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Short communication

The importance of rainfall to a cavity-nesting species

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Reproductive success in birds is influenced by a variety of factors, which differ widely among species (Newton 1989). Although nest predation is often believed to be the most important of these variables (Ricklefs 1969, McCleery & Perrins 1991), weather conditions may also play a key role (Elkins 1983). In addition to influencing food availability (Bryant 1978, Martins & Wright 1993), weather may directly affect the energetic expenditure of flight and the cost of thermoregulation (Drent 1973, Tinbergen & Dietz 1994). Responses and impacts of climatic fluctuations range from apparently subtle change, such as variation in timing of nesting (e.g. McAuley & Longcore 1989) and clutch size (e.g. Rotenberry & Wiens 1989), to major perturbations, including the failure of a large proportion of a population to breed (Valle *et al.* 1987) or the loss of an entire year's reproductive effort to storms or other catastrophe (Wooller *et al.* 1992).

Species that nest in tree cavities might seem to be protected from the direct effects of adverse weather, such as rainfall, but this may depend on the inclination of the cavity entrance. Although several studies have investigated how hole orientation affects nest microclimate, in particular temperature (e.g. Hooge *et al.* 1999, Wiebe 2001), the importance of cavity inclination has generally been ignored. The Green Woodhoopoe *Phoeniculus purpureus* (also known as the Red-billed Woodhoopoe) is a co-operatively breeding, territorial bird found in a variety of forest types throughout much of sub-Saharan Africa. Like other secondary cavity-nesting species, they cannot excavate their own nests and are limited to either natural tree cavities or old woodpecker and barbet holes. The breeding season of the Green Woodhoopoe in South Africa (mid-November to mid-March) coincides with the summer rains, creating the possibility of nest flooding.

We investigated the impact of rainfall on fledging success over an 18-year period. We also examined the size and inclination of natural nest-hole entrances, and the importance of the latter on success rate. Using nestboxes, the importance of cavity inclination for rain intake was investigated following a number of heavy rainfall events.

METHODS

The study was conducted in the Morgan's Bay region of South Africa (32°43′S, 28°19′E). Daily rainfall data were made available by a local weather station situated *c.* 3 km north-west of the centre of the study area (32°42′S, 28°18′E). The mean annual rainfall (1973–99) was 982 mm, with 57% occurring during the Green Woodhoopoe breeding season. Between 10 and 29 groups of Woodhoopoes were closely monitored each breeding season from 1982 to 1999 (for a total of 418 flock years). When possible, nestling dates were established by watching the provisioning behaviour of group members or inferred from fledging dates. The number of fledglings per group was also noted. It was assumed that all groups attempted to breed each year (i.e. no fledglings represents nest failure) and each group had only one nesting attempt (data not shown). Thirty-four natural nests were measured for the size and angle of inclination of the entrance hole. The angle of inclination was determined by placing a ruler flush to the entrance and next to a spirit level, and measuring the ensuing angle with a protractor: a positive value indicated that the entrance hole faced upwards whereas a negative value indicated a downward angle. An angle of 0° implied that the entrance hole faced horizontally, and the larger the angle, the greater the deviation towards a vertical inclination.

In May 2001, three nestboxes (400 mm × 150 mm × 150 mm) were placed within 5 m of one another at each of 20 known nesting sites. Between November 2001 and February 2002, after five heavy rainfall events (mean ± se rain within 2 h: 48.0 ± 4.4 mm), the height of standing water within seven empty pairs of nestboxes was measured. Within each pair of nestboxes, one entrance hole had a positive angle of inclination (mean ± se: +14.3 ± 1.7°) and the other had a negative angle of inclination (–6.4 ± 2.8°). To enable matched-pair testing (positive vs. negative angle of inclination), we focused on only two of the available nestboxes at each chosen site. All seven pairs were checked within 2 h of the cessation of heavy rainfall and each nestbox was checked within 2 min of its partner. After measuring the height of water present, the nestbox was emptied. Although boxes were present at 20 sites, not all sites included one box with an upward-facing and one with a downward-facing entrance hole. Furthermore, it would not have been logistically feasible to collect data from more than the seven chosen sites within a realistic time period following the cessation of rainfall.

All statistics were completed using MINITAB v.12 (Minitab Inc. 1998) with a level of significance set at 0.05. Proportions were arcsine($\sqrt{x}$)-transformed prior to

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analysis. Data sets were first analysed for normality and homogeneity of variance, and parametric or non-parametric tests were used subsequently, depending on the results of this analysis.

RESULTS

We began by establishing a correlation between fledging success and rainfall during the breeding season. During the 18-year study period, 48.8% (range: 22.7–75.0%) of nests (n = 418) fledged at least one young. Considering breeding attempts that reached the chick stage, 92% of nestlings were present between 1 December and 15 March. The proportion of successful nests in a breeding season was significantly and negatively correlated with the total amount of rainfall between these dates (r^2 = 24.0%, $F_{1,16}$ = 5.07, P = 0.039; Fig. 1). There was no significant relationship between the average number of fledglings per nest and the amount of rainfall during the breeding season, either when considering all nests (r^2 = 11.6%, $F_{1,16}$ = 2.10, P = 0.167) or when considering only those that were successful (r^2 = 3.3%, $F_{1,16}$ = 0.54, P = 0.473).

We then established the importance of cavity entrance inclination. Thirty-eight per cent of natural nests (n = 34) were found to face upwards. Breeding attempts in natural holes were significantly more likely to be successful if the angle of inclination of the entrance hole was negative (11 of 15 attempts) than if it was horizontal or positive (seven of 19 attempts; *G*-test: G_1 = 4.96, P < 0.05).

We therefore postulated that nest flooding may have a serious impact on fledging success, and we tested this hypothesis through experimentation. Nestboxes with holes inclined upwards collected significantly more water (mean ± se: 5.54 ± 0.45 mm) than those facing downwards (0.28 ± 0.08 mm; paired *t*-test on means: t_7 = 12.70, P < 0.001). The entrance holes to natural nest-sites were significantly larger than those in nestboxes (median: natural = 2010 mm^2, nestbox = 1590 mm^2; Mann–Whitney U = 1043, P < 0.001). For nestboxes (mean ± se: +14.3 ± 1.7°) and natural holes (+31.2 ± 5.3°) with a positive angle of inclination, natural holes were found to be significantly more positive (t_{18} = 2.27, P = 0.036).

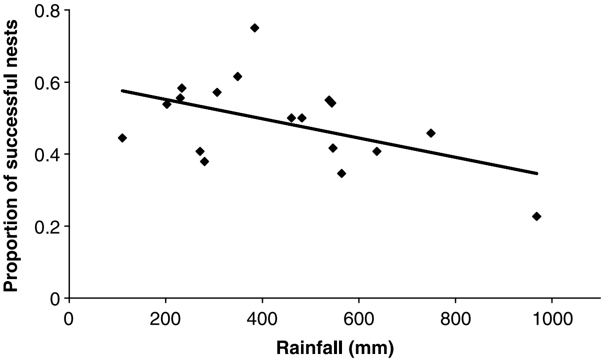

Figure 1. Relationship between the total rainfall from 1 December to 15 March (when 92% of nests have chicks present) and the proportion of Green Woodhoopoe nests that produced at least one fledgling. n = 18 years. A best-fit line is shown.

DISCUSSION

Green Woodhoopoes suffered lowered nesting success in wet breeding seasons, with 25% of the variation in fledging success explained by the total rainfall in that period. The likelihood of fledging young could have been affected adversely in two main ways. First, wet conditions might have reduced the amount of food delivered to the young, either because food was harder to find during rain (e.g. Siikamäki 1996) or because adults sheltered during heavy rainfall to avoid problems associated with waterlogged feathers (Radford *et al.* 2001). However, poor foraging conditions should also have led to brood reduction in some cases, and there was no relationship between the average number of fledglings per nest and the amount of rainfall during the breeding season. Reduced foraging opportunities might theoretically have led to a decrease in average fledging weight, and a consequent reduction in subsequent survival chances of the young (e.g. Tinbergen & Boerlijst 1990, Magrath 1991). We have no data to test this, but since Green Woodhoopoes are not dependent on aerial foraging, and garner much of their diet from the probing of holes in tree bark (Ligon & Ligon 1978), adverse effects of rainfall on diet might be minimal.

The second way in which rainfall could have affected fledging success was through the flooding of nest cavities. Du Plessis (1989) estimated that 11.4% (n = 79) of Green Woodhoopoe nest failures in the area resulted from flooding. Although the amount of water found in nestboxes following individual rain showers was not large, four factors may have increased the impact of rain in natural holes. First, the entrance holes of natural cavities were significantly larger than those of nestboxes, enabling the entry of more rain. Secondly, the mean angle of inclination of upward-facing natural holes was significantly greater than that of nestboxes, again increasing the likelihood of water entering the cavity. Thirdly, rainwater flowing down the trunk (stem flow) might have entered positively inclined natural holes that were flush with the trunk. Finally, there may have been less seepage from the bottom of natural holes and rain may therefore have accumulated over the 4-week nestling period, causing longer-lasting problems to the occupants. There may have been insufficient flooding to cause drowning (although Dennis (1971) reported several instances in which Pileated Woodpecker *Dryocopus pileatus* nests were filled with water, and full flooding of Vasa Parrot *Coracopsis vasa* nests has been recorded, J. Ekstrom pers. comm.). However, accumulation of water in the nest may have led to thermoregulatory problems, especially for young chicks that were unable to maintain their own body temperature (King & Farner 1961). It is also possible that recently fledged young caught in heavy rainfall may have suffered fatal reductions in body temperature, thus reducing observed fledging success (J.D. Ligon pers. comm.).

Natural nests with downward-facing entrances were more likely to be successful than those that had a cavity opening with a positive angle of inclination. Although nest openings that point downwards are believed to aid in nest defence, there is no evidence to support this (e.g. Hooge *et al.* 1999). Predation plays an important role in Green Woodhoopoe reproductive success – nests may be invaded by driver ants, genets or snakes – but the data presented here suggest that rainfall was also a key element in the fledging success of this species. Given that nest openings facing even slightly downwards tended to prevent rain from entering the cavity, even during strong winds, why do individuals choose cavities that face upwards and are thus susceptible to potential flooding? The benefits of a cavity nest-site result from a complex interplay of factors, including predation risk (Nilsson 1984, Li & Martin 1991), proximity to food, temperature and lack of parasites (Wiebe 2001), and so the selected upward-facing holes may be superior in other ways. In addition, nest-sites are known to limit habitat occupancy in the Green Woodhoopoe (Du Plessis 1992). There may therefore be little choice in available sites (Ligon 2001) and it is better to attempt breeding in an upward-facing cavity than not at all.

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