Corella, 2006, 30(1): 16–20

EFFECT OF RAINFALL ON BREEDING OF GREY SHRIKE-THRUSHES *Colluricincla harmonica*

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Received: 9 September 2005

Observational data from 24 nests in a single area in central New South Wales over eight years were used to determine whether the reproductive output (eggs laid, chicks fledged, number of broods) in a breeding season was related to rainfall before and during the breeding season in an endemic passerine, the Grey Shrike-thrush *Colluricincla harmonica*. In a species where clutch size is low and relatively fixed, annual rainfall nevertheless influenced both clutch size (correlation coefficient r = 0.62) and number of successful nests (r = 0.94). There was a strong relationship (r = 0.98) between annual rainfall and number of chicks fledged over the breeding season. It appears that the Grey Shrike-thrush can fine-tune reproductive output in response to rainfall (presumably mediated via food availability), an ability that would assist adult survival while maximizing reproductive output where climate and resources fluctuate markedly.

INTRODUCTION

Determinants of clutch size and reproductive output in passerine birds have been discussed for many years. Environmental factors such as food, climate, predators, latitude and elevation are thought to influence clutch size and therefore reproductive output (Cody 1966; Ricklefs 2000). Birds may respond to greater resource availability with a range of strategies including laying larger clutches, initiating breeding earlier or fledging chicks more rapidly, which allows the laying of additional clutches within a breeding season (Snow 1958; Martin 1987).

With a highly variable climate, especially in terms of rainfall, Australia is noted for opportunistic breeding in many terrestrial birds as a response to this variability (McGilp 1923a, 1923b, 1924; Keast 1959 Schodde 1982). For instance, cyclonic weather systems in semi-arid areas of Western Australia in 1953 and 1955 triggered breeding in several species of passerines, and similar weather in 1992 stimulated breeding at Barrow Island, Western Australia (Serventy and Marshall 1957; Ambrose and Murphy 1994). Chats (Meliphagidae; *Epthianura* spp.) inhabiting arid and semi-arid areas have been recorded breeding opportunistically after abundant rain, with the more xeric species showing greater flexibility in response than more mesic species (White 1950; Williams 1979). The breeding times of Superb Fairy-wrens *Malurus cyaneus* in low rainfall areas was less seasonal than in high rainfall areas, and followed good rains (Tidemann and Marples 1987).

While nomadic arid-zone birds were more likely to breed opportunistically, sedentary arid-zone species showed a spring-breeding peak, the extent of which varied according to the amount of rainfall in the preceding summer, autumn and winter (Schodde 1982). White-browed Treecreepers *Climacteris affinis* adjusted the commencement of breeding and number of clutches laid per season in response to variation in rainfall (Radford 2004). The ultimate factor underlying the breeding response to rainfall is assumed to be fluctuation in the food supply (Schodde 1982).

Few studies have looked explicitly at the relationship linking breeding and rain and it is clear that many environmental effects on avian life histories have not been fully explored. The present study evaluated the influence of rainfall on reproductive output (clutch size, number of breeding attempts and number of chicks fledged) in the Grey Shrike-thrush *Colluricincla harmonica*, a sedentary, 65 gram member of the family Pachycephalidae and a common inhabitant of forests, woodlands and scrubs throughout Australia. It shows slight sexual dichromatism and is known to breed in socially monogamous pairs (Higgins and Peter 2002) with a high level of biparental care (Stevens and Watson 2005). Reproductive output over eight breeding seasons is compared with rainfall in the same calendar years. As well as documenting the effect of rainfall on reproductive performance of this endemic species the influence of resource availability on reproduction in general is also discussed.

METHODS

Study sites

Grey Shrike-thrush ('shrike-thrush') nests were studied at a homestead in the Warrumbungle Mountains (31°17'S, 149°03'E; 800 m asl) approximately 25 kilometres west of Coonabarabran in central New South Wales. The homestead is in eucalypt forest with trees to within 50 metres. In this district, shrike-thrushes nest in spring/summer, between August and February. Clutch size was recorded for 24 nests over the breeding seasons 1995/96 to 2003/04: 21 of these were in five different locations in four hanging planters, all within three metres of each other, on the outside walls of the homestead; one nest was at another property three kilometres from the homestead and two nests were in eucalypt forest 400 metres from the homestead. All the nests at the homestead were situated under the eaves of the house and were therefore protected from rain.

For determination of the number of nests in a season and annual reproductive success, the study was restricted to the 20 nests at the homestead over eight breeding seasons (1996/97 to 2003/04), involving four females and three males. One female, paired with two different males, provided data for five of those seasons (1996/97 to 2000/01), three for one season each. For these parts of the study, the data from nests in 1995/96, at the other property and in the bush were not included as knowledge of re-nestings was incomplete for these other birds.

Observational methods

Shrike-thrush nests were studied by direct observation with the aid of 8 × 30 Swarovski binoculars. Because all nests in this study were at heights of less than two metres, contents could be checked by holding a mirror over the nest. Male and female shrike-thrushes were distinguished mainly by the plumage of the head and neck and the colour of the bill. Individual shrike-thrushes were identified by a combination of appearance (subtle difference in plumage of the head and upper body) and behaviour, i.e. whether they were habituated to the presence of people or not (see Stevens and Watson (2005) for description of the process of habituation).

Rainfall was measured using a Nylex rain gauge situated 100 metres from the homestead. The number of eggs laid, nesting attempts (both successful and unsuccessful) and chicks fledged by the female occupying the homestead territory during each of eight breeding seasons was recorded and plotted against rainfall. The reproductive data were analysed in terms of rainfall in the calendar year (January–December) in which the breeding season started and rainfall just prior to and during the main breeding season (July–December).

Analyses

Mean values are given with standard errors (SE). Linear Regression Analysis and univariate Analysis of Variance (ANOVA) were performed using the statistical package SPSS (SPSS Inc. 2003). Probability-Probability (P-P) plots and scatterplots of residuals were prepared using the linear regression model in SPSS, to see if the assumptions of the model (including normality) hold for each response variable. The values for Type III F-tests were used to see to what extent reproductive performance depended on rainfall and female identity (the latter included as a factor, given that one female provided results for five seasons). A further factor, clutch order, was included in clutch size analyses, to see whether there were differences between first and later clutches in a season. Pearson product-moment correlation coefficients (r) and coefficients of determination (r^2) from these analyses were used to show to what extent the model accounted for the number of eggs laid, nesting attempts and chicks fledged by a female shrike-thrush during the breeding season.

RESULTS

Rainfall

The longer-term average rainfall at the study site for the years 1986–2003 was 1042.0 ± 69.5 millimetres (annual) and 553.9 ± 50.6 millimetres (July–December) (Table 1). Rainfall over the study period showed great variation from these average values. Years were arbitrarily classified as wet (more than 120% of average rainfall), average to below average rainfall (between 120% and 70% of average rainfall) and well-below-average rainfall (less than 70% of average rainfall). Under this classification, 1996, 1998, 1999 and 2000 were wet years and 2002 had well-below-average rainfall. Rainfall in the wettest year (2000) in the study period was 152 per cent of the longer-term average, while rainfall in the driest year (2002) was 51 per cent of the longer-term average.

TABLE 1

Annual and July–December rainfall over eight breeding seasons and number of nesting attempts, eggs laid and chicks fledged by the female Grey Shrike-thrush occupying the territory at the homestead. Annual rainfall is rainfall in the calendar year January–December in which the breeding season commenced. The total number of eggs laid or chicks fledged in a breeding season is shown, with individual clutch and brood sizes in brackets. Means are given with standard errors (SE).

Calender year (Breeding season)	Annual rainfall (mm)	July to December rain (mm)	Number of nestings	Total number of eggs laid (clutch sizes)	Total number of chicks fledged (individual nestings)
1996 (1996/97)	1 268	704	3	8 (3, 2, 3)	8 (3, 2, 3)
1997 (1997/98)	1 031	589	2	6 (3, 3)	6 (3, 3)
1998 (1998/99)	1 525.5	971.5	3	11 (3, 4, 4)	10 (2, 4, 4)
1999 (1999/00)	1 316	667	3	9 (3, 3, 3)	9 (3, 3, 3)
2000 (2000/01)	1 588.5	956.5	3	10 (3, 3, 4)	10 (3, 3, 4)
2001 2001/02)	790.5	507.5	2	5 (2, 3)	5 (2, 3)
2002 (2002/03)	535	169.5	1	2 (2)	2 (2)
2003 (2003/04	818.5	439.5	3	9 (3, 3, 3)	6 (0, 3, 3)
Average clutch or brood size (mean ± SE)				3.0 ± 0.1	2.8 ± 0.2
Average rainfall 1996–2003 (mean ± SE)	1 109.1 ± 1 33.2	625.6 ± 94.5			
Longer-term average rainfall (1986–2003) (mean ± SE)	1 042.0 ± 69.5	553.9 ± 50.6			

Effect of rainfall on clutch size

The relationship between the size of 24 clutches, laid by six different females in the breeding seasons 1995/96 to 2003/04 inclusive, and annual rainfall is shown in Figure 1, with fitted regression line. Twenty of these clutches were laid by shrike-thrushes during breeding seasons 1996/97 to 2003/04 (Table 1). The remaining four clutches were laid in an earlier season (1995/96; one clutch of three), at a nearby property (one clutch of three) and in the adjoining forest (two clutches of two and three respectively).

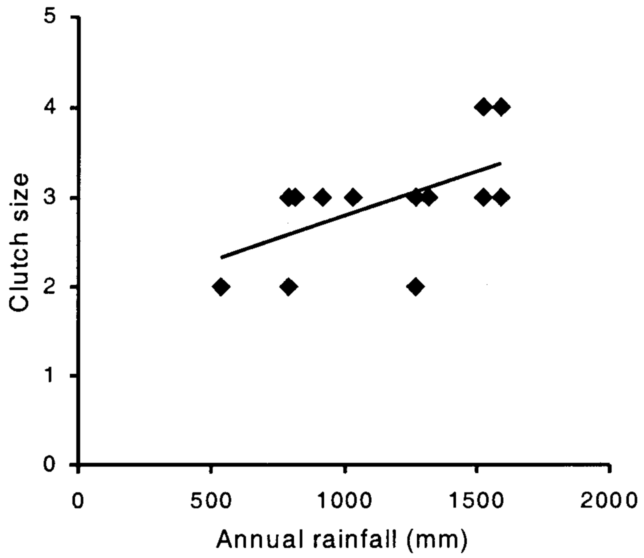

Figure 1. *Relationship between annual rainfall and clutch size for six female Grey Shrike-thrushes and 24 nests in the breeding seasons 1995/96 to 2003/04. One female laid 15 of these clutches, two laid three clutches each, and three laid one clutch each. Annual rainfall is January–December rainfall in the year in which the breeding season began.*

Shrike-thrushes laid an average of 3.1 ± 0.1 eggs per clutch in wet years, 2.9 ± 0.1 in average to below average years, and 2.0 ± 0.0 in the well-below-average year. With small sample sizes, these differences were not significant. Four-egg clutches occurred only in very wet years (breeding seasons 1998/99 and 2000/01), with rainfall more than 40 per cent above the longer-term average, while the driest year (2002/03) had two 2-egg clutches.

The P-P plot and plot of residuals confirmed that the data were approximately normal, though there was evidence of decreasing variance with increasing clutch size. Pearson correlation indicated a significant positive association between clutch size and annual rainfall, with rainfall accounting for 38 per cent of the variation in clutch size ($r = 0.62$, $r^2 = 0.38$, d.f. = 23, $P = 0.007$). ANOVA showed that the rainfall effect was significant ($F_{1,20} = 10.62$, $P = 0.004$) while the effects of different females and clutch order (first versus later clutches) were not significant ($F_{1,21} = 1.33$, $P = 0.26$ for female effect; $F_{1,21} = 4.22$, $P = 0.053$ for clutch order).

Effect of rainfall on number and timing of nests

The number of nests in a season was only known for the birds nesting at the homestead. The same female laid all eggs in the years 1996/97–2000/01 inc., while three other females laid the eggs in 2001/02, 2002/03 and 2003/04. In wet years, shrike-thrushes had three successful nests. They had two successful nests in average to below average years, and one in the well-below-average year. In wet and average to below average years, shrike-thrushes laid their first clutches in mid to late August and their second in October. In the well-below-average year, the single clutch at the homestead was laid in October. In wet years, the August and October nests were followed by third nests in either November, December, January or February.

The P-P plot and scatterplot of residuals showed that the data approximate normality and that the linear regression model is appropriate for the analysis. There was a total of 20 nests and a strong relationship between total number of nests in a season and rainfall ($r = 0.78$, $r^2 = 0.60$, d.f. = 7, $P = 0.024$). Of these 20 nests, 19 were successful. Pearson correlation indicated a significant positive association between number of successful nests and annual rainfall, with rainfall accounting for 88 per cent of the variation ($r = 0.94$, $r^2 = 0.88$, d.f. = 7, $P = 0.005$) (Fig. 2). ANOVA showed that the rainfall effect was significant ($F_{1,5} = 15.56$, $P = 0.011$) while the effect of different females was not significant ($F_{1,5} = 0.014$, $P = 0.91$).

Effect of rainfall on eggs laid or chicks fledged

The shrike-thrushes nesting at the homestead had a mean clutch size of 3.0 ± 0.1 and a high success rate of chicks fledged to eggs laid (56/60 or 93%) (Table 1). The number of chicks fledged by the breeding female in the homestead territory was related to annual rainfall: see Table 1 and Figure 3. No nests failed due to inclement weather because the eaves of the house protected the nests from falling rain.

The P-P plot and scatterplot of residuals showed that the data approximate normality and that the linear regression model is appropriate for the analysis. Pearson correlation indicated a significant positive association between eggs laid and annual rainfall ($r = 0.85$, $r^2 = 0.73$, d.f. = 7, $P = 0.004$) and chicks fledged and annual rainfall, ($r = 0.975$,

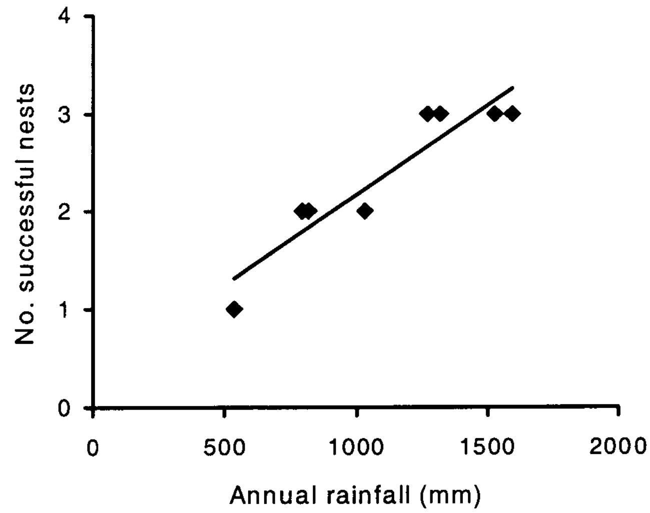

Figure 2. *Relationship between annual rainfall and number of successful nests, fledging at least one chick, in a season for four female Grey Shrike-thrushes. One female provided data for five seasons and three for one season each in eight breeding seasons, 1996/97 to 2003/04.*

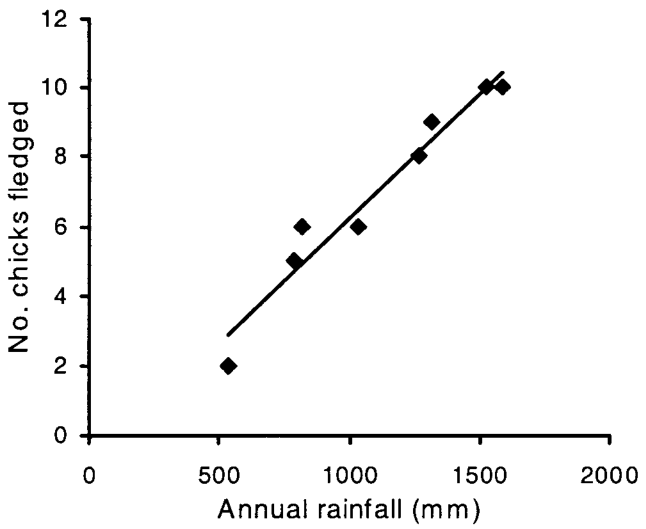

Figure 3. *Relationship between annual rainfall and number of chicks fledged in a season for four female Grey Shrike-thrushes. One female provided data for five seasons and three for one season each in eight breeding seasons, 1996/97 to 2003/04.*

r^2 = 0.95, d.f. = 7, P < 0.001), with rainfall accounting for 95 per cent of the variation in chicks fledged. ANOVA showed that the rainfall effect was significant ($F_{1,5}$ = 75.35, P = 0.0003) while the effect of different females was not significant ($F_{1,5}$ = 2.17, P = 0.20). Annual rainfall gave a higher correlation than other measures of rainfall (March–December, April–December and July–December, with r^2 values of 0.92, 0.90 and 0.91 respectively).

DISCUSSION

The breeding activities of habituated Grey Shrike-thrushes at the homestead provided a unique opportunity to examine reproductive output over eight breeding seasons and the effects of an environmental variable, namely rainfall, on reproductive output. There was no systematic attempt to find other nest sites some distance from the homestead in this study, and it is possible that the birds may have nested away from as well as at the homestead. However, the birds showed continuing interest in the nest site between breeding attempts and after fledging the last brood of chicks. The observed time for re-nesting at the homestead (median 16 days) was very short compared with the length of the breeding cycle (34.1 ± 0.5 days; Stevens and Watson 2005). Only one period to re-nesting, namely 49 days, was longer than 34 days, and occurred in somewhat unusual circumstances, i.e. the laying of a third clutch of four eggs in a new nest after fledging four young (Stevens and Watson 2005). Thus it is unlikely that the pair nesting at the homestead nested elsewhere in the same breeding season.

Most of the data on reproductive output and its relationship to rainfall are from one female paired with two different males over five breeding seasons (1996/97 to 2000/01), and it is therefore possible that the results are not representative. Because the data from the three other females fitted the same pattern, however, this is unlikely, and we are confident that these data are not overly influenced by this single individual.

In the present study, the range of clutch sizes was 2–4 with a modal clutch size of three. Clutch sizes of 1–4, generally three, have been reported for this species previously (Higgins and Peter 2002), and are similar to other palaeoendemic Australian passerines with small, relatively fixed clutch sizes (Yom-Tov 1987). The high success rate (93%) of habituated shrike-thrushes at the homestead is substantially greater than the figure of 20.3 per cent for this species reported in the Nest Record Scheme (Higgins and Peter 2002). Predation is thought to be the major cause of nest failure in open-nesting Australian passerines (Ford 1999), and the high success rate of shrike-thrushes in the present study is most likely due to deterrence of predators by human activity at the homestead (Stevens and Watson 2005).

In most seasons, shrike-thrushes were multibrooded, laying up to three clutches and 11 eggs in a season in the present study, with up to four clutches in a season observed by others (Higgins and Peter 2002). The present study has shown that annual rainfall accounted for 60 per cent of the variation in total number of clutches and 88 per cent of the variation in number of successful clutches. In wet years, shrike-thrushes had three successful nests. They had two successful nests in average to below average years, and one in the well-below-average year. The combined effects of variation in clutch size and number of successful nests resulted in the total number of chicks fledged in a season showing a strong positive correlation with annual rainfall. This allowed a four- to five-fold increase in annual reproductive output in unusually wet years compared with an unusually dry year, indicating a previously unrecorded degree of behavioural plasticity for this species.

Studies on other Australian passerines have documented that the White-fronted Chat *Epthianura albifrons* and Superb and Blue-breasted Fairy-wrens, *Malurus cyaneus* and *M. pulcherrimus*, laid smaller clutches in dry years (Williams 1979; Ford 1989; Rowley and Russell 2002). The Splendid Fairy-wren *Malurus splendens* and White-browed Scrubwren *Sericornis frontalis* varied the number of breeding attempts in a season but not clutch size (Russell and Rowley 1993; Magrath *et al.* 2000). Splendid Fairy-wrens laid more clutches in years when predation or brood parasitism were high, particularly in the two years after a major fire (Russell and Rowley 1993) but reasons for the year-to-year variation in the breeding effort of White-browed Scrubwrens were not examined. In the Purple-crowned Fairy-wren *M. coronatus*, however, there was some evidence for more clutches being laid in wet than dry years, with no breeding apparent in some dry years (Rowley and Russell 1993).

While rainfall is known to act as a stimulus to breeding in many arid-zone birds (Serventy and Marshall 1957; Keast 1959; Maclean 1976; Williams 1979; Ambrose and Murphy 1994; Zann *et al.* 1995), it may also trigger nesting in more mesic habitats. Silvereyes *Zosterops lateralis chlorocephala* on Heron Island began nest-building after heavy rain, while the Little Grassbird *Megalurus gramineus* in south-western Australia showed a breeding peak one month after rain (Kikkawa and Wilson 1983; Halse and Jaensch 1989). Rainfall probably acts by influencing the amount of food available (Schodde 1982;

Ford 1989). Food supply has been shown to influence the initiation of egg-laying, length of the breeding season, clutch size, egg mass, and nestling size and mass. Food shortage was considered to be responsible for reduced breeding success (shorter breeding season, lighter eggs though no reduction in clutch size, and smaller nestlings) in Eastern Yellow Robins *Eopsaltria australis* (Zanette *et al.* 2000).

Grey Shrike-thrushes are woodland and forest residents which consume a wide variety of animal and plant food items (Barker and Vestjens 1990), gathering food from all heights from ground level to canopy (Recher and Holmes 1985). Woinarski (1985) found that Australian forests provide a relatively stable food supply throughout the year with only a minor broad peak in abundance during the breeding season. It is likely that this minor peak is accentuated in years of good rainfall and reduced in poor years. Moreover, the increased breeding activities of other bird species in wet years could provide quite a large peak in available eggs and thus nutrients for breeding shrike-thrushes, given that shrike-thrushes are known major nest predators. Hence, the ability to modify clutch size in response to resource availability would afford a strong selective advantage, maximizing reproductive output when resources were plentiful. This ability, coupled with multiple breeding attempts within a single breeding season led to broad variation in reproductive output (2–10 chicks fledged in a single breeding season) and a close association between reproductive output and resource availability as measured by annual rainfall. We suggest that the plasticity of reproductive output in response to environmental conditions might help explain the success of this widespread species.

ACKNOWLEDGMENTS

The authors wish to thank Sonia Tidemann and Paul McDonald for constructive criticism of the manuscript.

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