The importance of low host densities for successful parasitism of diederik cuckoos on red bishop birds

J.W.H. Ferguson
Zoology Department, Pretoria University, Pretoria, 0002 Republic of South Africa

Received 24 May 1993; accepted 5 August 1993

Parasitism by diederik cuckoos *Chrysococcyx caprius* on their main southern African host, the red bishop bird *Euplectes orix*, was studied. Virtually all the cases of parasitism occurred where there were low densities of red bishop nests. Data from the present study were combined with published observations to show that the incidence of parasitism is much higher in small breeding colonies of red bishops than in large colonies. Aggression of red bishops towards diederiks is described. I suggest that diederik cuckoos cannot approach red bishop nests undetected where large concentrations of red bishops are found. High levels of brood failure in small red bishop colonies caused by brood parasitism may constitute a selective force for colonial breeding in this host species.

In hierdie studie word parasitisme deur diederik-koekoeke *Chrysococcyx caprius* op hulle belangrikste suider-Afrikaanse gasheer, die rooivink *Euplectes orix*, ondersoek. Bykans alle gevalle van parasitisme het voorgekom waar rooivinkneste in lae digthede voorgekom het. Data uit hierdie studie is gekombineer met dié van ander outeurs en dui daarop dat broei-parasitisme baie hoër is by klein rooivink-broeikolonies as by groot kolonies. Aggressie van rooivinke teenoor diederikke word beskryf en dit skyn dat die koekoeke nie neste onopgemerk kan nader as daar baie rooivinke is nie. Hoë mortaliteit van rooivink-broeisels a.g.v. parasitisme in klein kolonies mag 'n bron wees waardeur daar seleksie plaasvind vir koloniale broeigewoontes.

The diederik cuckoo *Chrysococcyx caprius* is one of the commonest cuckoo species in southern Africa (Rowan 1983; Fry 1988) and lays its eggs in the nests of a range of passerine birds. Diederik cuckoos appear to include several *gentes* or 'host races', each of which specializes in parasitizing a particular host species (Jensen & Vernon 1970). In central Africa the masked weaver *Ploceus velatus* appears to be the most-used host species (Friedmann 1948). However, the red bishop bird *Euplectes orix* is the species most commonly parasitized by diederiks in southern Africa outside of the Cape Province (Payne & Payne 1967; Jensen & Jensen 1969). The long-term relationship between a parasite and its host is subject to several constraints, one of which is that the parasite should not be so successful in its parasitic behaviour that the survival of the host species is at stake. Consequently the parasite is really dependent on its host being able to evade it efficiently. Davies & Brooke (1988) observed that reed warblers *Acrocephalus scripaceus* have a range of behavioural adaptations which make it quite difficult for a cuckoo to successfully parasitize a warbler brood: these behavioural patterns include the rejection of eggs which are not laid at the right time of day and the rejection of clutches after sighting a cuckoo close to the nest. One expects that similar phenomena exist between red bishop birds and diederik cuckoos.

A continuing study on breeding and the mating biology of red bishops has offered the opportunity to observe several broods which had been parasitized by diederik cuckoos. This enabled the quantification of nest site characteristics of diederiks and relating these to the breeding behaviour of bishops. I will offer two lines of evidence that the intensity of parasitism is much higher where bishop nests occur at low densities or in small numbers and that the intensity of parasitism in small colonies is so high that the reproductive success of the colony as a whole is seriously impaired. I will then discuss why the intensity of parasitism in large bishop colonies is much less than in small colonies.

Study area and Methods

Study area

The study was conducted in a reed bed at Colbyn Valley, Pretoria. The site is located in a large relatively undeveloped area comprising the experimental farm of Pretoria University and adjoining areas under municipal control. The red bishops breed in a reed bed 1,2 ha in size. The dominant reed species is *Phragmites australis*. The reed bed is adjacent to a stream and standing water is found only after significant rainfall. The reeds are cut during winter. Red bishops breed in the reed bed from early December until about the end of February. Diederik cuckoos are vocally active and often seen during December and January. This report includes data accumulated during two breeding seasons; 1990/1 and 1991/2.

Methods

Incidence of parasitism

The breeding success of red bishop nests was followed by direct observation. The whole reed bed was traversed once every week during the breeding season. The chicks of diederik cuckoos are diagnostic in that they have a darker colour than red bishop chicks and have very thick tarsi at a very early age. This resulted in the detection of parasitized nests within a few days of hatching. All active red bishop nests were marked with nursery tags some 50–100 cm below each nest. The localities of all active nests were noted using markers which had been mapped during a trigonometric survey. During the 1991/2 breeding season, observations ended during the first week of February. However, only a small amount of breeding took place after this date.

Plant physiognomy

The physiognomic characteristics at sites where red bishop nests had been parasitized were compared to those at sites with unparasitized nests. Measurements of reed height, reed density and reed diameter were made at the height of the breeding season during January 1992, by choosing 73 sites in a grid-like pattern which covered the whole reed bed and which included some non-gridded locations (chosen because some patches of different physiognomic characteristics were missed during sampling). Reed height was obtained by measuring the height of the four closest reeds to the sampling site. The diameter of these four reeds was also noted, as was the number of reeds within a 1-m^2 quadrant. Geographical effects in the reed bed were measured using a gridded map with grid units 10 m apart. In order to obtain physiognomic data for each grid block, Kriging (Clark 1979) was used as a means of interpolation between physiognomic sampling points.

Bishop nest density

The number of active nests in a 10 m × 10 m grid block of the reed bed was measured by mapping the location of each nest. Jensen & Vernon (1970) suggested that the term 'incident parasitism frequency' be used for the intensity of parasitism in a particular place and point in time, while 'overall parasitism frequency' should be used for the rate of parasitism over extended periods of time or over a wide geographic area. I use the terms 'incident parasitism rate' and 'overall parasitism rate' in an analogous way to denote intensity of parasitism.

Results

Incident parasitism rate and temporal characteristics of parasitism

Diederik cuckoos were present at the study site throughout both breeding seasons. However, they were vocal and often observed during the period November to early February. Red bishop breeding at Colbyn continued through February but at highly reduced levels. At Colbyn the percentage of successful red bishop broods dropped from 51% during January to less than 20% during February. During the two breeding seasons complete breeding histories were obtained for 377 red bishop nests, of which 28 were parasitized by diederik cuckoos, a mean incident parasitism rate of 0,074 (Table 1). The incident rate of parasitism was 0,105 during 1990/1 when few red bishops nested, compared with a lower value of 0,066 during 1991/2 when many more red bishops nested (Table 1). This difference is, however, not statistically significant (binomial $p = 0,085$). The highest incidence of parasitism during 1990/1 (21–31 December 1990; Table 1) was, however, significantly higher than the highest incidence during 1991/2 (11–20 January 1992; binomial $p < 0,005$). During both years brood parasitism largely coincided with the peak of the red bishop breeding season (Table 1), i.e. during the last half of December and the first half of January at Colbyn.

Table 1 Temporal distribution of the number of red bishop nests parasitized by diederik cuckoos at Colbyn. The date of the first location of each individual parasitized nest is indicated here in terms of a 10-day period within December or January. The total number of active red bishop nests is also indicated for each period and for each breeding season

		December			January			
Year		1–10	11–20	21–31	1–10	11–20	21–31	Total
1990/1	No. parasitized	0	0	7	1	0	0	8
	Red bishop nests	3	17	32	25	23	16	
1991/2	No. parasitized	0	2	6	4	7	1	20
	Red bishop nests	38	55	125	155	102	68	
Total no. parasitized nests		0	2	13	5	7	1	28

Spatial differences in intensity of parasitism within a colony

Quadrants of size 10 m × 10 m in the reed bed were divided into two groups: those with parasitized nests and those without. One-tailed Wilcoxon 2-sample rank sum tests were used to compare some of the characteristics of these quadrants and indicated that none of the physiognomic characteristics of the reeds differed between parasitized and non-parasitized quadrants (reed height $z = 0,9$; $p < 0,18$; reed density $z = 1,6$; $p < 0,07$; reed diameter $z = 0,87$; $p < 0,17$). These figures suggest that the cuckoos did not select red bishop nests associated with reeds with any particular physical characteristic. When these two classes were compared there was, however, a significant difference in the number of red bishop nests per quadrant (Wilcoxon $z = 1,96$; $p < 0,026$). Except for four cases, parasitized nests were all located outside quadrants with high red bishop nest densities (Figure 1). This indicates that diederik cuckoos

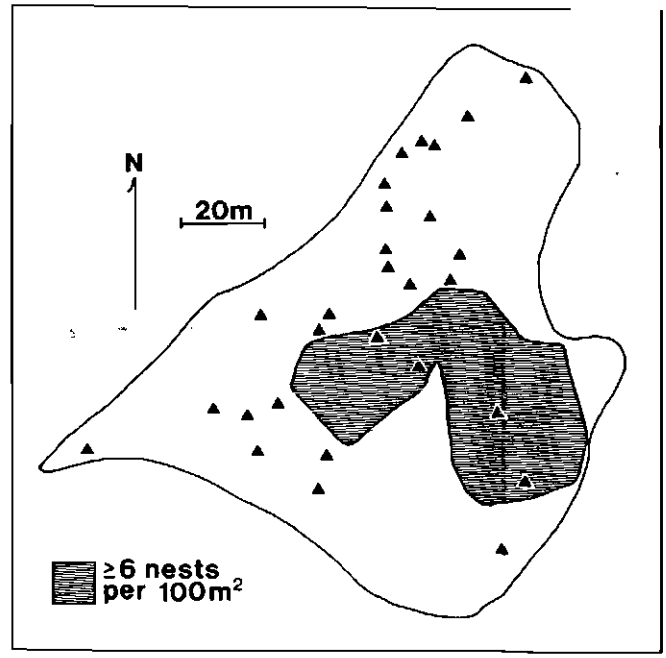

Figure 1 A map of the reed bed at Colbyn indicating the sites of diederik cuckoo parasitism (1990/1 and 1991/2) on red bishops relative to red bishop nest densities. The hatching indicates the area with nest densities equal to or higher than 6 nests/100 m^2, comprising 54% of all the active red bishop nests (1991/2).

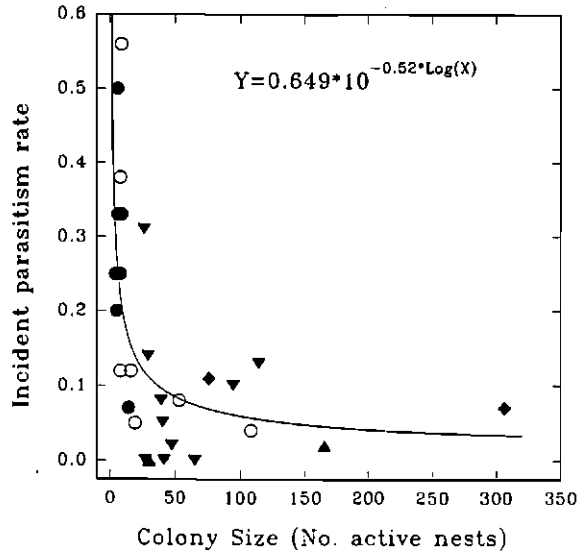

Figure 2 The relationship between red bishop colony size and the incidence of parasitism by diederik cuckoos. Data obtained from following sources: Diamonds — this study; broad-based triangles — Craig (1982); broad-topped triangles — Jensen & Vernon (1970); open circles — Payne & Payne (1967); solid circles — Reed (1968). A regression line and its equation are also indicated.

were more active in quadrants with low nest densities (Fisher's G = 12,2; df = 1; p < 0,001).

Differences in intensity of parasitism in large and small red bishop colonies

When the data from this study were combined with results of four other published studies (Figure 2), a clear trend emerged where the rate of brood parasitism by diederik cuckoos increased dramatically in small red bishop colonies. The relationship between incident parasitism rate and red bishop colony size was strongly non-linear and could only be linearized by means of a log/log transformation of the data after which magnitudes of the residuals were unaffected by those of the red bishop colony sizes (p > 0,4). The regression is highly significant (p < 0,005), and contributes 48% of the total sum-of-squares. Figure 2 indicates the regression line obtained via back-transformation of the log/log regression equation to linear axes. Colonies with fewer than 50 nests show a marked increase in incident parasitism rate of up to more than half of the total number of nests. The highest incidence of parasitism encountered in the literature was a colony of nine nests in Zimbabwe with a rate of parasitism of 0,56 (Payne & Payne 1967). The colonies with the five highest incident parasitism rates all had fewer than 10 active red bishop nests.

Although the records are too scanty for statistical analysis, there is an indication that red bishop broods have a lower incident parasitism rate during December (n = 6; mean = 0,05) than January (n = 7; mean = 0,17) and February (n = 4; mean = 0,3).

Discussion

Both Reed (1968) and Jensen & Vernon (1970) commented on the large degree of variation in incidence of diederik/red bishop parasitism. This study has shown that the size of a red bishop colony affects incidence of parasitism and that broods later in the breeding season may have higher incidences of parasitism. Schulze-Hagen (1992) also showed that the intensity of parasitism in the case of the European cuckoo varies with time as well as between geographical areas. The terminological distinction between 'incident parasitism frequency' and 'overall parasitism frequency' (Jensen & Vernon 1970) is therefore perhaps too simplistic: the intensity of parasitism is not a simple constant in a population but is affected by many factors.

I have shown that the regression of red bishop colony size with intensity of parasitism contributes 48% of the total sum-of-squares of the data presented in Figure 2. I suspect that the factors mentioned in the previous paragraph account for a large part of the remaining variation in intensity of parasitism. The trend for a high incidence of parasitism at Colbyn during 1990/1 compared with the following year when many more nests were active (Table 1) is consistent with these results. How does this phenomenon relate to the observation that the cuckoos parasitized red bishop nests mostly where these occured in low densities within the colony (Fig. 1)? In both these situations there are relatively few red bishops which could locate a cuckoo in search of a nest. I suggest that a situation with fewer hosts which could locate a cuckoo near nests is required for successful parasitism by diederik cuckoos.

Numerous reports have been published of aggression by individuals of host species towards cuckoos (e.g. Lack 1968, Moksnes & Røskaft 1989, Braa, Moksnes & Røskaft 1992). The relationship between diederik cuckoos and red bishops is no exception to this rule since adult diederiks are often attacked by red bishops (Friedmann 1948; Brooke 1953; Ottow & Duve 1965; Reed 1968). One such attack was observed during the present study when a diederik male ventured out into the reed bed. In addition Reed (1968) reported ferocious attacks of red bishop males even on diederik cuckoo chicks that had already left the nest. These behavioural patterns suggest that cryptic colouration, secretive behaviour and indistinct calls (Ottow & Duve 1965; Jensen & Jensen 1969) of diederik females are advantageous for successful egg laying. Friedmann (1948) mentions a case where a male diederik cuckoo acted as a decoy while the female cuckoo attempted to lay eggs. These observations lead to the conclusion that it is not easy for a female diederik to approach a red bishop nest. In the case of the European cuckoo *Cuculus canorus*, Moksnes & Røskaft (1989) showed that the sight of a cuckoo near a pipit nest predisposes the host towards rejecting cuckoo eggs; a phenomenon that could also apply to red bishops. Situations which favour an undetected approach to a red bishop nest are therefore more likely to occur where there are fewer red bishops to detect a cuckoo. This would be the case in small colonies of red bishops, where their nests do not occur in dense concentrations. I suggest that the incidence of parasitism is low in large red bishop colonies and where dense concentrations of red bishop nests occur because the probability of a female diederik approaching a nest unnoticed in this situation is relatively small. Diederik cuckoos were not conspicuous during February and this suggests that red bishops may avoid brood parasitism by

breeding late in the season. However, the low reproductive success of red bishops during February suggests that this is not the case.

The high incidence of brood parasitism among small red bishop colonies could constitute a strong selective force for colonial breeding in this species. Breeding success varies considerably from locality to locality. A breeding success of 45% has been recorded by Schmidt (1968) and a success of only 10% was recorded by Craig (1982). Predation was the largest source of brood failure. The additional effect of high levels of brood parasitism, as described above for small red bishop colonies, could affect their survival, leaving only large colonies which are relatively unaffected by parasitism. Indeed, Reed (1968) reported the decline of a red bishop population subject to high rates of parasitism. However, he could not quantitatively show that this decline was due to the observed high incidence of parasitism. The fact that diederiks do not parasitize red bishops in the Cape Province also implies that these red bishop populations are not subject to the same constraints regarding parasitism as are the red bishops reported on here. The importance of brood parasitism as a source of selection for colonial breeding would largely be determined by the degree to which parasitism and predation are compensatory sources of mortality. Further studies should focus on the reproductive success of different-sized colonies in reasonably close proximity and the contribution of brood parasitism towards lack of successful breeding.

Acknowledgements

A large number of people assisted in field work. Jaco Greeff did most of the field work during December/January 1990/1. Willie Ferguson, Johan Ferguson and Nicholas Mnguni assisted with field work during the 1991/2 breeding season. George Ellison, Johan Kritzinger, Walter Neser, Niall Corbet, Chris Styles, Frans Jonker and Jonathan Bloomer all assisted in a trigonometric survey of the reed bed and the Surveying Department at Pretoria University supplied equipment for this survey. Joos Esterhuisen assisted in processing data from the trigonometric survey. My sincere appreciation goes to all these people. Thanks also to Adrian Craig for constructive criticism of the manuscript. This work was funded by the FRD and the University of Pretoria.

References

BRAA, A.T, MOKSNES, A. & RØSKAFT, E. 1992. Adaptations of bramblings and chaffinches towards parasitism by the common cuckoo. *Anim. Behav.* 43; 67–78.

BROOKE, R.K. 1953. A mounted Didric Cuckoo. *Bokmakierie* 5: 72.

CLARK, I. 1979. Practical Geostatistics. Applied Science Publishers, London.

CRAIG, A.J.F.K. 1982. Breeding success of a red bishop colony. *Ostrich* 53: 182–188.

DAVIES, N.B. & BROOKE, M. 1988. Cuckoos versus reed warblers: Adaptations and counteradaptations. *Anim. Behav.* 36: 262–284.

FRIEDMANN, L. 1948. The parasitic cuckoos of Africa. *Washington Acad. Sci. Monogr. 1.*

FRY, C.H. 1988. The Birds of Africa. Volume 3. Academic Press, London.

JENSEN, R.A.C. & JENSEN, M.K. 1969. On the breeding biology of the African cuckoos. *Ostrich* 40: 163–181.

JENSEN, R.A.C. & VERNON, C.J. 1970. On the biology of the didric cuckoo in southern Africa. *Ostrich* 41: 237–246.

LACK, D. 1968. Ecological adaptations for breeding in birds. Methuen, London.

MOKSNES, A. & RØSKAFT, E. 1989. Adaptations of meadow pipits to parasitism by the common cuckoo. *Behav. Ecol. Sociobiol.* 24: 25–30.

OTTOW, J. & DUVE, G. 1965. Zur Kenntnis der Fortpflantzung von *Chrysococcyx caprius* und *Cuculus canorus* in Süd-Afrika. *J. f. Orn.* 106: 431–439.

PAYNE, R.B. & PAYNE, K. 1967. Cuckoo hosts in southern Africa. *Ostrich* 38: 135–143.

REED, R.A. 1968. Studies of the diederik cuckoo *Chrysococcyx caprius* in the Transvaal. *Ibis* 110: 321–331.

ROWAN, M.K. 1983. The doves, parrots, louries and cuckoos of southern Africa. David Philip, Cape Town.

SCHULTZE-HAGEN, K. 1992. Parasitierung und Brut verluste durch den Kuckuck (*Cuculus canorus*) bei Teich- und Sumpfrohsänger (*Acrocephalus scirpaceus, A. palustris*) in Mittel und Westeuropa. *J. f. Orn.* 133: 237–249.

SCHMIDT, R.K. 1968. A colony of red bishops *Euplectes orix* in the south-western cape. *Ostrich* 39: 25–27.