The breeding biology of the greywing francolin *Francolinus africanus* and its implications for hunting and management

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We studied the breeding biology of the greywing francolin *Francolinus africanus* on the Stormberg Plateau of the eastern Cape Province, South Africa during 1988–1991. Timing of breeding, nesting behaviour, clutch size, egg size, and clutch survival rates were recorded and compared with published and unpublished information from Natal, the eastern Orange Free State and south-western Cape Province. The greywing breeds during the austral summer throughout its range, with peak laying activity during August–November. However, the nesting period is contracted in the south-western Cape, where it starts about one month earlier and ends three months earlier than in the eastern Orange Free State and the eastern Cape, where laying was recorded from August to March. The greywing's breeding season is more consistently positively correlated with measures of environmental variation in the summer rainfall region than in the winter rainfall region. Flushed single birds were the best indicators of nesting sites. Clutches were incubated by hens only. Mean clutch size was 5,5 (*SD* = 1,2) and mean egg dimensions were 39,9 mm × 30,1 mm (*SD* = 1,9 and 0,9). Incubation period was 21,7 days (*SD* = 0,5), hatching success (the probability that eggs present at hatching time actually produced living young) was 90% and clutch survival rate (the probability that a clutch will survive 21,7 days of incubation) was 31%. Hunting seasons for the greywing should be from 15 April to 31 July in the summer rainfall region and from 1 April to 30 June in the winter rainfall region. Veld burning should cease at the end of August throughout the greywing's range so that disturbance of breeding birds is minimized.

Ons het die broeibiologie van die bergpatrys *Francolinus africanus* op die Stormbergplato in die Oos-Kaap, Suid-Afrika, tussen 1988 en 1991 bestudeer. Tydsberekening van broeiaktiwiteit, broeigedrag, broeisel- en eiergroottes, en broeisukses is aangeteken en vergelyk met gepubliseerde en ongepubliseerde inligting vanuit Natal, die Oranje Vrystaat en Suidwes-Kaapland. Bergpatryse broei gedurende die suidelike somer dwarsoor hul verspreidingsgebied met 'n piek in eierlê-aktiwiteit tussen Augustus en November. Die broeiperiode is egter korter in die Suidwes-Kaap deurdat dit 'n maand vroeër begin en ongeveer drie maande vroeër eindig as in die oostelike Vrystaat en die Oos-Kaap, waar spits-lêtyd tussen Augustus en Maart is. Die bergpatrys se broeiseisoen is gedurende die somer meer konsekwent positief gekorreleer met faktore wat omgewingsvariasie weerspieël, as gedurende die winter. Opgejaagde enkelvoëls was die beste aanduiders van neste en slegs wyfies het gebroei. Gemiddelde broeiselgrootte was 5,5 (*SD* = 1,2) en gemiddelde eiergroottes was 39,9 mm × 30,1 mm (*SD* = 1,9 en 0,9). Inkubasietydperk was 21,7 dae, uitbroeisukses was 90% en broeisel-oorlewing was 31%. Bergpatrys-jagseisoene behoort tussen 15 April en 31 Julie in die somerreënvalstreek, en tussen 1 April en 30 Junie in die winterreënvalstreek, te val. Die brand van veld moet dwarsdeur die spesie se verspreidingsgebied teen die einde van Augustus gestaak word, sodat versteuring van broeiende voëls so laag moontlik gehou word.

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The greywing francolin *Francolinus africanus* (hereafter called greywing) is endemic to southern Africa (Clancey 1986). The nesting habits and breeding season of the greywing have been discussed by Gilfillan (1908), Clancey (1967), Winterbottom (1968, 1971), Mentis (1973), Mentis & Bigalke (1980), Maclean (1985) and Crowe, Keith & Brown (1986). Clancey (1967) suggested that greywing populations in the eastern, southern and western Cape Province breed significantly earlier than populations from Lesotho, Natal and the extreme eastern Cape. Liversidge (1987) also reported that the greywing breeds earlier in the south-western Cape Province, where rain falls predominantly in the austral winter (May–August), than elsewhere within its range, where the onset of breeding coincides with the initiation of the rains of the austral summer. Therefore, if reproduction in the greywing is influenced by rainfall, as is the case in the helmeted guineafowl *Numida meleagris* (Crowe 1978; Crowe *et al.* 1986), significant variation would be expected between the timing of breeding in populations from winter and summer rainfall regions. The greywing is a popular and commercially important gamebird (Mentis & Bigalke 1985; Johnson & Wannenburgh 1987; Hickman 1988), and should any significant variation occur in its breeding season, it will be necessary to time the hunting season and certain management activities (e.g. veld burning) to coincide with its non-breeding season to minimize their impact on population losses and trends. Furthermore, for sustainable hunting of greywing it is necessary to have information on their annual productivity.

The objectives of this study are to investigate the variation in timing of breeding in three geographic regions within the range of this species, and to estimate the clutch size, incubation period, hatching success and clutch survival rates of the greywing populations from commercially grazed grasslands of the Stormberg Plateau in the eastern Cape Province, i.e. at the extreme south-western range of *F. a. proximus* (Clancey 1957). Comparative published and unpublished breeding information for greywing populations from conservation areas in Natal, and from the eastern Orange Free State and a range of areas from the south-western Cape

Province were obtained. These data, plus various measures of environmental variation and availability of food were used to determine: (i) timing of breeding in relation to environmental and other variables, (ii) breeding biology and nesting success, and (iii) implications for hunting and management.

Study area and methods

Most of our observations on the breeding biology of the greywing were made on farms on the Stormberg Plateau (31°15′S / 26°30′E), in the eastern Cape Province of South Africa from 1988–1990 (Figure 1). Additional observations were made on the timing of egg laying in the eastern Cape, and gonad size and pairing behaviour of greywing from the south-western Cape, during 1991. The Stormberg study area is dominated by open grasslands ranging in elevation from 1 700 m to 2 000 m above sea level. Greywing populations within the study area are subjected to annual hunting at 35–40% removal levels. However, significant alteration of the results of this study by hunting is unlikely, because these socially structured populations display naturally high rates of turnover (Grant & Little 1992) and little between-population variation in demography or genetics between hunted and unhunted populations, at these levels of offtake (Little, Grant & Crowe in prep.).

Greywing reproduction was monitored by measuring gonadal development and by observing the timing of pairing and egg laying. Testis and ovarian follicle size were measured for greywing shot monthly during July 1988–December 1990. For male birds, gonad size was the anterio-posterior length of the larger testis (usually the left one) and for females, the diameter of the largest follicle. Greywing were classified as adult if they had a rounded tenth primary, or juvenile (< one year) if this feather was pointed (Little & Crowe 1992). The percentage of coveys comprising two birds reflect pairing rates. The presence of chicks was estimated by advancing the nesting curve for greywing by one month, i.e. about 10 days longer than the 20–23 day incubation period for most francolin species studied to date (Crowe *et al.* 1986).

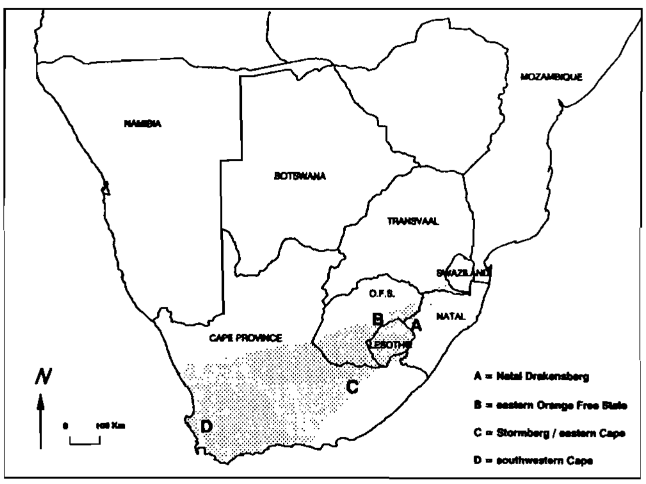

Figure 1 Range of the greywing francolin (stippled; Maclean 1985) and location of study areas.

We compared our results with measures of reproductive condition and pairing behaviour of greywing populations from Giant's Castle Game Reserve, Natal Drakensberg (29° 15′S / 29°30′E) (Mentis 1973; Mentis & Bigalke 1980) and with unpublished nest records from a range of sites in the south-western Cape and eastern Orange Free State (Nest Record Card Scheme of the Southern African Ornithological Society) (Figure 1).

We used the multiway frequency tables: log-linear model (4F) from the BMDP statistical package (Dixon, Brown, Engelman & Jennrich 1990) to test the hypothesis of independence, and departures from expectations, of nesting times in the three geographical regions. BMDP-4F tests for independence of the rows and columns (regions and months) using a likelihood-ratio χ^2 (G-statistic), and also tests for levels of adjusted standardized deviation (ASD) from expected values at each cell (in this case number of nests per region per month). Adjusted standardized deviates are significant if the absolute value is greater than $t_{\infty, 0{,}05}$ = 1,96 (Everitt 1977).

Simple correlation analyses were done between seasonal variation in pairing, follicle size, nesting and the presence of chicks for the three regions and measurements of monthly rainfall, ambient temperature, day length and the availability of arthropod food, to investigate relationships between greywing breeding and environmental variation.

Environmental variables were extracted from the Agro Climatical Reports (Anon. 1983–1991) for the farm Buffelsfontein (31°22′S / 26°42′E) in the eastern Cape and from the Weather Bureau (Anon. 1979) for Cedara (29°32′S / 30°17′E) in Natal and D.F. Malan Airport (33°58′S / 18°36′E) in the south-western Cape. Day length was the number of hours between standardized sunrise and sunset for Buffelsfontein, Cedara and D.F. Malan (CSIR 1973). Variation in arthropod numbers in the eastern Cape was recorded monthly using a 0,25 m^2 quadrant. Arthropods were counted for 1 min per quadrant, at 30 quadrants about 2 m apart, per survey. Two surveys were conducted per month, on calm clear days and between 10h00 and 15h00. Data on availability of arthropods were extracted from Earlé (1981) and Siegfried (1969) for Natal and the south-western Cape, respectively.

We measured eggs and examined nests on site. Nest dimensions were the mean of two diameters within the lining of the nest bowl and depth, from a horizontal line across the top of the bowl to the floor of the bowl. Clutch size was the largest number of eggs in the nest during incubation. Egg length was measured with Vernier calipers along the longitudinal axis, and egg width across the widest part of the egg. Incubation period was the number of days from the laying of the last egg in a clutch to the hatching of that egg (Campbell & Lack 1985).

Nesting success was determined using methods described by Mayfield (1975) and Johnson (1979). Hensler & Nichols (1981) suggest that the measure of nest success proposed by Mayfield (1975) is a maximum likelihood estimator.

Results

Timing of breeding

There was highly significant geographical variation in the

Table 1 Monthly distribution of greywing francolin nest records for the eastern Cape (eCape), eastern Orange Free State (eOFS) and south-western Cape (swCape)

Region	J	A	S	O	N	D	J	F	M	A	M	J	Total
eOFS[2]		2	2	4	6	1	1	3^+	2^+				21
eCape[1]	$^-$	5	11	12	7	4	1		1				41
swCape[2]	6^+	9	13	10	6	3							47
Total	6	16	26	26	19	8	2	3	3				109

$^-$ negative significant deviation (ASD>1,96; p = 0,05).
$^+$ positive significant deviation (ASD>1,96; p = 0,05).
[1] this study.
[2] Nest Record Card Scheme of S.A.O.S.

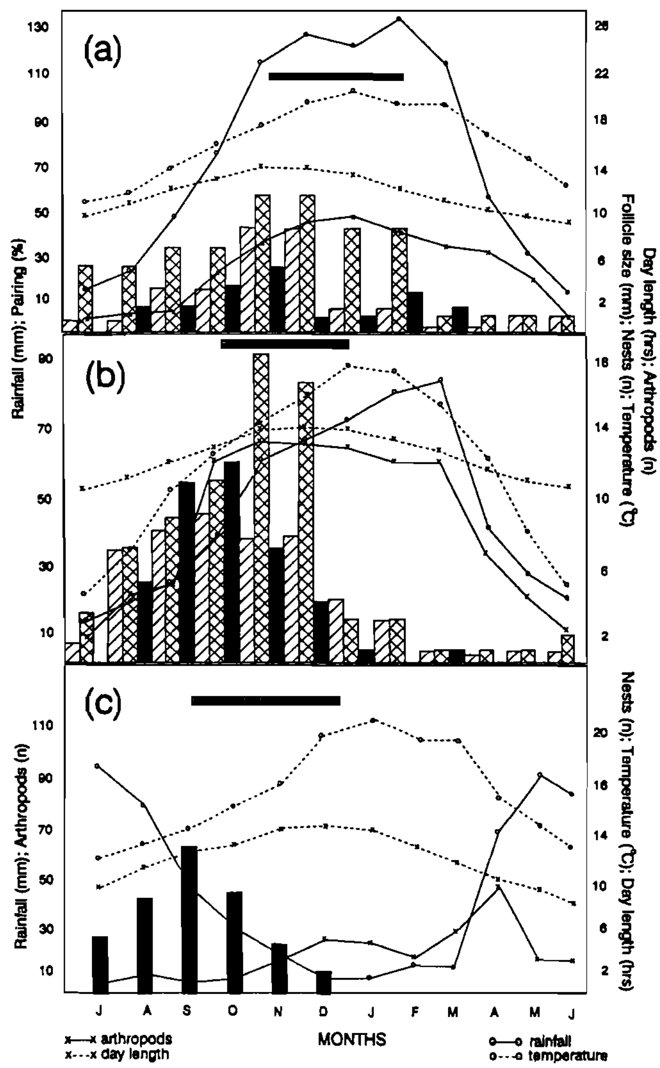

Figure 2 Reproductive activity of greywing francolin (vertical bars) and environmental variables (lines) for (a) Natal/eastern Orange Free State, (b) the eastern Cape Province, and (c) the south-western Cape Province. Hatched bars = pairing frequency; cross hatched bars = mean follicle diameter; solid bars = nests; horizontal stippled bars = peak chick 'windows'. Sources: follicle size and pairing for Natal (Mentis 1973); nesting for Natal and south-western Cape (Nest Record Card Scheme of the S.A.O.S.); climatic variables (Anon. 1979, 1983–1991); arthropods for Natal (Earlé 1981) and for the south-western Cape (Siegfried 1969).

timing of nesting of greywing between Natal, the eastern Cape and the south-western Cape (G = 34,4; df = 16; p = 0,005; Table 1).

Natal

Gonadal development of adult greywing from Natal was greatest during July–December (Mentis 1973; Mentis & Bigalke 1980). Furthermore, the frequency of paired greywing was greatest during September–December (Figure 2a). Although there are few nesting data available for Natal, data for 21 nests from the nearby eastern Orange Ftee State indicate that nesting peaks there during October–November (Table 1). There was significantly more nesting activity during February–March in the eastern Orange Free State (ASD = 3,6 & 2,1 respectively, p < 0,05) than in the eastern and south-western Cape. Measurements of monthly pairing behaviour, follicle size and the presence of chicks were significantly positively correlated with environmental variables (Table 2).

Eastern Cape Province

As with greywing from Natal, the gonads of 929 greywing from the eastern Cape, examined during July 1988–March 1990, showed greatest adult reproductive activity during July–December (Table 3). Adult males had enlarged testes

Table 2 Correlation coefficients (r) for monthly breeding activity of greywing francolin and monthly environmental variables (July–December)

Correlation variables	Regional statistics: Natal r	eCape r	swCape r
Pairing *vs*			
Temperature	0,91 *	0,60 ns	–
Rainfall	0,96 **	0,43 ns	–
Day length	0,95 **	0,58 ns	–
Arthropods	0,93[1]**	0,57 ns	–
Follicle size *vs*			
Temperature	0,90 *	0,96 **	–
Rainfall	0,95 **	0,98 **	–
Day length	0,95 **	0,97 **	–
Arthropods	0,93[1]**	0,92 **	–
Nesting *vs*			
Temperature	0,54 ns	0,37 ns	–0,53 ns
Rainfall	0,48 ns	0,17 ns	0,23 ns
Day length	0,53 ns	0,36 ns	–0,35 ns
Arthropods	0,42[1]ns	0,37 ns	–0,78[2]ns
Chicks *vs*			
Temperature	0,92 **	0,82 *	0,48 ns
Rainfall	0,95 **	0,77 ns	–0,69 ns
Day length	0,95 **	0,84 *	0,63 ns
Arthropods	0,93[1]**	0,89 *	0,10[2]ns

* = significant at p < 0,05.
** = significant at p < 0,01.
ns = not significant (p > 0,05).
[1] arthropod availability data from Earlé (1981).
[2] arthropod availability data from Siegfried (1969).

Table 3 Monthly variation in gonadal size of greywing francolin (Stormberg: July 1988–March 1990)

		Months											
		J	A	S	O	N	D	J	F	M	A	M	J
Male (testis length, mm)													
Ad	$\bar{x}$	12,5	13,6	14,6	14,3	15,5	16,2	13,7	11,9	13,3	9,4	8,0	8,5
	SD	3,7	1,8	2,7	1,5	1,8	2,6	2,3	1,9	2,0	2,3	1,6	2,0
	n	69	17	7	4	11	5	10	9	9	47	80	78
J	$\bar{x}$	9,5	9,4	14,6	13,3	13,0	6,0	5,5	10,0	6,8	5,8	6,5	6,9
	SD	3,9	2,7	0,9	4,3	–	0,0	1,3	–	1,5	2,0	1,1	1,1
	n	45	11	5	4	1	2	4	1	5	17	32	34
Female (follicle diameter, mm)													
Ad	$\bar{x}$	3,0	6,7	8,5	10,8	18,5	17,3	3,4	2,6	1,3	1,2	1,2	1,5
	SD	2,1	6,8	9,1	9,8	18,2	17,2	1,3	1,3	0,5	0,4	0,5	0,6
	n	44	20	8	5	4	4	5	7	4	22	47	32
J	$\bar{x}$	1,1	3,1	3,0	3,3	1,0	–	1,0	1,3	1,1	1,1	1,0	1,1
	SD	0,9	4,2	0,0	0,5	0,0	–	–	0,5	0,3	0,4	0,0	0,3
	n	57	17	3	4	2	–	1	4	9	28	36	59
Total *n*		215	65	23	17	18	11	20	21	26	114	195	203

Ad = adult
J = juvenile (first-year)

(>10 mm) between July and March, and the testes of juvenile males were not significantly different from those of adults during September–November (p = 0,43; Mann-Whitney U test). Gonadal development in adult females peaked during August–December (Figure 2b), and follicle size of juvenile females was greatest during August–October (Table 3).

Gonadal development in 89 greywing measured during July–December 1990 showed testicular development similar to that for 1988–1989. However, follicle size of adults was significantly greater for birds collected in August 1990 ($\bar{x}$ = 38,0 mm; SD = 1,0; n = 3 *vs* 6,7 mm; $p < 0{,}01$, Mann-Whitney U test). The onset of egg laying was also earlier in 1990 (in early August) than in the two previous seasons.

Egg laying in 1991 commenced in late August, before the start of the spring rains and following a dry winter, despite the lowest August temperatures in nine years (mean minimum temperature = –5,1°C; SD = 6,4), nearly 3,0°C colder than the 1983–1990 mean minimum temperature.

All two-bird coveys collected during August–March (n = 10) consisted of a male and a female in breeding condition. The incidence of such pairing was greatest during August–December (Figure 2b). Incubating birds were observed during August–March, but excluding February, and the majority of nests (73%; n = 41) were found during September–November (Table 1; Figure 2b).

Although greywing nests were recorded during January–March, this extension of the breeding season was not significantly different from the general pattern for the three regions (Table 1; ASD = 0,4; –1,4 and –0,2 respectively; $p > 0{,}05$). However, the potential for early nesting in the eastern Cape was suggested by a significant negative deviation from expected in July, i.e. the model expected to detect breeding in July in the eastern Cape (ASD = –2,0; $p < 0{,}05$). Indeed, on 26 July 1991 a hen in breeding condition (3 follicles > 10 mm in diameter) was shot on the Stormberg Plateau.

The monthly incidence of follicle size and the presence of chicks were usually significantly positively correlated with monthly temperature, rainfall, day length and arthropod availability. Correlations with pairing and nesting were not significant (Table 2).

South-western Cape Province

Pairing frequency for greywing populations from the south-western Cape during August (33%; n = 6 coveys) was similar to that for the eastern Cape (35%), and the mean follicle size for 18 females from these populations was not significantly different ($p > 0{,}05$, Mann-Whitney U test) from that of the eastern Cape for April (1,8 mm), June (2,7 mm), August (5,3 mm) and November (17,6 mm) (Table 3). However, nest record cards (n = 47) from the south-western Cape indicate that nesting peaks during August–October (Table 1; Figure 2c), and that there is significantly earlier nesting in the south-western Cape, i.e. during July (ASD = 2,9; $p < 0{,}05$), than in the eastern Cape and eastern Orange Free State. There were no significant correlations between our measurements of greywing breeding activity and environmental variables in the south-western Cape (Table 2).

Nesting, clutch size and incubation

Of 41 nests examined on the Stormberg during the study period, all but two were found by searching areas from where single birds had flushed. One nest was located by pointing dogs during 73 h of searching, and the other was located by random searching (effort not recorded). Nests were all situated on the ground, under the canopy of a grass tuft, with the exception of one, which was placed in a lucerne *Medicago sativa* land. Greywing nests are scrapes in the earth lined with grass and occasionally feathers. Mean nest dimensions measured from eight nests were 16,9 cm diameter (SD = 0,3; range = 16,5–17,5) by 4,8 cm deep (SD = 1,0; range = 3,5–6,5).

Mean clutch size for the eastern Cape was 5,5 eggs (SD = 1,2; range = 4–8; n = 38), and was not significantly different between years (1988/89 $\bar{x}$ = 5,45; SD = 1,6; n = 11; 1989/90 $\bar{x}$ = 5,25; SD = 0,9; n = 12; 1990/91 $\bar{x}$ = 5,80; SD = 1,0; n = 15; $p > 0{,}05$; t test). Mean egg size was 39,93 mm × 30,11 mm (SD = 1,9 and 0,9; range = 37,2–44,6 × 28,3–32,1; n = 101). Egg coloration was consistent with the descriptions by Maclean (1985) and Crowe *et al.* (1986), i.e. yellowish brown, sometimes speckled with brown and slate. Mean incubation period for 13 eggs from two wild clutches was 21,7 days (SD = 0,5; range = 21–22), while three eggs of known laying date, incubated in an electronic incubator, hatched at 21 days. Clutches were incubated by the hen only, usually with the paired male close to the nest site.

Nest success

The clutch survival rate, hatching rate and the survival per egg-day were calculated for 21 nests from the Stormberg study period (Table 4). The hatching rate (i.e. the probability that eggs present at hatching time actually produce living young) was 44 young/49 eggs which equals a hatching probability of 0,898. That is, about 10% of the eggs present at hatching did not hatch. Nine clutches were lost during 172

Table 4 Nest success rates (as percentages) calculated for 21 greywing francolin clutches from 1988–1990 on the Stormberg Plateau

Success rate	Breeding season 1988/89 10 nests	1989/90 11 nests	Cumulative 21 nests
Clutch success			
Mortality/nest-day	10,26	1,06	5,23
Survival/nest-day	89,74	98,94	94,77
Survival/21,7 days	9,55	79,29	31,39
Egg success			
Overall			
Mortality/egg-day	1,21	0,41	0,78
Survival/egg-day	98,79	99,59	99,22
Survival/21,7 days	76,72	91,46	84,40
Persisting/nests			
Mortality/egg-day	0,76	0,25	0,45
Survival/egg-day	99,24	99,75	99,55
Survival/21,7 days	84,79	94,80	90,73
Hatching success			
Mortality/season	25,00	5,41	10,20
Survival/season	75,00	94,60	89,80

nest-days of incubation, the rate of clutch loss was therefore 9/172 = 0,052 per nest-day, and the clutch survival rate was 1 – 0,052 = 0,948 per nest-day. Thus, the probability that a clutch will survive 21,7 days of incubation is $0{,}948^{21{,}7}$ = 0,31. The variance of Mayfield's estimator of clutch survival per nest-day (s) using the method of Johnson (1979) is:

$$\mathrm{Var}(s) = [(172)^3/(172-9)9]^{-1}$$
$$= 2{,}883(10^{-4}),$$

and the standard error (the square root of the variance) = $1{,}698(10^{-2})$. The 95% confidence limits for s, calculated as the estimated value ± 2 standard errors, gives the boundary at 0,914 to 0,982 (usually: $\bar{x} \pm 2SD / \sqrt{n}$).

The overall mortality per egg-day from seven eggs lost individually during incubation, where the exposure was 899 egg-days, was $7{,}8(10^{-3})$ per egg-day. Therefore, the survival was 0,992 per egg-day, and the probability of an egg surviving the incubation period without the entire clutch being destroyed was 0,84.

The mortality per egg-day for the eight clutches which persisted until hatching was 3/671 = $4{,}5(10^{-3})$. Thus, the probability of an egg surviving the incubation period in a persisting nest was 0,907.

Discussion

Timing of breeding

The greywing francolin has a prolonged breeding season (August–March) in the summer rainfall region (i.e. the eastern Cape Province and Natal/eastern Orange Free State) and a contracted breeding season which begins significantly earlier (July–December) in the winter rainfall region. In the Stormberg study area, annual variation in August temperature appeared to have no effect on the timing of breeding. However, above-average winter rainfall during June 1990 did appear to induce earlier egg-laying in August 1990. The view that food availability is the chief ultimate factor influencing the onset of breeding (Marshall 1951; Nix 1976) and that breeding in gamebirds is timed to take advantage of a seasonal flush of arthropods (Potts 1986) is not supported by the negative relationship between laying, and the weak positive relationship between chick-rearing phase, and arthropod availability in the south-western Cape. Thus, it appears that the seasonal variation in suitable breeding conditions in the south-western Cape create a relatively small acceptable time 'window' for breeding in that region which necessitates both early onset and cessation of breeding. In the summer rainfall region, however, greywing breed when temperature, rainfall, day length and arthropod availability are increasing or peaking. The alternative for greywing from the south-western Cape would be to breed when there is maximum arthropod availability at the start of the rainy season (i.e. March–April). However, this is a time during which temperature is decreasing and winter rainfall is increasing. Since the survival of young gamebirds may be poor under cold and wet conditions (Pedersen & Steen 1979; Potts 1986) chick survival would be low.

The biological implications of this breeding pattern pose two, as yet unanswered, questions. First, is the greywing capable of the same reproductive success in the winter rainfall region as it is in the summer rainfall region? Second, if not, is reduced reproductive success in the winter rainfall region a result of inadequate arthropod availability? If so, this less-than-optimal breeding strategy may lead to reduced populations and hence its low utilization for hunting in that area.

Clutch and egg size

Mean clutch and egg sizes in this study were consistent with those in other studies for this species, except for the upper range of clutch size, which was less than that reported by Gilfillan (1908), Maclean (1985) and Crowe *et al.* (1986). These authors suggest that larger clutches may result from two hens laying in the same nest, a behaviour which was not observed during this study.

Mean greywing clutch size is less than that of nine species of northern hemisphere quails and partridges (Johnsgard 1988), but is similar to that of 10 other southern African francolin species (Crowe *et al.* 1986). Lack (1968) suggested that smaller clutch sizes, characteristic of tropical partridges, may reflect either reduced amounts of nutritious foods, shorter diurnal foraging periods, or longer nesting seasons making it more feasible to raise two or more broods per season. No evidence was found during this study to support the multiple-broods hypothesis for the greywing, despite previous circumstantial evidence of 'old' hens raising more than one brood per season (Mentis & Bigalke 1980). Indeed, parents stayed with their chicks throughout the breeding season, and chicks of different sizes and ages were never observed with only one pair of adults. However, we suggest that the apparently extended breeding season, particularly in the summer rainfall region, would allow successful re-nesting after failure of the first clutch.

Nest success

Nesting losses for the greywing were as highly variable between years as for most other gamebirds (Johnsgard 1988). However, the between-year difference in nesting success would be reduced if corrections were possible for the disturbing influence of sampling during the 1988/89 season. Nevertheless, the cumulative nesting success of 31,4% for the Stormberg is not significantly different from the mean of 40,7% (SD = 18,1) reported by Johnsgard (1988) for several studies of northern hemisphere quails and partridges. During the 1988/89 season, we visited nests daily, and hens were flushed from the nest at each visit. This may have contributed to the higher predation rate and one case of nest desertion during the first season. Visits to nests were not made as frequently, and hens were flushed less often, during the 1989/90 breeding season.

Although we recorded high seasonal variation in hatching rate, the cumulative egg failure rate of greywing closely matches the egg failure rates of less than 10% for three gamebird species reported by Johnsgard (1988).

Individual egg losses were low (i.e. when eggs were lost to predation either all the eggs were taken or the nest was deserted). Therefore we used Mayfield's (1975) assumption that the product of the probabilities of hatching success and clutch survival will give the probability that an egg present at the start of incubation produces a chick. This probability for greywing is 0,90 × 0,31 = 0,28. Thus, the mean clutch size of 5,5 eggs × 28% probability of chick production = ± 2 chicks hatched per pair per season. Mentis & Bigalke (1980) report an average annual turnover of birds in a population of 50% for the Natal Drakensberg populations. We recorded adult : juvenile ratios of 55–60% : 40–45% in non-breeding (winter) populations on the Stormberg during this study (Little & Crowe in prep). These production levels suggest that our estimates of chick production are conservative.

Regional and seasonal differences may be found in the rates of nest success, particularly where influenced by different levels of predation. During this study, two nests were preyed on by crows (*Corvus* spp.), three by small carnivores and one by a common egg-eater (*Dasypeltis scabra*). Greywing egg-shells located in the grassland indicated additional predation by crows and snakes. We suggest that nest predation by small carnivores and crows is possibly the major cause of nest failure on the Stormberg Plateau, and that the high incidence of losses of entire clutches is attributable to this cause [as found by Myrberget (1985) for willow grouse *Lagopus lagopus lagopus*]. However, further study is required on the effects of predator removal on the nesting success of the greywing before this can be tested fully.

Other causes of nest failure observed during this study were destruction by management fires (one case in August and two cases in September), human disturbance (one) and trampling by sheep (one).

Management implications

The management implications of a geographically variable breeding season in the greywing create the need for regional differences in the timing of hunting. We suggest that the hunting season for the greywing should be from 15 April to 31 July in the summer rainfall region and from 1 April to 30 June in the winter rainfall region (presently 1 April–15 July in the Cape Province, and 31 May–31 August in Natal).

Although previous literature reports that a fine-scale fire mosaic maintains high densities of grassland francolins (Mentis & Bigalke 1981), it has been suggested that late spring burning is detrimental to the reproductive success of these grassland francolins (Little & Bainbridge 1988). The common practice of burning grasslands shortly after the first spring rains usually encroaches into the breeding season of greywing francolin. We therefore recommend that grasslands in the summer rainfall region be burned not later than the end of August.

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