Burrow depth, carbon dioxide and reproductive success in Sand Martins (*Riparia riparia*)

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Short title: Breeding costs in sand martins

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

Summary

Capsule: Carbon dioxide (CO_2) concentrations in the burrows of sand martins *Riparia riparia* increase with depth but have no detectable impact on fledging success.

Aims: To investigate whether burrow depth and CO_2 concentrations influence reproductive success in sand martins.

Methods: We monitored two Sand Martin colonies along the River Lune, Lancashire (UK) to investigate the effect of burrow depth on reproductive success. We also measured CO_2 levels in a sample of burrows to test whether burrow depth predicts CO_2 concentration, and to test for a relationship between CO_2 concentration and breeding success.

Results: Burrow depth was significantly correlated with fledging success, but the correlation was positive in first broods and negative in second broods. The highest CO_2 concentration recorded was 73 650 ppm and the mean concentration across burrows was 31 757 ppm. However, while CO_2 concentrations were positively correlated with burrow depth after controlling for the number and age of nestlings, they were not correlated with reproductive success.

Conclusion: There are reproductive costs associated with deeper burrows in second broods, but these could not be attributed to CO_2 concentrations despite the exceptionally high levels recorded. This study highlights the need for further investigation into gas exchange and the potential impacts of, or adaptations to, CO_2 accumulation in avian burrows.

Introduction

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

Gas exchange presents another significant physiological challenge to burrowing animals. Models suggest that in burrows with narrow entrances, the main source of air flow is through the soil, potentially leading to a significant accumulation of carbon dioxide (CO_2) and corresponding decrease in oxygen (O_2) concentration (Wilson & Kilgore 1978, Withers 1978). The CO_2 concentration of free air is typically around 400 ppm but concentrations over 50 000 ppm have been recorded in the burrows of some species and these levels are likely to have severe physiological effects (Boggs *et al*. 1984, Schmidt-Nielsen 1997). The concentration of CO_2 is positively correlated with the metabolising mass of the burrow's occupants due to respiration (White *et al.* 1978, Wickler & Marsh 1981), but even in unoccupied burrows CO_2 concentrations are higher than in free air (Birchard *et al.* 1984), presumably due to soil microbe and root respiration in the substrate. The levels also depend on abiotic factors such as the substrate, season, burrow depth and structure (Wilson & Kilgore 1978, Arieli 1979, Birchard *et al.* 1984), but more work is needed to understand how biotic and abiotic influences interact.

Most studies investigating the impact of exposure to high CO_2 concentrations on burrowing animals have addressed physiological responses, specifically how fossorial and semi-fossorial species (i.e. animals which spend all or some of their lives underground, respectively) may be adapted to such conditions. Burrowing birds, for example, have a lower ventilatory response to elevated CO_2 concentrations than non-burrowing species (Boggs & Kilgore 1983; Boggs *et al*. 1984). Comparisons between closely related fossorial and non-fossorial mammals have shown higher skeletal muscle myoglobin concentrations and slower metabolisms in the former (McNab 1966, Lechner 1976). Other research has examined the effects of elevated CO_2 levels on survival in poultry farms, where concentrations are high due to bird densities and low ventilation. In these farms, CO_2 levels greater than 2500 ppm increase the risk of heart disease (Frame *et al.* 1999) and when greater than 4000 ppm can cause chick mortality through lethargy and reduced feeding (Donaldson *et al.* 1995).

Despite the implications of this research, very little is known about the potentially adverse effects of CO_2 on the reproductive success of animals which raise their young in burrows. The young of semi-fossorial species may be particularly susceptible because they are exposed to high CO_2 and low O_2 concentrations for extended periods of time, yet may not show the same adaptations to these conditions as fossorial species (Soholt *et al.* 1973). A study of the European Bee-Eater *Merops apiaster* showed that chicks raised in burrows with CO_2 concentrations above 60 000 ppm had noticeably laboured and rapid breathing, averaging about 100 breaths/min compared with 68 breaths/min for chicks exposed to concentrations of 30 000 ppm (White *et al.* 1978). Being exposed to such high concentrations could inhibit development (Scheid 1982) and reduce begging and feeding (Donaldson *et al.* 1995). This could be especially problematic in birds, where adults take direct cues from begging chicks when making choices about food distribution and feeding frequency (Kilner & Johnstone 1997, Leonard & Horn 2001). However, only a small number of other studies have measured CO_2 levels in the burrows of wild birds (Birchard *et al.* 1984, Ar & Piontkewitz 1992, Lill & Fell 2007) and the relationship between burrow depth and CO_2 accumulation has rarely been investigated.

Sand Martins *Riparia riparia* are colonial Afro-Palearctic migrant birds that nest in burrows excavated into river banks and man-made quarries. They are a Species of European Conservation Concern (BirdLife International 2004), but the underlying causes of within-colony variation in reproductive success are poorly known. Sand Martins arrive in Europe from West Africa in spring and start digging new burrows or renovate pre-existing ones (Szép *et al.* 2003, Turner & Rose 2010). Each burrow has a single entrance and the nest is placed in a small chamber at the far end at a depth varying from 30cm to over 100cm (Heneberg 2003, Turner & Rose 2010). In a comparative study of three burrowing bird species – Sand Martins, Rhinoceros Auklets *Cerorhinca monocerata* and Burrowing Owls *Athene cunicularia* – the burrows of Sand Martins had the highest mean CO_2 concentrations (32 000 ppm), the highest overall CO_2 concentration (67 000 ppm) and the widest range (4000 ppm to 67 000 ppm, Birchard *et al.* 1984). They are therefore an ideal model system for understanding the relationship between burrow depth, CO_2 concentration and reproductive success.

Wickler and Marsh (1981) took gas samples from Sand Martin burrows and reported a positive correlation between CO_2 content and burrow depth. Burrow depth is likely to exacerbate CO_2 accumulation because air convection, due to either wind or the movement of occupants, is typically the most important mechanism of gas exchange in animal burrows yet may be restricted at greater depths (White *et al.* 1978, Wilson & Kilgore 1978, Withers 1978, Wickler & Marsh 1981, Birchard *et al.* 1984, Lill & Fell 2007). Another previous study of Sand Martins reported a negative correlation between burrow depth and breeding success, but CO_2 concentrations were not measured (Cruickshank 2013). In our study, we monitored all nesting attempts at two colonies during a single season in order to: (1) investigate how different components of reproductive success vary with burrow depth; (2) test whether burrow depth predicts CO_2 concentration after controlling for other influences; and (3) test whether CO_2 concentration is correlated with breeding success.

Materials and methods

STUDY POPULATION AND NEST MONITORING

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

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

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

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

A total of 824 nests were monitored throughout the breeding season. All dates were converted to a Julian Date (JD, days since 1st January) for analyses. Active nests were sometimes found late in the season in burrows that had previously been unoccupied; these were considered unlikely to be first breeding attempts, especially as pairs are known to sometimes change burrow between broods (Cowley 1983). Second broods were therefore classified as follows: ‘true’ second broods were first identified as a second breeding attempt in a nest that had previously fledged; the lay date for the earliest known true second brood was 15th June (JD 165) and this was then used as a threshold for determining second broods in other burrows. All eggs laid on or after this date were considered part of a second brood and all those before, a first brood (i.e. including replacement clutches).

CARBON DIOXIDE CONCENTRATION

CO_2 was measured (in ppm) throughout the breeding season using a GM70 CARBOCAP probe (Vaisala, Vantaa, Finland) calibrated to 10% CO_2 concentrations. The probe was placed directly alongside the nest at the end of the burrow and left in place until the reading stabilised (approximately five minutes), and the time of day was then recorded. The probe was allowed to return to ambient CO_2 concentrations (measured as 380-450 ppm during each day of the study), before the next sample was taken; 228 samples were taken throughout the season. Many nests were only sampled once ($n = 122$) but repeat measurements were made for those nests which survived long enough ($n = 53$ nests, each sampled twice). Repeat measurements were taken once within the first part of the nestling period (day 1-10) and once within the last nine days before fledging (day 11-20). For burrows in which chicks may have been old enough to fly (age 16-20), all chicks were counted and the CO_2 probe inserted only if all were present. CO_2 concentration was also measured in a sample of unoccupied burrows ($n = 66$) for which depth was measured. Ambient air temperature was obtained to the nearest 0.01°C from TGP-4017 Tinytag data loggers (Gemini, Chichester, UK) placed in trees between the colonies and set to record every 30 minutes throughout the entire breeding season. These were calibrated in a United Kingdom Accreditation Service approved laboratory using 0 and 30°C calibration points.

STATISTICAL ANALYSES

Burrow Depth and Reproductive Success

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

The distribution of the number of fledglings showed high zero inflation and so a hurdle model was fitted (Zuur *et al.* 2009). The *glmmADMB* package (Fournier *et al.* 2012) in R version 3.2.3 (R Core Team 2015) was used to fit two separate generalised linear mixed effects models (GLMMs). In one, the response variable was a binary indicator of whether or not the nest fledged at least one chick, hereafter ‘fledging success’. In the other, restricted to successful nests, the response variable was the number of chicks fledged, hereafter ‘fledgling number’.

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

Burrow Depth and Carbon Dioxide Concentration

Linear mixed effect models (LMEs) were used to investigate the relationship between burrow depth and CO_2 levels; models were fitted with the *lme4* package (Bates *et al.* 2015). CO_2 concentration was fitted as the response variable and burrow depth, brood number (1 or 2), colony (north or south), brood size and chick age (measured in days from hatch date) were fitted as fixed effects (number of samples per age group: age 0-5, n = 55; age 6-10, n = 69; age 11-15, n = 59; age 16+, n = 45); the latter two were included together with their interactions with burrow depth because these factors were considered likely to influence CO_2 levels based on previous work (Wickler & Marsh 1981). Time of day (timing of the samples throughout the day: 07.00-10.00, n = 36; 11.00-14.00, n = 54; 15.00-18.00, n = 121; 18.00 or later, n = 17) and ambient air temperature are also likely to affect CO_2 concentrations due to the impact of light levels and temperature on soil microbe respiration (Lloyd & Taylor 1994), and so were included as fixed effects together with their interactions with burrow depth. Burrow identity was included as a random effect in order to control for repeated measures. Continuous variables were centred and standardised before analysis; brood number and colony were centred (Schielzeth 2010). All variables were included in the analyses because correlations between them were weak ($r < 0.3$) and VIFs small (< 2; Zuur *et al.* 2009). Models were compared, averaged and validated using the same approach described above. To compare CO_2 concentrations in occupied and unoccupied burrows, the mean level per burrow was analysed using a Mann-Whitney U Test. A linear regression was used to investigate the relationship between unoccupied burrow depth and CO_2 concentration.

Carbon Dioxide Concentration and Reproductive Success

GLMMs were used to investigate the relationship between carbon dioxide concentration and fledging success using the *lme4* package (Bates *et al.* 2015). The effect of CO_2 on fledgling number was not considered as fledgling number was very strongly correlated with brood size, an important determinant of CO_2 concentration. Due to missing fledging success data, analyses were carried out using a sub-sample of the dataset (*n* = 221 samples from 175 nests). Fledging success was fitted as the response variable in a model with a binary error distribution and logit link function. CO_2 concentration, brood number (1 or 2), colony (north or south) and the interaction between CO_2 concentration and brood number were fitted as explanatory variables. The interaction term was included because reproductive costs are likely to differ between broods, and the potential costs associated with CO_2 concentrations may therefore also differ. Burrow identity was included as a random effect to control for repeated measures. CO_2 concentration was centred and standardised before analysis; brood number and colony were centred (Schielzeth 2010). All variables were included in the analyses as correlations between them were weak ($r < 0.4$) and VIFs small (< 2; Zuur *et al.* 2009). Models were compared, averaged and validated using the same approach described above.

Results

BURROW DEPTH AND REPRODUCTIVE SUCCESS

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

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

BURROW DEPTH AND CARBON DIOXIDE CONCENTRATION

The average CO_2 concentration in occupied burrows was 31 757 ppm (± 17 152 sd), but ranged from 570 ppm to 73 650 ppm. In the analysis of the factors affecting these levels, all fixed effects and interactions were contained in the model set used for averaging (Table 3, Table A3). Brood number had the largest effect, with CO_2 concentrations significantly lower in nests containing second broods (Table 3, first brood mean: 35 356 ppm ± 16 905 sd, second brood mean: 24 557 ppm ± 15 053 sd). Time of day and air temperature were negatively and positively correlated with CO_2, respectively (Table 3). CO_2 concentration was also positively correlated with chick age, brood size and burrow depth (Table 3). The interaction between brood size and burrow depth revealed a more marked effect of depth on CO_2 in smaller broods (Fig. 2), but the effect sizes for all other interactions were extremely small (Table 3).

In unoccupied burrows, CO_2 concentration ranged from 350 ppm to 33 180 ppm with a mean of 6700 ppm, significantly lower than in occupied burrows ($W = 27866$, $P < 0.001$). CO_2 concentration in unoccupied burrows was also positively correlated with burrow depth (linear regression: $r = 0.415$, $P < 0.001$).

CARBON DIOXIDE CONCENTRATION AND REPRODUCTIVE SUCCESS

Fledging success was not correlated with burrow CO_2 concentrations. Colony and brood number were retained in the best-fitting model set but effect sizes were low and therefore unlikely to be biologically meaningful (Table 4, Table A4).

Discussion

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

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

Whatever the mechanism behind the positive relationship between burrow depth and reproductive success in first broods, the benefits of a deeper burrow are apparently outweighed by the associated costs in second broods. Declines in reproductive success throughout the season are not uncommon in birds, for example due to reduced food availability (Crick *et al.* 1993, Møller 2002) or the energetic costs associated with second breeding attempts (Verhulst & Tinbergen 1991). However, this does not explain the negative effect of burrow depth on reproductive success in second broods. It could be that birds using deep burrows for their first brood, in which there was generally higher fledging success, face trade-offs which lead to reduced success in their second. Such trade-offs are difficult to determine because Sand Martins often change burrows between broods (Cowley 1983), but they may be driven by the accumulation of ectoparasites which impose significant costs on nestlings (Szép & Muller 2000). The relationship between parasite load and burrow depth requires further study.

CO_2 concentrations in occupied burrows were significantly higher than in unoccupied burrows and, in common with other studies, increased with the age and number of chicks (Wilson & Kilgore 1978, Withers 1978, Wickler and Marsh 1981, Birchard *et al.* 1984). High CO_2 levels can reduce begging and feeding behaviour, leading to lower growth rates and increased mortality through reduced food consumption (Donaldson *et al.* 1995, Frame *et al.* 1999). Indeed, it was expected that high CO_2 would be one of the primary drivers of reduced fledging success in deeper burrows. Our findings suggest, however, that it had no influence on fledging success. CO_2 concentration in burrows was positively correlated with ambient air temperature, and warmer temperatures are likely to correspond with a higher abundance of the insects on which Sand Martins feed (Bale *et al.* 2002, Turner & Rose 2010). It could be that this increase in prey abundance offsets any negative effects of elevated CO_2 concentration, meaning that chicks remain well fed despite having reduced begging capabilities. Alternatively, the effects of CO_2 concentration on chicks may not have been detected in our study. CO_2 varied significantly throughout the day and those in deeper burrows may be exposed to higher concentrations for longer periods of time; this would not be reflected in our measures of CO_2 concentration. It could also be that Sand Martins are unaffected by high CO_2 levels due to physiological adaptations (Boggs *et al.* 1984), or that there are post-fledging fitness costs such as reduced offspring survival. Investigating these possibilities would increase our understanding of avian behaviour and physiology in burrowing species.

The positive correlation between burrow depth and CO_2 concentration was stronger in small broods, perhaps indicating that large broods produce enough CO_2 to mask any effect of depth. This may be because airflow in shallower burrows can reduce CO_2 levels providing that broods are relatively small. It is also possible that a significant proportion of CO_2 accumulation is accounted for by bacteria within the burrows; bacteria may be enhanced by large broods producing more faecal matter. This might explain why temperature is highly correlated with CO_2 concentration as soil microbe respiration is greater at higher temperatures (Lloyd & Taylor 1994). The large overall effect size of burrow depth indicates that, even after accounting for other abiotic and biotic factors, it is an important determinant of the gas composition of burrows, as suggested by previous studies (Maclean 1981, Wickler & Marsh 1981). In fact, as far as we are aware, the CO_2 concentrations reported here are the highest found in burrows of any vertebrate species to date, and far greater than those thought to be dangerous for birds in poultry farms (Donaldson *et al.* 1995). This makes the absence of any relationship between CO_2 concentration and reproductive success all the more intriguing.

Acknowledgements

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

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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

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

Table A4. The full set of GLMMs of the effect of CO_2 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**	**CO_2**	**Col**	**BN xCO_2**	**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

Tables

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**
Intercept	1.299	0.137
Brood number	-0.847	0.162
Burrow depth	0.200	0.112
Colony	-0.958	0.179
Brood number x burrow depth	-0.608	0.166
Random effect	**Variance**	
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	
Brood number	-0.127	0.057	1.00
Burrow depth	0.002	0.013	0.22
Colony	-0.003	0.027	0.21
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 CO_2 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.

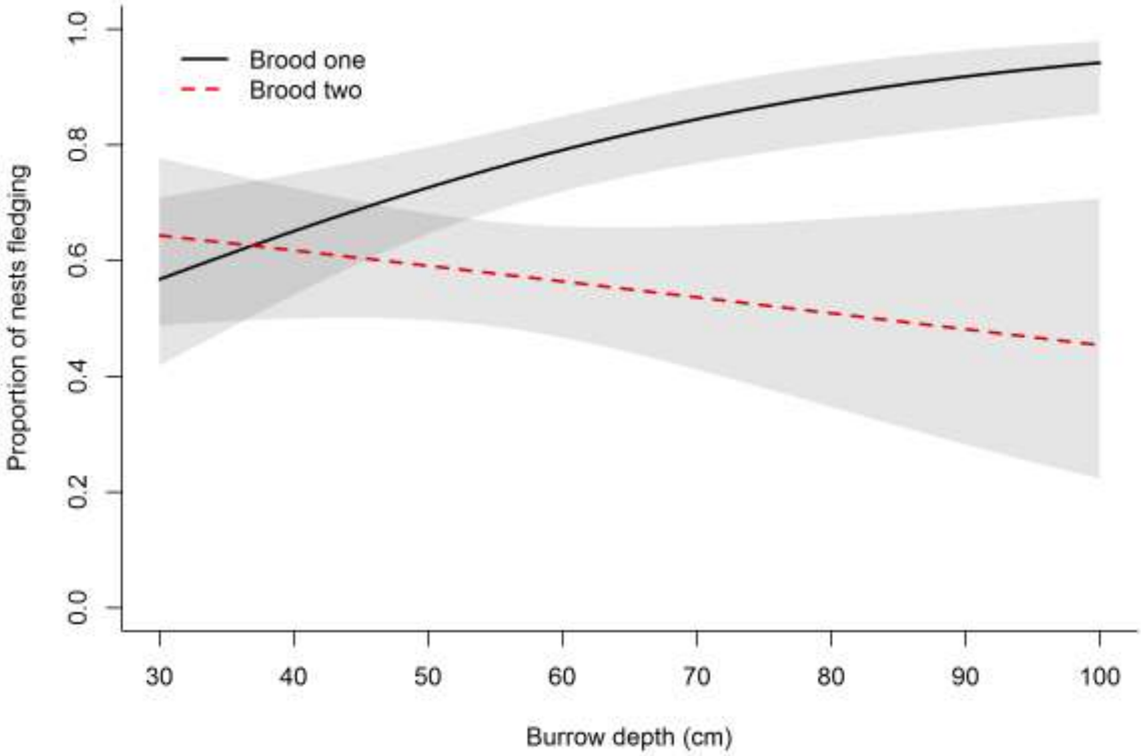
Fixed effects	**Estimates**	**Adjusted SE**	**Relative importance**
Intercept	13.363	2.287	
Colony	-0.933	3.283	0.28
Brood number	-0.366	1.452	0.22
Random effects	**Variance**		
Burrow identity	1985		

Legends to figures

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

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

550 # Figures



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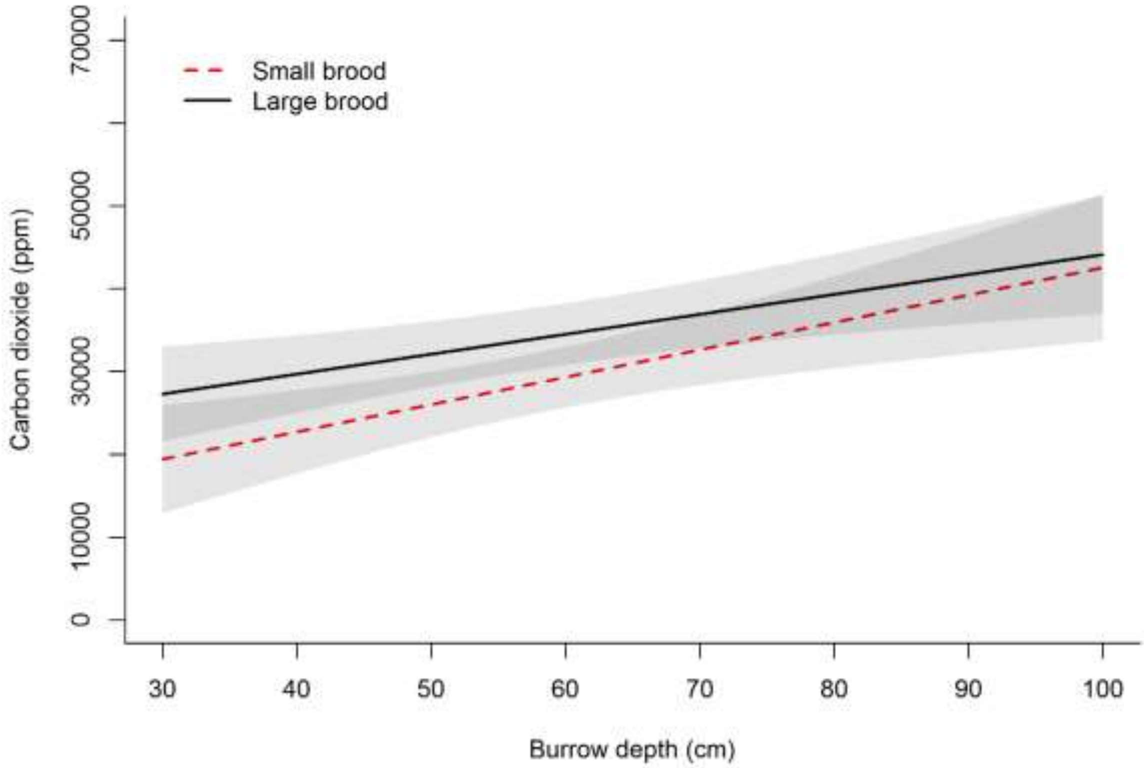
552 **Figure 1**



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554 **Figure 2**