burrowing mammals and birds. *Comp. Biochem. Physiol.* **77**:1-7.
- 399 **Clutton-Brock, T.H., O’Riain, M.J., Brotherton, P.N.M., Gaynor, D., Kansky, R.,**
400 **Griffin, A.S. and Manser, M.** 1999. Selfish sentinels in cooperative mammals. *Science*
401 **284**:1640-1644.
- 402 **Collett, D.** 2002. *Modelling Binary Data*. CRC Press.
- 403 **Cowles, R.B. and Bogert, C.M.** 1944. A preliminary study of the thermal requirements of
404 desert reptiles. *Bull. Am. Mus. Nat. Hist.* **83**:261-296.
- 405 **Cowley, E.** 1983. Multi-brooding and mate infidelity in the Sand Martin. *Bird Study* **30**:1-8.
- 406 **Crick, H.Q., Gibbons, D.W. and Magrath, R.D.** 1993. Seasonal changes in clutch size in
407 British birds. *J. Anim. Ecol.* **62**:263-273.
- 408 **Cruickshank, A.** 2013. Reproductive success and provisioning rate in the Sand Martin,
409 *Riparia riparia*: the effect of colony size and structure. MSc, Lancaster Environment
410 Centre, Lancaster University, UK.

411 **Donaldson, W., Christensen, V., Garlich, J., McMurtry, J. and Olson, N.** 1995. Exposure
412 to excessive carbon dioxide: A risk factor for early poult mortality. *J. Appl. Poultry. Res.*
413 **4**:249-253.

414 **Ebensperger, L.A. and Bozinovic, F.** 2000. Energetics and burrowing behaviour in the
415 semifossorial degu *Octodon degus* (Rodentia: Octodontidae). *J. Zool.* **252**:179-186.

416 **Fernaz, J.M., Schifferli, L. and Gruebler, M.U.** 2012. Ageing nestling barn swallows
417 *Hirundo rustica*: an illustrated guide and cautionary comments. *Ringing & Migration*
418 **27**:65-75.

419 **Fournier, D., Skaug, H., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M., Nielsen,**
420 **A. and Sibert, J.** 2012. AD Model Builder: using automatic differentiation for statistical
421 inference of highly parameterized complex nonlinear models. *Optim. Method Softw.*
422 **27**:233-249.

423 **Frame, D.D., Buckner, R.E. and Anderson, G.L.** 1999. Causes and control of spontaneous
424 cardiomyopathy or roundheart disease in Utah turkeys. All Archived Publications Paper
425 26. Utah State University Extension.

426 **Hampton, S.L., Ryan, P.G. and Underhill, L.G.** 2009. The effect of flipper banding on the
427 breeding success of African penguins *Spheniscus demersus* at Boulders Beach, South
428 Africa. *Ostrich* **80**:77-80.

429 **Heg, D. and Rasa, O.A.E.** 2004. Effects of parental body condition and size on reproductive
430 success in a tenebrionid beetle with biparental care. *Ecol. Entomol.* **29**:410-419.

- 431 **Heneberg, P.** 2003. Soil particle composition affects the physical characteristics of Sand
432 *Martin Riparia riparia* holes. *Ibis* **145**:392-399.
- 433 **Ke, D. and Lu, X.** 2009. Burrow use by Tibetan ground tits *Pseudopodoces humilis*: coping
434 with life at high altitudes. *Ibis* **151**:321-331.
- 435 **Kilner, R. and Johnstone, R.A.** 1997. Begging the question: are offspring solicitation
436 behaviours signals of need? *Trends Ecol. Evol.* **12**:11-15.
- 437 **Lechner, A.J.** 1976. Respiratory adaptations in burrowing pocket gophers from sea level and
438 high altitude. *J. Appl. Physiol.* **41**:168-173.
- 439 **Leonard, M.L. and Horn, A.G.** 2001. Begging calls and parental feeding decisions in tree
440 swallows (*Tachycineta bicolor*). *Behav. Ecol. Sociobiol.* **49**:170-175.
- 441 **Lill, A. and Fell, P.J.** 2007. Microclimate of nesting burrows of the Rainbow Bee-eater.
442 *Emu* **107**:108-114.
- 443 **Lloyd, J. and Taylor, J.A.** 1994. On the temperature dependence of soil respiration. *Funct.*
444 *Ecol.* **8**:315-323.
- 445 **Lovegrove, B. 1989.** The cost of burrowing by the social mole rats (Bathyergidae)
446 *Cryptomys damarensis* and *Heterocephalus glaber*: the role of soil moisture. *Physiol.*
447 *Zool.* **62**:449-469.

448 **Maclean, G.S.** 1981. Factors influencing the composition of respiratory gases in mammal
449 burrows. *Comp. Biochem. Phys. A* **69**:373-380.

450 **McNab, B.K.** 1966. The metabolism of fossorial rodents: a study of convergence. *Ecology*
451 **47**:712-733.

452 **Møller, A.P.** 2002. North Atlantic Oscillation (NAO) effects of climate on the relative
453 importance of first and second clutches in a migratory passerine bird. *J. Anim. Ecol.*
454 **71**:201-210.

455 **Patricia, R.Y.B. and Passmore, N.I.** 1996. Time constraints and multiple choice criteria in
456 the sampling behaviour and mate choice of the fiddler crab, *Uca annulipes*. *Behav. Ecol.*
457 *Sociobiol.* **38**:407-416.

458 R Core Team 2015. R: a language and environment for statistical computing. R Foundation
459 for Statistical Computing. Vienna, Austria.

460 **Randall, J.A., Rogovin, K.A. and Shier, D.M.** 2000. Antipredator behavior of a social
461 desert rodent: footdrumming and alarm calling in the great gerbil, *Rhombomys opimus*.
462 *Behav. Ecol. Sociobiol.* **48**:110-118.

463 **Scheid, P.** 1982. Respiration and control of breathing. *Avian Biol.* **6**:405-453.

464 **Schielzeth, H.** 2010. Simple means to improve the interpretability of regression coefficients.
465 *Method Ecol. Evol.* **1**:103-113.

- 466 **Schmidt-Nielsen, K.** 1997. *Animal Physiology: Adaptation and Environment*. Cambridge
467 University Press, UK.
- 468 **Seymour, R., Withers, P. and Weathers, W.** 1998. Energetics of burrowing, running, and
469 free-living in the Namib Desert golden mole (*Eremitalpa namibensis*). *J. Zool.* **244**:107-
470 117.
- 471 **Shenbrot, G., Krasnov, B., Khokhlova, I., Demidova, T. and Fielden, L.** 2002. Habitat-
472 dependent differences in architecture and microclimate of the burrows of Sundevall's jird
473 (*Meriones crassus*) (Rodentia: Gerbillinae) in the Negev Desert, Israel. *J. Arid Environ.*
474 **51**:265-279.
- 475 **Soholt, L.F., Yousef, M.K. and Dill, D.B.** 1973. Responses of Merriam's kangaroo rats,
476 *Dipodomys merriami*, to various levels of carbon dioxide concentration. *Comp. Biochem.*
477 *Phys. A* **45**:455-462.
- 478 **Szabo, Z.D. and Szep, T.** 2010. Breeding dispersal patterns within a large Sand Martin
479 (*Riparia riparia*) colony. *J. Ornith.* **151**:185-191.
- 480 **Szép, T. and Muller, A.P.** 2000. Exposure to ectoparasites increases within-brood variability
481 in size and body mass in the Sand Martin. *Oecologia* **125**:201-207.
- 482 **Szép, T., Moller, A.P., Vallner, J., Kovács, B. and Norman, D.** 2003. Use of trace
483 elements of Sand Martin *Riparia riparia* for identifying moulting areas. *J. Avian. Biol.*
484 **34**:307-320.

- 485 **Turner, A. and Rose, C.** 2010. *A Handbook to the Swallows and Martins of the World.*
486 A&C Black.
- 487 **Verhulst, S. and Tinbergen, J.M.** 1991. Experimental evidence for a causal relationship
488 between timing and success of reproduction in the great tit *Parus m. major*. *J. Anim.*
489 *Ecol.* **60**:269-282.
- 490 **Vleck, D.** 1979. The energy cost of burrowing by the pocket gopher *Thomomys bottae*.
491 *Physiol. Zool.* **52**:122-136.
- 492 **White, F.N., Bartholomew, G.A. and Kinney, J.L.** 1978. Physiological and ecological
493 correlates of tunnel nesting in the European bee-eater, *Merops apiaster*. *Physiol. Zool.*
494 **51**:140-154.
- 495 **Wickler, S.J. and Marsh, R.L.** 1981. Effects of nestling age and burrow depth on CO₂ and
496 O₂ concentrations in the burrows of bank swallows (*Riparia riparia*). *Physiol. Zool.*
497 **54**:132-136.
- 498 **Wilson, K.J. and Kilgore, D.L.** 1978. The effects of location and design on the diffusion of
499 respiratory gases in mammal burrows. *J. Theor. Biol.* **71**:73-101.
- 500 **Withers, P.C.** 1978. Models of diffusion-mediated gas exchange in animal burrows. *Am.*
501 *Nat.* **112**:1101-1112.
- 502 **Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. and Smith, G.M.** 2009. *Mixed effects*
503 *models and extensions in ecology with R.* Springer Science & Business Media.

505 **Appendices**

Table A1. The full set of GLMMs of the factors affecting fledging success in Sand Martins. Burrow identity was fitted as a random effect in each case. Model averaging was carried out on the models within 2 AICc units of the best-fitting model (shown in bold). Int = Intercept, BN = Brood Number, Col = Colony, BD = Burrow Depth.

Model ID	Int	BN	Col	BD	BN x BD	AICc	ΔAICc	Weight
16	1.299	+	+	0.200	+	944.896	0.000	0.992
4	1.310	+	+	-	-	955.178	10.282	0.006
8	1.289	+	+	-0.053	-	956.825	11.928	0.003
14	0.867	+	-	-0.008	+	972.243	27.346	0.000
6	0.865	+	-	-0.246	-	983.980	39.084	0.000
3	0.893	-	+	-	-	984.703	39.807	0.000
7	0.862	-	+	-0.098	-	985.372	40.476	0.000
2	0.867	+	-	-	-	992.363	47.467	0.000
5	0.536	-	-	-0.263	-	1006.703	61.807	0.000
1	0.528	-	-	-	-	1017.062	72.165	0.000

506

Table A2. The full set of GLMMs of the factors affecting fledgling number in Sand Martins. Burrow identity was fitted as a random effect in each case. Model averaging was carried out on the models within 2 AICc units of the best-fitting model (shown in bold). Int = Intercept, BN = Brood Number, Col = Colony, BD = Burrow Depth.

Model ID	Int	BN	Col	BD	BN x BD	AICc	ΔAICc	Weight
2	1.261	+	-	-	-	1644.352	0.000	0.401
6	1.262	+	-	0.009	-	1646.282	1.930	0.153
4	1.266	+	+	-	-	1646.344	1.992	0.148
1	1.221	-	-	-	-	1647.481	3.129	0.084
8	1.271	+	+	0.013	-	1648.192	3.840	0.059
14	1.262	+	-	0.007	+	1648.308	3.956	0.055
5	1.222	-	-	0.012	-	1649.310	4.958	0.034
3	1.214	-	+	-	-	1649.354	5.002	0.033
16	1.271	+	+	0.011	+	1650.232	5.880	0.021
7	1.217	-	+	0.009	-	1651.288	6.936	0.013

Table A3. The set of LMEs within 5 AICc units of the best-fitting model of the factors affecting carbon dioxide concentration in Sand Martins. Burrow identity was fitted as a random effect in each case. Model averaging was carried out on the models within 2 AICc units of the best-fitting model (shown in bold). For an electronic copy of the full set of LMEs, contact the corresponding author. Int = Intercept, BN = Brood Number, AT = Air Temperature, CA = Chick Age, BS = Brood Size, Col = Colony, BD = Burrow Depth, T = Time of Day.

Model ID	Int	BN	AT	CA	BS	Col	BD	T	AT X BD	CA x BD	CN x BD	BD x T	AICc	ΔAICc	Weight
240	33773.3	+	2987.6	3703.3	2625.6	-	4800.7	-6221.2	1733.9	-	-	-	5009.4	0	0.07
752	33858.6	+	3013.1	3719.8	2597.4	-	5124.5	-6233.3	1636.9	-	-1489.5	-	5009.6	0.145	0.065
624	33893	+	3019.4	3748.5	2631.8	-	5100.9	-6009.4	-	-	-1598	-	5009.9	0.47	0.055
112	33803.2	+	2992.3	3732.6	2664.4	-	4750.4	-5982	-	-	-	-	5010.1	0.639	0.051
256	32623.5	+	2843	3677.6	2663.5	+	4290.5	-6312.7	1831.8	-	-	-	5010.1	0.647	0.051
768	32767.7	+	2875.4	3694.8	2634.3	+	4628.9	-6319.4	1733.4	-	-1429.2	-	5010.4	0.969	0.043
640	32926.9	+	2897.5	3727.8	2666.4	+	4659.9	-6074	-	-	-1550.1	-	5011	1.578	0.032
128	32779.6	+	2863.7	3711.1	2700.1	+	4293	-6051.6	-	-	-	-	5011	1.595	0.031
880	33757.2	+	3017.8	3729.8	2640.3	-	5084.6	-6105.8	-	712.7	-1681	-	5011.5	2.062	0.025
496	33748.4	+	2987.2	3700.5	2628.5	-	4793.2	-6232.5	1690.7	129.7	-	-	5011.6	2.19	0.023

1264	33773.5	+	2992.1	3706.7	2624.3	-	4800.9	-6223	1742.9	-	-	-36.6944	5011.6	2.207	0.023
1008	33802.6	+	3012.8	3713.6	2603.2	-	5116	-6260.4	1532.2	305.7	-1532	-	5011.7	2.27	0.022
239	32398.3	-	2983.5	4014.8	2931.5	-	4889.3	-6541	1702.6	-	-	-	5011.7	2.329	0.022
1776	33858.7	+	3014.1	3720.5	2597.1	-	5124.6	-6233.7	1638.8	-	-1489.3	-7.78201	5011.8	2.374	0.021
368	33692	+	2989.9	3717.2	2672.5	-	4723.1	-6057.3	-	564.4	-	-	5011.9	2.441	0.021
1648	33890.1	+	2982.7	3720.4	2640.8	-	5101.8	-6005	-	-	-1600.6	294.8258	5012	2.569	0.019
751	32447.6	-	3010.8	4040.2	2906.8	-	5192.1	-6558.9	1607.2	-	-1417.3	-	5012.1	2.689	0.018
1136	33800.3	+	2956.8	3705.4	2673.2	-	4750.7	-5977.7	-	-	-	284.3556	5012.1	2.727	0.018
111	32440.8	-	2991.1	4042.7	2962.6	-	4833	-6302.5	-	-	-	-	5012.2	2.831	0.017
512	32575.3	+	2841.1	3673.1	2668.1	+	4274.4	-6330.7	1767.3	196	-	-	5012.2	2.833	0.017
1280	32623.8	+	2844.9	3678.9	2662.9	+	4290.7	-6313.4	1835.4	-	-	-15.0268	5012.3	2.876	0.017
623	32494.7	-	3017	4065.3	2937.7	-	5168.3	-6335.9	-	-	-1524.5	-	5012.3	2.893	0.016
896	32720.5	+	2888.6	3706	2677.8	+	4616	-6184.1	-	784.7	-1638.7	-	5012.5	3.06	0.015
1024	32683.6	+	2872.8	3687	2641.9	+	4610.8	-6352.9	1610.7	362.7	-1478.7	-	5012.5	3.072	0.015
1792	32767.5	+	2873.9	3693.7	2634.8	+	4628.8	-6318.8	1730.6	-	-1429.4	11.55793	5012.6	3.218	0.014
384	32603.2	+	2854.7	3692.4	2711.1	+	4239.7	-6140.8	-	644	-	-	5012.7	3.3	0.013

255	31346.3	-	2861.3	4007.8	2971.8	+	4443.7	-6632.3	1783.6	-	-	-	5012.8	3.368	0.013
1664	32912.1	+	2855.3	3696.3	2676.8	+	4655.6	-6069.9	-	-	-1552.4	327.3966	5013.1	3.672	0.011
1152	32764.9	+	2822.4	3680.3	2710.4	+	4288.2	-6047.6	-	-	-	319.2677	5013.1	3.676	0.011
879	32428.8	-	3014.9	4009	2921.5	-	5138.5	-6444.7	-	1028	-1651.1	-	5013.2	3.783	0.011
767	31462.8	-	2892.4	4029.7	2949.1	+	4769	-6643.9	1689	-	-1363	-	5013.3	3.878	0.01
367	32382.2	-	2986.9	3991.7	2952.2	-	4787.1	-6393.7	-	879.2	-	-	5013.5	4.048	0.009
127	31519.2	-	2881.1	4035	3002.5	+	4443.6	-6372.7	-	-	-	-	5013.5	4.111	0.009
495	32368.4	-	2981.8	3988.9	2928	-	4856.8	-6569.7	1536.9	499.8	-	-	5013.6	4.231	0.008
1904	33761.4	+	2995.3	3713.4	2645.5	-	5085.8	-6098.9	-	681.5	-1678.9	180.8622	5013.7	4.251	0.008
639	31635.9	-	2913.8	4057.2	2976	+	4797.2	-6400.3	-	-	-1481.8	-	5013.7	4.306	0.008
1007	32411	-	3010.3	4006.7	2900.6	-	5169.1	-6598.6	1377.5	676	-1515.8	-	5013.8	4.38	0.008
1520	33747.6	+	2993.6	3705.1	2626.7	-	4793.1	-6235.6	1701.3	135.9	-	-51.8564	5013.8	4.415	0.008
1263	32399.2	-	2989.2	4018.8	2930.3	-	4890.7	-6543.4	1715.3	-	-	-50.1515	5013.9	4.514	0.007
2032	33801.9	+	3018	3717.3	2601.8	-	5115.9	-6262.8	1540.8	310.6	-1531.6	-41.612	5013.9	4.518	0.007
1392	33696.6	+	2965.7	3699.4	2678.1	-	4724.9	-6049.9	-	530.8	-	195.1827	5014	4.603	0.007
1775	32447.7	-	3011.9	4041	2906.5	-	5192.1	-6559.4	1609.5	-	-1417	-9.32123	5014.3	4.897	0.006

1135	32436.7	-	2956.5	4016.6	2970.7	-	4832.4	-6298.5	-	-	-	278.085	5014.3	4.905	0.006
1647	32491.2	-	2981.1	4038	2946.7	-	5169.2	-6331.8	-	-	-1527	287.9306	5014.4	4.979	0.006

508

Table A4. The full set of GLMMs of the effect of CO₂ on fledging success in Sand Martins. Burrow identity was fitted as a random effect in each case. Model averaging was carried out on the models within 2 AICc units of the best-fitting model (shown in bold). Int = Intercept, BN = Brood Number, Col = Colony.

Model ID	Intercept	BN	CO₂	Col	BN xCO₂	AICc	ΔAICc	Weight
1	13.038	-	-	-	-	63.674	0	0.314
5	13.741	-	-	-3.389	-	64.890	1.216	0.171
2	13.639	+	-	-	-	65.350	1.675	0.136
3	13.042	-	0.135	-	-	65.719	2.045	0.113
6	14.538	+	-	-3.747	-	66.370	2.696	0.082
7	13.781	-	0.421	-3.596	-	66.863	3.189	0.064
4	13.659	+	-0.090	-	-	67.419	3.745	0.048
8	14.676	+	0.466	-4.150	-	68.360	4.686	0.030
16	26.879	+	0.316	-25.778	+	68.691	5.016	0.026
12	13.638	+	0.160	-	+	69.489	5.815	0.017

Table 1. The results of the best-fitting GLMM of the factors affecting fledging success in Sand Martins. Analyses were restricted to those nests for which complete data were available ($n = 768$).

Fixed effect	Estimate	SE	514
Intercept	1.299	0.137	515
Brood number	-0.847	0.162	516
Burrow depth	0.200	0.112	517
Colony	-0.958	0.179	518
Brood number x burrow depth	-0.608	0.166	519
Random effect	Variance		520
Burrow identity	8.681e-06		

Table 2. The results of the best-fitting GLMMs of the factors affecting fledgling number in Sand Martins. Analyses were restricted to those nests for which complete data were available ($n = 768$). Details of fixed effects were obtained by averaging the models within 2 AIC_c units of the best-fitting model. The random effect variance was obtained from the best-fitting model. Relative importance values are the sum of Akaike weights over all the models containing the explanatory variable.

Fixed effect	Estimate	Adjusted SE	Relative importance
Intercept	1.262	0.033	1.00
Brood number	-0.127	0.057	0.22
Burrow depth	0.002	0.013	0.21
Colony	-0.003	0.027	
Random effect			
	Variance		
Burrow identity	1.13e-7		

Table 3. The results of the best-fitting LMEs of the factors affecting carbon dioxide concentration. Analyses were restricted to those nests for which complete data were available ($n = 228$). Details of fixed effects were returned from averaging the models within 2 AIC_c units of the best-fitting model. The random effect variance was obtained from the best-fitting model. Relative importance values are the sum of Akaike weights over all the models containing the explanatory variable.

Fixed effect	Estimate	Adjusted SE	Relative importance
Intercept	33406.5	1365.8	
Brood number	-4409.0	2034	1.00
Air temperature	2949.3	938.5	1.00
Chick age	3714.4	967.6	1.00
Brood size	2641.7	946.1	1.00
Burrow depth	4754.0	1006.6	1.00
Time of day	-6160.3	943.2	1.00
Colony	924.5	1713.9	0.39
Air temperature x burrow depth	992.6	1159.8	0.57
Brood size x burrow depth	-743.8	1052.9	0.49
Random effect	Variance		
Burrow identity	6.70e-6		

Table 4 The results of the best-fitting GLMMs of the effect of CO₂ on breeding success. Analyses were restricted to those nests for which complete data were available ($n = 221$). Details of fixed effects were returned from averaging the models within 2 AIC_c units of the best-fitting model. The random effect variance was obtained from the best-fitting model. Relative importance values are the sum of Akaike weights over all the models containing the explanatory variable.

Fixed effects	Estimates	Adjusted SE	Relative importance
Intercept	13.363	2.287	
Colony	-0.933	3.283	0.28
Brood number	-0.366	1.452	0.22
Random effects	Variance		
Burrow identity	1985		

539

540

541 **Legends to figures**

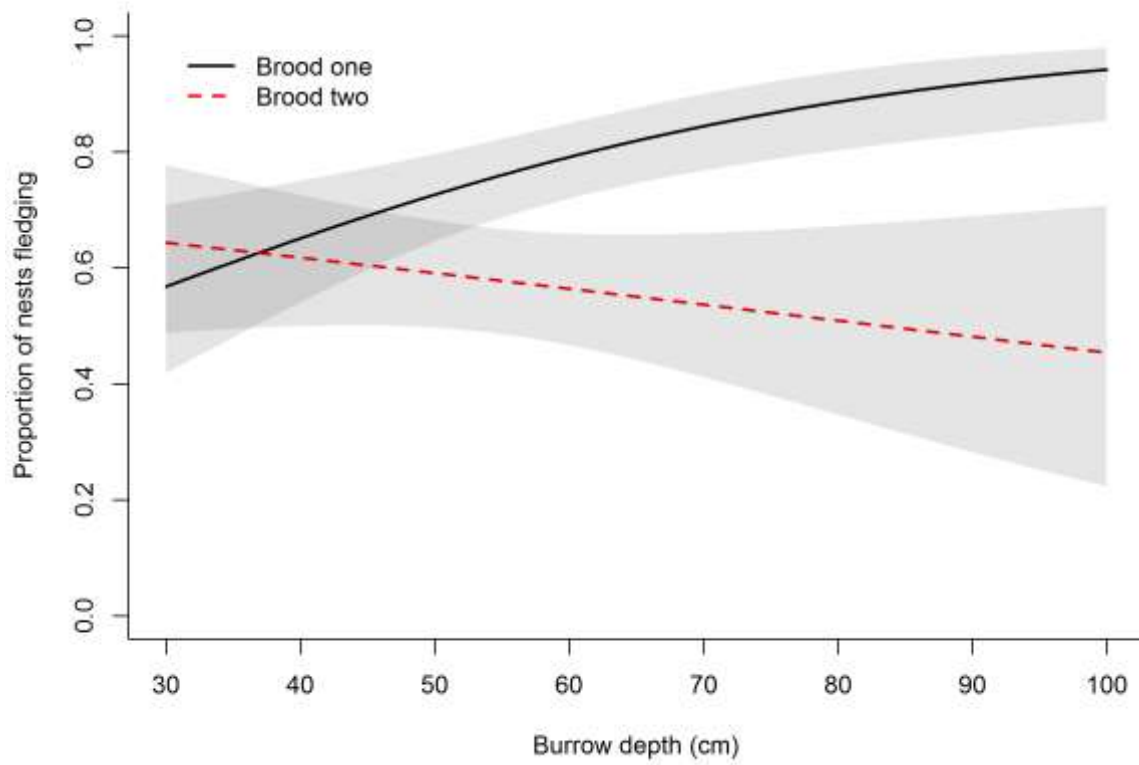
542

543 **Fig. 1** The relationship between fledging success and burrow depth in broods 1 and 2. Lines
544 show predicted values from a GLMM; shaded areas show 95% confidence intervals.

545 **Fig. 2** The relationship between carbon dioxide concentrations and burrow depth in large
546 broods (5 chicks) and small broods (2 chicks). These brood sizes are one standard deviation
547 higher and lower than the mean and rounded to the nearest whole number. Lines show
548 predicted values from an LME; shaded areas show 95% confidence intervals.

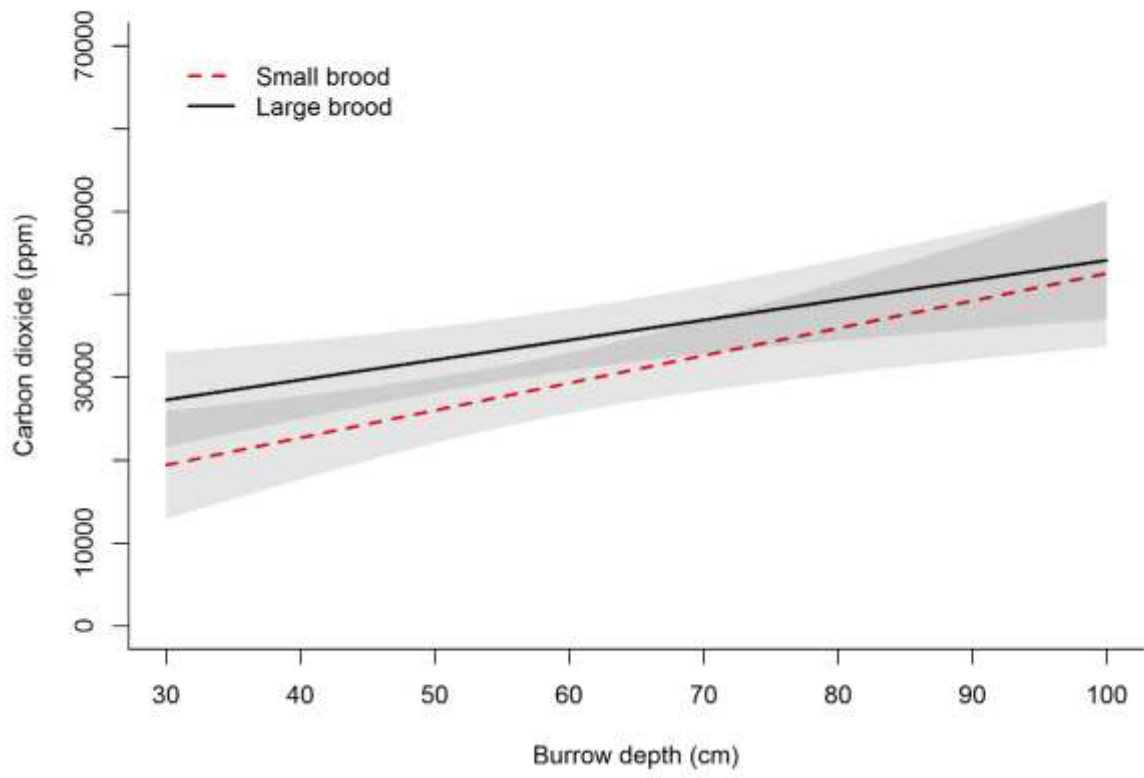
549

550 **Figures**



551

552 **Figure 1**



553

554 **Figure 2**