COOPERATIVE BREEDING AND DELAYED DISPERSAL IN THE PALE CHANTING GOSHAWK *Melierax canorus*

by

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Thesis submitted for the degree of Doctor of Philosophy

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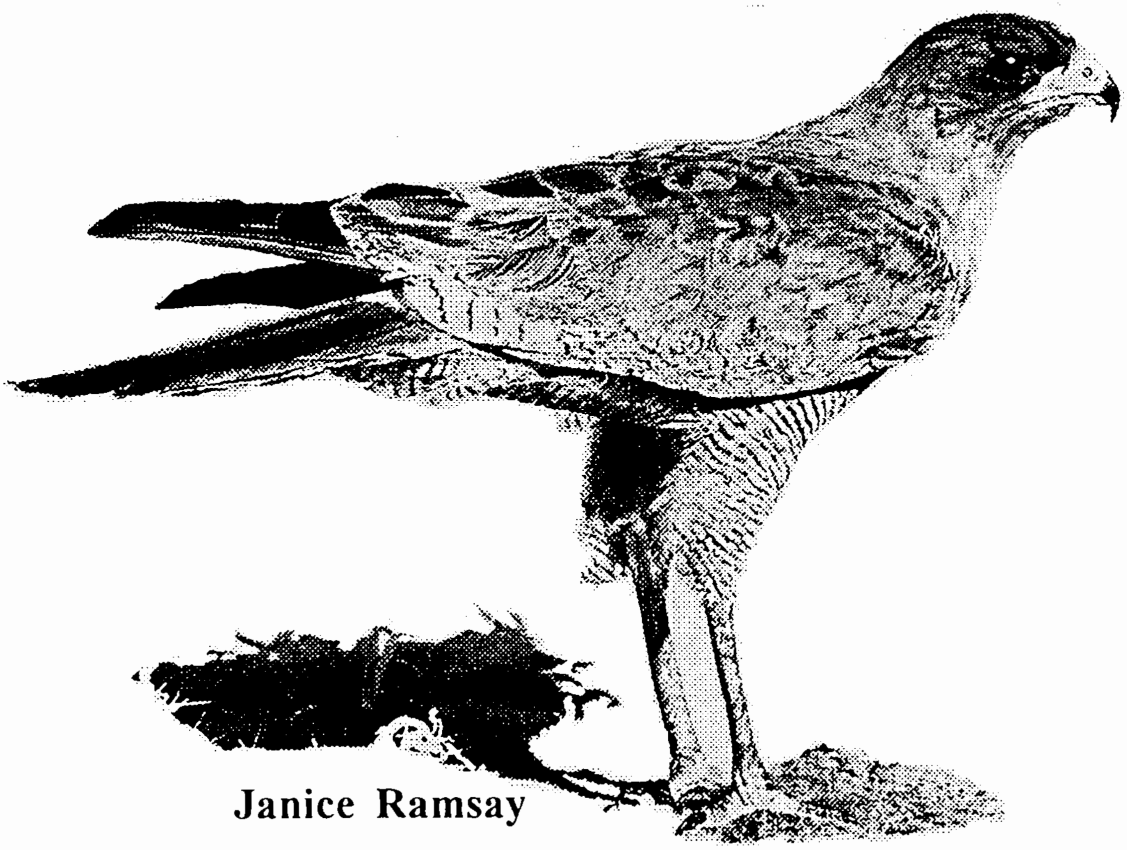
DECLARATION

This thesis reports the results of original research I conducted under the auspices of the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, between 1988 and 1995. All assistance that I received has been fully acknowledged. This work has not been submitted for a degree at any other university.

Gerard Malan

There is an immense pleasure and fascination
to be gained from studying an animal
day-to-day in its own environment.
Ian Newton



Janice Ramsay

Dedicated to my parents, Christo and Rina,

and my wife, Marianne

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ABSTRACT

Malan, G. 1995. Cooperative breeding and delayed dispersal in the Pale Chanting Goshawk Melierax canorus. *Ph.D. Thesis, FitzPatrick Institute, Department of Zoology, University of Cape Town, Rondebosch 7700, South Africa, (xx)+277p.*

A population of Pale Chanting Goshawks *Melierax canorus*, some of which live in families, was studied during 1988-1992 for a total of 117 group-years near Calitzdorp, South Africa. The aims of the study were to identify ecological and social factors that might predispose individuals in the population to delay dispersal and become non-breeding or co-breeding members of Pale Chanting Goshawk families, and to determine why co-breeders breed cooperatively in polyandrous trios.

In all vegetation types within the study area, non-breeders, as juvenile and adult offspring, delayed dispersal from their natal territories. However, co-breeding males occurred only in one vegetation type, Karroid Broken Veld. Co-breeding males participated in all reproductive activities, including copulation. Karroid Broken Veld also supported the largest known groups of Pale Chanting Goshawks and the highest frequency of groups with non-breeders, which resulted in some of the highest recorded single species raptor densities in the Afrotropics. Pale Chanting Goshawks in Karroid Broken Veld preyed primarily on two otomyinid rodents, *Otomys unisulcatus* (42-48% of prey biomass) and *Parotomys brantsii* (18-32%). The habitat quality of Karroid Broken Veld for Pale Chanting Goshawks was high since, compared with other vegetation types, it incorporated: (1) optimal habitat for otomyinid prey, (2) a very high estimated biomass of otomyinids, almost twice that of other vegetation types, and (3) a hunting habitat with an optimum combination of prey visibility and perch availability that facilitated hunting efficiency.

Territorial space was limited throughout the study area, constraining the number of non-breeders per group to two and inhibiting new breeders from establishing territories. Juvenile non-breeders probably delayed dispersal to increase their probability of survival,

and dispersed later as sexually mature adults, since they could not increase their fitness further by becoming helpers at the nest. During the nestling period, co-breeding beta males provided prey at an equal rate to dominant males, that enabled polyandrous trios to undertake more frequent and successful breeding attempts in years of high prey abundance. The help provided by co-breeders contributed more to this success than did density of dominant prey and territory size. In Karroid Broken Veld co-breeders delayed dispersal since their fitness as subordinate sibling males was probably higher than fitness achieved due from dispersing to a breeding vacancy in habitat of lower quality. I suggest that those ecological factors which contribute to habitat quality provided the proximate impetus, and the resulting saturation of the habitat the ultimate impetus, in promoting the establishment of Pale Chanting Goshawk family units.

Once Pale Chanting Goshawk formed families, a range of secondary benefits evolved as birds adjusted their behaviour to benefit from the presence of other group members. For example, although breeders in high-quality habitat produced the highest number of offspring, the lack of territorial space probably forced more offspring to disperse. To increase offspring survival, breeders may have adjusted their reproductive strategy and allow non-breeders to partake and share in returns of cooperative hunts. Other secondary benefits included the possibility of inheriting a natal territory, budding-off onto territorial borders or helping close relatives as an experienced co-breeder.

ACKNOWLEDGEMENTS

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Without the landowners at Calitzdorp who allowed me access to their properties, fieldwork would not have been possible. I apologise to these gentleman for the roads I created on their farms travelling to Pale Chanting Goshawk nesting sites: the late Johan Geyser, Gerrit Lategan, Harry Lewitton, Gerrie Mathee, Jan Meiring, Lourens Oosthuizen, Nellis Oosthuizen, the late Erenst Potgieter, Kobus Potgieter, Jan and Johan

Potgieter, Okkie Scholtz, Daantjie Strydom, Hennie Terblanche, Saag Jonker, Hans Fouche and Fanie Fourie. Johan Potgieter, Okkie Scholtz, the late Koot Pretorius, Johan Marais and Boy Terry assisted whenever they could, even if I got stuck.

Without the assistance of my parents this study would not have been possible. They allowed me free lodging and abundant time for fieldwork. My wife supported wherever and whenever she could and allowed me to delay dispersal for so long.

Lastly, it is impossible to convey the atmosphere of studying Pale Chanting Goshawks in the Little Karoo. Perhaps a slate grey Pale Chanting Goshawk flying against the emerald green Spekboomveld, the red foothills of the Rooikoppe in the background. Summer was exciting as summer visitors, Booted Eagles, Lanner Falcons, and buzzards arrived, and Pale Chanting Goshawks bred, and sometimes bred again. In winter the weather was sunny, cool, almost without any wind or cloud, the perfect study environment for a student of behavioural ecology.

GENERAL INTRODUCTION

CHAPTER 1

INTRODUCTION

1.1 Avian cooperative-breeding systems

Cooperative breeding in birds occurs when individuals in addition to the genetic parents exhibit parent-like or helping behaviour towards the young of a single nest (Emlen 1991). The social systems of the more than 200 cooperative-breeding bird species vary considerably, but consist generally of a monogamous pair with related adult offspring that delay dispersal and help at the nest (see Brown 1987b). However, cooperative breeding may not only include non-breeding helpers at the nest, but also helpers that participate in reproductive activities (Faaborg & Patterson 1981). Cooperative polygamy can be subdivided into polygyny, females sharing one male, or polyandry, co-breeding males sharing one female (Brown 1987b; Davies 1991). Polyandry can again be subdivided into sequential and cooperative polyandry, in which the female has persistent bonds with two or more males, with all males being involved in copulation and parental care (Faaborg & Patterson 1981). Cooperative polyandry is rare in birds and has been reported in fewer than 15 species (Faaborg 1986). Four of these are raptors, the Harris' Hawk *Parabuteo unicinctus*, Galapagos Hawk *Buteo galapagoensis* (Faaborg & Bednarz 1990), Bearded Vulture *Gypaetus barbatus* (Heredia & Donazar 1990) and Egyptian Vulture *Neophron percnopterus* (Tella 1993).

1.2 The social system and how it functions

It is important to study the social behaviour and relatedness of cooperatively breeding individuals, since only when the fitness consequences of a specific social arrangement are known, can one choose between alternative hypotheses relating to benefits and constraints of phenomena such as delayed dispersal and helping (Emlen 1984; Joste *et al.* 1982; Russell & Rowley 1988; Emlen 1990; Koenig *et al.* 1992; Emlen 1994). The social behaviour of non-breeding *vs* breeding helpers (co-breeders) that delay dispersal also needs investigation since the ecological and social conditions that lead to these phenomena are poorly understood (Koenig *et al.* 1992). If helping does not confer any fitness advantages to breeders or co-breeders, helping behaviour can be judged to be selectively neutral (Emlen & Wrege 1989). To assess the neutrality of helping, one can measure various indices of reproductive success, such as prey provisioning to young at the nest site which may release breeders from some parental duties and increase the probability of further breeding attempts, or detection and deterrence of predators at nest sites or territorial borders (Brown & Brown 1981; Gayou 1986; Russell & Rowley 1988; Rabenold 1990; Reyer 1990; Davies 1991; Mumme 1992a). If helping does confer fitness advantages to breeders or related co-breeders by the production of descendant and non-descendant kin, individuals gain direct and indirect fitness benefits (Maynard-Smith 1964; Joste *et al.* 1982). Since the loss in direct fitness can be compensated by a gain in indirect fitness and paternity is diluted by the number of individuals participating in reproduction, one can expect the development of dominance hierarchies with an ensuing adjustment in reproductive roles (Stacey 1979; Vehrencamp 1980). To protect their genetic investment, co-breeders may guard their mates, copulate as frequently as possible and provision offspring at rates equal to those of dominant breeders (Davies 1985; 1990; Birkhead & Moller 1992).

1.3 Why delay dispersal and why act as a co-breeder?

1.3.1 Population densities and territorial space

Effective population density could be the primary factor distinguishing between extrinsic constraints or intrinsic benefits as conditions that regulate the intensity and configuration of cooperative-breeding systems (Koenig & Mumme 1987; Stacey & Koenig 1990; Koenig *et al.* 1992; Komdeur *et al.* 1991). Koenig *et al.* (1992) predicted that, if an extrinsic constraint, such as the lack of territorial space, provides the proximate impetus, offspring would experience higher fitness by delaying dispersal rather than dispersing to a vacant territory of lower quality. If intrinsic benefits provide the impetus, then living in groups will yield higher fitness than living as pairs, and the density and availability of high-quality territorial space will have little impact on individuals that delay dispersal. Intrinsic benefits are normally socially-derived and include benefits of philopatry such as the learning of hunting skills, protection from predation, indirect fitness gains from helping close relatives or the possibility of inheriting or occupying a territory nearby (Stacey & Ligon 1987; Heinsohn *et al.* 1990; Emlen 1994).

1.3.2 Habitat quality: prey abundance and habitat parameters

Habitat quality is one of the ecological factors that might explain the evolution of cooperative breeding and delayed dispersal (Lack 1968; Koenig & Pitelka 1981; Bednarz & Ligon 1988; Stacey & Ligon 1991; Koenig *et al.* 1992; Komdeur 1992). The determination of habitat quality is difficult, and factors such as characteristics of the prey abundance and associated habitat parameters have to be defined (Koenig & Pitelka 1981; Bednarz & Ligon 1988; Koenig *et al.* 1992; Komdeur 1992). The prey supply may be subject to considerable spatial and temporal environmental variation, and the quantity, diversity and stability of prey may favour group living by providing benefits to birds that occupy territories with a superior prey supply (Bednarz & Ligon 1988; Waser 1988; Stacey & Ligon 1991). In a bird species that searches visually for terrestrial prey and hunts from a perch, habitat parameters such as perch height and abundance, vegetation density and prey visibility, may all influence hunting success (Fitzpatrick 1980; Simmons 1989; Sonerud 1992; Yosef 1992; Widen 1994). Greater hunting success and the different foraging strategies employed under different habitat regimes may favour cooperative breeding because of the intrinsic benefit of increased hunting efficiency of group members (Bednarz 1988; Yosef 1992).

1.3.3 The demographic impact of habitat quality

The 'decision' to delay dispersal and to help is based on the assumption that each individual will try to maximise its reproductive and survival fitness (Emlen & Wrege 1994). To do so, birds will occupy habitat in rank order of quality until all suitable habitat is occupied (Komdeur *et al.* 1991; 1992). Once such a point of saturation is reached, access by offspring to breeding opportunities will be limited (Woolfenden & Fitzpatrick 1984; Mumme 1992b). Furthermore, if the population is stable and breeder recruitment low, offspring are further constrained in obtaining a breeding opportunity (Woolfenden &

Fitzpatrick 1984; Russell & Rowley 1988). If offspring, especially juveniles, are constrained by a lack of territorial space and survival or hunting skills, they will prefer to remain in their natal territories if the cost of missed breeding opportunities is less than the fitness loss by dispersing to a habitat of poorer quality (Brown 1987b; Heinsohn *et al.* 1990; Emlen 1991; Koenig *et al.* 1992). However, as soon as birds live in families, individuals may adjust their behaviour in order to benefit from the presence of other group members (Fitzpatrick & Woolfenden 1986; Emlen 1994). The result is that many of the benefits of family living, such as enhanced survival or helping close relatives, may be the result of intense competition for high-quality territorial space in the first place (Emlen 1994). The conclusion can therefore be drawn that, only if a range of social and ecological benefits and constraints are examined, can the evolutionary causes and consequences of cooperative breeding and delayed dispersal be understood (Mumme 1992b).

1.4 The Pale Chanting Goshawk

Although the Pale Chanting Goshawk (PCG) *Melierax canorus* is a widespread, common, resident and readily-observed species in southwestern Africa, its behaviour and ecology were remarkably poorly known at the onset of this study (Steyn 1982). Some of its basic natural history had been studied (Biggs *et al.* 1984; Steyn & Myburgh 1992), but there was very little quantitative information on any aspect of its behaviour or ecology. For example, it was known that adult PCGs stay in the same areas for up to six years (Biggs *et al.* 1984). Finch-Davies & Kemp (1980) suggested that, because juveniles remained in the parental territory for several months, some form of relatively complex social organization might exist. They further hypothesised that, although the PCG appears to breed monogamously, its breeding system might be more highly specialised through complex social arrangements than had been documented. At the start of my study in 1988, I discovered that, although raptors normally expel their young from the natal territory (Brown 1970), PCG juveniles and adult offspring (non-breeders) were often allowed to delay dispersal. Furthermore, in the beginning of August of that year, I discovered that

PCGs were cooperatively polyandrous breeders when I observed two colour-marked males copulating with the same marked female in a single pre-laying period.

1.5 Aims

The aims of this study are to investigate and review a range of ecological and social factors that may predispose PCGs to delay dispersal and breed cooperatively. I compare behaviour, breeding biology, diet and population ecology between polyandrous and monogamous groups (as individual and group members) in three quite distinct vegetation types at my primary Calitzdorp study area (see Chapter 2). From a PCG's perspective, each vegetation type potentially represents different habitat quality, and opportunities for changes in mating systems, densities and demography. Whenever possible, aspects of population ecology are compared with other less intensively studied PCG populations.

1.6 Outline of the thesis

Chapter 2 describes the three vegetation types, as well as the general ecology of the Calitzdorp study area. In the first section (Chapters 3-5) of the thesis that outlines research results, I analyse aspects of the social biology of the PCG. I ask the question if co-breeders really help and, if they help, how they help. I also examine how kinship impacts on the polyandrous breeders' reproductive roles. In the second section (Chapters 6-9), I analyse ecological and social factors that may predispose PCGs to delay dispersal and breed cooperatively. Chapter 6 is an examination of relative population densities and the availability of territorial space that may indicate if the decision to delay dispersal was influenced by intrinsic benefits and extrinsic constraints. I examine the PCG's diet, the abundance of dominant prey species and habitat parameters associated with these prey. Chapter 8 investigates characteristics of the PCG's hunting habitat, *e.g.* perch height and abundance, and ground and perch cover that may influence perch availability and prey visibility, as well as cooperative hunting by PCGs. In the last chapter, I quantify habitat quality and assess the demographic impact, such as recruitment, fidelity and survival, of PCGs living in habitats of differing quality.

CHAPTER 2

STUDY AREAS, GENERAL METHODS AND THE GENERAL BIOLOGY OF THE PALE CHANTING GOSHAWK

2.1 Study areas

2.1.1 Calitzdorp study area

2.1.1.1 Locality

The main study area was located near Calitzdorp (33°32'S; 21°48'E) in the Western Cape, South Africa, near the southern limit of the Pale Chanting Goshawk's (PCG) distribution (Fig. 2.1).

2.1.1.2. Farming practices

The study area is 145.75 km^2 in extent and is encompassed totally by farms within which no PCGs occur (Fig. 2.2). To the east of the study area are intensive irrigated fruit, grape and lucerne farms, to the south and west semi-intensive, dry-land (non-irregated) wheat and lucerne farms, and, there are to the north, extensive cattle farms. The study area itself and the unstudied surrounding areas are unoccupied by humans and were utilised almost exclusively for extensive ostrich farming and, occasionally, for cattle and horse grazing. Two main roads run east-west across the area, an asphalt road that carries the bulk of the traffic, and a cement road to a separate farming community (Fig. 2.2). Apart from these and two secondary gravel roads, roads are private and closed to the public.

2.1.1.3 Vegetation types

Three karroid vegetation types occur in the study area, lying in parallel bands from Spekboomveld in the north, through Karroid Broken Veld to Succulent Karoo in the south (Fig. 2.2) (Acocks 1988). In order to map the vegetation types, the study area was divided into 500x500 m quadrats. Each quadrat was searched and categorised according to the dominant vegetation type. Spekboomveld or Succulent Mountain Scrub were divided into Open Spekboomveld (where PCGs occur) and Closed Spekboomveld (no PCGs). To avoid subjective judgement, the presence or absence of Spekboom (*Portulacaria afra*), a species closely associated with dense scrub (Acocks 1988), was used as an indicator species

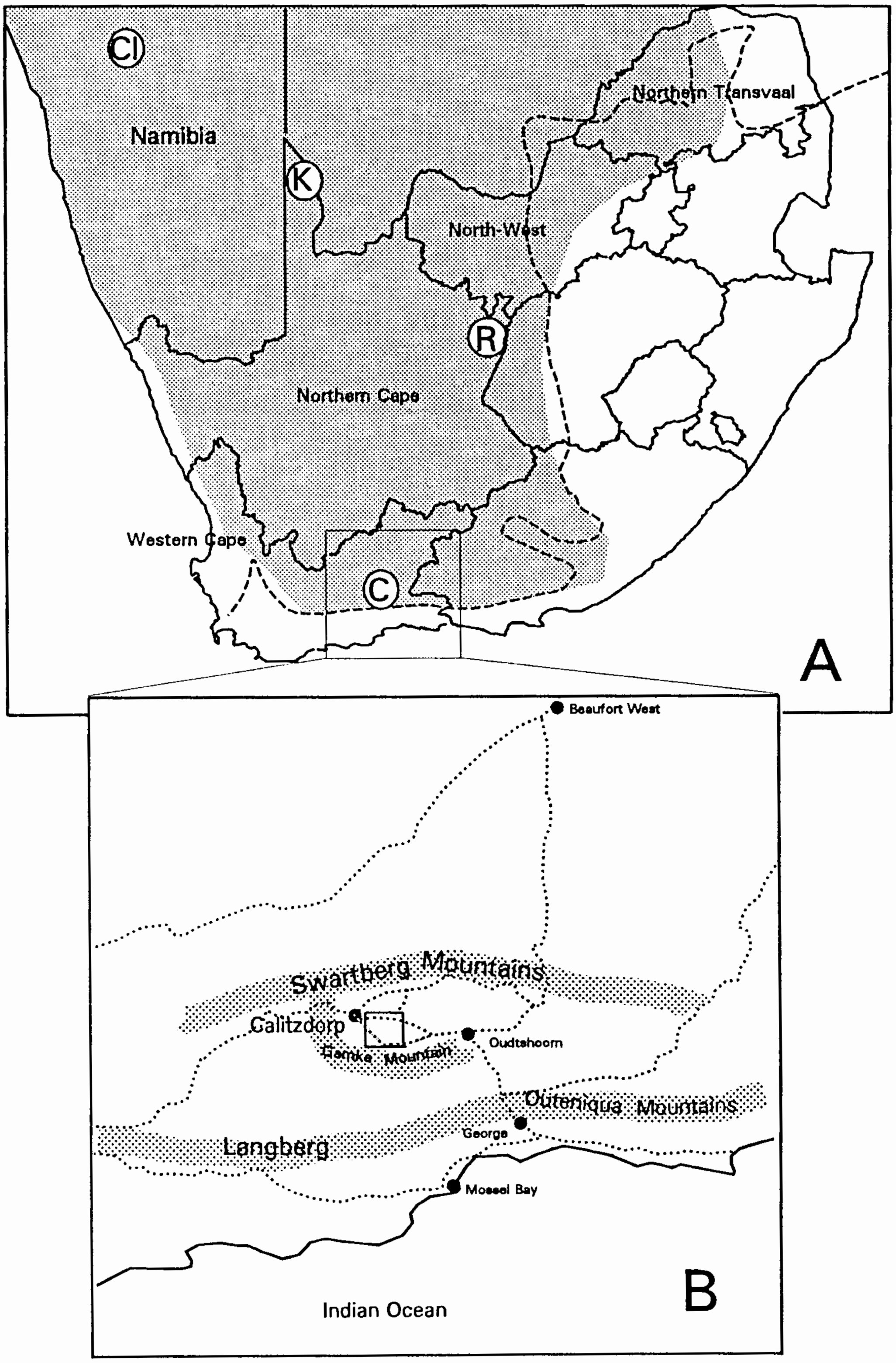

Fig. 2.1 Locality of Calitzdorp study area. (A) Shaded area Pale Chanting Goshawk distribution in South Africa (Maclean 1985). Dashed line is 500 mm rainfall isoline. R = Rooipoort, K = Kalahari Gemsbok National Park, Cl = Claratal, C = Calitzdorp. (B) Mountain ranges surrounding the Calitzdorp study area, dotted lines are roads.

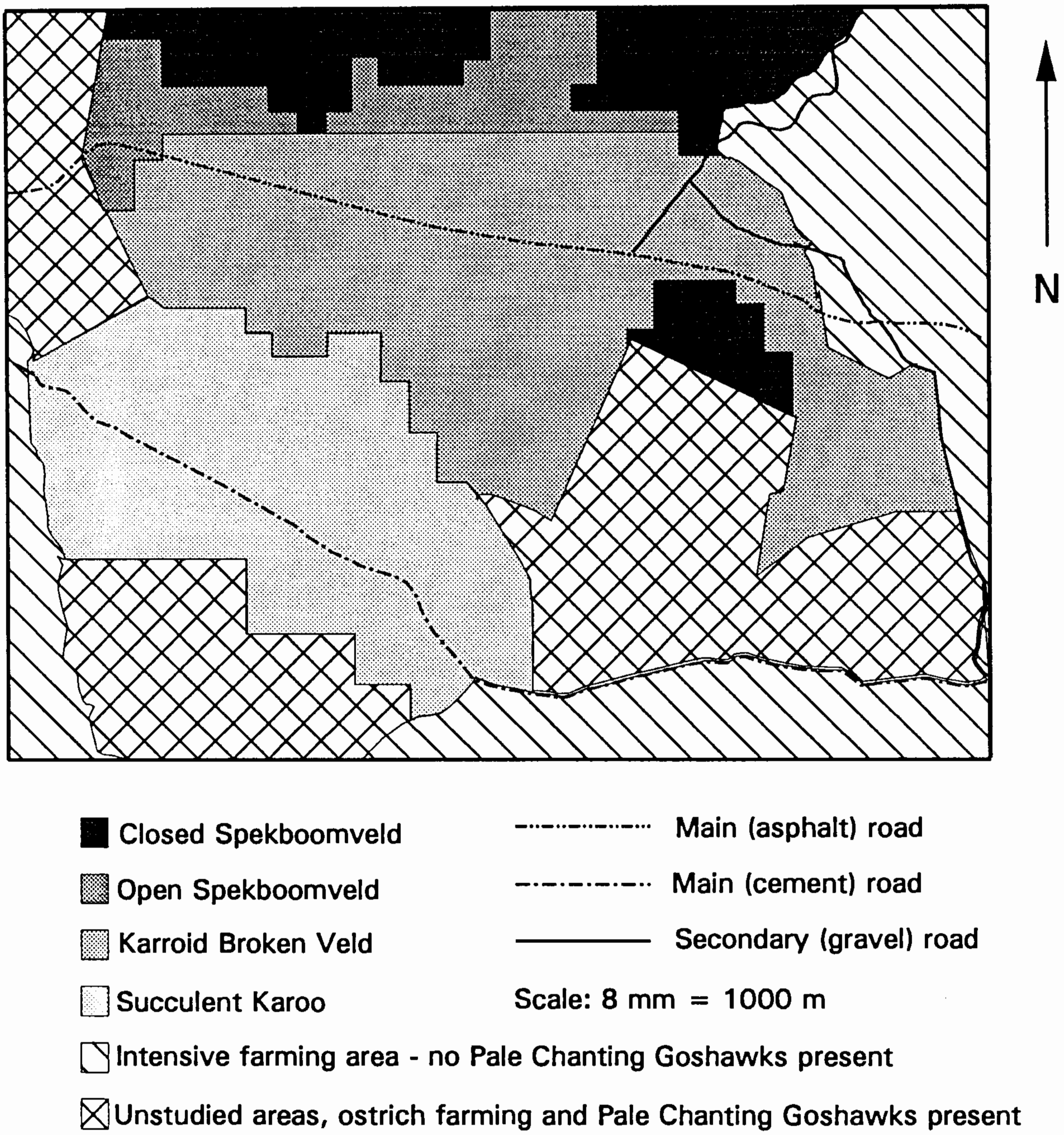

Fig. 2.2 The Calitzdorp study area (shaded area), vegetation types, farming practices and major roads.

to separate Closed (Spekboom present) from Open Spekboomveld. Closed Spekboomveld consists of a dense stands of trees and shrubs 2-5 m tall, whereas Open Spekboomveld is more open with fewer trees and shrubs. *Portulacaria afra* and *Pappea capensis* are dominant Spekboomveld trees. Karroid Broken Veld consists of a layer of small plants with dwarf trees and shrubs 1-3 m tall scattered throughout. Dominant small plants (bushes and mesembs) are *Zegophyllum microphyllum* and *Drosanthemum uniflorum* and often grow in dense clumps, especially on the Mima-like mounds or heuweltjies (Lovegrove & Siegfried 1986; Acocks 1988). Dominant trees and shrubs are *Euclea undulata, Maytenus undata, Pappea capensis, Rhus lucida* and *Carissa haematocarpa*. Succulent Karoo virtually lacks trees and shrubs and consists only of a sparsely distributed layer of succulents, normally *Augea capensis*, less than 0.15 m tall. Within this vegetation type, PCGs did not occur without man-made (*e.g.* telephone and fence) or planted (Sisal *Agave mericana*) perches (GM pers. obs.). Very few grasses occurred in any of the vegetation types (Acocks 1988).

2.1.1.4 Topography and soil types

Geologically, the study area falls within the Little Karoo, a level sedimentary basin (140 km long and at places 50 km wide) set between two parallel ranges of mountains, the Swartberge in the north and the Langeberg and Outeniqua ranges in the southeast (Fig. 2.1). Soils are shallow (< 400 mm), usually coarsely textured and overlaying hardpan (a hard chalk deposit), but are generally rich in plant nutrients (Ellis & Lambrechts 1986). The topography of the study area is generally flat, but slopes from 446 m.a.s.l. in the north to 257 m.a.s.l in the south. No rivers occur and water is dispersed by drainage lines.

2.1.1.5 Rainfall and temperature

Calitzdorp has an average annual rainfall of 198.8 mm (n = 116 years) (Anon. 1993). The low rainfall is, amongst other reasons, the result of the Little Karoo being in the rainfall shadow of the Langeberg/Outeniqua Mountain ranges (Schulze & McGee 1978).

The southern section of the study area (Succulent Karoo) receives approximately 40 mm less annual rainfall than the north (Closed Spekboomveld) (landowners pers. comm.). The rainfall is bi-seasonal with peaks in February-April and October-November (Fig. 2.3). Within South Africa, the Little Karoo rainfall district is subject to moderate year-to-year fluctuations compared to other rainfall districts within the PCG's distribution range (CV of rainfall distribution = 25%, range 21 - 47; Onesta & Verhoef 1976). Mean monthly maximum temperature range from 31-16°C and mean monthly minimum temperature from 19-5°C (n = 26 years; Anon. 1993) (Fig. 2.3). Mean annual temperature is 14°C (South Africa range 14-22) (see Schulze & McGee 1978). In conclusion, although the low rainfall classified the study area as being located in a semi-desert (Maclean 1990), its climate was moderate as it was situated on the ecotone of the mesic (> 500 mm annual rainfall; Fig. 2.1) and arid parts of South Africa (Zucchini *et al.* 1992).

2.1.2 Other study areas

To place the Calitzdorp study population in perspective, it was compared with populations from: the farm Claratal (22°50'S 18°50'E) on the Khomas Hochland, Namibia; the Kalahari Gemsbok National Park (KGNP) (25°25'S 20°35'E); and Rooipoort (28°45'S 24°05'E), a private nature reserve in the Northern Cape Province. Rooipoort's vegetation consists mainly of dense shrub and open grass savanna. However, on the reserve PCGs inhabit fairly flat and open terrain (Crowe *et al.* 1981). The KGNP consists of open flat savanna with red sand dunes and two dry river systems, the Nossob and Auob (Liversidge 1984). The large trees in these river systems provide nesting and perching opportunities for raptors. The vegetation at Claratal is open savanna with rolling hills, interspersed with dry river courses (Biggs *et al.* 1984).

2.2 Field work

2.2.1 Trapping and marking

Perching PCGs were caught with a bal-chatri trap. Birds incubating were caught on the nest with a nest-ring (Newton 1986) using two hard-boiled chicken eggs as replacement eggs. The goshawk eggs were kept in a warm safe place for not longer than one hour. Birds with nestlings were caught with a nest-dome (bal-chatri without a floor) tied over the nest with nestlings inside. Birds were marked with individual colour combinations, using colour rings (1988-1990) and patagial tags (1991-1992) (Simmons 1991). Between 1988 and 1992, 148 PCGs were marked inside the study area.

2.2.2 Instantaneous sampling

To study the behaviour of an individual in the non-breeding period and pre-laying period (from first copulation to egg laying) I employed instantaneous sampling (Lehner 1979). Instantaneous samples are discrete samples of acts, a 'behaviour' with an appreciable duration, *e.g.* a PCG hunting by flying down from a perch, chasing a rodent through the shrub and catching it (Altmann 1974). An individual's behaviour was recorded at predetermined 'points' in time (Lehner 1979). I used 60-second intervals, with a metronome 'bleeping' to provide the signal to record the behaviour. Behavioural acts recorded are described in Appendix 1. The behavioural acts were noted on cassette tape, with a pocket size tape recorder and microphone, either held in hand or attached to my collar. The advantage of the latter method was that by simply switching the machine 'on' (with a switch on the microphone itself), the behaviour could be recorded without taking my eyes off the focal bird.

I followed an individual in a light utility truck and, in some instances, on foot. The truck was preferred as the PCGs were not disturbed by its presence and it enabled me to actively pursue birds flying across a territory. An observation period stopped if a bird was lost from view for longer than 1 minute and all observation periods of less than 30 minutes were discarded. I tried to record each focal bird's behaviour for an observation period of at least 210 minutes, but because of the various obstacles hindering my pursuit (*e.g.* a fence without a gate, dense vegetation or ditches), observation periods varied in length. The mean duration of the observation periods on adult breeders was 144 minutes, and 86

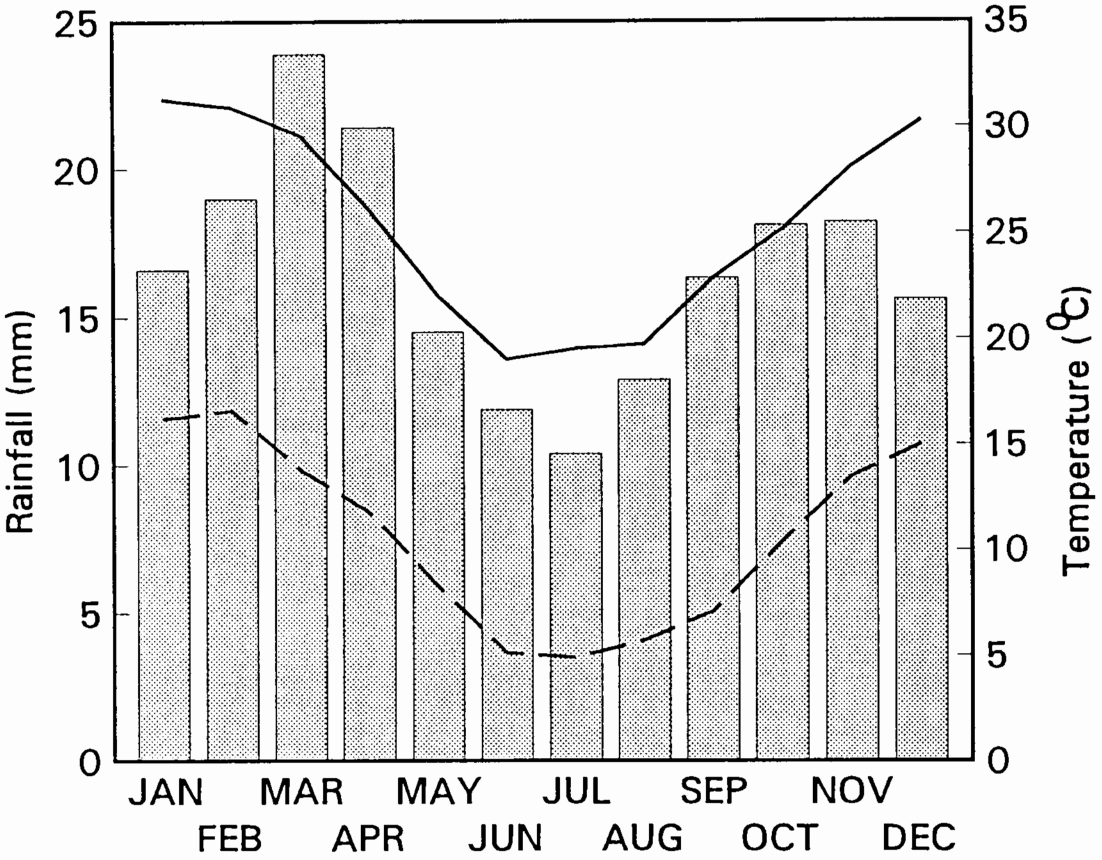

Fig. 2.3 Mean monthly rainfall (bars), mean maximum daily temperature (solid line) and mean minimum daily temperature (dashed line) at the Calitzdorp study area.

observation periods totalling 12 368 minutes or 206 hours were recorded. Observation periods were conducted in all daylight hours with peaks in the mid morning and late afternoon. The dense vegetation in the Open Spekboomveld vegetation type made it practically impossible to follow a PCG, therefore instantaneous sampling data were only recorded in Karroid Broken Veld and Succulent Karoo.

2.2.3 Scan sampling

Once the female of a group had laid a clutch of eggs, I studied the group's behaviour from a hide overlooking the nest area. A hide was secured on top of a 5 m scaffolding and was placed 5-15 m from nests. As the hides were higher than the nest and surrounding vegetation, I had an panoramic view of the birds' behaviour. The PCGs showed no adverse reactions to the presence of the hides, and used them regularly as perches. Employing scan sampling (Lehner 1979) each individual's behaviour was noted at 60 second intervals and behavioural acts recorded are described in Appendix 1. Behaviour was noted only within a 100 m radius from the nest and in the airspace above the nest. In the incubation period, observation periods varied in length, but in the nestling period, observation periods of eight hours (480 min.) were employed. Forty observation periods totalling 18 369 minutes or 306 hours were conducted. Scan sampling data were recorded in all vegetation types.

2.3 General Pale Chanting Goshawk biology

2.3.1 Distribution and taxonomy

Francois Le Vaillant named the PCG in 1799: "The yellow at the base of the feet, as well as of the feet; the elegant colours and the sustained warbling, characterise one of Africa's most beautiful birds of prey; one which I have named the Singing Falcon (*faucon chanteur*). This organ, which he alone seems endowed, to the exclusion of all other birds of prey deserves indeed to enjoy a particular appellation, as if being privileged in this sense".

Table 2.1 Body mass and wing measurements for adult Pale Chanting Goshawk from three localities in southern Africa. Mean (± 1 standard deviation) and (sample size) below. Records for Namibia and Transvaal from Mendelsohn *et al.* (1989) and Kalahari Gemsbok National Park (KGNP) from Herholdt (1993).

	Calitzdorp	KGNP	Namibia and Transvaal
Body mass (g)			
Males	729 (41) (20)	666 (38) (58)	647 (42) (35)
Females	936 (71) (29)	869 (80) (53)	809 (51) (27)
Standard wing length (mm)			
Males	355 (9) (20)	342 (12) (30)	342 (8) (35)
Females	384 (10) (19)	370 (13) (26)	340 (8) (28)
Ulna (mm)			
Males	123 (5) (18)		120 (3) (35)
Females	131 (6) (17)		130 (3) (28)

The PCG is a characteristic species of the Southwest Arid Subregion of Africa (Crowe & Crowe 1982) and inhabits low-rainfall areas ranging from true desert to open arid savanna (Steyn 1982). This species is distributed throughout the former Cape Province (except in the southwest), the western parts of the Orange Free State and Transvaal, Namibia, Botswana, southwestern Zimbabwe and southern Angola (Brown *et al.* 1982). The PCG's closest relatives are the Dark Chanting Goshawk *Melierax metabates*, distributed northwards through Africa to the Sahara but not in the forested regions of Zaire, or the dry north-east where the Eastern Chanting Goshawk *M. poliopterus* occurs (Brown *et al.* 1982; Amadon & Bull 1988). Taxonomically the PCG has been grouped with the sparrowhawks and goshawks (*Accipiter*), but recent phylogenetic and biogeographic studies suggest that the genera *Melierax, Micronisus, Kaupifalco* (from the Afrotropics) and *Leucopternis* (from the Neotropics) should be grouped into a buzzard-like melieraci clade (Kemp & Crowe 1990).

2.3.2 Morphometrics

PCGs showed reverse sexual size dimorphism and, at Calitzdorp, females weighed, on average, 28% more than males (Table 2.1). In the field, females appeared more stocky, their stance was more upright and their wing-beat slower when flying (GM pers. obs.). Birds from Calitzdorp were heavier than their counterparts in the warmer climates to the north (Bergmann's Rule) (Fig. 2.1).

2.3.3 Habits

PCGs are normally found as singletons or pairs, but groups of three or more adults together have been recorded (Biggs *et al.* 1984). This goshawk's grey body, bright orange legs and cere, and upright stance makes it easily identifiable, and its habit of perching on top of trees, poles and fenceposts makes it easy to observe (Maclean 1985). It flies with slow wing-beats interspersed with gliding and hunt from perches, gently swooping to the ground. It often walks on the ground and may pursue prey on foot (Steyn 1982).

2.3.4 Prey

PCGs are opportunistic and generalist hunters and take a broad range of prey in terms of size and diversity , *e.g.* birds, rodents, small mammals (to the size of a hare), snakes, lizards, beetles, grasshoppers, termites, carrion and even frogs (Hare 1932; Biggs *et al.* 1984; Steyn 1984; Steyn & Myburgh 1992).

2.3.5 Breeding

The PCG's breeding season is from June to December. Nests are placed in the canopy or near the canopy of a tree or shrub (Steyn 1982). The nest is lined with miscellaneous items such as dung, goat hair, sheep wool and hessian, as well as *Stegodyphus* spider nests (Malan 1992). Normally, two eggs are laid and the nesting period is 85-94 days (Maclean 1985).

2.4 Statistical analyses

All large data sets (*e.g.* instantaneous and scan sampling, and ecological data) were stored on the u-VAX computer system at the Information Technical Services, University of Cape Town. On this system, the BMDP (1990) package was employed for statistical analyses. Throughout this thesis, I have made use of multiple comparison tests (BMDP-7D). For normally distributed data, I performed a one-way analysis of variance to test between group differences (Dixon *et al.* 1990). If significant, and for a small number of groups, a pairwise $\underline{t}$ tests were preformed. When group variances were unequal (Levene's test for variances not significant) separate variance $\underline{t}$ tests were employed and, when group variances were equal, pooled variance $\underline{t}$ tests. When more than two groups were analysed, Bonferroni-adjusted significant levels were applied by dividing the number of pairwise comparisons by the significance level. When there was a large number of groups, I performed the more powerful Tukey test (Zar 1984). When the data were not distributed normally, I performed a nonparametric analysis of variance (Kruskal-Wallis test). Other statistical tests executed with the BMDP (1990) package were two-sample tests ($\underline{t}$ test and Mann-Whitney) and simple linear regressions and correlations. To analyse contingency tables I employed the Statgraphics statistical package (Anon. 1986) in either a chi-square analysis or, if frequencies were too small, Fisher's exact test.

SECTION 1

SOCIAL BIOLOGY

CHAPTER 3

THE SOCIAL SYSTEM OF THE PALE CHANTING GOSHAWK: DO CO-BREEDERS AND NON-BREEDERS HELP?

SUMMARY

The social organization of four Pale Chanting Goshawk (PCG) populations (Calitzdorp, Claratal, Rooipoort and Kalahari Gemsbok National Park) was investigated. Delayed dispersal by adult PCGs was recorded in two populations (Kalahari Gemsbok National Park and all vegetation types at the primary Calitzdorp study area). However, cooperative polyandry was observed only at Calitzdorp, and only in one vegetation type, Karroid Broken Veld (KBV). The PCG is a polyandrous, facultative, cooperatively breeding species since this mode of breeding was recorded in 20% of breeding attempts in KBV. At Calitzdorp, non-breeders were retained in the natal territories, but were actively excluded by breeders from the nest area during the breeding season. Before addressing the questions "Why delay dispersal and help at the nest", it is important to try and determine if co-breeders really help? To do this, I compared laying dates, the number of two-egg clutches, reproductive success, and nest failures of three PCG populations and from two vegetation types at Calitzdorp with that in KBV at Calitzdorp. At Calitzdorp, PCGs fledged more young per group than at Claratal and, at Calitzdorp, groups in KBV fledged more young than groups from other vegetation types. Within KBV, reproductive success per group was not significantly different between polyandrous trios and monogamous pairs, although polyandrous trios were able to attempt more second broods. Whereas PCGs only lay a maximum of two eggs per clutch, at Calitzdorp during 1989-1990, certain groups double-brooded successfully. Two polyandrous trios in KBV even double-brooded successfully in both years, each group fledging seven young. Furthermore, the second brood was attempted directly after the first. The occurrence of two males may therefore enable polyandrous trios to undertake more frequent and successful breeding attempts, and to pursue and endure, prolonged breeding seasons.

3.1.1 INTRODUCTION

Cooperative breeding occurs when individuals in addition to the genetic parents exhibit parent-like or helping behaviour to the young of a single nest (Emlen 1991). The social systems of cooperative-breeding birds vary considerably, but consist generally of a monogamous pair with related adult offspring that delay dispersal from a natal territory and help at the nest (see Brown 1987b). Delayed dispersal and helping behaviour usually co-occur (Koenig *et al.* 1992), but exceptions are known. For example, cooperative breeders' offspring often do not delay dispersal and, in systems where the offspring delay dispersal, helping does not occur at the nest (*e.g.* Texas Green Jay *Cyanocorax yncas*; Gayou 1986). Helpers' parental duties range from non-nesting duties (*e.g.* territorial defence) and occasional nesting duties (*e.g.* prey delivery to the nesting female or young), to helpers that participate fully in all reproductive duties (Brown 1987b).

Before becoming independent breeders, offspring of cooperative breeders delay dispersal, disperse and breed, or float (Koenig *et al.* 1992) and, secondly, they may or may not become helpers (Emlen 1984). Before investigating factors which influence these alternative forms of behaviour, it is important to try to determine if helpers really help (Emlen 1990). The term 'helper' is ambiguous and does not imply that the presence of helpers at the nest benefits the young or breeding birds (Brown 1987b). Helpers may have a positive impact on reproduction (Emlen 1990), no impact at all (Bednarz 1987b) or may even disrupt the breeding attempt (Brown & Brown 1990; Zahavi 1990). Craig & Jamieson (1990) suggested that the provisioning behaviour by helpers is simply an unselected response to the stimulus of young begging for food and that no explanation is therefore required to explain the evolution of helping *per se*. The hypothesis that helping behaviour is selectively neutral can only be accepted if there are no direct or indirect fitness advantages to breeders or kin (Emlen & Wrege 1989). To assess the presence of helping neutrality, one can measure various indices of reproductive success such as increased clutch size, reproductive success at the various stages of the breeding cycle, or breeding attempts per breeding season (Brown & Brown 1981; Russell & Rowley 1988; Craig & Jamieson 1990; Reyer 1990).

3.1.2 Pale Chanting Goshawk - the *status antequo*

At the onset of this study, the PCG was thought to be a monogamous breeder (Steyn & Myburgh 1992), although Biggs *et al.* (1984) recorded a group comprising two adult males and a female PCGs hunting together, and Finch-Davies & Kemp (1980) suggested that the species might have a specialised social system.

At the Calitzdorp study area, PCGs occur in three major vegetation types (see Chapter 2), Open Spekboomveld (OSBV), Karroid Broken Veld (KBV) and Succulent Karoo (SK) (Acocks 1988). To place the Calitzdorp study population in perspective, it was compared with populations from Claratal, the Kalahari Gemsbok National Park (KGNP) and Rooipoort (see Chapter 2).

The aims of this chapter are to compare: 1) social systems of four populations of PCGs, not only within and between different vegetation types at Calitzdorp, but also between Calitzdorp and three other study populations and, 2) reproductive indices for PCG breeding groups within a specific vegetation type, KBV, with that within two other vegetation types at Calitzdorp, and with PCG populations at three other study areas.

3.2 METHODS

3.2.1 Data

Data for the Claratal study area was provided by Drs. R. & H.C. Biggs and Mr. J.J. Herholdt (National Parks Board) provided data from the Kalahari Gemsbok National Park. I collected data from the PCG populations at Calitzdorp and Rooipoort.

3.2.2 Marking methods and moult

At the Calitzdorp study area, perching PCGs were trapped and marked as described in Chapter 2. At Claratal, birds were marked with colour rings and, at Rooipoort, with patagial tags. At Calitzdorp, the stage of moult was recorded to determine the age of first adult plumage.

3.2.3 Terminology

The following terminology was used to designate the apparent status of individuals and groups of PCGs:

1) Breeder - an adult participating in breeding activities, *e.g.* nest building, successful copulations, incubation, brooding and feeding the offspring, and territorial defense;
2) Co-breeder - an additional adult (apart from male and female) participating in breeding as outlined above;
3) Non-breeder - offspring, either a one year old juvenile, a moulting bird or adult, which lived within the territory of the breeders and co-breeders, but which did not breed;
4) Juvenile - offspring in juvenile plumage less than one year old;
5) Monogamous pair - a breeding group comprising only one male and one female breeder;
6) Monogamous group - a social group comprising one male and one female breeder, and one or more non-breeder(s).
7) Polyandrous trio - a breeding group comprising two males (alpha and beta) and one female breeder;
8) Polyandrous group - a social group comprising two males (alpha and beta) and one female breeder, and non-breeder(s);
9) Breeder group - a monogamous pair or polyandrous trio;
10) Group - a monogamous pair, monogamous group, polyandrous trio or polyandrous group.

3.2.4 Breeding status and group size

At Calitzdorp, for each group, the number of marked breeder males that copulated with a marked breeder female was recorded in the pre-laying periods (first copulation until egg laying) of 1988-1989. In the breeding season, 51 visits to nests were carried out over five years, 21 during 1988, 16 during 1989, four during 1990, three during 1991 and seven during 1992. The breeding status (*i.e.* monogamous or polyandrous) was determined by counting the number of adults at or near the nest during each nest visit. Cases were included in the analysis only when: the nest was visited when either eggs or chicks were present (1988-1989); either eggs, chicks or fledglings were present in or near the nest (1990-1992); or if a group did not breed (1988-1992) (in which case the territory was searched from the position of the previous year's nest(s)) and only cases included with at least one adult was sighted. In addition, the behaviour of non-breeders was recorded during nest visits (1988-1992) and/or while studying the behaviour of all PCGs present at nest sites in the breeding seasons (1988-1989).

At Calitzdorp, the presence of non-breeders was recorded *en route* between nest sites and during nest site visits. Roughly the same route was followed each year, but no special effort was made to systematically search each territory. Nest sites were visited irregularly at the other study areas and, only at KGNP, was the presence of additional breeders and non-breeders not recorded.

3.2.5 Reproductive success and breeding biology

At all study areas, the status of the nest contents was recorded during each visit. If the age of the chick was recorded, laying dates were calculated backwards using 35 day incubation and 49 day nestling periods (GM unpubl. data). If not, the known record(s) (either from eggs or chicks) was assumed to be the median for either of the two periods and laying dates calculated accordingly. In addition, the Southern African Ornithological Society provided me with breeding records from their Nest Record Card Scheme, and laying dates were calculated as above. No replacement clutch or double-brood laying dates were included in the laying date analysis. To determine if groups that double-brooded lay their first clutch earlier that those with single broods, I calculated for 1989 (a year with sufficient data) the number of days groups laid after 1 June (the first day of a month before which no eggs were laid), and converted the results back to calender days. The numbers of one-egg and two-egg clutches laid were compared between status groupings, vegetation types and study areas. At all study areas, a nesting attempt was judged to have been initiated if at least one egg was laid, not by birds copulating or building a nest.

At Calitzdorp, the reproductive success of each group was assigned to the vegetation type which contained the nest. A nesting attempt was judged as successful if a nestling was present in the last three weeks of the seven-week nestling period. At other study areas, because of a lower and irregular nest visiting pattern, a nesting attempt was successful if a chick was recorded in the nest. Presumed nest failures were compared between the various status groupings, vegetation types and study areas.

At Calitzdorp, polyandrous trios were only recorded in KBV. The reproductive variables were therefore only compared between polyandrous trios and monogamous pairs from that vegetation type, and not with breeding groups from other vegetation types or with breeding groups from the three other study areas. Reproductive success was investigated for all study years combined. The ratio of groups succeeding in reaching each stage of the nesting cycle (laying, hatching and fledging) was also compared for first and second broods. Only data for years when double-brooding was recorded (1989-1990) were included in the second brood analysis. In cases in which the first breeding attempt failed, data for the replacement clutches were included in the analysis.

3.3 RESULTS

3.3.1 Calitzdorp population

3.3.1.1 Moult

PCGs 9-13 months of age (n = 7) have not yet started moulting into adult plumage (no grey feathers could be detected). However, birds 14-18 months of age (n = 14) were at varying stages of moult, whereas birds 18 months and older possessed no detectable juvenile plumage.

3.3.1.2 Breeding status

The breeding biology of PCGs was studied for 117 group years (11-29 groups) over five breeding seasons (Table 3.1). On various occasions, involving three different groups, two males were observed copulating with a single female. On 67% (24/36) of nest visits to these groups, the marked polyandrous trio was present at the nest. For an additional 13 groups, the presence of two males and one female was recorded in 60% (38/63) of nest visits. In a further 407 nest visits to 101 (117-(3+13)) groups, the presence of a third adult was recorded in 5% (19/407) of visits. However, a third adult was recorded at 11 of the 101 groups or 33% (19/58) of nest visits. I therefore judged the breeding status of 16 groups to be polyandrous and 101 groups to be monogamous.

In 506 nest visits, the presence of a non-breeder male was recorded in 3% of visits (n = 14), and that of a non-breeder female in 1% of visits (n = 5). During these nest visits, non-breeders were only recorded at nests of monogamous pairs or groups. Non-breeders normally perched approximately 50-200 m from the nest and no intragroup aggression was observed. Aggressive interactions between breeders and non-breeders were limited to three observations. In the field, during 18 067 minutes of observations at six nest sites in the breeding season (see Chapter 4), only once was a non-breeder recorded approaching the nesting site. An unmarked non-breeder female arrived, briefly perched 15 m from the nest, and was chased off by the female in the presence of her two males. In the second, included in the laying date analysis. To determine if groups that double-brooded lay their first clutch earlier that those with single broods, I calculated for 1989 (a year with sufficient data) the number of days groups laid after 1 June (the first day of a month before which no eggs were laid), and converted the results back to calender days. The numbers of one-egg and two-egg clutches laid were compared between status groupings, vegetation types and study areas. At all study areas, a nesting attempt was judged to have been initiated if at least one egg was laid, not by birds copulating or building a nest.

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Table 3.1 Pale Chanting Goshawk monogamous pairs and polyandrous trios (**in bold and underlined**) studied at Calitzdorp from 1988-1992, vegetation types they nested in, the number of offspring fledged and non-breeders present (Y) or absent (N) per group.

Vegetation type No.	Group name	1988	1989	1990	1991	1992
Open Spekboomveld						
1	Nellis		1 (Y)	2 (N)	0 (Y)	0 (N)
2	1stKloof	0 (Y)	1 (Y)	3 (Y)	0 (N)	0 (N)
3	2ndKloof			1 (N)	0 (N)	
18	KweekK		1 (N)			
19	Unknown			1 (Y)	0 (N)	2 (N)
20	Erenst		1 (N)	0 (N)	0 (N)	0 (N)
28	BoKuile			2 (N)	1 (N)	2 (Y)
Karroid Broken Veld						
4	Okkies	**1 (Y)**	**4 (Y)**	**3 (Y)**	**0 (Y)**	0 (Y)
5	JohanG	**0 (Y)**	**2 (N)**	**2 (Y)**	0 (Y)	0 (Y)
6	Ridge			4 (N)	0 (N)	0 (N)
7	Cutting	1 (Y)	2 (N)	2 (Y)	0 (N)	**0 (N)**
8	Kraal	2 (Y)	2 (Y)	2 (N)	0 (Y)	2 (N)
9	DGates			**1 (N)**	**0 (N)**	1 (N)
11	Vlakte		1 (N)	1 (Y)	0 (Y)	2 (N)
12	Zwartkop		**2 (N)**	**3 (Y)**	**4 (N)**	0 (Y)
13	Bloubosvlei	0 (Y)	2 (Y)	2 (Y)	0 (Y)	0 (Y)
14	AndriesK		**2 (Y)**	0 (Y)	0 (N)	0 (N)
15	TarRoad		2 (Y)	2 (N)	0 (N)	2 (Y)
16	Secretary		2 (Y)	3 (Y)	0 (Y)	2 (Y)
17	Kuile		1 (N)		1 (N)	0 (Y)
21	Kruisrivier	**1 (Y)**	0 (N)	2 (N)	1 (Y)	0 (Y)
22	Rietfontein		1 (N)	2 (N)	0 (N)	0 (N)
23	Vleirivier		2 (Y)	2 (Y)	0 (Y)	2 (Y)
24	BaasF		2 (Y)	2 (N)	0 (Y)	2 (N)
25	Saayman		**1 (N)**	1 (Y)	0 (Y)	2 (N)
29	Pickniks				0 (N)	2 (Y)
30	BoOkkies					1 (N)
31	ErnieF				2 (N)	2 (Y)
Succulent Karoo						
10	Engelskamp	0 (N)	2 (N)	3 (Y)	0 (Y)	0 (N)
26	Badsaf	1 (N)	2 (Y)	1 (Y)	0 (Y)	0 (Y)
27	Remhog	0 (N)	1 (N)	1 (N)	0 (Y)	2 (N)

a breeder female was caught on eggs with a nest-ring. While marking the female 100 m from the nest, a marked non-breeder female arrived, landed on the nest rim, but was chased off the nest by the male. In the third incident, the nest contained two four-week old chicks and I caught the breeder female with the nest-dome. While marking the female 50 m from the nest, a marked non-breeder female landed on the nest with prey and tried to feed the chicks. On release of the breeding female, the non-breeder immediately flew off from the nesting site.

3.3.1.3 Reproductive success in all vegetation types

Eighty-six percent (n = 14) of clutches laid by groups in the OSBV were two-egg clutches, compared with 94% (n = 65) in the KBV and 93% (n = 14) in the SK (Chi-square; $P > 0.05$). The number of chicks fledged per group did not differ significantly between vegetation types (Table 3.2).

Table 3.2 Reproductive success and group size estimates (mean ± 1 standard deviation below) for Calitzdorp, calculated over a five year period (1988-1992) for the three vegetation types, OSBV (Open Spekboomveld), KBV (Karroid Broken Veld) and SK (Succulent Karoo). NS = Not significant.

Vegetation types	OSBV	KBV	SK	ANOVA
Group years	22	80	15	
Chicks fledged per group	0.82 (0.91)	1.19 (1.10)	0.87 (0.99)	NS

At the Calitzdorp study area, it was mostly groups in KBV and polyandrous trios that double-brooded, *i.e.* laying an additional clutch after at least one chick fledged from the first (Figs. 3.1-3.5). During 1989, all groups laid, and seven groups double-brooded successfully *i.e.* at least one chick fledged from the second brood. In KBV, one polyandrous trio double-brooded successfully and fledged four chicks (Group no. 4; Fig. 3.2). In addition, one monogamous pair, after fledging two chicks, laid a further two clutches, only to abandon both (Group no. 13; Fig. 3.2). A monogamous pair breeding in the SK also double-brooded, although unsuccessfully (Group no. 10; Fig. 3.2). During

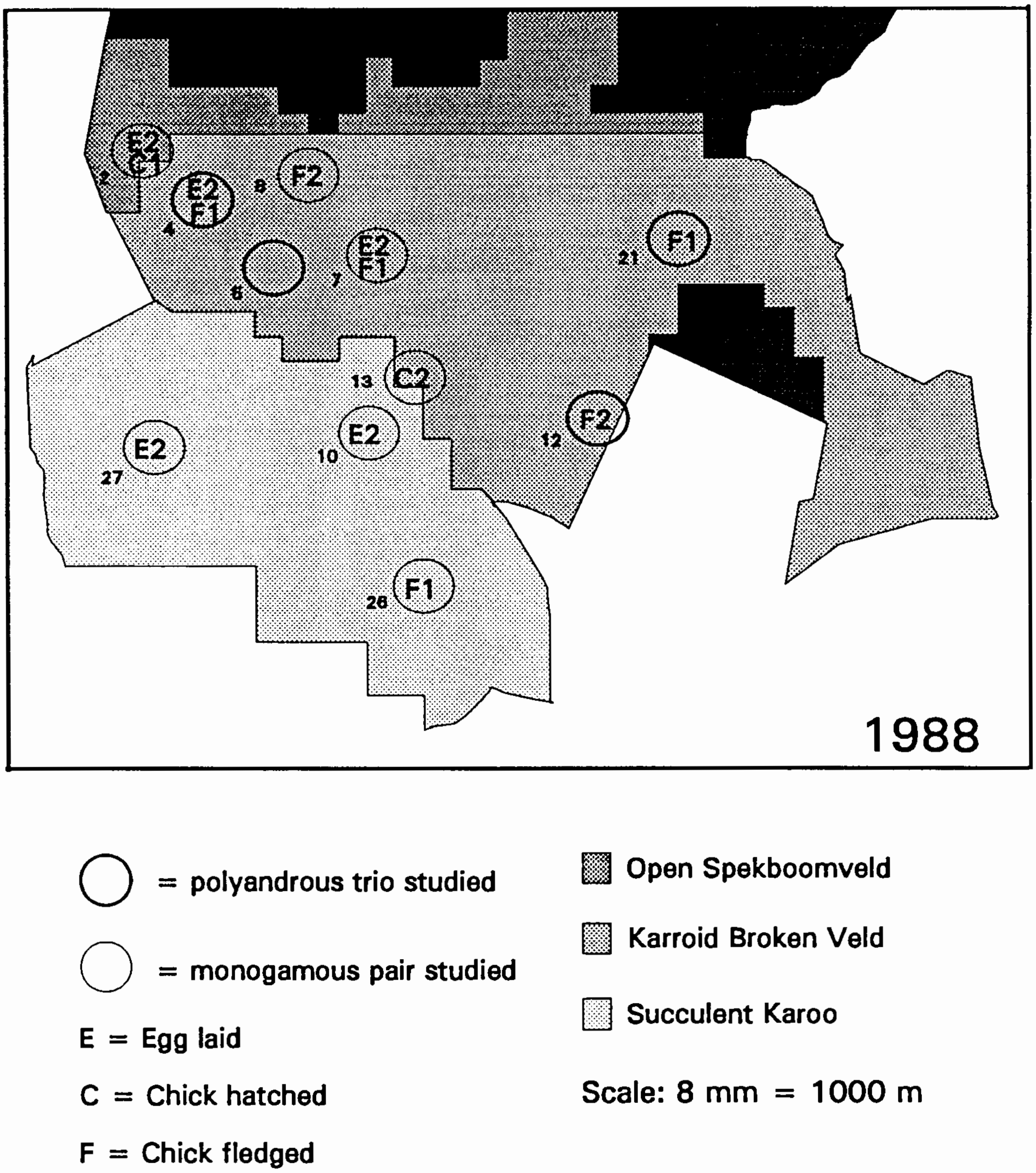

Fig. 3.1 Reproductive success of groups studied at Calitzdorp during 1988. Circles indicate approximate nest site positions. Group numbers correspond with that in Table 3.1.

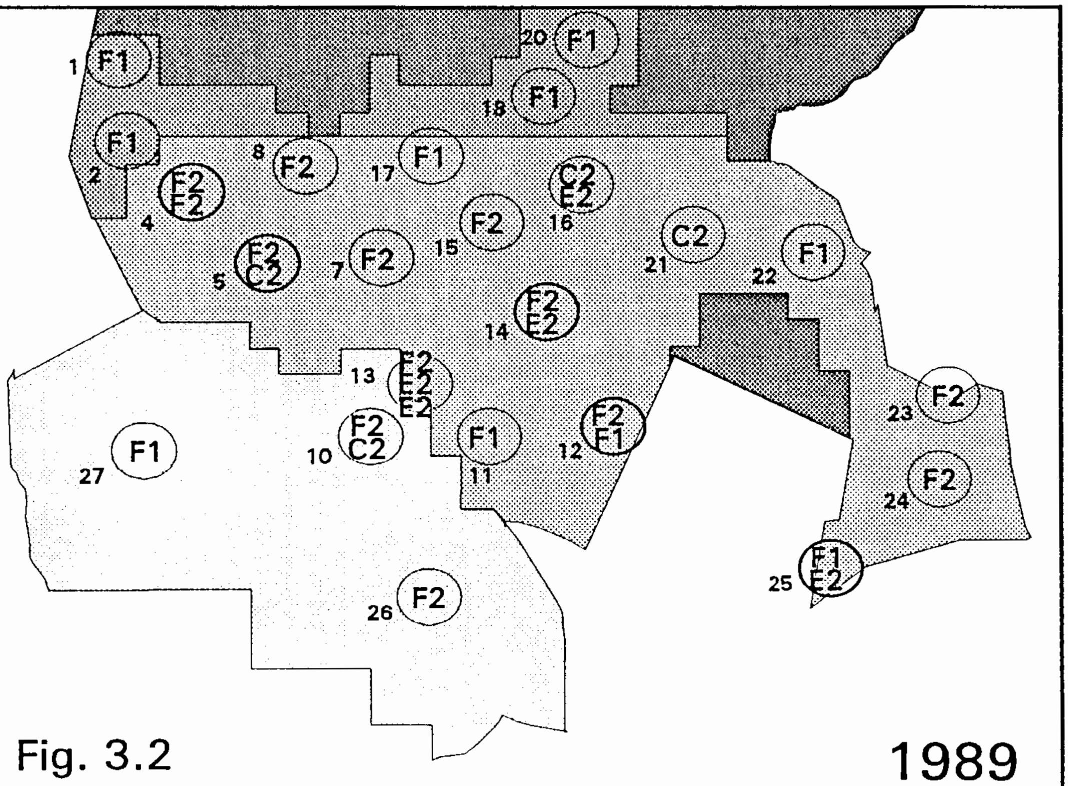

Fig. 3.2

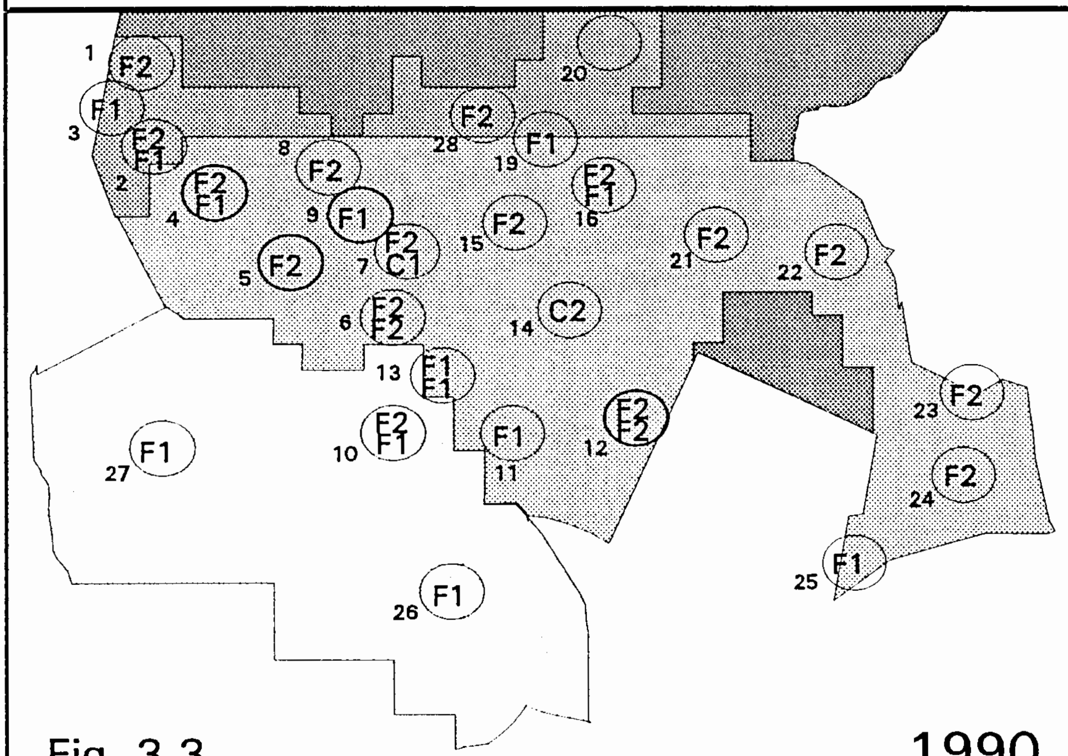

Fig. 3.3

Fig(s). 3.2 & 3.3 Reproductive success of groups studied at Calitzdorp during 1989-1990. Circles indicate approximate nest site positions. Group numbers correspond with that in Table 3.1. Captions as in Fig. 3.1.

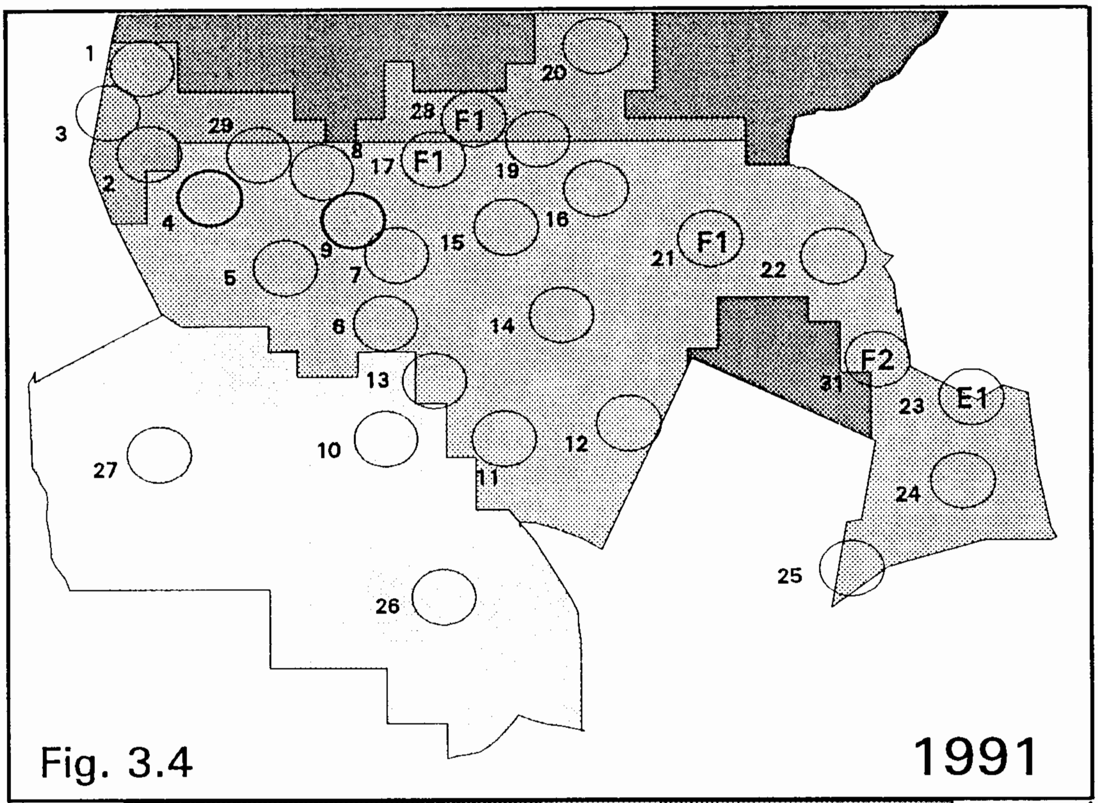

Fig. 3.4 1991

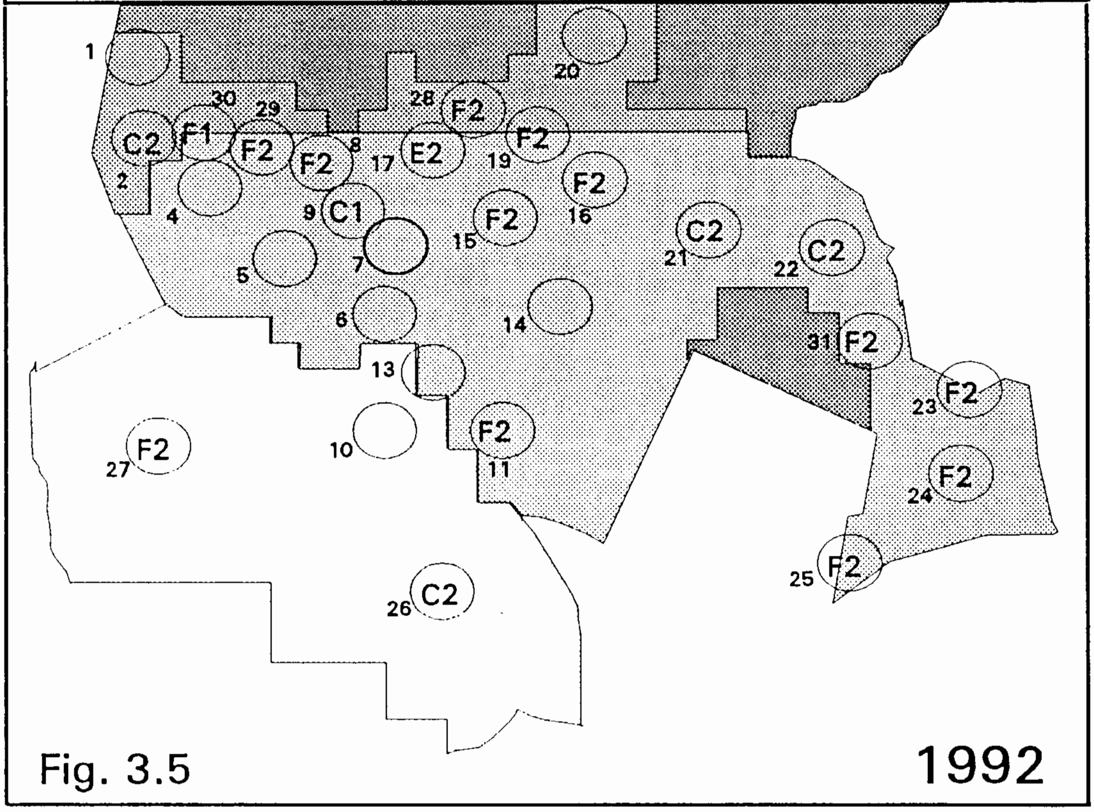

Fig. 3.5 1992

Fig. 3.4 & 3.5 Reproductive success of groups studied at Calitzdorp during 1991-1992. Circles indicate approximate nest site positions. Group numbers correspond with that in Table 3.1. Captions as in Fig. 3.1.

1990, successful double-brooding not only occurred in KBV, but also in SK and OSBV (Fig. 3.3; Groups no. 2 & 10). Although a different polyandrous trio (Group no. 12 as opposed to no. 4) succeeded in fledging four chicks, a monogamous pair, did likewise (Group no. 6; Fig. 3.3). Two polyandrous trios (Groups no. 4 & 12) succeeded in double-brooding successfully for two years in succession, each group fledging seven chicks (Figs. 3.2 & 3.3).

During 1989, groups that double-brooded laid significantly earlier (mean = 8 July; range 7 June-7 August; n = 8) than groups that single-brooded (mean = 29 August; range = 12 July-28 September; n = 14; P < 0.001; t test). Replacement clutches were laid significantly later (after the failure of the first clutch) (35 ± 6 days; n = 4), compared with double-brood clutches (after the success of the first) (24 ± 9 days; n = 8; P < 0.05; t test). Presumed causes of nest failures of egg or chicks were 37% in the OSBV (n = 27), 33% in the SK (n = 24) and 30% in the KBV (n = 128) (Chi-square; P > 0.05).

3.3.1.4 Reproductive success in Karroid Broken Veld

All polyandrous trios studied were in KBV (Figs. 3.1-3.5; Table 3.1). Ninety-five percent (n = 19) of clutches laid by polyandrous trios were two-egg clutches, compared with 94% (n = 46) for monogamous pairs. Double-brooding polyandrous trios laid from 7 June to 31 July (mean = 3 July; n = 5), and monogamous pairs 28 June to 7 August (mean = 18 July; n = 2). The number of chicks fledged per group did not differ significantly between polyandrous trios and monogamous pairs for all years combined, or for first and second broods (Table 3.3). During 1991 and 1992, however, none of the polyandrous trios bred. Presumed causes of nest failures involving egg or chicks were 30% for both polyandrous trios (n = 37) and monogamous pairs (n = 91).

The frequency of groups succeeding in reaching each stage of the nesting cycle (laying, hatching and fledging) did not differ significantly between polyandrous trios and monogamous pairs in the first breeding cycle (Table 3.3), although all polyandrous trios that laid fledged at least one chick, compared with 39/44 monogamous pairs (Table 3.4). In the second breeding cycle, the frequency of groups succeeding in reaching the laying and hatching stages differ significantly between polyandrous trios and monogamous pairs (Table 3.3). Seventy-eight percent (n = 9) of the polyandrous trios succeeded in laying one egg and 56% (n = 9) in hatching one egg, whereas only 24% (n = 25) and 16% (n = 25) of the monogamous pairs did likewise. However, at the fledging stage, the breeding attempts of polyandrous trios suffered as many failures as monogamous pairs (n = 3), as to render the difference nonsignificant.

3.3.1.5 Non-breeders

Non-breeders were recorded in half (58/117) of the groups (Table 3.1). Thirty-two percent (n = 7) of the groups from OSBV had non-breeders, 56% (n = 35) from KBV, and 47% (n = 7) from SK (Chi-square; $P > 0.05$). In KBV, non-breeders were recorded in 56% of polyandrous (n = 16) and monogamous (n = 64) groups.

Table 3.3 Reproductive success per year, combined, and per brood, calculated over a five year period (1988-1992) for polyandrous trios and monogamous pairs in the Karroid Broken Veld. Mean (± 1 standard deviation); NS = Not significant.

	Polyandrous trios	Monogamous pairs	*t* test
All years	16	64	
Chicks fledged per group	1.63 (1.36)	1.08 (1.01)	NS
Chicks fledged per group - 1988	1.00 (0.82)	1.00 (1.00)	NS
(n) (4)	(3)		
Chicks fledged per group - 1989	2.40 (1.14)	1.55 (0.69)	NS
(n) (5)	(11)		
Chicks fledged per group - 1990	2.50 (1.29)	1.92 (0.95)	NS
(n) (4)	(14)		
Chicks fledged per group - 1991	0.00	0.22 (0.56)	
(n) (2)	(17)		
Chicks fledged per group - 1992	0.00	1.05 (0.97)	
(n) (1)	(19)		
First brood - 1989	1.80 (0.45)	1.55 (0.69)	NS
(n) (5)	(11)		
Second brood - 1989	0.60 (0.89)	0.00	NS
(n) (5)	(3)		
First brood - 1990	1.75 (0.50)	1.62 (0.65)	NS
(n) (4)	(13)		
Second brood -1990	1.50 (0.71)	1.00 (0.82)	NS
(n) (2)	(4)		

Table 3.4 A comparison of the frequencies of groups succeeding in laying at least one egg, hatching at least one egg, and succeeding in fledging at least one chick. Data for polyandrous trios and monogamous pairs from Karroid Broken Veld, analysed for first and second broods.

	Polyandrous trios	Monogamous pairs	Fisher's Exact Test
First broods - All years			
Groups studied	16	64	
Succeed in laying one egg			
Yes	12	44	NS
No	4	20	
Succeed in hatching one egg			
Yes	12	42	NS
No	4	22	
Succeed in fledging one chick			
Yes	12	39	NS
No	4	25	
Second broods 1989-1990			
Groups studied	9	25	
Succeed in laying one egg			
Yes	7	6	$P < 0.01$
No	2	19	
Succeed in hatching one egg			
Yes	5	4	$P < 0.05$
No	4	21	
Succeed in fledging one chick			
Yes	4	3	NS
No	5	22	

3.3.2 Four study populations

3.3.2.1 Demography

At Rooipoort and Claratal, there were always only two breeders (Table 3.5). At Calitzdorp and the KGNP, non-breeders were present (Table 3.5). In the KGNP, two adult males and females were caught in close proximity over eight months and, in a second case, two adult males and a female over 12 months.

Table 3.5 A presence of cooperative breeding and delayed dispersal at four Pale Chanting Goshawk populations in southern Africa. KGNP = Kalahari Gemsbok National Park.

	Calitzdorp	Rooipoort	Claratal	KGNP
Cooperative breeders	Yes	No	No	Unknown
Non-breeders present	Yes	No	Seldom	Yes

3.3.2.2 Reproductive success

For all study years combined, territorial groups at Calitzdorp on average fledged 1.1 young/year, and those at Claratal 0.4 young/year. The mean number of young fledged between years varied greatly at Calitzdorp (CV = 65%), but even more so at Claratal (CV = 112%) (Table 3.6). Calitzdorp's reproductive output followed a cyclic nature, starting of with an intermediate reproductive year (1988), followed by two high years (1989-1990), a low year (1991) and back to a intermediate reproductive year (1992).

3.3.2.3 Laying dates and nest failures

Laying dates for southern African PCGs ranged from March to December with a peak from July to September at Calitzdorp (Fig. 3.6). The laying dates of a further 26 fledglings from 1990 could only be calculated to late June or early July. It would therefore appear that the PCGs in Calitzdorp lay earlier than other South African populations, since these populations lay predominantly from August to November. Namibia follow the Calitzdorp trend with Claratals' birds laying primarily in September. Groups attempted to breed in 82/117 (70%)

Table 3.6 Reproductive success of four Pale Chanting Goshawk populations in southern Africa. Records from Claratal for 1980-82 from Biggs *et al.* 1984.

Study area (year)	Number of groups on territories	Number of groups laying at least one egg	Number of nests in which at least 1 egg laid	Number of nests in which at least 1 egg hatched	Number of nests from which at least 1 young fledged	Clutch size (sample size)	Mean number of young per clutch started	Mean number of young per territorial group
Calitzdorp								
1988	11	10	13	8	6	2 (12); 1 (2)	0.6	0.7
1989	23	23	32	27	24	2 (30); 1 (2)	1.1	1.6
1990	26	25	35	33	31	2 (26); 1 (1)	1.4	1.9
1991	29	5	5	4	4	2 (1); 1 (1)	1.0	0.2
1992	28	19	19	18	14	2 (17); 1 (1)	1.4	0.9
Rooipoort								
1988	8	6	6	5	4	2 (6)	1.0	0.8
KGNP								
1988		7	8	7	6	2 (7); 1 (1)	1.2	
Claratal								
1980	7						0.0	0.0
1981	7						0.0	0.0
1982	6				2		1.5	0.5
1983	6						0.0	0.0
1984	6				4		1.3	1.2
1985	6			5	3		0.6	0.5
1986	6	6	7	5	5	2 (2); 1 (2)	1.1	1.3
1987	6	2	2	1	0	1 (2)	0.0	0.0
1988	6			1	1		1.0	0.2
1989	6			5	4	2 (1); 1 (1)	1.0	0.8

group years at Calitzdorp (Table 3.6). Thirteen percent of nest failures happened during incubation and 12% during the nestling period. On average, 1.2 chicks hatched from clutches at Calitzdorp. Groups at Calitzdorp laid significantly more two-egg clutches (86/93; 93%) than groups at the other study areas combined (18/24; 75%: Chi-square; $P > 0.05$). However, this difference is the result of the low number of two-egg clutches (3/8) laid at Claratal. Mean overall clutch size was 1.88 ($n = 115$). Three three-egg and one four-egg clutches have been recorded (J.J. Herholdt in litt.; GM pers. obs.), but were probably replacement clutches laid in the same nest. At Calitzdorp, a female laid a third egg in the same nest after a two-egg clutch had addled.

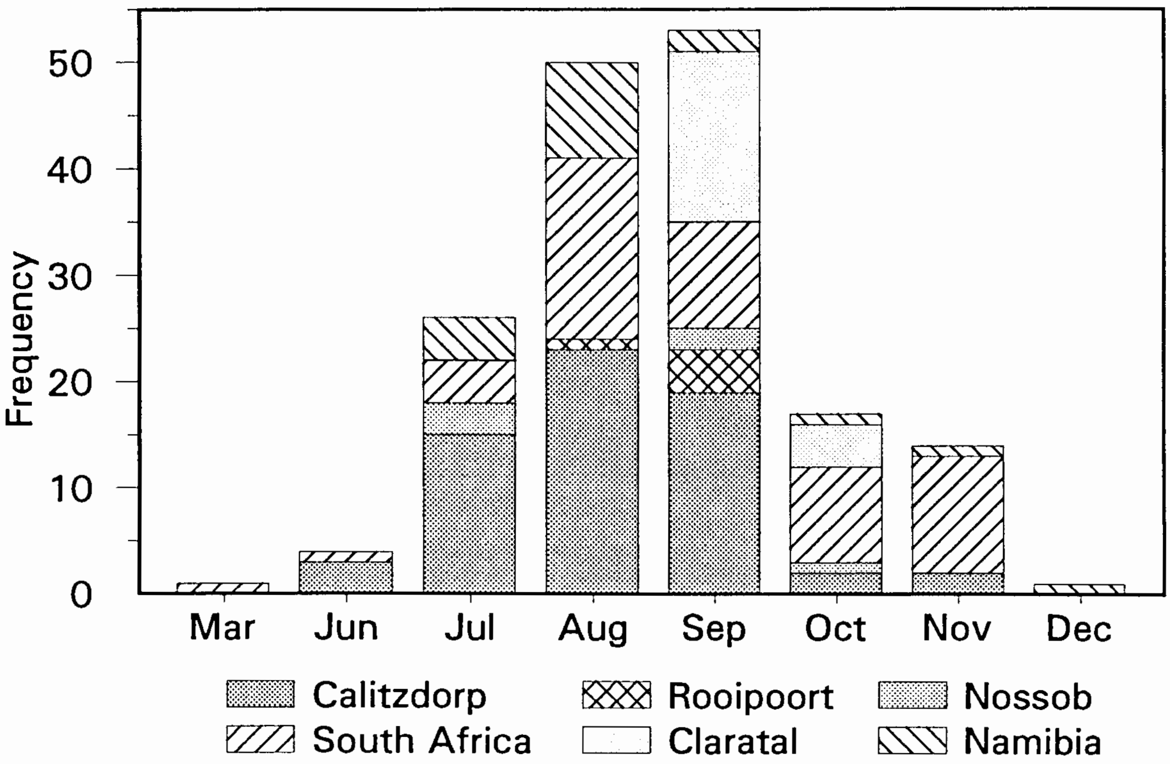

Fig. 3.6 Laying dates for Pale Chanting Goshawks in southern Africa. Namibia and South Africa records do not include data from other sites.

Calitzdorp had a nest failure rate (*i.e.* eggs or nestlings) of 61/179 (34%), not significantly different from the 17/67 (25%) of other PCG populations (Table 3.7) (Chi-square; P > 0.05). The lower failure rate at Calitzdorp could be the result of more visits to nests by observers in the breeding season, compared with other areas. Overall, predation of eggs or nestlings was the main cause of failure (26/78; 33%), followed by sibling aggression or other natural causes (16/78: 21%), eggs abandoned (14/75:19%) and eggs addled (13/75:17%). At Calitzdorp, unknown causes of nest failure included the collapsing of a nest tree and possible human disturbance at the nest.

Table 3.7 Presumed causes of nest failure in four Pale Chanting Goshawk populations in southern Africa. Analysis only include known cases of failures.

	Number eggs or chicks that failed (%)	Eggs addled	Eggs abandoned	Eggs broken	Eggs or chicks predated	Sibling aggression or natural causes	Other
Calitzdorp							
1988	15/26 (58)		1	1	6	2	5
1989	24/62 (39)	3	10		5	6	
1990	11/53 (21)	7			1	3	
1991	1/3 (33)	1					
1992	10/35 (29)		1	1	8		
Rooipoort							
1988	5/12 (42)		2			3	
KGNP							
1988	5/15 (33)	2			2	1	
Claratal							
1985	2/6 (33)				2		
1986	2/9 (22)				1		1
1987	2/2				1		1
1989	1/6 (17)					1	
Total	78/229 (34)	13	14	2	26	16	7

3.4 DISCUSSION

3.4.1 Mating system

If the offspring of a polyandrous trio are fathered by one or both males, and both assist with the rearing of the young (see Chapter 4), one or both males qualify as helpers (Brown 1987b). At Calitzdorp, both males assisted with the rearing of young (see Chapters 4). PCGs therefore qualify as cooperative breeders as one member of a social group provides care to young that are not his own offspring (Stacey & Koenig 1990). Faaborg & Patterson (1981) defined the above mating system as cooperative polyandry in which the female has persistent and bonds simultaneously with two or more males, copulates with these males, and all males share in parental care.

The PCG, a species characteristic to the Southwest Arid Subregion of Africa (Crowe & Crowe 1982) is a facultatively-cooperative species, since cooperative polyandry in the Calitzdorp population was recorded in 20% of groups (n = 80) and only in KBV. Frequency of cooperative breeding ranged from 5% to 83% in various Harris' Hawk populations (see Bednarz 1987b), and from 32% to 68% in the Galapagos Hawk (Faaborg 1986). The only other known localities where PCG 'groups' have been observed were near Worcester (Western Cape Province), Etosha National Park, Namibia (GM pers. obs.) and Port Nolloth (Northern Cape Province; P.G. Ryan pers. comm.). At Calitzdorp, the additional non-breeders and occasional co-breeders at the nest resulted in PCGs living in groups. From the few PCG populations studied in some detail, it would appear that group living is certainly more widespread than facultative, cooperative polyandry, since more than two adults in association were recorded at Calitzdorp, in the KGNP, Etosha and Claratal (Biggs *et al.* 1984).

3.4.2 Social system

At Calitzdorp, the PCG's social system consists of monogamous pairs, with or without an additional breeder, and each breeding group with or without non-breeders. Non-breeders delayed dispersal, were retained in their natal territories, but were not allowed to participate in any breeding activities. Since the behaviour of the non-breeder males was not studied in the non-breeding and pre-laying periods, as well as that of non-breeder males and females away from the nest site in the nesting period, it is not possible to state whether these birds perform helping functions, such as territorial defence, that would qualify them as helpers. In fact, in a casual observation, a marked non-breeder male was observed chasing off an intraspecific intruder. Even if further research suggests that non-breeder males are helpers away from the nest site, the social system is still unique. An almost similar social system was reported for the Texas Green Jay in which offspring deferred dispersal and defended the natal territory without helping with nest activities (Gayou 1986). The difference was that all one-year old young were expelled from their natal territory as soon as the young from the following year fledged, whereas at Calitzdorp, non-breeders was retained in their natal territories for up to five years (see Chapter 9). A social system that consists of non-breeders not allowed to participate in nest activities, and co-breeders that participate fully in all nest activities is, to my knowledge, unique among cooperative-breeding birds.

It is unusual for breeders that allow offspring to delay dispersal in their natal territory to prevent them from helping at the nest (Brown 1987b). Extra helpers at the nest (apart from the occasional beta male) may increase the group's reproductive success and increase breeder survival (Emlen 1991). The two non-breeding females certainly tried to gain access to the nest, but were prevented from doing so. It is suggested that, in a predatory bird, an offspring in breeding condition could be highly disruptive in the social order of the group and the value of inexperienced breeder and hunter may be too costly (Faaborg 1986). However, in the cooperative-breeding Harris' Hawk, beta and gamma helpers were allowed limited participation in nesting activities, even incubation and feeding the offspring (Dawson 1988). If offspring helping at the nest depress the fitness of the breeders, helping may only be allowed if the PCG, by fully participating in all breeding and territorial activities, increases the fitness of polyandrous trios. Perhaps benefits gained by the breeders in having a partly participating helper do not exceed the costs.

At Calitzdorp, delayed dispersal and co-breeding occurred at two distinct levels, with co-breeders, but not non-breeders discriminating between vegetation types. Why is there then delayed dispersal and group living in all vegetation types, and why does helping occur only in KBV. These are intriguing and interesting questions that will be addressed in the remaining chapters.

3.4.3 Reproductive success

Within KBV, the presence of co-breeders did not automatically result in a higher reproductive success. This result has been reported for numerous other cooperative-breeding species (see references in Stacey & Koenig 1990). The only difference was that polyandrous trios were able to attempt more second broods. Double-brooding by a raptor in the temperate regions is rare (Newton 1979). It is interesting that both the other two known cooperative-breeding raptors double-brood, the Harris' Hawk (Bednarz 1987a) and Galapagos Hawk (De Vries 1975), although the effect of the secondary males on this phenomenon has not been analysed.

PCGs are unusual for birds of their size in that they only lay 1-2 egg clutches, a clutch size normally associated with eagles and small vultures (Newton 1979). However, the limitations imposed by small clutch size are offset by the occurrence of double-brooding. Due to the significant linear relationship between female body size and the length of the breeding cycle (see Newton 1979), the ability to double-brood in one year is not only limited by the length of the individual breeding cycle, but also by female body mass. The breeding cycle must obviously be shorter than six months, which excludes species with females weighing more than 1050 g (recalculated from Newton 1979). The mean body mass of PCG females at Calitzdorp was 936 g (see Table 2.1). Furthermore, the second successful breeding attempt was undertaken almost directly after the first, not as the tropical Galapagos Hawk (De Vries 1975) and Eastern Chanting Goshawk *Melierax poliopterus* (Smeenk & Smeenk-Enserink 1976) which has a bi-seasonal breeding pattern correlated to bi-seasonal rainfall. Given a pre-laying period of 31 days (from the start of nest building; Chapters 4 & 5), incubation period of 35 days, nestling period of 49 days, inter-brood period of 24 days, and a post-fledging period of between 30 and 81 days (Chapters 4 & 5), a double breeding cycle at Calitzdorp can take between 253 and 303 days. The two polyandrous trios that double-brooded successfully for two years in succession were therefore involved in breeding for a large part of those two years. The earlier laying by the Calitzdorp population in general, and the significantly earlier laying by the double-brooders in particular, was probably necessary to accommodate such a long breeding season.

The occurrence of double-brooding may suggest that, although the presence of two male breeders does not necessarily result in an increase in productivity per breeding attempt, it may enable polyandrous trios to lay earlier, to undertake more frequent and successful breeding attempts and to pursue and endure a prolonged breeding season. The extra male at the nest therefore certainly helped the breeders to increase their reproductive effort. At this stage, I can only speculate on how the above situation may have evolved. For two males it could be easier to feed the female at a sufficient high rate at the coldest time of the year with the shortest day lengths, as to enable her to lay two eggs early enough as complete two successful breeding attempts in one season (Brown & Brown 1981; Russell & Rowley 1988). Furthermore, by feeding the fledglings, male breeders at the nest may free the female breeder to initiate a further breeding attempt. Alternatively, the breeders may, by sharing the work. not work as hard as monogamous pairs, resulting in an increased survivorship and lifetime fitness (Woolfenden & Fitzpatrick 1984). After establishing that co-breeders help I can progress to the general questions Why delaying dispersal and Why help?

CHAPTER 4

THE ROLES OF POLYANDROUS ALPHA AND BETA MALE PALE CHANTING GOSHAWKS IN REPRODUCTION AND COOPERATIVE-BREEDING

SUMMARY

The Pale Chanting Goshawk (PCG) breeds either in monogamous pairs or polyandrous trios. Breeders remain together throughout the year, often with non-breeding offspring. Since male breeders may be closely related, variation in fitness values with the different mating arrangements may promote cooperation and/or conflict among group members. The reproductive roles of PCG breeder groups were studied in detail during the non-breeding period of 1988 and nesting seasons of 1988-1989. The inclusive fitness of groups which bred in Karroid Broken Veld was determined for the 1988-1992 breeding seasons. During the non-breeding and pre-laying periods, beta (subordinate) males contributed less than alpha (dominant) males in all aspects of reproductive duties (*e.g.* female attendance, copulation frequency, prey provisioning and nest construction). However, during the incubation and nestling periods, beta males increased their participation in parental activities (*e.g.* incubation frequency, prey provisioning to female and chicks) as well as aggression and soliciting-calling towards other breeder members, especially alpha males. One polyandrous trio studied began its second nesting cycle while still feeding its first brood. The behaviour of two males differed in that the alpha male spent more time building the second nest and advertising its presence, whereas the beta male hunted to provide prey. The genetic relationships of one polyandrous trio were analysed by means of DNA fingerprinting. The males were full sibs (brothers or father and son), but were not related to the female. Indirect fitness compensation for subordinate kin (beta male) may allow alpha males to skew paternity. If beta males lost direct reproductive fitness benefits, they may gain other direct benefits such as breeding experience. Alpha males and even polyandrous females appear to alter their reproductive roles to accommodate related beta males, thereby increasing their inclusive fitness.

4.1 INTRODUCTION

Helping behaviour appears to be altruistic in that individuals contribute to the rearing of offspring of breeders when they could be raising their own young (Russell & Rowley 1988). Individuals that contribute, also genetically, may not only gain direct fitness from descendant kin, but also indirect fitness benefits from non-descendant kin (Hamilton 1964; Brown 1987b). If the indirect component of fitness is increased by the production of non-descendant kin, related breeders should become helpers (Maynard-Smith 1964). Since the loss of direct fitness can be compensated by a gain in indirect fitness, related males will skew paternity by attempting to father a disproportionately large number of offspring (Vehrencamp 1980; Koenig 1990). If a dominance hierarchy exists, as is the case in many cooperative breeders (Brown 1987b), and with different fitness values at stake, one can expect intra- and inter-sexual differences to develop in a specific social system (Joste *et al.* 1982).

If more than one male participates in copulations, the probability of paternity will be diluted by the number of individuals participating (Stacey 1979). However, co-breeding males can increase their paternity by guarding their females or attempting to copulate as frequently as possible during the fertile period (Davies 1985; 1990; Birkhead & Moller 1992). Females, on the other hand, may benefit by allowing extra-male copulations. To protect their genetic investment, males may progressively increase prey provisioning to offspring, allowing an increase in the number of chicks fledged or even the possibility of a second brood which, in turn, may increase the reproductive success of both sexes (Davies 1985).

The aims of this chapter are to: (1) analyse the behaviour of polyandrous and monogamous breeders in non-breeding, pre-laying, incubation and nestling periods, and (2) study female attendance, copulation behaviour, nest construction, prey provisioning, nest site presence, dominance, morphometrics, kinship and inclusive fitness values in polyandrous and monogamous males.

4.2 METHODS

4.2.1 Non-breeding and pre-laying periods

4.2.1.1 Male behaviour during the non-breeding and pre-laying periods

During the non-breeding period and pre-laying period (from first copulation until egg laying) of 1988, I employed instantaneous sampling (see Chapter 2) in Karroid Broken Veld (KBV) and Succulent Karoo (SK) vegetation types. Behavioural acts recorded are described in Appendix 1. The mean duration of observation periods on males was 138 ± 71 minutes and 44 observation periods totalling 6 056 minutes were conducted (Table 4.1). Males were grouped into demographic groupings, *i.e.* according to status (polyandrous alpha and beta, and monogamous males) and the vegetation type within which they nested. The status of polyandrous males was determined by observing dominance behaviour of alpha over beta males, such as alpha males mantling prey from beta males, or physically shouldering beta males from the eggs. For polyandrous trios where the dominant behaviour of males were not studied, I assumed a dominance hierarchy. Demographic groupings with fewer than four observation periods were excluded from the analysis, resulting in a comparison of behaviour of polyandrous breeders in KBV and monogamous breeders in SK. Behavioural acts were classified into the following behavioural groupings: PERCH ALERT, PERCH PREENING, FLY DIRECT, FLY THERMALLING, FORAGING BEHAVIOUR, AGGRESSION - INTERGROUP AND INTERSPECIFIC, AGGRESSION - INTRAGROUP and REPRODUCTIVE BEHAVIOUR (see Appendix 2). In addition, all behavioural acts recorded while birds were on the ground were classified ON GROUND. Chanting-calls were recorded if the melodious piping WIP-pi-pi-pi-pi-pip (Maclean 1985) was heard at the recording point.

To calculate time activity budgets, I analysed instantaneous sampling data (or spot samples) to estimate the percentage of time each demographic grouping spent in each behavioural grouping (Lehner 1979; Yosef 1992). The duration of the behavioural acts was, in all

Table 4.1 The number and the duration of the observation periods carried out on different individuals in the non-breeding and pre-laying (first copulation until egg laying) periods of 1988. Name is code of colour rings used to identify individual (*e.g.* BB = blue-blue), lower case notation after name indicates unmarked individual (*e.g.* OLf = OL's female). Poly = polyandrous female, Alpha = alpha male, Beta = beta male, Monog = either male or female of monogamous pair, KBV = Karroid Broken Veld and SK = Succulent Karoo. Underlined observation periods were recorded in pre-laying period. Group numbers correspond to that in Chapter 3.

Sex Name	Group (number)	Status	Vegetation type	Observation periods (min)
Males				
BB	JohanG (5)	Beta	KBV	244, 108, 122
BW	Okkies (4)	Alpha	KBV	53
EW	Badsaf (26)	Monog	SK	134, 148, 124, 98, 210
LL	Kruisrivier (21)	Alpha	KBV	121, 35, 100, 32, 64, 110, 89, 76
LWWL	Engelskamp (10)	Monog	SK	218, 249, 209, 238, 116
OL	JohanG (5)	Alpha	KBV	203, 151, 225
RL	Okkies (4)	Beta	KBV	60, 62, 217
WE	Kruisrivier (21)	Beta	KBV	57, 297, 173, 43, 185
WO	Remhog (27)	Monog	SK	73, 147, 89, 212, 212, 213, 83, 196, 169
WR	Cutting (7)	Monog	KBV	42, 49
Females				
LW	Okkies (4)	Poly	KBV	31, 31, 46, 76, 55, 145 300, 106, 210, 236, 87 241, 164, 188, 219, 221
LY	Engelskamp (10)	Monog	SK	114, 241, 251
OLf	JohanG (5)	Poly	KBV	258, 277, 151, 120, 154
RW	Remhog (27)	Monog	SK	66, 129, 218, 210, 141
WL	Badsaf (26)	Monog	SK	50, 158, 127, 81, 163, 123, 255
WRf	Cutting (7)	Monog	KBV	184, 74
YY	Kruisrivier (21)	Poly	KBV	31, 63, 180, 137,

Table 4.2 The group names, status, the number of chick(s) in the nest and observation periods of groups studied in the 1988 and 1989 nestling periods (from hatching until fledging). OSBV = Open Spekboomveld, KBV = Karroid Broken Veld and SK = Succulent Karoo.

Year/ Group	Veld type	Status	No. of chick(s) in the nest	No. of 8 hr. observation periods
1988				
Badsaf	SK	Monogamous pair	1	9
Cutting	KBV	Monogamous pair	1	7
Okkies	KBV	Polyandrous trio	1	7
1989				
BaasF	KBV	Monogamous pair	2	3
Erenst	OSBV	Monogamous pair	1	3
Zwartkop	KBV	Polyandrous trio	2[1]	5

[1] First of two successful nesting attempts

cases, longer than 60 seconds. Since this interval between instantaneous samples was short enough that no more than one transition could occur between consecutive samples, the resulting data were essentially equivalent to focal-animal sampling (Altmann 1974). Therefore, using percentage time spent as input data, an analysis of variance, with arcsine transformations, was performed for each behavioural grouping to test for differences between demographic and behavioural groupings (Zar 1984).

4.2.1.2 Female attendance

While recording instantaneous sampling data for both sexes (Table 4.1), I recorded the attendance of all other PCG breeders within a 100 m radius of the focal bird. For each observation period, the percentage time a breeder spent in attendance of the opposite sex was calculated, as well as the attendance of a polyandrous male (alpha or beta) to the female.

4.2.1.3 Copulation behaviour

I differentiated between contact copulations (the male mounted the female, the tail of each bird was displayed laterally and the two cloacae came into juxtaposition) and non-contact copulations (the female by either shaking her body and/or stepping aside, discouraged the mounting male from copulating) (Chardine 1987). Copulations were recorded during the 1988 pre-laying period for three polyandrous trios in KBV and three monogamous pairs in SK, all starting their first clutch of the season.

During 1989, copulation data were recorded at the double-brooding Zwartkop polyandrous trio's nest (scan sampling; see below) and, because this group had two young in the nest, I analysed the data for groups without and with nestlings separately. Copulation rates were calculated by dividing the number of copulations recorded per observation period by the length of the observation period in hours. For polyandrous trios, I also calculated the number of polyandrous males present during each copulation and if the female 'allowed' males a contact copulation within 20 minutes after they provisioned her.

4.2.1.4 Nest construction and pre-laying prey provisioning

The number of prey provisions to the female, as well as nest construction (nest structure and nest lining) rates were recorded during the 1988 pre-laying period for three polyandrous trios in KBV and three monogamous pairs in SK. Only observation periods from the first prey provisioning or nest construction activity to egg laying were included in the analysis since these activities started after the first copulations were recorded.

4.2.2 Incubation and nestling periods

4.2.2.1 Male behaviour during the nesting season

Scan sampling was employed to record behavioural data once the female of each group had laid (see Chapter 2). During the incubation period, observation periods varied in length, and six observation periods (2 049 min.; range = 120-547) were recorded. During the nestling period, observation periods of eight hours (480 min.) were employed and 34 eight-hour (16 320 min.) observation periods were recorded. Data were collected from different polyandrous trios and monogamous pairs during 1988 and 1989, all from KBV, from a monogamous pair in SK during 1988, and a monogamous pair in OSBV during 1989 (Table 4.2).

As the data for each demographic grouping were analysed separately, 34 observation periods resulted in 46 'male' observation periods being examined. Since the population's reproductive success differed substantially between 1988 and 1989 (Chapter 3), data from these two years were analysed separately. Apart from the Zwartkop polyandrous trio (Group no. 12; Table 3.1; Fig. 3.2), all other groups studied were attending their first and only broods. Behavioural acts were grouped into the following behavioural groupings: FEEDING SELF, FEEDING CHICK(S), FORAGING BEHAVIOUR AT NEST SITE, AGGRESSION-INTERSPECIFIC, AGGRESSION-INTRAGROUP, FLY THERMALLING, NEST ACTIVITIES, and REPRODUCTIVE BEHAVIOUR (see Appendix 3). Chanting-calls were also recorded during this period. I assumed that the proportion time spent in each of the above behavioural groupings followed a linear trend (see Section 4.2.2.2) and behaviour such as brooding chicks, that decrease in the nestling period, were therefore not included in the analysis.

4.2.2.2 Male presence at the nest site

For each observation period recorded during the nestling period, the number of minutes each male was not within the 100 m radius from the nest was extracted from the scan sampling data. Since breeding raptors spend more time away from the nest during the later nestling period, so obtain prey to meet the needs of the growing young (Newton 1979), I analysed nest attendance data (for groups as in Table 4.2) by employing a one-way analysis of covariance with days after fledging as the independent variable, and minutes per observation period outside the 100 m radius as the dependent variable.

4.2.2.3 Prey provisioning

The prey provisions to the nest site by alpha, beta and monogamous males in the nestling period were categorised according to the transfer route of the prey: male provisions female, female feeds and then feeds chick; beta male provisions, prey taken over by alpha male, transfer to female, female feeds and then feeds chick (for polyandrous trios); male provisions and feeds chick; male provisions female and female only feeds; male provisions and only male feeds; and all deliveries by males combined. Rates per hour were calculated by dividing the number of provisions observed by the eight hours of the observation period and analysed for groups as in Table 4.2.

4.2.2.4 Soliciting-calls and dominance

Soliciting-calls were recorded during the nestling period as described for prey provisions, and extracted accordingly. The soliciting-call is a rapid ke-ke-ke-ke-ke-ke made by breeders when copulations or begging prey (Steyn 1982). Aggressive interactions recorded between alpha and beta males, always accompanied by soliciting-calling, are described in Section 4.3.9. Dominance hierarchies of polyandrous males were determined by observing egg displacement sequences (dominant alpha males were able to physically displace subordinate beta males from eggs) or the route prey was transferred, *e.g.* male provisions, prey taken over by dominant male which transfer to female).

4.2.3 Morphometrics and kinship

4.2.3.1 Body mass

When captured, each male was weighed to the nearest 10 g and marked with an individual colour combination (see Chapter 2). Mass data for monogamous males from KBV and SK were combined.

4.2.3.2 Inclusive fitness and kinship

In calculating inclusive fitness (measured in offspring equivalents; Koenig & Pitelka 1981) for each breeder (regardless of their status), I have taken into account the ratio of relatedness of the concerned individuals (kinship) as well as potential paternity, determined by their contact copulation ratio (paternity split). Only the present component of reproductive indirect fitness was taken into account (Brown 1987b, 1980; Emlen & Wrege 1994). Members of the Kruisrivier polyandrous trio were removed from the population to ascertain the coefficient of relatedness of a group of polyandrous breeders. Breast, heart and liver tissue was stored in liquid nitrogen and transported to the Department of Genetics, University of Nottingham, where they were studied by Roy Carter employing DNA fingerprinting (Parkin & Wetton 1990). In the absence of other genetic analysis, I speculatively reviewed three reproductive strategies for polyandrous breeders in KBV; independent breeding, co-breeding and beta male not breeding in the presence of an alpha male. Offspring equivalent values were calculated from each polyandrous breeder's perspective with males either unrelated or full sibs, and reproductive data for the study period (1988-1992) were pooled. Koenig & Pitelka's (1981) inclusive fitness formula was used to calculate values for co-breeders, but to avoid double accounting (Brown 1987b), breeders were only accredited for unaided offspring production.

4.3 RESULTS

4.3.1 Male behaviour during the non-breeding and pre-laying periods

In the non-breeding and pre-laying periods, no significant differences were found between the behaviour of alpha, beta and monogamous males, except for REPRODUCTIVE BEHAVIOUR which increased, as expected, in the pre-laying period (Table 4.3). In both periods, these males spent on average 79.8% (± 2.1) of their time PERCH ALERT, followed by FORAGING BEHAVIOUR 5.9% (± 1.8), FLY DIRECT 5.1% (± 0.7), PERCH PREENING 4.2% (± 2.3), FLY THERMALLING 0.3% (± 0.9), AGGRESSION - INTRAGROUP 0.06% (± 0.31), CHANTING CALLS 0.01 (± 0.2) and AGGRESSION - INTERGROUP AND INTERSPECIFIC 0.01% (± 0.11). In addition, males spent on average 4.7% (± 1.3) of their time on the ground. In the non-breeding period, no reproductive behaviour was recorded for beta males (*i.e.* nuptial display flights; GM unpubl. data).

4.3.2 Female attendance

Nest attendance by monogamous breeders from KBV and SK did not differ significantly (Mann-Whitney test; $P > 0.05$) and data were combined. The attendance of beta males to females increased significantly from the non-breeding period to pre-laying period, resulting in a significant increase in attendance of polyandrous males (Table 4.4).

4.3.3 Copulation behaviour

Contact and non-contact copulation frequencies did not differ significantly between polyandrous alpha and beta, and monogamous males without nestlings (Chi-square; $P > 0.05$) (Table 4.5). Copulation frequencies did not differ significantly between polyandrous males with nestlings (Chi-square; $P > 0.05$). For polyandrous trios the copulation frequency differed significantly between males without (23:7 or 77% contact ratio) and with nestlings (8:15 or 35% contact ratio) (Chi-square; $P < 0.05$). Alpha males without nestlings were successful (*i.e.* contact copulation) in 84% of their copulations attempts,

Table 4.3 Significant results of analysis of variance to test for percentage time differences between different male demographic (status and vegetation type) and behavioural groupings in the non-breeding and pre-laying periods (first copulation until egg laying). Below each behavioural grouping the results for pairwise comparisons. A = alpha male, B = beta male, M = monogamous male, n = non-breeding period, p = pre-laying period, K = Karroid Broken Veld and S = Succulent Karoo. ANOVA; mean percentage time, Tukey tests below; ** = $P < 0.01$; NS = not significant; n = observation periods.

Groupings	AnK	BnK	MnS	MpS	ANOVA
REPRODUCTIVE BEHAVIOUR	0.3	0.0	0.2	3.5	$P < 0.001$
AnK		NS	NS	**	
BnK			NS	**	
MnS				**	
MbS					
n	12	9	15	4	

Table 4.4 The mean percentage time (± 1 standard deviations) per observation period polyandrous and monogamous males were recorded within a 100 m radius from their female. NS = not significant, * = $P < 0.05$; n = number of observation periods.

	Non-breeding period	Pre-laying period	Mann-Whitney test
Monogamous male with female	23 (24)	40 (32)	NS
n	29	3	
Alpha male with female	25 (28)	35 (22)	NS
n	17	13	
Beta male with female	12 (18)	28 (21)	*
n	16	13	
A polyandrous male with female	24 (22)	52 (21)	*
n	7	13	

beta males 64% and monogamous males, 62% (Table 4.5). The alpha male with nestlings performed 46% contact copulations and the beta male, 25% (Table 4.5). The earliest contact copulation recorded was performed by the alpha male of the Okkies polyandrous group 89 days before laying. The contact copulation rate of this alpha male decreased from day 31 (the next observation period) to day five before laying, whereas the beta male only achieved contact copulations on days five and three (Fig. 4.1). The clutch was abandoned after one egg broke and the female laid a second clutch 34 days later. In the further three observation periods, the beta male achieved all contact copulations.

Table 4.5 Contact and non-contact copulation frequencies recorded for polyandrous and monogamous male Pale Chanting Goshawks in groups without or with offspring.

	Contact copulations	Non-contact copulations	Total
Groups without nestlings			
Alpha male	16 (84)	3 (16)	19
Beta male	7 (64)	4 (36)	11
Monogamous male	5 (63)	3 (37)	8
Group with nestlings			
Alpha male	5 (45)	6 (55)	11
Beta male	3 (25)	9 (75)	12

During the first clutch, the alpha male performed no non-contact copulations, but, in the second clutch, this occurred only during the last observation period. No reverse dominance could be detected during observation periods when the beta male achieved a higher contact copulation rate. The contact copulation rate of the Zwartkop group (with nestlings) followed the same trend as Okkies' first clutch, although not as clear cut (Fig. 4.1). Again, contact copulation rates of the beta male exceeded that of the alpha male prior to laying.

Contact copulation rates of females differed significantly between groups, and rates for polyandrous females without nestlings were significantly higher than that of polyandrous females with nestlings ($P < 0.05$; pairwise t test) (Table 4.6). Male contact copulation rates only differed significantly between groups without nestlings (Table 4.6).

No significant differences were found between the number of males present (within a 100 m radius from female) during contact and non-contact copulations for polyandrous trios either with or without nestlings (all $P > 0.05$; Fisher's Exact Test). For polyandrous trios without nestlings, a second male was present during 28% (8/29) contact and 29% (2/7) non-contact copulations. For the polyandrous trio with nestlings, a second male was present during 50% (4/8) contact and 50% (5/10) non-contact copulations. A second male

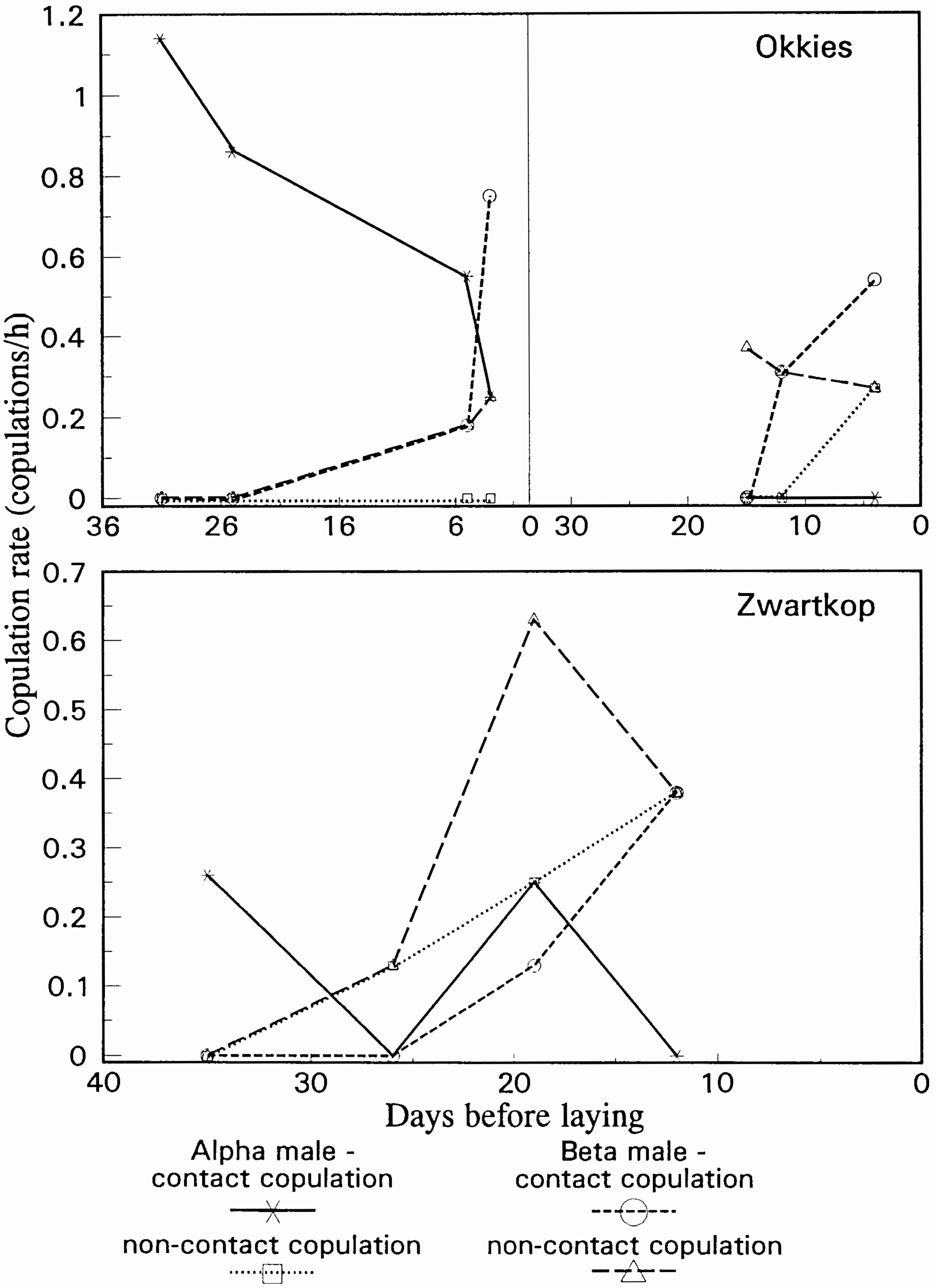

Fig. 4.1 Contact and non-contact copulation rates for alpha and beta males of two polyandrous groups. Polyandrous trio Okkies laid a second clutch after the first clutch failed.

Table 4.6 Mean copulation rates (per hour) recorded for polyandrous and monogamous females and males without or with nestlings. N = number of observation hours.

	Contact copulations	Non-contact copulations	Observation periods
Females			
Polyandrous trio without nestlings	0.75	0.27	10
Monogamous pair without nestlings	0.33	0.20	5
Polyandrous trio with nestlings	0.25	0.44	4
ANOVA	$P < 0.05$	NS	
Males without nestlings			
Alpha	0.55	0.11	10
Beta	0.21	0.16	10
Monogamous	0.33	0.20	5
ANOVA	$P < 0.05$	NS	
Males with nestlings			
Alpha	0.16	0.19	4
Beta	0.10	0.25	4
t test	NS	NS	

present during a contact copulation never displayed physical aggression towards the copulating male.

In all copulations observed for monogamous pairs with no nestlings (n = 8), a male only once tried to achieve a contact copulation directly after feeding the female (< 20 min.). In the 19 copulations observed for alpha males of groups without nestlings, the male only once achieved a contact copulation directly after feeding the female. In the 11 copulations observed for the polyandrous trio without nestlings, the alpha male achieved no copulation directly after feeding the female, but the beta male contact copulated and non-contact copulated once.

4.3.4 Nest construction and pre-lay prey provisioning

Mean nest construction and pre-lay prey provisioning rates did not differ significantly between polyandrous alpha, beta and monogamous males (Table 4.7).

Table 4.7 Mean prey provisioning and nest construction rates (nest structure and nest lining deliveries) (± 1 standard deviations) per hour recorded per observation period for polyandrous and monogamous males in the pre-laying period.

	Prey provisions to female	Nest construction	Observation periods
Alpha male	0.09 (0.20)	0.75 (0.89)	9
Beta male	0.03 (0.09)	0.25 (0.33)	9
Monogamous male	0.08 (0.13)	0.59 (0.55)	6
ANOVA	NS	NS	

4.3.5 Incubation

Monogamous and polyandrous females and beta males incubated the longest periods and most frequently (Table 4.8). In three instances, at three polyandrous groups, I observed alpha males displacing beta males by physically shouldering them from the eggs. In all cases, in the absence of any physical aggression, the beta males' soliciting-calls indicated that they were subordinate to alpha males.

Table 4.8 A comparison of minutes observed incubating between a monogamous pair and polyandrous trio. Mean bout lengths (± 1 standard deviations) and below the number of bouts recorded for each observation period.

Group	Female	Alpha or monogamous male	Beta male	Minutes observed
Monogamous pair	116 (169) 3	37 (35) 2		464
Polyandrous trio				
	60 (33) 3	3 1	34 (34) 2	547
	79 (26) 4	0	66 (41) 3	497
	56 (24) 3	22 (6) 3	19 1	238

4.3.6 Male behaviour during the nestling period

The behaviour of male demographic groupings differed significantly between all behavioural groupings, except AGGRESSION INTERSPECIFIC, AGGRESSION INTRAGROUP and FLY THERMALLING (Table 4.9). Pairwise comparisons revealed that it was only during 1989, and predominantly with regards to males from the double-brooding polyandrous trio, where significant behavioural differences were observed. These males were significantly more involved in NEST ACTIVITIES (0.70 and 0.31%), REPRODUCTIVE BEHAVIOUR (0.31 and 0.33%), FORAGING BEHAVIOUR AT THE NEST SITE (2.13 and 3.38%), the alpha male in CHANTING-CALLING(0.15%), and beta male in FEEDING SELF (4.39%).

4.3.7 Nest site presence

Time spent at the nest site did not differ significantly between monogamous males for 1988 and 1989, and data were combined for each year. During 1988, the regressions and adjusted means of time spent at the nest sites for monogamous and polyandrous males did not differ significantly. On average, males were away from the nest site for 95% (456/480 minutes) of time. During 1989, again the slopes did not differ significantly, but the adjusted means did ($F = 93.9$; $P < 0.001$). On average, the alpha male spent 42% (217/480) of their time away from the nest site, significantly less than the beta (53% or 255 min.) ($P < 0.05$; t test) and monogamous males (89% or 427 min.) ($P < 0.001$; t test).

4.3.8 Prey provisioning

No significant differences were found between prey provisioning rates for monogamous males between years, and thus data were combined. During 1988 no significant differences were found between provisioning rates for each prey provision route (Table 4.10). During 1989, the beta male provisioned the male-female-chick route at a significantly higher rate than monogamous males ($P < 0.05$ significance level; pairwise t test). Monogamous males also provided prey directly to the chick at a higher rate than polyandrous males (P < 0.05; pairwise t test).

Table 4.9 Results of analysis of variance to test for percentage time differences between different male demographic (status and vegetation type) and behavioural groupings in the nestling periods (hatching until fledging) of 1988 and 1989. Below each behavioural grouping the significant results for pairwise comparisons. A = Alpha male, B = Beta male, M = monogamous male, K = Karroid Broken Veld, S = Succulent Karoo, O = Open Spekboomveld. Tukey test; * = P < 0.05, ** = P < 0.01; n = number of observation periods

groupings	1988					1989				
	AK	BK	MK	MS	ANOVA	AK	BK	MK	MO	ANOVA
FEEDING SELF	1.6	7.6	2.0	0.1	NS	7.1	22.5	10.0	5.5	NS
FEEDING CHICK(S)	0.0	0.1	0.3	0.0	NS	0.2	0.0	8.1	7.8	P < 0.01
MK89							*			
MO89							*			
AGGRESSION INTER-SPECIFIC	0.1	0.2	0.1	0.0	NS	0.6	0.6	0.0	0.0	NS
AGGRESSION INTRAGROUP	1.3	1.4	0.0	0.0	NS	0.5	0.6	0.0	0.0	NS
FLY THERMALLING	0.7	0.9	0.1	0.5	NS	1.5	2.1	1.6	0.3	NS
NEST ACTIVITIES	0.0	0.0	0.0	0.0	NS	3.3	1.5	0.0	0.0	NS
REPRO-DUCTIVE BEHAVIOUR	0.0	0.0	0.0	0.0	NS	1.5	1.7	0.0	0.0	P < 0.05
FORAGING BEHAVIOUR AT NEST SITE	0.4	0.4	1.9	0.8	NS	10.3	16.7	1.4	0.1	P < 0.01
MK89							*			
MO89						*	**			
CALLING-CHANTING	0.0	0.1	0.0	0.0	NS	0.7	0.4	0.0	0.0	NS
n	7	7	7	9		5	5	3	3	

Table 4.10 Results of analysis of variance to test for differences in prey provisioning rates in the nestling period between polyandrous and monogamous males in an intermediate reproductive year (1988) and high reproductive year (1989). Means per hour (± 1 standard deviations), NS = not significant, n = number of eight hour observation periods.

Provisioning route	Alpha male	Beta male	Monogamous male	ANOVA
1988				
Male-female-chick	0.13 (0.18)	0.11 (0.11)	0.06 (0.10)	NS
Beta male -alpha male -female-chick		0.02 (0.05)		
Male-chick	0.00	0.06 (0.14)	0.04 (0.08)	NS
Male-female	0.00	0.02 (0.05)	0.05 (0.07)	NS
Male	0.04 (0.06)	0.02 (0.05)	0.00	NS
All male(s)	0.16 (0.18)	0.20 (0.16)	0.15 (0.16)	NS
n	7	7	13	
1989				
Male-female-chick	0.15 (0.11)	0.25 (0.13)	0.06 (0.11)	$P < 0.05$
Beta male -alpha male -female-chick		0.03 (0.06)		
Male-chick	0.08 (0.07)	0.03 (0.06)	0.17 (0.10)	$P < 0.05$
Male-female	0.13 (0.09)	0.05 (0.11)	0.02 (0.05)	NS
Male	0.08 (0.07)	0.13 (0.09)	0.02 (0.05)	NS
All male(s)	0.44 (0.15)	0.46 (0.21)	0.28 (0.09)	NS
n	5	5	6	

4.3.9 Soliciting calls and aggressive behaviour

Soliciting calls were generally recorded at very low rates (Table 4.11). During 1988, for the polyandrous trio, the highest mean soliciting-call rate was recorded for alpha and beta males calling at each other (0.554/h or once every 108 min.), followed by beta male at alpha male, and female at alpha and beta male. During 1989, it was again the alpha and

Table 4.11 Soliciting-call rates eight hour observation period of polyandrous trios and monogamous pairs in the nestling period of an intermediate reproductive year (1988) and high reproductive year (1989). Sex-status groupings in brackets indicate individual the calls are directed to, but individual is not responding. Means per eight hour and (± 1 standard deviations), n = number of eight hour observation periods

	1988	1989
Polyandrous trios		
Alpha male-female	0.036 (0.094)	0.025 (0.056)
Beta male-female	0.054 (0.142)	0.025 (0.056)
Alpha male-beta male	0.554 (0.946)	0.350 (0.487)
Female-(alpha male)	0.125 (0.331)	0.025 (0.056)
Female-(beta male)	0.107 (0.233)	0.050 (0.068)
Alpha male-(female)	0.00	0.050 (0.068)
Alpha male-(beta male)	0.00	0.075 (0.068)
Beta male-(female)	0.054 (0.142)	0.100 (0.163)
Beta male-(alpha male)	0.179 (0.374)	0.050 (0.068)
n	7	5
Monogamous pairs		
Male-female	0.047 (0.188)	0.042 (0.102)
Male-(female)	0.039 (0.156)	0.021 (0.051)
Female-(male)	0.070 (0.137)	0.271 (0.550)
n	16	6

beta male calling at each other that recorded the highest rate followed by the beta male calling at the female. For monogamous pairs, only during 1989, did the female calling at the male recorded a rate of above 0.100/h or once every 10 h.

The behavioural act, PERCH AGGRESSIVE, where one of the polyandrous males perches in close proximity to the other with wings vibrating against the body and soliciting-calling, was recorded on seven instances. During the first four of these instances, after the beta male provisioned prey, both males perched aggressively for 11 minutes in total, the beta male alone for four minutes (the alpha male not responding) and the alpha male alone for three minutes. In three cases, the alpha male provisioned prey, and both males perched aggressively for eight minutes and the beta male alone for nine minutes.

4.3.10 Male body mass

Mean body mass differed significantly between the three status males ($P < 0.05$; Kruskal-Wallis test) (Table 4.12). Beta males weighed significantly less than monogamous males ($P < 0.05$; Tukey test). In three cases where both males from polyandrous trios were trapped, the beta male always weighed less than the alpha male.

Table 4.12 Body mass of monogamous and polyandrous males during breeding seasons. Males were weighed to the nearest 10 g. Monogamous males are from Karroid Broken Veld (KBV) and Succulent Karoo (SK).

Status Group	Alpha male	Beta male	Monogamous male
Polyandrous trios			
Okkies	770	740	
Kruisrivier	770	670	
JohanG	720	640	
Zwartkop		720	
Cutting		710	
Monogamous pairs			
Badsaf (SK)			750
Remhog (SK)			750
Cutting (KBV)			780
Engelskamp (SK)			750
Secretary (KBV)			750
Means (SD)	753 (29)	696 (40)	756 (13)

4.3.11 Kinship, paternity and inclusive fitness

The genetic analysis revealed that the female shared 17% of her restriction fragment length polymorphisms (RFLPs) with the alpha male and 16% with the beta male. This female was judged not to be related to the males. The two males however shared 81% of their RFLPs and were judged to be first order relatives or full sibs, *i.e.* father and son, or brothers. From the contact copulation ratio, the split in paternity was determined to be 68:32 in favour of alpha males.

Polyandrous females achieved the highest fitness (= offspring equivalent) if they co-breed (Table 4.13; Fig. 4.2). Polyandrous males achieved the highest inclusive fitness, if as full sibs, they breed independently. Alpha males achieved higher fitness than monogamous males (= 0.54) by co-breeding with a full sib (= 0.69) or unrelated male (= 0.55). Offspring equivalent values for beta males co-breeding with a full sib equaled that of monogamous males. Moreover, the fitness of a beta male not breeding (0.27) equaled that of co-breeding with an unrelated male (Table 4.13).

Table 4.13 The number of offspring equivalents produced in the Karroid Broken Veld for five breeding seasons by polyandrous and monogamous males and females, calculated out of the female's, and alpha and beta male's perspectives. Different scenarios are presented with males either not related or full sibs, and with paternity split of 68:32 in favour of the alpha male. Indirect fitness calculations are underlined.

	Polyandrous trios	Monogamous pairs
No. of group years	16	64
No. of males	32	64
No. of young	26	69
Offspring per group	1.63	1.08
FEMALE'S PERSPECTIVE		
Independent breeding	0.54	(0.5x1.08)
Co-breeding	0.815	(0.5x1.63)
Beta male not breeding	0.54	(0.5x1.08)
ALPHA MALE'S PERSPECTIVE AND PATERNITY SPLIT 68:32		
Males not related		
Independent breeding	0.54	(0.5x1.08)
Co-breeding	0.55	0.5(0.68x1.63)
Beta male not breeding	0.54	(0.5x1.08)
Males full sibs		
Independent breeding	0.81	(0.5x1.08)+0.5(0.5x1.08)
Co-breeding	0.69	(0.68x0.815)+0.5(0.32x0.815)
Beta male not breeding	0.54	(0.5x1.08)
BETA MALE'S PERSPECTIVE AND PATERNITY SPLIT 32:68		
Males not related		
Independent breeding	0.54	(0.5x1.08)
Co-breeding	0.26	0.5(0.32x1.63)
Beta male not breeding	0	
Males full sibs		
Independent breeding	0.81	(0.5x1.08)+0.5(0.5x1.08)
Co-breeding	0.54	(0.32x0.815)+0.5(0.68x0.815)
Beta male not breeding	0.27	0.5(0.5x1.08)

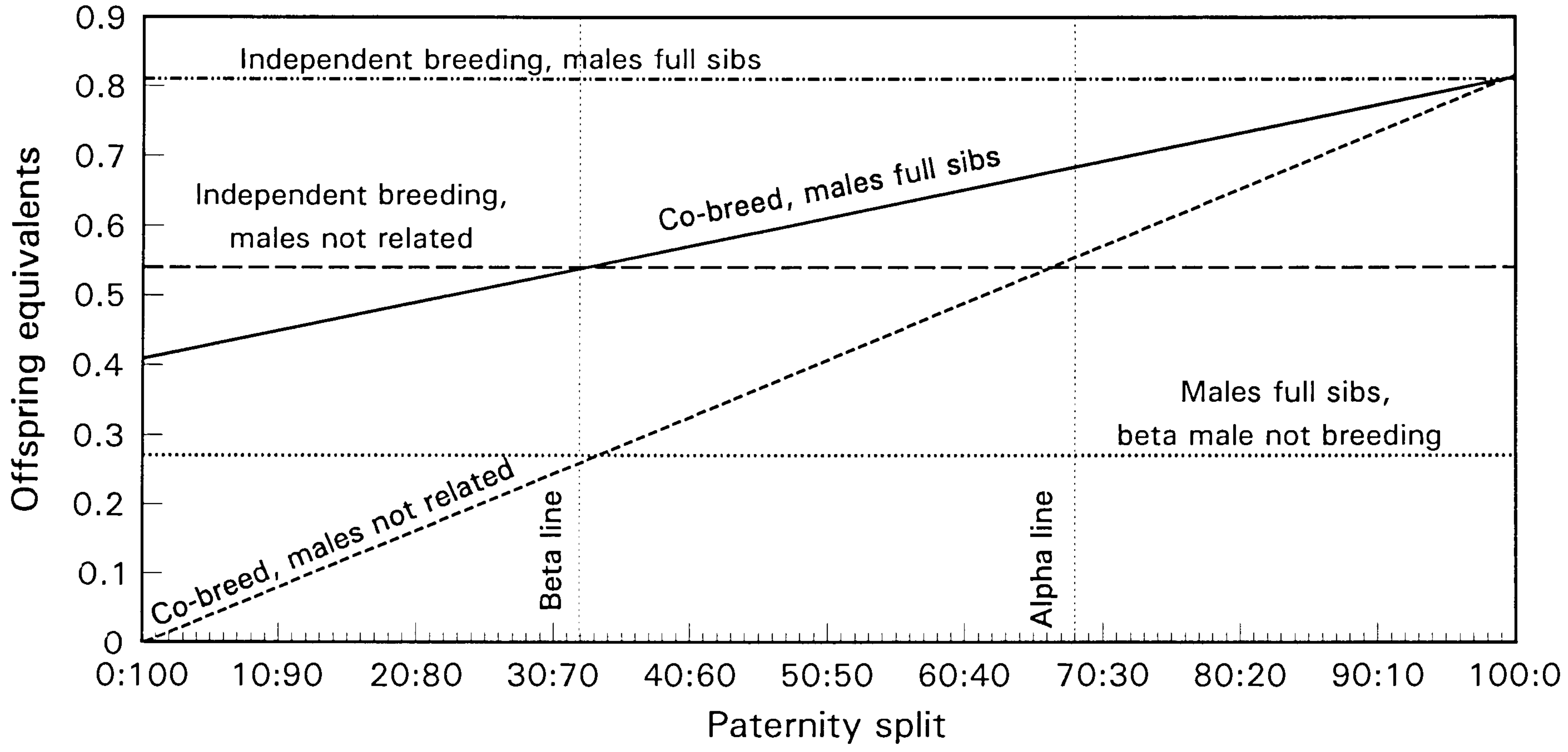

Fig. 4.2 The possible number of offspring equivalents that can be produced under different scenarios: polyandrous males can either be full sibs or unrelated, and can either breed independently, co-breed or beta male not breeding. The alpha and beta lines indicate paternity split of 68:32.

4.4 DISCUSSION

4.4.1 Beta male's reproductive role differs

During the pre-laying period, all reproductive behaviours of beta males were less intense than those of other breeding males. However, during the nesting season, beta males significantly increased their involvement in parental activities. They outperformed alpha males in incubation, fed more in close proximity to the nest site and provisioned prey via the female-chick route (1989). They were the group member most often involved in soliciting-calling and aggressive behaviour. Whether the beta male's behaviour can be attributed to inexperience, subordination or being in competition with the alpha male is difficult to substantiate. The beta male certainly displayed an eagerness to participate in incubation and prey provisioning, an eagerness not observed in the non-breeding and pre-laying periods. Perhaps, prior to egg laying, the alpha male suppresses the reproductive behaviour of the beta male by some dominant behaviour. Thus, it may only after laying that the beta male is allowed to participate fully in all reproductive activities.

Although the comparison of behaviour between polyandrous males (from one polyandrous trio) and other male groups during 1989 in fact represents a comparison of double- *vs* single-brooding groups, it provides insights into the reproductive roles of polyandrous males under different reproductive situations. The nesting activities and reproductive behaviour recorded for these two males can therefore be attributed directly to this double-brooding group starting their second nesting cycle while still feeding the first brood (see Chapter 3). Compared with the alpha male, the beta male concentrated his efforts on hunting and provisioning . The beta male spent more time (3.38%) foraging in a very small section (0.0314 km^2 or $< 1\%$) of the territory (3.95 km^2; recalculated from Chapter 6). During the nestling period, he also provisioned at a higher rate and spent significantly more time feeding at the nest site. Alternatively the alpha male spent more time, either nest building (the second nest) or chanting, presumably to advertise the locality of the nest he was building (Brown 1970). The difference in nest site presence can therefore be attributed to the alpha male spending more time on the second breeding attempt (more at the nest site) and the beta male on provisioning (less at the nest site). By directing his efforts at the second nesting attempt, the alpha male secured a further genetic investment by increasing the possibility of a second breeding attempt. The high incubation and provision rate of the beta male may, in fact, relieve the alpha male from those duties, providing the opportunity for him to start the second breeding cycle (Woolfenden & Fitzpatrick 1984; Russell & Rowley 1988).

4.4.2 Copulation behaviour and fertile period

Males can firstly guard their paternity by guarding the females but, since attendance of the female by PCG males was less than 60% of time, they did not qualify (see references in Birkhead & Moller 1992). They may also guard paternity by copulating frequently in the fertile period (Birkhead & Moller 1992). If PCGs started the first copulation 37-89 days before laying, and contact copulated at a mean rate of 0.75 per hour, then females copulated 300-721 times before laying. Between 447 and 589 copulations per clutch have been recorded for the European Goshawk *Accipiter gentillis*, and Moller (1987) hypothesised that this high number is a response to the inability of the male to guard the female continuously. While hunting to provision female, the male leaves the female for long periods and copulates upon his return, presumably so that his sperm may compete with sperm from possible extra-male copulations. PCG males also provision females in the fertile period and leave them for long periods unattended (50-58% of time). Although the study area is relatively flat and open, perching females were certainly out of view for high proportions of the time. Extra-male copulations were never observed among the marked study population, but are reported to occur regularly among raptors (see Moller 1987).

Paternity is not only determined by the rate and number of contact copulations, but also by the temporal distribution of contact copulations. Various anatomical and physiological factors play a role in fertilization, including the length of the fertile period, the duration of sperm storage, and intervals between ovipositions, and ovulation and fertilization (Birkhead & Moller 1992). Since the above are unknown for PCGs, one can only speculate on paternity. At first glance, it would appear that beta males were assured of paternity since, the last male to copulate normally fertilises a disproportionately large proportion of the eggs (Birkhead 1988). However, since beta males only started contact copulating late in the pre-laying period, they may have overvalued their matings, since most of the clutch could have been fertilised (Davies *et al.* 1992). Secondly, prey provision rates to offspring provides a good prediction of the male's assurance of paternity but, if males are related, beta males may benefit by feeding offspring even if they did not participate in any copulations (Koenig 1990; McDonald & Potts 1994). Alternatively, alpha males guarded their paternity by contact copulating at a higher rate and therefore delivered more sperm. It is an open question if the dominant and larger alpha male would have decreased his contact copulation rate if there were an equal probability of decreasing his paternity. The decreasing pattern of contact copulations, as observed for alpha males, is not unusual, and convergent patterns had been recorded in other taxa in which breeders copulate frequently, such as raptors, owls, shrikes and colonial breeders (Birkhead *et al.* 1987). Furthermore, although PCG males did not guard their females, a male's access to the female gives a good prediction of his chances of paternity (Davies *et al.* 1992). In the pre-lay period, the attendance of the female by the alpha male and his presence at the nest site were higher than beta, and even monogamous males. A preliminary conclusion can therefore be drawn that, in polyandrous trios, alpha males had the highest probability of fertilizing eggs laid by females.

4.4.3 Sexual conflict

In general, females that allow more than one male to copulate may benefit reproductively through an increase in parental care (Davies 1985; Birkhead & Moller 1992). This was indeed the case with polyandrous females (see Chapter 5). Although males may father offspring disproportionately to their genetic investment, as may be the case with PCG beta males, it is in the interest of the female to secure their cooperation by allowing them to participate in copulations (Stacey 1979; Davies 1985). Although contact copulation rates of polyandrous females (without and with nestlings) and monogamous females differed significantly, all eggs subsequently laid were fertile (GM unpubl. data). The average contact copulation rate of once every 1/80 minutes recorded for polyandrous females without nestlings, and even the low rate of 1/240 minutes for polyandrous females with nestlings, were therefore not essential to fertilise eggs (Birkhead & Moller 1992), but possibly to secure the cooperation of males.

In the fertile period, the lack of inter-male aggression between polyandrous males was surprising since one would expect males to guard their paternity actively. However, it is during this period that the dominant breeders, the female and alpha male may allow the beta male to copulate, since securing his full cooperation allowed the polyandrous trios to undertake more frequent and successful breeding attempts (see Chapter 3). Females did not respond to courtship feeding by allowing the male that provisioned to copulate. If she did, males would have been able to 'claim' a contact copulation which, in turn, would have made it impossible for females to 'control' the temporal distribution of copulations.

Why then the aggressive behaviour and high calling rate recorded between polyandrous males and the beta male and female in the nestling period? Calling and aggressive behaviour may, as reproductive functions, indicate vigour and dominance in an individual or even solicit subordination (Welty 1982). Evidence of soliciting was seen during 1989 when monogamous males predominantly provisioned chicks directly, resulting in high soliciting-call rates by females. During 1988, the higher calling and aggression rate of members of the polyandrous trio, compared with the 1989 polyandrous trio may be the result of lower prey densities (see Chapter 7), influencing the dynamics and interactions around provisioning and soliciting.

4.4.4 Reproductive roles

Vehrencamp (1980) predicted that, if polyandrous males enjoy on average higher reproductive success than monogamous males, alpha (dominant) males will not skew paternity since beta (subordinates) males may leave and breed on their own. In addition, co-breeding males may be unrelated since their direct fitness may be greater than that of monogamous males. However, polyandrous PCG males produced on average 0.815 offspring (0.5x1.63) and monogamous males 1.08. Under these circumstances Vehrencamp's (1980) model predicts that alpha males will skew paternity and males are likely to be related to gain indirect fitness benefits. The closer the two males are related, the more paternity may be skewed, since the loss in direct fitness to beta males is compensated for by a gain in indirect fitness (Vehrencamp 1980).

One can only speculate on a possible paternity skew and the results thereof. The mechanism through which the dominant breeders, the female and alpha male, controlled the copulation frequency and timing, is still an open question, since no observation was made of alpha males actually preventing beta males from copulating. It is probably of little importance to the female which male copulates when, as long as both males contact copulate (for reasons discussed above).

In the absence of any paternity tests, I could first of all assign paternity in compliance with the contact copulation ratio. According to this ratio, alpha males skewed paternity to the point where the inclusive fitness of beta males equaled that of monogamous males (see Fig. 4.2). At that point, the direct fitness of beta males (0.26) is lower than that of monogamous males (0.54) but, as predicted, the difference is compensated for by gains in indirect fitness (0.28; 0.26 + 0.28 = 0.54). If beta males fathered no offspring, the inclusive fitness of beta males (0.41) would still be higher than that of a beta male not breeding in the presence of an alpha male (0.27). This threshold is reached when a beta male delays dispersal in the territory of a full sib or, if he disperses with his father or brother and either one of them breeds.

However, there are two reasons why co-breeding may be more advantageous when compared with delaying dispersal and not breeding. One should compare the inclusive fitness of beta males, not with that off alpha males, but with non-breeding males.

Compared with subordinate males not allowed near the nest site, beta males may not only achieve higher inclusive fitness, but more importantly gain some reproductive and survival skills (Brown 1986; Heinsohn *et al.* 1990; Stacey & Koenig 1990; Heinsohn 1991). It is therefore not entirely to the disadvantage of the beta male to co-breed. Even if beta males achieved no direct reproductive fitness, they could still gain other direct fitness benefits such as breeding experience and ascension to a higher status (Stacey & Koenig 1990; McDonald & Potts 1994). The status of a beta male may be a stepping stone in the social ladder from non-breeder, subordinate breeder (beta male) to dominant breeder (alpha male). For both alpha and beta males, the establishment of beta males as dominant (monogamous) males holds the highest benefit since all reproductive scenarios, except 100:0 in favour of alpha males, falls short of the 0.81 offspring equivalents produced if the two sibs would breed independently, either as neighbours or perhaps in the same population.

As expected, the male dominance hierarchy resulted in a degree of reproductive competition, but PCG males demonstrated more cooperation than conflict. The advantages of this strategy, especially to the alpha male, have clearly been demonstrated. Interpreting the behaviour of beta males is difficult given the ratio of direct *vs* indirect fitness benefits achieved through breeding with a full sib. Only with removal experiments could one explain some of the apparent anomalies between paternity and reproductive roles (Koenig 1990; Davies *et al.* 1992). This was especially apparent in the case of beta males if one compares their relatively low genetic input (contact copulations) with their relative high provisioning rate. Furthermore, paternity tests on offspring will reveal if beta males were duped into believing that they fathered offspring. It will also reveal if their apparent minor genetic contributions were offset by indirect fitness benefits?. How will beta males respond after gaining more breeding experience, *i.e.* will they leave the group or try to change their status? The potential exists for such a relationship to be unstable. The demographic consequences of this relationship will be discussed in Chapter 9.

CHAPTER 5

HOW DO CO-BREEDERS HELP?: PREY PROVISIONING AND TERRITORIAL DEFENSE IN THE COOPERATIVE-BREEDING PALE CHANTING GOSHAWK

SUMMARY

Polyandrous and monogamous Pale Chanting Goshawks (PCG) were investigated to determine how co-breeders helped polyandrous trios to produce more young, defend the territory and nest more efficient, and increase prey provisioning and parental duties. PCG males were involved predominantly in interspecific and, often aggressive, intraspecific interactions against other males on territory borders. Females occasionally defended their territories, but against other females, and only within the territory. Territorial intraspecific interactions were almost exclusively recorded in Karroid Broken Veld (KBV), as well as interspecific interactions at nest sites. Over a period of five years (1988-1992), 16% (12/77) of the nests of monogamous pairs and only 5% (1/20) of the nests of polyandrous trios were apparently predated. Since polyandrous breeders had a lower interaction frequency than monogamous breeders, and polyandrous males largely occupied exclusive parts of a territory, it is suggested that co-breeders helped by decreasing the interaction frequency per breeder.

In the breeding season, a clear division of parental duties was found between the sexes. Females performed duties such as brooding, feeding and guarding nestlings, whereas males performed nest construction and prey provisioning. Furthermore, in the nestling period, a relationship existed between presence of females at the nest site and male prey provisioning (combined in the case of polyandrous males). For example, at a provisioning rate of 0.14 items per hour, a monogamous female left the nest site, presumable to hunt, for 73% of time. At the other extreme, a polyandrous trio's nest site provisioned by males at a rate of 0.90 items per hour, the female not only stayed at the nest site for 94% of time, but also double-brooded. Since polyandrous offspring were not fed at a significantly different rate, or were not significantly different in body mass from monogamous offspring, it is suggested that beta males helped in lessening the female's workload, thus allowing her to accumulate the necessary body reserves for laying a second clutch. Since the help provided by beta males increased the reproductive success of polyandrous trios, beta males would at least gain indirect fitness benefits if co-breeding with related males.

5.1 INTRODUCTION

The occurrence of two breeding males in some PCG groups enabled polyandrous trios to undertake more frequent and successful breeding attempts and produce more young (Chapters 3 & 4). However, it is still not known how these co-breeders helped to achieve this higher reproductive success. Helpers may help by providing more food to nestlings which may reduce the workload of breeders, *e.g.* fledgling care (Brown *et al.* 1978, du Plessis 1991). This may, in turn, increase the probability of further breeding attempts (Brown & Brown 1981; Russell & Rowley 1988; Davies 1991). Helpers may also help with the early detection and deterrence of predators resulting in reduced predation of nests (Gayou 1986; Rabenold 1990; Mumme 1992a).

Within polyandrous trios, co-breeding beta males participate fully in all reproductive activities such as prey provisioning and nest construction (Chapter 4). Prey provisioned to nest sites during the nestling period were eaten in part or in full by male(s), female and nestlings. Since PCGs lay a maximum of two eggs per clutch, they can only increase their reproductive success by double-brooding (Chapter 3). To do so in one breeding season, their two breeding cycles overlap, the nestling period of the first cycle with the pre-laying period (nest construction, prey provisioning and copulations) of the second.

The aims of this chapter are to study: (1) parental duties, prey provisioning, territorial defense and nest predation in male and female PCGs in different vegetation types, and (2) the impact of equal parental effort by two polyandrous males on the behaviour of the female and the success of the reproduction of polyandrous trios.

5.2 METHODS

5.2.1 Behaviour during the non-breeding, pre-laying and nestling periods

During the non-breeding period and pre-laying period (from first copulation until egg laying) of 1988 I studied PCGs employing instantaneous sampling (see Chapter 2) to investigate breeder behaviour in the Karroid Broken Veld (KBV) and Succulent Karoo

(SK) vegetation types. The mean duration of observation periods on adult breeders was 144 ± 73 minutes and 86 observation periods totalling 12 368 minutes were conducted (see Table 4.1). Breeders were classified into demographic groupings according to status (polyandrous or monogamous), sex, the vegetation type the group nested in and reproductive period. Demographic groupings with less than four observation periods were excluded from the analysis. Behavioural acts related to territorial defense were classified into the following behavioural groupings: FLY THERMALLING and AGGRESSION - INTRASPECIFIC AND INTERSPECIFIC (see Appendix 2). Nest construction activities and pre-laying prey provisioning for males and females from KBV and SK were extracted from instantaneous sampling data.

Scan sampling (see Chapter 2) was employed to record behavioural data once the female of each group laid. For 1988 and 1989, during the nestling period, 34 eight-hour (16 320 min.) observation periods were recorded for two different polyandrous trios and two monogamous pairs, all from KBV, during 1988 from a monogamous pair in SK, and during 1989 a monogamous pair in the Open Spekboomveld (OSBV) (see Table 4.2). Since the population's reproductive success differed substantially between 1988 and 1989 (Chapter 3), data from these two years were analysed separately. Apart from the Zwartkop polyandrous trio (Group no. 12; Table 3.1; Fig. 3.2), all other groups studied were attending their first and only broods. Breeders were classified into demographic groupings according to status (polyandrous or monogamous), sex, the vegetation type the group nested in, and reproductive period. Behavioural acts were classified into the following behavioural groupings: FEEDING CHICK(S), AGGRESSION - INTERSPECIFIC, AGGRESSION - INTRAGROUP, FLY THERMALLING, NEST ACTIVITIES and FORAGING BEHAVIOUR AT NEST SITE (see Appendix 3).

5.2.2 Nest site presence

For each observation period recorded during the nestling period, the number of minutes each breeder was not within the 100 m radius from the nest was extracted from scan sampling data. Since breeding raptors spend more time away from the nest during the later nestling period, so as to meet the prey needs of the growing young (Newton 1979), I analysed nest attendance data by employing a one-way analysis of covariance with days after fledging as the independent variable, and minutes per observation period outside the 100 m radius as the dependent variable.

5.2.3 Prey provisioning during the nestling period

Rates of prey provisioning to the nest site during the nestling period were calculated from scan sapling data for polyandrous and monogamous males and females, Since no significant differences were found between prey provisioning of alpha and beta males (Chapter 4), data were combined to reflect the total effort of polyandrous males to the nest site. Prey that were fed to chicks were calculated similarly. Provisions per hour per observation period were analysed for 1988 and 1989 separately.

5.2.4 Nest predation

For each of the 51 nest visits during the breeding seasons of 1988-1992 (Chapter 3), the following data were recorded: the presence/absence of eggs/chicks, disturbance to nest lining and structure and, the presence of chick remains on the ground below the nest.

5.2.5 Fledgling body mass

During week seven of the eight week nestling period, young were weighed (to the nearest 10 g) and sexed (at that age the chicks were already showing clear-cut reverse sexual size dimorphism; GM unpubl. data).

5.2.6 Interspecific and intraspecific interactions

An interaction was defined as an encounter between a territorial PCG and an intruder (interspecific or intraspecific), which elicited an action or reaction from the PCG. I recognised the following interaction modes and ordered them in sequence of aggression according to physical and vocal expression: FLY DIVING AT - PCG fly and dives at intruder, only a few dives are performed, dives are shallow; FLY MOB - PCG fly and dive repeatedly at intruder, dives are deep and to within one metre from intruder; FLY MOB AND CALL - fly mob is accompanied by alarm-call, a quavering ee-e-e-e-e-e-e (Maclean 1985); FLY STRIKING - PCGs fly mob and physically strike intruder with talon (no physical damage was ever obvious); SPIRAL FLIGHT AND AGGRESSIVE-CALL - PCG thermals, flying in small circles with very fast and shallow wingbeats (this flight is accompanied by aggressive-call, loud fast bursts of staccato Kikiki-Kikiki-Kikiki-Kikiki); and CARTWHEEL FLIGHT - birds lock feet in mid air and whirl down in a vertically-oriented plane. All interactions were recorded during instantaneous and scan sampling during 1988-1989 and ad hoc observations during 1988-1992. Interactions were divided into interspecific and intraspecific (between neighboring PCG groups). The territorial position of intraspecific interactions was noted as either border (on the border of two territories) or internal (more than 500 m from territory boundary). At nest sites, I recorded the presence or absence, as well as the passive or active participation, of male(s) and female in interactions.

5.2.7 Territorial occupancy

During all observations in the study area, I searched for marked breeders and recorded their positions on a map. In addition, during instantaneous sampling, the quadrat (500x500 m) position of the focal animal was recorded every 60 seconds. For two pairs of polyandrous males (JohanG's OL & BB and Kruisrivier's LL & WE; Table 4.1), for which I studied the behaviour of each male for more than seven hours (after which time the new quadrats visited decreased; GM unpubl. data), I calculated a proportional occupation per quadrat.

5.3 RESULTS

5.3.1 Behaviour during pre-laying and nestling periods

Polyandrous females thermalled for significantly longer time during the pre-laying period than did other males and females (Table 5.1). Nest construction (nest structure or lining) was observed on 35 occasions by males and on three by females, all monogamous females. Pre-lay prey provisioning of females by males was observed on five occasions. Prey was brought to a polyandrous female, respectively 15, four and three days before laying and to two monogamous females, 33 and 14 days before laying.

Table 5.1 Results of analysis of variance to test for percentage time differences between different demographic (status, sex and vegetation type) and behavioural groupings in the non-breeding and pre-laying periods (first copulation till egg laying). F = female, M = male, T = polyandrous trio, P = monogamous pair, n = non-breeding period, p = pre-laying period, K = Karroid Broken Veld and S = Succulent Karoo. ANOVA; mean percentage time; NS = not significant. Tukey test below; * = $P < 0.05$, ** = $P < 0.01$; n = number of observation periods.

Groupings	FTnK	FTbK	FPnS	MTnK	MPnS	MPbS	ANOVA
FLY THERMALLING	0.39	4.39	0.15	0.54	0.12	0.44	$P < 0.01$
FTbK	*		**	**	**		
AGGRESSION - INTRASPECIFIC AND INTERSPECIFIC	0.02	0.02	0.01	0.00	0.04	0.06	NS
n	12	13	12	21	15	4	

5.3.2 Nestling period behaviour

No significant difference was found between mean prey provisioning rates for the two monogamous pairs during 1988 and 1989, and data were thus combined. During 1988 and 1989, mean provisioning rates differed significantly between polyandrous males and all other groupings (Table 5.3). Mean provisioning rates to chicks did not differ significantly between polyandrous trios and monogamous pairs during 1988 (0.32 *vs* 0.22; n = 20 observation periods; $P > 0.05$; t test) or 1989 (0.55 *vs* 0.22; n = 12; $P > 0.05$; t test).

During 1988, monogamous females spent significantly more time on FEEDING CHICKS and polyandrous females on NEST ACTIVITIES (Table 5.2). During 1989, the polyandrous female (from the double-brooding group) fed the chicks over a longer period than did her two males, who spent more time than other demographic groupings hunting within a 100 m radius of the nest (Table 5.2).

Table 5.2 Results for 1988 and 1989 of an analysis of variance to test for percentage time differences between different demographic (status, sex and vegetation type) and behavioural groupings in the nestling period (hatching until fledging). Below each behavioural grouping the significant results for pairwise comparisons. F = female, M = male, T = polyandrous trio, P = monogamous pair, K = Karroid Broken Veld and S = Succulent Karoo and O = Open Spekboomveld. ANOVA; mean percentage time; NS = not significant. Tukey tests below; * = $P < 0.05$, ** = $P < 0.01$; n = number of observation periods.

1988 groupings		FTK	MTK	FPK	MPK	FPS	MPS	ANOVA
FEEDING CHICK(S)		1.1	0.0	1.5	0.1	0.3	0.0	$P < 0.05$
	MTK			*				
	MPS			*				
AGGRESSION INTERSPECIFIC		0.0	0.0	0.1	0.0	0.0	0.0	NS
FLY THERMALLING		0.4	0.2	0.1	0.0	0.1	0.1	NS
NEST ACTIVITIES		0.1	0.0	0.0	0.0	0.0	0.0	$P < 0.001$
	FTK		**	**	**	**	**	
FORAGING BEHAVIOUR AT NEST SIT		0.3	0.1	0.4	0.4	0.4	0.2	NS
n		7	14	7	7	9	9	

1989 groupings		FTK	MTK	FPK	MPK	FPO	MPO	ANOVA
FEEDING CHICK(S)		3.7	0.0	0.2	1.7	0.8	1.6	$P < 0.05$
	FTK		**					
AGGRESSION INTERSPECIFIC		0.0	0.1	0.0	0.0	0.0	0.0	NS
FLY THERMALLING		0.5	0.4	0.0	0.3	0.1	0.1	NS
NEST ACTIVITIES		0.0	0.5	0.0	0.0	0.0	0.0	$P < 0.05$
FORAGING BEHAVIOUR AT NEST SIT		0.8	2.7	0.1	0.3	0.1	0.0	$P < 0.001$
	MTK			*	*	**	**	
n		5	10	3	3	3	3	

Table 5.3 Results of an analysis of variance to test for differences of prey provisioning rates between polyandrous and monogamous males and females in the nestling periods of an intermediate reproductive year (1988) and high reproductive year (1989). F = female, M = male, T = polyandrous trio, P = monogamous pair, K = Karroid Broken veld, S = Succulent Karoo, MTKC = polyandrous males combined. Means per hour, NS = not significant. Tukey tests below; ** = P < 0.01; n = number of eight observation periods.

	FTK	FPS	MTKC	MPS	ANOVA
1988					
	0.018	0.135	0.393	0.144	P < 0.01
FTK		NS	**	NS	
FPS			**	NS	
MTKC				**	
n	7	13	7	13	
1989					
	0.075	0.104	0.900	0.292	P < 0.001
FTK		NS	**	NS	
FPS			**	NS	
MTKC				**	
n	6	6	5	6	

5.3.3 Brooding

Of the two sexes, only females were recorded brooding hatchlings. During 480 minute observation periods during 1988, two monogamous females brooded for 84 min. on day five, and 156 min. on day seven of the nestling period. A polyandrous female brooded 327 min. on day six, and 275 min. on day 15 of the nestling period.

5.3.4 Nest site presence

During 1988, time spend away from the nest site did not differ significantly between monogamous and polyandrous males and data were thus combined (see Chapter 4). The adjusted means (ANCOVA; F = 49.0; P < 0.001) and regression slopes (F = 15.9; P < 0.001) of time spend away from the nest site differed significantly between males, polyandrous female and monogamous females (Fig. 5.1). The regression slope of males

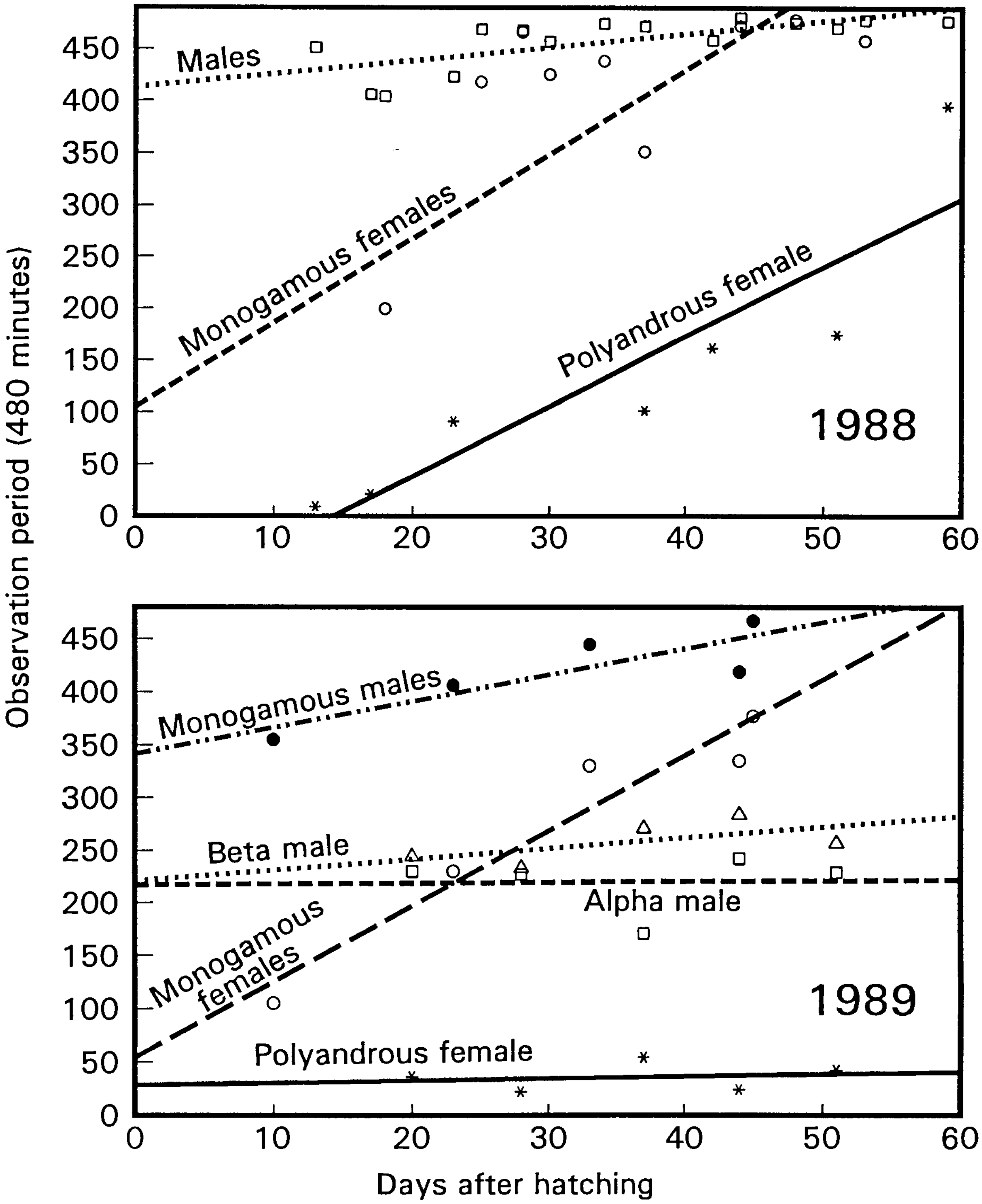

Fig. 5.1 Minutes per observation period Pale Chanting Goshawk breeders were not within 100 m radius from the nest site in the nestling periods of 1988 and 1989.

(ANCOVA; $F = 31.9$; $P < 0.001$) and monogamous females ($F = 16.1$; $P < 0.001$) differed significantly from all other classes. On average, males were away from the nest site 95% (456/480 minutes) of the time, monogamous females 73% (351/480), and the polyandrous female, 28% (135/480).

During 1989, time spend away from the nest site did not differ significantly between monogamous males and data were thus combined (see Chapter 4). The adjusted means (ANCOVA; $F = 52.8$; $P < 0.001$) and regression slopes ($F = 7.2$; $P < 0.01$) differed significantly between polyandrous and monogamous males and females (Fig. 5.1). The regression slope of monogamous females (ANCOVA; $F = 25.9$; $P < 0.001$) differed significantly from all other classes. On average, monogamous males spent 89% min. (429/480) away from the nest site, followed by monogamous females (61% or 291 min.), the beta male (53% or 252 min.), the alpha male (45% or 214 min.), and the polyandrous female (6% or 30 min.).

For both years, mean prey provisioning rates by monogamous and polyandrous males combined were closely correlated with nest site absence of their respective females ($r = -0.93$; $P < 0.10$; $n = 4$).

5.3.5 Nest predation

Nest predation was highest during 1988 and 1992, and at its lowest during 1989 and 1990 (Table 5.4). During 1991, when only three out of 29 groups bred, no predation was recorded. Of the 97 breeding attempts documented over five years (1988-1992), 16% (12/77) of the nests of monogamous pairs and only one (5%; 1/20) nest of a polyandrous trio were predated. Half of the nests (6/13) showed visual signs of nest lining or structured disturbance, often with traces of blood on the nest lining (GM pers. obs.), and were in most cases (77%; 10/13) from first broods (or single broods in years when only one brood was raised). The majority of chicks (67%; 8/12) were predated in the first half of the seven week nestling period. Offspring remains found below nests were all from large chicks.

Table 5.4 Alleged nest predation of Pale Chanting Goshawk eggs and chicks in five breeding seasons (1988-1992). Poly trio = polyandrous trio, Mono pair = monogamous pair.

Year	Status	Egg/ Chick	Numbers	Age (weeks)	Second successful brood per season	Nest lining/ structure disturbed	Remains on ground (5-7 weeks)
1988	Mono pair	Chick	2	1	No	Yes	
	Mono pair	Chick	1	3	No	No	
	Mono pair	Chick	1	6	No	No	Yes
	Mono pair	Egg	2		No	No	
	Mono pair	Chick	1	3	No	*No	
1989	Poly trio	Chick	2	1	Yes	No	
	Mono pair	Chick	1	2	Yes	No	
	Mono pair	Chick	1	6	No	No	Yes
1990	Mono pair	Chick	1	7	Yes	Yes	Yes
1991		No predation					
1992	Mono pair	Chick	2	5	No	Yes	Yes
	Mono pair	Chick	2	3	No	Yes	
	Mono pair	Chick	2	1	No	Yes	
	Mono pair	Chick	2	1	No	Yes	

* second chick still in nest

5.3.6 Fledgling body mass

There were no significant differences between the body mass of female fledglings from polyandrous trios (810 ± 44 g; n = 9) and monogamous pairs (790 ± 48 g; n = 31; $P > 0.05$; t test), nor did the body mass of male fledglings from polyandrous trios (648 ± 29 g; n = 4) and monogamous pairs differed (648 ± 46 g; n = 31; $P > 0.05$; t test).

5.3.7 Interspecific and intraspecific interactions

Of the 31 interspecific interactions observed in territories during the non-breeding and pre-laying periods, males were involved in 26 (84%) and were the aggressor in 25 of these (Table 5.5). Among polyandrous males, beta males were recorded in eight interactions and alpha males twice. Females were the aggressors in three out of five interactions. All intruders were chased approximately one hundred metre, except Blackshouldered Kites *Elanus caeruleus*, Jackal Buzzards *Buteo rufofuscus* and Whitenecked Ravens *Corvus albicollis* which were chased until they had left the territory. In SK, territorial interspecific interactions were observed at a rate of once every 311 min. (n = 5 595 min.) (Table 5.5). In KBV interactions were observed once every 599 min. by polyandrous breeders (n = 7 188 min.); and once every 175 min. by monogamous breeders (n = 349 min.).

Table 5.5 Interspecific interactions recorded in the non-breeding and pre-laying periods on 1988-1989. All intruders were mobbed. KBV = Karroid Broken veld, SK = Succulent Karoo. Asterisk indicate birds pursued to the border of the territory.

Aggressor	Vegetation type	Status	Aggressee
MALE			
PCG	KBV	Beta	*Blackshouldered Kite (4x) *Elanus caeruleus*
PCG	KBV	Alpha	Two Black Crows (2x) *Corvus capensis*
PCG	KBV	Beta	*Whitenecked Raven *Corvus albicollis*
PCG	KBV	Beta	*Jackal Buzzard (3x) *Buteo rufofuscus*
PCG	SK[1]	Monogamous	Two Black Crows (4x)
PCG	SK[1]	Monogamous	Black Harrier *Circus maurus*
PCG	SK[1]	Monogamous	Lanner Falcon *Falco biarmicus*
PCG	SK	Monogamous	*Blackshouldered Kite (6x)
PCG	SK	Monogamous	Rock Kestrel *Falco tinnunculus*
PCG	SK	Monogamous	Two Egyptian Geese *Alopochen aegyptiacus*
PCG	SK	Monogamous	Yellow Mongoose *Cynictis penicillata*
Two Black Crows	SK[1]	Monogamous	PCG
FEMALE			
PCG	KBV	Monogamous	Steppe Buzzard (2x) *Buteo buteo*
PCG	KBV	Polyandrous	*Blackshouldered Kite
Two Blackshouldered Kites	KBV	Polyandrous	PCG
Black Crow	SK[1]	Monogamous	PCG

1 Interactions recorded in SK territory on the border of KBV

Apart from two interactions, intraspecific interactions in the non-breeding season, were all between members of the same sex (Table 5.6). Males were involved in more aggressive interactions (cartwheel flights), as well as in more interactions (69%; 9/13). Males were significantly more involved in interactions on the border of territories, whereas females where also involved internally (P < 0.01; Fisher's Exact test). No intraspecific interactions were observed in SK, 13 in KBV and four in OSBV (Table 5.6). In KBV, during instantaneous and scan sampling of 1988-1989, an interaction was recorded once every 1 049 min. (n = 7 345 min.).

Overall, males and females shared equally in defending the nest contents when both sexes were present (Table 5.7). Males called in 50% (6/12) of interactions and females in 33% (5/15). Females were involved in physically striking the potential predator, all Yellow Mongooses *Cynictis penicillata*, in four instances. PCGs appeared 'nervous' (*e.g.* flying with continuous wingbeats) during interactions with Gymnogenes *Polyboroides typus* and Martial Eagles *Polemaetus bellicosus*. In one instance, a Martial Eagle was chased in turn by three consecutive groups as it flew along a drainage line which contained PCG nests with chicks. In a particularly aggressive interaction, a polyandrous trio attacked a terrestrial, but unidentified, animal. The female perching near the nest spotted the possible predator advancing down a drainage line and called (alarm call). The two males arrived almost instantaneously and all three birds started calling and diving at the animal in a continuing sequence. The predator was stopped 20 m from the nest, from where it was forced to follow a circular route round the nest and back into the drainage line. During the same observation period, the interaction was repeated from the opposite direction.

At nest sites in KBV, interactions were recorded once every 675 min. (n = 12 145 min.), once in 5 248 min. in SK and none in 1 440 min. in OSBV. Of the 18 interactions recorded in KBV, polyandrous and monogamous breeders were involved in nine each, although polyandrous breeders were involved once every 816 min. and monogamous breeders once every 533 min.

Table 5.6 Intraspecific interactions recorded in the non-breeding and pre-laying periods of 1988-1992. See text for explanations of interact modes. Birds in parenthesis present but did not participate in interaction. Asterisk indicate interactions recorded in casual observations. Poly = polyandrous, Mono = monogamous, KBV = Karroid Broken Veld and OSBV = Open Spekboomveld.

Aggressor (Vegetation type)	Interact mode	Aggressee	Internal or border interaction
MALES			
Beta male (KBV)	Fly mob	Mono male (2x)	Border
Alpha male (KBV)	Fly mob	Mono male and female	Border
Beta male (KBV)	Fly striking	Mono male (and female)	Border
Alpha male (KBV)	Spiral flight and call, cartwheel flight	Mono male	Border
Mono male* (KBV)	Spiral flight and call	Mono male (4x)	Border
Alpha & beta males* (KBV)	Spiral flight and call	Mono male	Border
Mono male* (OSBV)	Spiral flight and call	Mono male (2x)	Border
Mono male* (OSBV)	Spiral flight and call, cartwheel flight	Mono male (and female)	Border
FEMALES			
Poly female (KBV)	Fly mob	Non-breeder female (from poly trio)	Internal
Mono female* (KBV)	Fly mob	Non-breeder female (from mono pair)	Internal
Mono female (KBV)	Fly mob each other	Alpha male and female	Border
Mono female* (OSBV)	Fly mob	Mono female	Internal

Table 5.7 Interspecific and intraspecific interactions recorded at nest sites in breeding seasons of 1988-1989. See text for explanations of interact modes. Asterisk indicate birds pursued too the border of the territory. Poly = polyandrous, mono = monogamous, KBV = Karroid Broken Veld, SK = Succulent Karoo.

Aggressor (Vegetation type)	Interaction mode	Aggressee
<u>All breeders attack</u>		
Beta male and female (KBV)	Fly mob (and rob)	Booted Eagle (3x) *Hieraaetus pennatus*
Mono male and female (KBV)	Fly mob and call	*Martial eagle *Polemaetus bellicosus*
Poly males and female (KBV)	Fly diving at	Booted Eagle (2x)
Poly males and female (KBV)	Fly mob and call	Terrestrial predator (2x)
<u>Female attack, male(s) present</u>		
Mono female (KBV)	Fly mob	*Jackal Buzzard
Mono female (SK)	Fly striking and call	Yellow Mongoose *Cynictis penicillata*
Poly female (KBV)	Fly diving at	PCG female
<u>Male attack, female present</u>		
Alpha male (KBV)	Fly mob and call	*Gymnogene *Polyboroides typus*
Mono male (KBV)	Fly mob	Lanner Falcon
Mono male (KBV)	Fly mob and call	*Jackal Buzzard
Mono male (KBV)	Fly mob and call	Steppe Buzzard
<u>Female attack, male not present</u>		
Mono female (KBV)	Fly striking	Yellow Mongoose (2x)
Mono female (KBV)	Fly striking and call	Yellow Mongoose
Mono female (KBV)	Fly mob	*Jackal Buzzard

5.3.8 Territorial occupancy

Twenty-eight breeders were marked during the five years spent in the field. These birds were observed for 86.5 breeder years within their breeding territories, and no bird was ever seen in the territory of another group. No clear-cut differences were found in the spatial arrangement of proportional quadrat occupation by polyandrous males (Fig. 5.2). However, occupation per quadrat by both males did not exceed 10 and 14% for JohanG and 21 and 8% for Kruisrivier. Moreover, JohanG's beta male occupied quadrats at a higher proportion in the west of the territory and the alpha male in the east (Fig. 5.2). For Kruisrivier, the beta male occupied quadrats at a higher proportion in the south and the alpha male in the north.

JohanG

	B=6	A=8 B=10	A=14
B=4	B=15	A=10 B=14	
B=15	A=16	A=9 B=4	
B=1		B=21	A=3 B=10
		A=12	A=7
		A=3	A=18

Kruisrivier

	A=2		A=9 B=2
	A=8 B=6	A=14	B=1
	A=23 B=1	A=21 B=8	A=7 B=21
B=3	A=1 B=4	A=11	B=5
	B=17	A=4 B=12	B=21

Fig. 5.2 Proportional quadrat occupation by polyandrous alpha (A) and beta (B) males from two polyandrous trio territories. Values represent percentages.

5.4 DISCUSSION

5.4.1 Territorial defense

For territorial PCGs, males predominantly defended the territory against interspecific intruders. The chasing of Blackshouldered Kites and Jackal Buzzards to the border of territories was probably because both resident species share the PCG's predominantly rodent diet, and Blackshouldered Kites bred in the study area (Steyn 1982; GM pers. obs.). Other raptor species involved in interactions, *e.g.* Black Harrier *Circus maurus*, Lanner Falcon *Falco biarmicus* and Rock Kestrel *Falco tinnunculus*, also shared the PCG's diet, but to a lesser extend (Steyn 1982). Egyptian Geese *Alopochen aegyptiacus* frequently utilised PCG nests before and after being occupied by PCGs (GM pers. obs.) and were chased from nest sites. Against conspecifics, males were once again, involved in the highest frequency of interactions, but this time almost exclusively against other males. Interactions between territorial males were particularly aggressive since the majority involved spiral and cartwheel flights (*sensu* Simmons & Mendelsohn 1993). Since females, on the other hand, chased intruder females, and in two out of three cases non-breeders, they were preventing unpaired females from entering territories in KBV. Restricting your partner's access to additional mates is common in species that defend territories (Davies 1985). It was also in this vegetation type that polyandrous females thermalled significantly more. Thermalling behaviour can possibly be interpreted as having a display function (Newton 1986). A female thermalling to the periphery of human vision, as they often do (GM pers. obs.), should be visible to many surrounding groups and, in doing so during the pre-laying period, they could advertise territorial occupation. The nest construction and pre-laying prey provisioning of polyandrous males may have helped to release polyandrous females from these duties. This, in turn, may have allowed them time to advertise the occupation and defend the territory against other females.

During the non-breeding and pre-laying periods, interspecific interactions were recorded in more or less equal proportions in SK and KBV. However, since intraspecific interactions were recorded almost exclusively in KBV, it appears that resources, such as prey and nest sites, but also the possibility of acquiring a mate within this vegetation type was of particular importance to PCGs. Moreover, within KBV, the interspecific interaction frequency was lower for polyandrous compared with monogamous males. The inclination of polyandrous males to occupy different sections of a territory may have additional advantages in that each male only need to defend a sub-section. The conclusions can therefore be drawn that a co-breeding male actively defending a territory in KBV may have helped by lowering the interaction frequency per individual breeder.

5.4.2 Nest site defense

Since nest predation was never observed directly, it is not know which predator species were accountable. Whitenecked Ravens, for example, were treated with more aggression by PCGs than Black Crows *Corvus capensis*, probably because ravens are perceived as potential nest predators (Winterbottom 1975). Yellow Mongooses that were frequently and violently chased from near nest trees, have in fact not been reported as a tree climber or major bird eater (Smithers 1983). Caracal *Felis caracal*, Large-spotted Genet *Genetta tigrina* and African Wild Cat *Felis lybica*, all proficient climbers and bird eaters (Smithers 1983), were observed in the study area (GM pers. obs.). Since signs of a struggle were found in half the nests, some chicks and/or parents put up a struggle against predators. Nests that were predated without a visible struggle could have been from aerial predators lifting chicks out of a nest, or bird-eating snakes such as Boomslang *Dispholidus typus* (periodically observed near nest trees), quietly removing envenomated offspring. Larger chicks' remains discovered below nests could be the result of either chicks accidentally falling out of the nest and then being eaten, or flushed out of the nest during the predation act itself. Apart from the reasons why polyandrous females stayed at the nest site for longer periods (to be discussed below), the larger sex would be more capable of physically defending the nest contents. It is noteworthy that the majority of nests were predated during the first three weeks of the nestling period, the period when the female still spent the largest proportion of her time at the nest site brooding hatchlings. Some nest predators that are sufficient in skill and size may therefore prey on nestlings, irrespective of the presence of any number of breeders.

In Chapter 3 I demonstrated that the predation of eggs or chicks was the major cause of nest failures (including siblicide) at four PCG study areas (33%; 26/78), including the Calitzdorp study area (33%; 20/61) (Table 3.7). At Calitzdorp, predation was at its highest during 1988 and 1992, years of intermediate PCG reproductive success (Table 3.7). During years with high reproduction, 1989 and 1990, only one out of 49 groups did not breed and 16 groups laid a second clutch (See Chapter 3), only four cases of predation were recorded. Since both 1988 and 1992 were preceded by below average rainfall years (1987 = 102.5 mm; 1991 = 120.8 mm; mean = 198.8 mm), it may be that predators switch to alternative prey (PCG chicks) in years when their general prey numbers decrease because of low rainfall. Evidence is provided by the fact that mostly first broods were predated. One would expect second broods to be predated given that breeders then not only have to provision hatchlings, but also fledglings, and would probably leave nest sites for longer periods to hunt. Ironically, nest guarding may only be required in years of intermediate and low PCG reproduction and prey abundance, when potential predators switch to 'alternative' prey such as PCG nestlings and 'nest guarding' females are more likely to leave the nest site to hunt.

Apart from the advantage of having a female guarding the nest site, the female may alert male(s) to assist in nest defense, a strategy clearly demonstrated by one polyandrous trio. This is also the case in the Stripe-backed Wren *Campylorhynchus nuchalis*, where groups of 2-3 adults suffer 79% nest failures and larger groups, 32% (Rabenold 1990). Whereas large groups were able to scold predators and attract up to 30 individuals of different species to join in the attack, the desultory scolding of small groups seldom attracted other species. Likewise, Mumme (1992a) found that groups of Florida Scrub Jays *Aphelocoma c. coerulescens* with one to four helpers suffered lower nestling predation (33%) than groups whose helpers were removed (63%). During PCG nestling periods, interspecific interactions were recorded almost exclusively in KBV, and again the interaction frequency was lower for polyandrous compared to monogamous breeders. The co-breeding male may therefore help by defending on request and by easing the defense load of polyandrous breeders.

5.4.3 Prey provisioning

In the breeding season, a clear division in parental duties was found between the sexes. Males built the nests, provisioned the females during the pre-laying period, and were predominant in provisioning prey to nest site during the nestling period. Females, on the other hand, incubated (Chapter 4), attended the nest, and brooded, fed, guarded and defended nestlings. During 1988, polyandrous females spent more time on nest activities (restructuring the rim and cleaning the nest lining; GM unpubl. data). This behaviour may prevent the nest from collapsing and spilling its contents, or ectoparasites to establish in prey remains (see Malan 1992). Although I did not calculate the energy expenditure of the above parental duties, it can be argued that duties males preformed, such as prey provisioning that involved hunting and flying, were energetically more expensive than incubation, brooding and guarding nestlings. However, this largely inactive period in the annual life-cycle of females changed when the prey needs of the growing young necessitated spending more time away from the nest during the later stages of the nestling period (Newton 1979). In this respect, for groups studied, the probable energy expenditure of monogamous females exceeded that of polyandrous females since polyandrous females remained at the nest site for longer periods. The double-brooding polyandrous female, studied during 1989, had probably an even lower energy expenditure in that she (that weighed 1 040 g; GM unpubl. data), over a period of 60 days, spent on average 94% of her time within a 100 m radius circle from the nest.

Male provisioning rates of 0.14-0.20 per hour, combined with that of the female, appeared to satisfy the prey needs of the growing young. Surprisingly, polyandrous offspring weighed no more than those of monogamous offspring, as is often the case in cooperative *vs* monogamous breeders (see Davies 1985; Mumme 1992a, but also du Plessis 1991 and references therein). A second objective of prey provisioning would be to retain the female at the nest site to guard nestlings. Since provisioning rates by males were linked directly to the presence of females at the nest site, male prey provisioning was pivotal in this respect. A male provisioning rate of 0.39 per hour and higher fulfilled this requirement. It is noteworthy that, at these provisioning rates, females as well as males were feeding on prey not fed to offspring (see Table 4.10). A third objective would be to provide at a rate sufficient for the female to accumulate body reserves (Newton 1979) for a second breeding attempt directly after the first. To achieve this objective, a provisioning rate of 0.90 per hour was sufficient. At this rate, the polyandrous female was almost totally relieved of hunting duties away from the nest site. The energy saved and body reserves accumulated could then be channeled into laying a second clutch directly after fledging the first brood.

As suggested in Chapter 7, the higher provisioning rate for 1989 could be attributed directly to prey abundance. The double-brooding could therefore not only be attributed to the help of a co-breeder *per se* but also to the quality of the habitat (Lennartz *et al.* 1987). Walters (1990) has shown that for of Red-cockaded Woodpeckers *Picoides borealis*, when the quality of the habitat was controlled for, the relationship between the help provided by helpers and reproductive success no longer existed. Alternatively, for White-fronted Bee-eaters *Merops bullockoides* Emlen & Wrege (1991) found that, when environmental conditions were controlled for, the provisions by additional individuals still greatly increased fledgling success. Some evidence of the influence of prey abundance on prey provisioning rates and reproduction is found in the fact that, during 1989, the double-brooding polyandrous males spent significantly more time than single-brooding monogamous males hunting in the immediate vicinity of the nest site.

Even if the influence of male provisioning rates on reproduction was overshadowed by prey availability, polyandrous males helped, by provisioning at an equal rate, for polyandrous trios to attempt a second breeding attempt under favourable conditions. Alpha males played an important role in reproduction in that they did not decrease their provisioning rate in the presence of other individuals helping, as often the case with dominant breeders (Brown & Brown 1981; du Plessis 1991). The reproductive effort of two polyandrous males thus enabled polyandrous females and alpha males to increase their reproductive success, and hence inclusive fitness. The help provided by beta males, mainly in the form of prey provisioned to breeders at nest sites, enabled polyandrous trios to increase their reproductive success. There is thus evidence that beta males, if related to alpha males, gained at least indirect reproductive fitness benefits from helping. If they would father some offspring they would also gain direct fitness benefits (Chapter 4). An additional benefit of the help provided by co-breeders is the strategy of reduced parental effort on the residual reproductive value and longevity of the breeders (Brown *et al.* 1978; Rabenold 1990; Clutton-Brock & Godfray 1991). This may especially be true for females, and more so polyandrous females, in that the lower interaction frequency and energy expenditure may increase their survivorship and lifetime fitness.

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SECTION 2

POPULATION ECOLOGY

CHAPTER 6

POPULATION DENSITY IN COOPERATIVE-BREEDING PALE CHANTING GOSHAWKS: A BENEFIT OR CONSTRAINT THAT PROVIDES THE PRIMARY IMPETUS TO DELAY DISPERSAL

SUMMARY

According to Koenig *et al.* (1992) relative population density could be the primary factor distinguishing the conditions leading to delayed dispersal and cooperative breeding. Density indices, territorial coverage and group sizes were therefore investigated for Pale Chanting Goshawks (PCG) in three vegetation types at Calitzdorp and between Calitzdorp and three other PCG study areas (Claratal, Rooipoort and Kalahari Gemsbok National Park). Roadcounts of all study areas were correlated to nearest neighbour distances, and were therefore directly representative of PCG breeding densities. At Calitzdorp, the roadcount (2.1 km/bird) and PCG densities (0.71-1.01 km^2/bird) observed in Karroid Broken Veld (KBV) and Open Spekboomveld (OSBV) vegetation types are among the highest recorded for single raptor species in the Afrotropics. Territorial space, acting as an extrinsic constraint, was limited in both KBV and OSBV. It is suggested that the observed PCG densities are close to the upper limit of density for this species and that territoriality may have prevented densities from increasing further. However, densities of PCGs overall and breeding PCGs did not differ between KBV and OSBV but, within KBV, groups were larger and polyandrous groups even larger due to the presence of a co-breeder. These results suggests that intrinsic benefits, and not only the lack of territorial space, may be the primary factors leading to delayed dispersal in the PCG.

6.1 INTRODUCTION

The intensity and configuration of cooperative breeding and delayed dispersal recorded in various bird populations, or even in closely related species, has been noted to correlate with differences in population density (Koenig & Mumme 1987; Stacey & Koenig 1990; Komdeur *et al.* 1991). Koenig *et al.* (1992) stated that "relative population density could be the primary factor distinguishing the conditions leading to cooperative breeding". Density itself may be manifested in many forms within a population. At one extreme, birds could be present or absent from a given area. For example, when the cooperatively breeding Seychelles Warbler *Acrocephalus sechellensis* was introduced to the uninhabited Aride island, they bred monogamously and young dispersed (Komdeur *et al.* 1991, 1991, 1992). At the other extreme, if the density increases, a situation is reached where all suitable habitat is occupied by territorial breeders, *i.e.* the 'habitat saturation' point (Brown 1969a, 1987b). However, various authors have stressed that a situation rarely exists where no suitable habitat is available (see Stacey & Ligon 1991). Therefore, rather than habitat saturation, one must examine the options of offspring in habitats of varying quality (Koenig & Pitelka 1981).

The aims of this chapter are firstly to: (1) examine and compare population density indices such as nearest neighbour distance and roadcount densities between Calitzdorp and three other PCG study areas, and to (2) compare density indices such as the availability of territorial space and group sizes between monogamous groups from three vegetation types, and polyandrous groups from one vegetation type at Calitzdorp.

6.2 METHODS

6.2.1 Study areas

At the Calitzdorp study area, PCGs occur in three major vegetation types, OSBV, KBV and Succulent Karoo (SK). To place the Calitzdorp study population in perspective it was compared with populations from Claratal, the Kalahari Gemsbok National Park (KGNP) and Rooipoort study areas (see Chapter 2).

6.2.2 Roadcount densities

At the Calitzdorp study area and surroundings, roadcounts were taken to be an index of relative density of PCGs. These were carried out along the 14 km asphalt road running through the study area and for 30 km outside the study area towards Oudtshoorn. The total length of this road runs through KBV. Forty-seven counts were carried out between March 1988 and April 1989. In addition, comparative roadcounts were carried out in the KGNP, inside and outside Rooipoort, and elsewhere in the Northern Cape Province. The literature was searched for comparative single and multi-species roadcount data for the Afrotropics.

6.2.3 Nearest neighbour distances

I calculated nearest neighbour distance (Boshoff 1988; Boshoff & Palmer 1988) for all four study areas. At Calitzdorp, Rooipoort and Claratal the distance to the nearest neighbour's nest site, as an index of nearest neighbour distances, was measured by plotting the nest sites on 1:50 000 scale maps. At Calitzdorp, the distance to the nearest neighbour's nest was measured irrespective of the vegetation type (*i.e.* the nearest neighbour could be breeding in a different vegetation type). Only nests from groups that bred actively were included and, if more than one nest was used per season, the distance to a central point between nests was measured. In OSBV and KBV at Calitzdorp, nesting sites were freely available, but not so in SK. In the KGNP, 29 groups were studied between 1988 and 1990, all of which nested in or in the immediate vicinity of the Nossob River bed. As nest sites for only four groups were known, I plotted trap positions (the position a bird was trapped with a bal-chatri) on 1:50 000 scale maps and, for each group, calculated a trap point (*i.e.* the centre point where all members were trapped). Since nearest nest distances were significantly correlated with inter-trap distances ($r = 0.99$; $n = 4$; $P < 0.001$), I used inter-trap distance data as an index of nearest neighbour distances for KGNP. Nearest neighbour distances for Claratal, KBV (vegetation type the asphalt road runs through) from Calitzdorp, Rooipoort and the KGNP were tested for correlation with roadcount data from the same areas and corresponding time periods.

6.2.4 Density indices

At Calitzdorp, 51 visits to nest sites were carried out during the breeding seasons of 1988-1992 (see Chapter 3). During each visit, the presence of a breeder and/or co-breeder was noted. The presence of non-breeders and juveniles was recorded *en route* between nest sites and during nest site visits. Roughly the same route was followed each year, but no special effort was made to search each territory systematically. Nest sites were visited irregularly at other study areas and, only at the KGNP, was the presence of additional breeders and non-breeders not investigated.

6.2.5 Territory sizes at Calitzdorp

At Calitzdorp, PCGs were marked with individual colour ring combinations (see Chapter 2). To determine territorial size, positions of group members were recorded during instantaneous sampling (see Chapter 4) and plotted on a 1:50 000 scale map. Seven PCG groups were observed for 12 677 minutes during the non-breeding and pre-laying periods of 1988 (mean = 1 811 min.; range 349-3 190 min.). In addition, during all travels in the study area, I searched for marked individuals and plotted their positions. To calculate territory sizes, data for members of each group were combined and each outlier point was linked to its nearest outlier point and a Minimum Convex Polygon drawn by hand (Stahlecker & Smith 1993). The study area was also searched for areas unoccupied by PCGs and areas occupied by other raptor species.

To calculate group densities, I divided the number of groups recorded in each vegetation type by the vegetation type size. I also calculated breeder (breeder and co-breeder), adult (breeder, co-breeder and non-breeder), and PCG (breeder, co-breeder, non-breeder and juvenile) densities for each vegetation type. The number of birds in each category was divided by either the recorded or estimated territory size (see below), and an analysis of variance was performed to test for differences in densities in each vegetation type. Since the presence of polyandrous trios at Calitzdorp was recorded only in KBV, the density and group size variables were only compared between polyandrous and monogamous groups from this vegetation type.

6.2.6 Territory coverage at Calitzdorp

Territory coverage, *i.e.* the surface areas for all territories within a vegetation type combined divided by the surface area of the vegetation type, was calculated for each vegetation type at Calitzdorp, and was used as an index of habitat saturation. During 1988, the territorial behaviour of all three groups in SK was studied, as well as known nest site positions, and territorial coverage could be calculated directly. During 1988 the nest sites of only seven groups in KBV were searched for but, during 1989, I searched this vegetation type in total and discovered the nest sites of 16 groups. However, due to the fact that I only studied the behaviour of groups with marked birds, the territorial behaviour of only four of these groups was studied. I therefore correlated nearest neighbour distances with territory size ($n = 4$; $r = 0.96$; $P < 0.05$) and estimated territory sizes for the remainder 14 groups using the regression formula $Y = -0.055 + 0.002X$ (X = nearest neighbour distance in m; Y = territory size in km^2). Territorial behaviour was not studied in OSBV. I made the assumption that a linear relationship between nearest neighbour distance and territory size also existed in OSBV and, using the above formula, during 1989, estimated territory sizes for four groups that were present in this vegetation type.

6.3 RESULTS

6.3.1 Roadcounts and raptor densities

Roadcount densities were more than twice as high inside the Calitzdorp study area than outside and far higher than other areas (Table 6.1). Roadcount densities for Claratal, KBV at Calitzdorp, Rooipoort and the KGNP were significantly positively correlated with nearest neighbour distances ($r = 0.97$; $n = 4$; $P = 0.03$). Calitzdorp roadcount densities exceeded that of the single and all species densities in the Afrotropics, except for the Whitebacked

Vultures *Gyps africanus* from Uganda (Table 6.2). Group densities of 4.39-8.60 km^2/group compared favourably with densities of pairs in areas of reputedly high raptor densities (Table 6.2).

Table 6.1 Comparative roadcount data for Pale Chanting Goshawks from southern Africa.

Locality	km/bird	Source
Study area (1988-1989)	2.1	
Outside study area (1988-1989)	5.6	
Kalahari Gemsbok National Park (1988)	13.7	
Kalahari Gemsbok National Park (1974-1980)	13.0	Liversidge (1984)
Outside Kalahari Gemsbok National Park (1974-1980)	38.9	Liversidge (1984)
Northern Cape Province (1988)	58	
Rooipoort (1990)	28	
Outside Rooipoort (1990)	19	
Northern Karoo (1950)	217	Rudebeck *in* Brown 1970
Northern Cape Province (1965)	172	Cade (1969)
Central Namibia (1977-1981)	34	Biggs *et al.* (1981)

6.3.2 Nearest neighbour distances

Nearest neighbour distances differed significantly between the study areas (Table 6.3) with Calitzdorp nearest neighbour distances being significantly lower than those at Claratal and Rooipoort. At Calitzdorp, nearest neighbour distances differed significantly between vegetation types (Table 6.4), but not between polyandrous trios and monogamous pairs in KBV (Table 6.5).

Table 6.2 Comparative roadcounts for single- and all-species raptor densities from the Afrotropics. KGNP = Kalahari Gemsbok National Park.

Category	Locality	Density	Source
ROADCOUNTS			
Single species			
Whitebacked Vulture *Gyps africanus*	Uganda national parks	1.1-4.5 km/bird	Thiollay (1978)
Eastern Chanting Goshawk *Melierax poliopterus*	Tsavo East National Park	27 km/bird	Smeenk (1974)
All species			
All species	Uganda national parks	0.4-0.8 km/bird	Thiollay (1978)
All species	East African rangelands	5 km/bird	Brown 1970
All species	KGNP	6 km/bird	Brown 1970
All species	Tsavo East National Park	7 km/bird	Smeenk 1974
All species	Kruger National Park	15 km/bird	Brown 1970
PAIR DENSITY			
Eastern Chanting Goshawk	Tsavo East National Park	1.7-2.0 km^2/pair	Brown *et al.* 1982
All species	Matopo Hills	1.5-2.8 km^2/pair	Gargett 1990
Eagles and buzzards	Kruger National Park	5 km^2/pair	C.J. Vernon *in* Gargett 1990

Table 6.3 An analysis of nearest neighbour distances (NND) and the presence of additional adults at four Pale Chanting Goshawk study areas in southern Africa. Means ($\pm$ 1 standard deviation), KGNP = Kalahari Gemsbok National Park. 1 = Calitzdorp *vs* Rooipoort; 2 = Rooipoort *vs* Claratal; 3 = Claratal *vs* KGNP; 4 = Calitzdorp *vs* Claratal; 5 = Rooipoort *vs* KGNP; 6 = Calitzdorp *vs* KGNP; NS = Not significant, * = $P < 0.05$; ** = $P < 0.01$; pairwise *t* tests.

	Calitzdorp	Rooipoort	Claratal	KGNP	ANOVA
Groups studied	77	6	9	29	
NND (m)	1 813 (927) *^{1} **^{4} NS^{6}	3 734 (1 179) NS^{2} NS^{5}	3 594 (1 125) NS^{3}	2 638 (1 494)	$P < 0.05$
Additional adults present	Yes	No	Seldom	Yes	

Table 6.4 An analysis of nearest neighbour distances (NND) and density indices (mean ± 1 standard deviation) calculated over a five year period (1988-1992) for the three vegetation types, Open Spekboomveld (OSBV), Karroid Broken Veld (KBV) and Succulent Karoo (SK). Group, breeder, adult and PCG density estimates are presented for 1989, the first year when the study area was searched for all groups. Mean (± 1 standard deviation); 1 = OSBV *vs* KBV; 2 = KBV *vs* SK; 3 = OSBV *vs* SK: NS = Not significant; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$; pairwise t tests.

Vegetation types	OSBV	KBV	SK	ANOVA
NND (m)	1154 (421) **1 **3	1684 (530) *2	2888 (1437)	P < 0.001
(n)	(13)	(50)	(14)	
Vegetation type area (km^2)	14.75	66.50	45.25	
Territorial area (km^2)	17.56	76.42	25.81	
Territorial coverage (vegetation type/territorial area)	119%	115%	57%	
Groups resident in 1989	4	16	3	
Group density (km^2/group)	4.39	4.77	8.60	
Breeder density (km^2/bird)	1.43 (0.43) NS ***	1.85 (0.43) ***	3.10 (0.61)	P < 0.001
Adult density (km^2/bird)	0.98 (0.09) NS ***	1.54 (0.57) **	2.68 (0.13)	P < 0.001
PCG density (km^2/bird)	0.71 (0.01) NS NS	1.01 (0.49) NS	1.58 (0.23)	P < 0.05
Group years	22	80	15	
Non-breeders per group	0.46 (0.74)	0.74 (0.76)	0.53 (0.64)	NS
Adults per group	2.46 (0.74) * NS	2.94 (0.86) NS	2.53 (0.64)	P < 0.05
PCGs per group	3.27 (1.24) * NS	4.13 (1.44) NS	3.40 (1.12)	P < 0.05

Table 6.5 An analysis of nearest neighbour distances (NND), density indices and group size estimates calculated over a five year period (1988-1992) for polyandrous and monogamous groups in Karroid Broken Veld (KBV). Group, breeder, adult and PCG density estimates are presented for 1989, the first year when the study area was searched for all groups. Mean (± 1 standard deviation); NS = Not significant.

Vegetation types	Polyandrous groups	Monogamous groups	t test
NND (m) (n)	1886 (456) (11)	1630 (537) (39)	NS
Group years	5	11	
Breeder density (km^2/bird)	1.63 (0.27)	1.95 (0.46)	NS
Adult density (km^2/bird)	1.36 (0.46)	1.61 (0.61)	NS
PCG density (km^2/bird)	0.80 (0.40)	1.07 (0.54)	NS
Group years	16	64	
Non-breeders per group	0.75 (0.78)	0.73 (0.76)	NS
Adults per group	3.75 (0.78)	2.73 (0.76)	$P < 0.001$
PCGs per group	5.38 (1.63)	3.81 (1.21)	$P < 0.001$

6.3.3 Territory sizes

At Calitzdorp, recorded territory sizes in KBV ranged from 3.6-4.5 km^2, all smaller than the 7.6-11.0 km^2 in SK (Table 6.6). Average territory sizes (recorded and estimated) differed significantly between vegetation types ($P < 0.001$, $n = 23$; ANOVA), but were not significantly different between SK, KBV and OSBV (all $P > 0.05$; pairwise t tests). Territories were largest in SK (8.0 ± 2.8 km^2), intermediate in KBV (4.3 ± 1.0) and the smallest in OSBV (2.9 ± 0.7).

Table 6.6 Territory sizes recorded for seven groups at Calitzdorp in 1988.

Vegetation type No. Name	km²
Karroid Broken Veld	
4 Okkies	3.9
5 JohanG	4.5
7 Cutting	3.6
21 Kruisrivier	4.1
Succulent Karoo	
10 Engelskamp	5.5
26 Badsaf	7.6
27 Remhog	11.0

6.3.4 Relative densities

Group densities in KBV and OSBV were almost double those in SK (Table 6.4). Breeder, adult and PCG densities differed significantly between vegetation types (Table 6.4). In KBV, all density indices were consistently higher for polyandrous groups, albeit not significantly (Table 6.5).

6.3.5 Territorial coverage

Territorial coverage was 57% in SK with large unoccupied areas surrounding the territories (Fig. 6.1). In KBV and OSBV, the territorial coverage was 115% and 119% respectively (Table 6.4; Fig. 6.1). In KBV, the estimated territorial boundaries were not limited to that vegetation type or to the borders of the study area. In KBV, three unstudied PCG groups existed, and in OSBV only one. In addition, in KBV, Jackal Buzzards and Blackshouldered Kites occupied areas and there was even one unoccupied area.

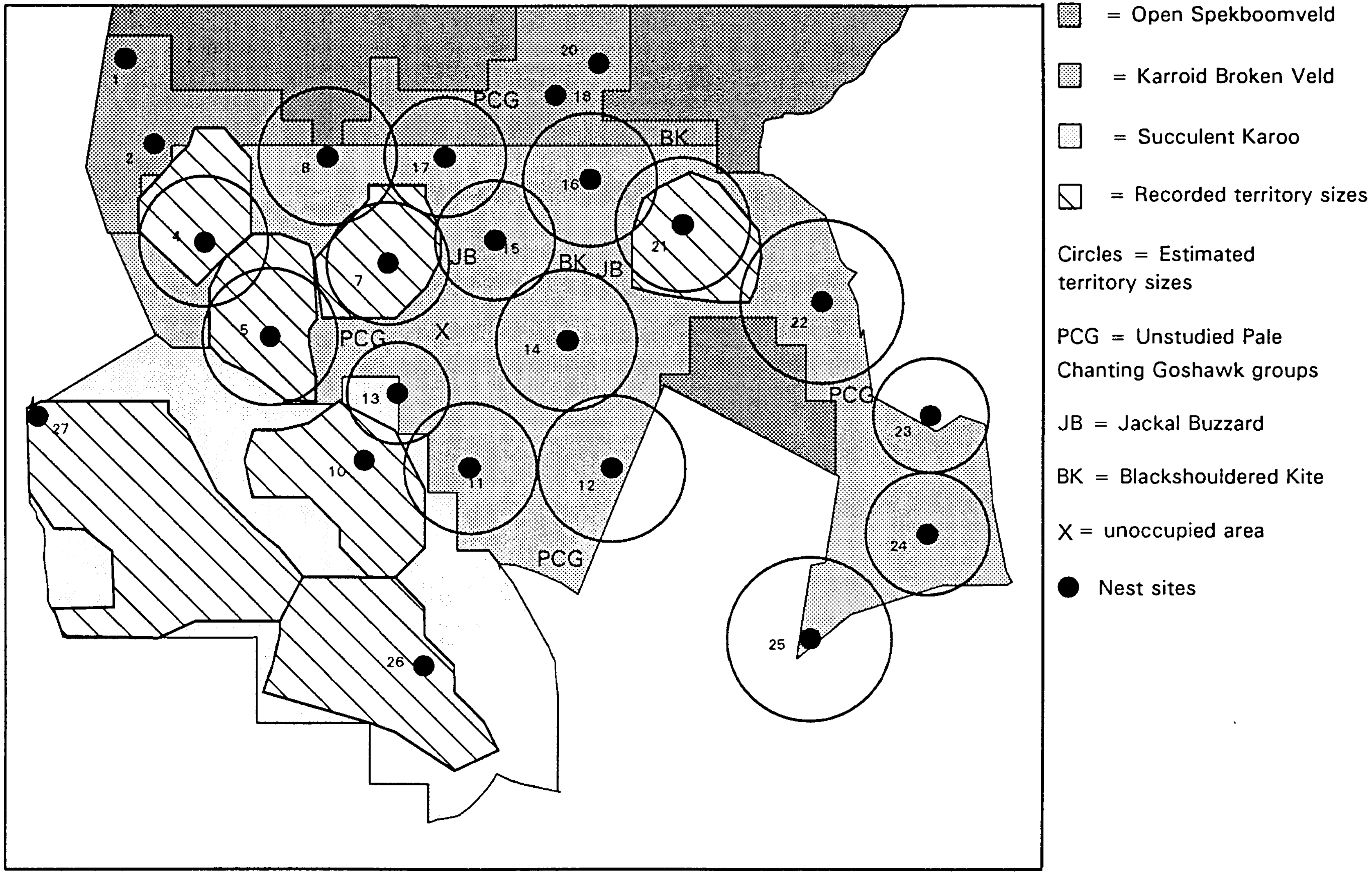

Table 6.1 Recorded Pale Chanting Goshawk territory sizes (cross hatch) and estimated territory sizes (circles), nest sites during 1989, groups not studied, areas occupied by other raptor species and unoccupied areas.

6.3.6 Group demography

At Rooipoort and Claratal, there were never more than two breeders, whereas additional adults were present at Calitzdorp and the KGNP (Table 6.3). In the KGNP, two adult males and females were caught in close proximity over eight months and, in a second case, two adult males and a female over 12 months (J.J. Herholdt in litt.). However, since this population was non-marked, one unmarked bird could have been replaced by another.

At Calitzdorp, group sizes varied from two to nine birds (Fig. 6.2). Group sizes differed significantly between vegetation types (Table 6.4) and between polyandrous and monogamous groups in KBV (Table 6.5). The most frequently recorded group size in OSBV was two birds, three in SK, four for monogamous groups and five for polyandrous groups, both in KBV (Fig. 6.2).

At Calitzdorp, the number of non-breeders per group ranged from zero to two (Table 6.7), and numbers did not differ significantly between vegetation types (Table 6.4) or between polyandrous groups and monogamous groups in KBV (Table 6.5). Non-breeders were recorded within 50% (59/117) of the groups (Table 6.7). Thirty-two percent of groups (7/22) in OSBV had non-breeders, 56% (45/80) in KBV and 47% (7/15) in SK (Table 6.7), but frequencies did not differ significantly (Chi-square; $P > 0.05$). In KBV, 56% of both polyandrous and monogamous groups had non-breeders in their groups (9/16 and 36/64 respectively).

Table 6.7 Pale Chanting Goshawk monogamous and polyandrous groups (**in bold and underlined**) studied at Calitzdorp from 1988 to 1992, including information on the vegetation types they nested in, the number of offspring fledged per group. Values for non-breeders in brackets, the number indicate the number of non-breeders.

Vegetation type No.	Group	1988	1989	1990	1991	1992
Open Spekboomveld						
1	Nellis		1 (2)	2	0 (1)	0
2	1stKloof	0 (2)	1 (2)	3 (1)	0	0
3	2ndKloof			1	0	
18	KweekK		1			
19	Unknown			1 (1)	0	2
20	Erenst		1	0	0	0
28	BoKuile			2	1	2 (1)
Karroid Broken Veld						
4	Okkies	**1 (2)**	**4 (2)**	**3 (1)**	**0 (2)**	0 (1)
5	JohanG	**0 (1)**	**2**	**2 (1)**	0 (2)	0 (1)
6	Ridge			4	0	0
7	Cutting	1 (1)	2	2 (1)	0	**0**
8	Kraal	2 (1)	2 (1)	2	0 (2)	2
9	DGates			**1**	**0**	1
11	Vlakte		1	1 (1)	0 (1)	2
12	Zwartkop		**2**	**3 (1)**	**4**	0 (1)
13	Bloubosvlei	0 (1)	2 (1)	2 (2)	0 (1)	0 (1)
14	AndriesK		**2 (1)**	0 (2)	0	0
15	TarRoad		2 (1)	2	0	2 (1)
16	Secretary		2 (1)	3 (2)	0 (2)	2 (2)
17	Kuile		1		1	0 (2)
21	Kruisrivier	**1 (1)**	0	2	1 (1)	0 (2)
22	Rietfontein		1	2	0	0
23	Vleirivier		2 (1)	2 (1)	0 (1)	2 (2)
24	BaasF		2 (1)	2	0 (2)	2
25	Saayman		**1**	1 (1)	0 (1)	2
29	Pickniks				0	2 (1)
30	BoOkkies					1
31	ErnieF				2	2 (2)
Succulent Karoo						
10	Engelskamp	0	2	3 (1)	0 (2)	0
26	Badsaf	1	2 (1)	1 (1)	0 (1)	0 (1)
27	Remhog	0	1	1	0 (1)	2

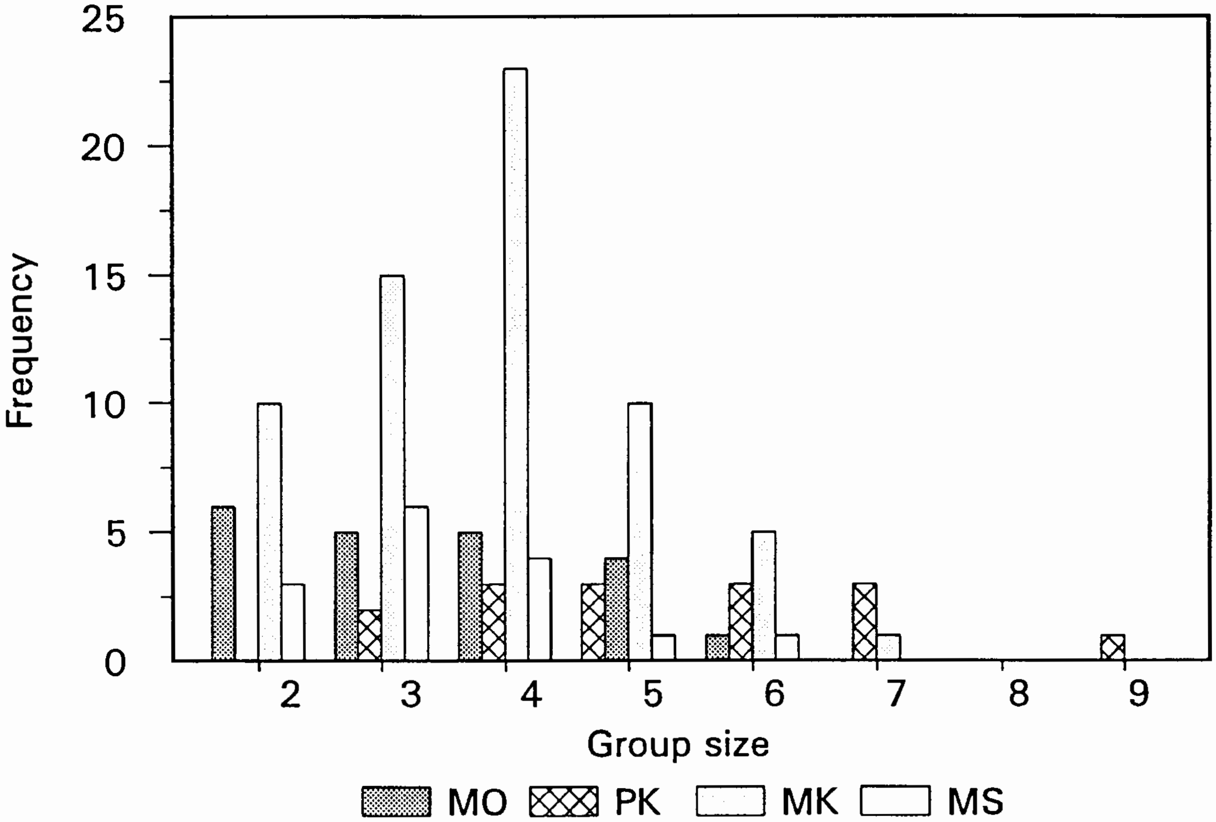

Fig. 6.2 Pale Chanting Goshawk group sizes from different status-vegetation type groupings at Calitzdorp. MO = Monogamous group-Open Spekboomveld, PK = Polyandrous group-Karroid Broken Veld, MK = Monogamous group-Karroid Broken Veld, and MS = Monogamous group-Succulent Karoo.

6.4 DISCUSSION

6.4.1 Pale Chanting Goshawk densities

The PCG's habit of perching on top of trees, shrubs and poles make it one of the easiest raptorial species to observe and record (Steyn 1982). Therefore, their high visibility and preference for open habitat (Steyn 1982) produced roadcount data that were directly representative of PCG nearest neighbour distances. Roadcount densities were not an underestimate as for example the Eastern Chanting Goshawk *M. poliopterus* in the substantial denser savanna of the Tsavo East National Park (27 km/bird *vs* 1.7-2.0 km^2/pair; Table 6.2). Although counted over a relative short distance (14 km) and probably at a greater intensity, KBV roadcount density of 2.1 km/bird by far exceeded that of all other PCG roadcounts, and also compared favourably with other species roadcount data. I cannot explain the higher roadcount density inside, compared with outside the Calitzdorp study area, except that the soil outside appeared more rocky, possibly resulting in lower prey production. It should be kept in mind that, in the Calitzdorp study area, PCGs are by far the dominant resident raptor, almost a 'monoculture', whereas at the other localities interspecific territorial behaviour might spatially separate species.

Nearest neighbour distances decreased from Rooipoort to Calitzdorp, and at Calitzdorp from SK to KBV and OSBV vegetation types. Average PCG densities of 0.71-1.01 km^2/bird compared favorably with Eastern Chanting Goshawk (1.7-2.0 km^2/pair) and even for all raptors densities in the Matopo Hills (1.5-2.8 km^2/pair), an area renowned for its raptor density (see Gargett 1990). Based on data presented here, the Calitzdorp study area, and especially areas of KBV and OSBV, contain not only the highest known density of PCGs, but also some of the highest recorded single-species raptor densities in the Afrotropics. Overall density indices point to the fact that the Calitzdorp study area contains some prime PCG habitat.

6.4.2 Intrinsic benefits and extrinsic constraints

Koenig *et al.* (1992) and Emlen (1994) proposed that one should examine intrinsic benefits and extrinsic constraints leading to delayed dispersal. Birds may delay dispersal because they gain intrinsic benefits, socially derived benefits such as indirect fitness from helping close relatives, lower predation, development of a skill or participation in a critical foraging strategy (Rabenold 1984; Bednarz 1988; Heinsohn 1991; Stacey & Ligon 1991). Alternatively, extrinsic constraints, normally ecologically derived, such as a lack of breeding territories or partners, or some critical recourse such as nest cavities may force them to delay dispersal (Koenig & Pitelka 1981; Faaborg & Bednarz 1990; Emlen 1991; du Plessis 1992; Emlen 1994). Recently Koenig *et al.* (1992) introduced their delayed-dispersal threshold model. It takes into account the fitness of different dispersal strategies in relation to territory quality. It essentially compares, in territories of varying quality, the cost of delayed dispersal (the reproductive success associated with delaying dispersal) with the loss of fitness reproducing in a poor quality territory (Emlen 1994). According to this model, population density may promote delayed dispersal in two different ways. If extrinsic constraints provide the proximate impetus and all the high-quality territories are occupied, offspring would experience higher fitness if they remain in the natal territory. If intrinsic benefits provide the impetus, living in groups will yield higher fitness and the density will have little impact on individuals that delay dispersal. However, "density will influence group size since, as density increases, individuals will continue to delay dispersal and group size will increase until the intrinsic benefits to those remaining no longer outweigh the cost". At this point, other factors such as the variability of resources come into play (Koenig *et al.* 1992).

6.4.3 Lack of territorial space - an extrinsic constraint

The territorial coverage analysis revealed that, in SK, large unoccupied areas existed whereas, in KBV, on face value, no territorial space was available. The KBV result however is an overestimate since: (1) territories of three groups were not included in the analysis, (2) estimated territory sizes (circles) included areas from outside the study area and the two surrounding vegetation types, (3) PCGs were strictly territorial (Chapter 5) and estimated territories boundaries (circles) showed some degree of overlap between neighbouring groups, (4) at least one area existed which was not unoccupied by PCGs, and (5) some areas were occupied by other resident diurnal raptor, and perhaps even nocturnal species. The same reasons can be listed for territorial coverage in OSBV, although PCG territorial behaviour was not studied in this vegetation type. The higher territorial coverage estimate for OSBV, compared with KBV, was probably the result of the existence of pockets of OSBV in Closed Spekboomveld (no PCGs). Since the dominant vegetation type per quadrat (500x500 m) was assigned to each quadrat (see Chapter 2), the actual OSBV area compared may have been an underestimate. Therefore, in view of reasons listed, it appears that territorial space was limiting in KBV and OSBV.

The question of why offspring do not disperse to the large 19.44 km^2 area unoccupied in SK needs to be addressed. In addition, the density of PCGs outside the study area was more than twice as low, and PCG densities were substantially lower in other regions of southern Africa. If the lack of territorial space, as an extrinsic constraint, provides the proximal impetus to delay dispersal, all high-quality and even lower quality habitats would have been occupied (Koenig *et al.* 1992). Furthermore, if there is a relationship between fitness and habitat quality, as assumed by the delayed-dispersal threshold model (Koenig *et al.* 1992), then territories in KBV and OSBV would be of higher quality, especially KBV with its higher PCG reproductive success. Moreover, Koenig *et al.* (1992) stated that a lack of territorial space "does not cause delayed dispersal and cooperative breeding, but is an important factor influencing the probability of these phenomena by affecting the expected fitness of individuals that disperse and breed in the best availability territory". The lack of territorial space could be the result, not the cause of delayed dispersal. Stacey & Koenig (1987) argued that the competition for space is the outcome of factors that causes delayed dispersal, and not the result thereof. If so, intrinsic benefits govern the decision and thus provide the proximate impetus to delay dispersal.

6.4.4 Group size - regulated by an intrinsic benefit

To gain intrinsic benefits, one can expect birds to converge into larger groups (Bednarz 1988; Stacey & Ligon 1991). Group sizes increased from OSBV to KBV and, in this vegetation type, the addition of a co-breeder resulted in larger polyandrous groups. If intrinsic benefits provide the impetus for PCGs to delay dispersal, individuals will continue to delay dispersal and group size will increase until the intrinsic benefits to those remaining no longer outweigh the costs (Brown 1987b; Koenig *et al.* 1992). At Calitzdorp, in spite of the fact that some groups fledged four young (n = 3), three (n = 5) or even two young (n = 35) per year, never more than two non-breeders were present in a territory. Therefore, there was a limit to the number of offspring that can, or may, delay dispersal in a single PCG territory. Furthermore, in KBV, the addition of a co-breeder that delayed dispersal significantly increased group size. It therefore appears that not only the number of non-breeders per group was limited, but also the number of co-breeders, since only one per group was ever recorded (Chapter 3). Thus, the number of non-breeders, and even co-breeders per group, may be density dependent.

A further factor that must be taken into account is that PCGs were strictly territorial and defended their territories and therefore the resources within (see Chapter 5). Territoriality "serves to ensure the individual certain needs" (Newton 1979). Since PCG densities increased as groups started breeding closer to each other, territoriality may have deleted all available space and thereby prevented offspring to breed independently (Brown 1969b). The significant result was that, although groups were larger and breeding further apart in KBV compared with OSBV, breeder, adult and PCG densities did not differ, indicating that these densities are close to the limit for this species. Thus, the larger groups in KBV, and especially the presence of co-breeders, may therefore also be linked to benefits of philopatry, and not only densities *per se*.

The delayed-dispersal threshold model of Koenig *et al.* (1992) plots the fitness of birds that delay dispersal under different density scenarios against territorial quality or suitability for breeding. Territorial quality, and what constitutes quality are at this stage unknown entities. It is therefore not possible to answer the question fully if population density were the primary factor distinguishing between intrinsic benefit or extrinsic constraint as conditions leading to delayed dispersal. However, the high density and apparent limitation to the number of co-breeders and non-breeders recorded in groups in KBV may point to the fact that intrinsic benefits provided the proximal impetus. Only when the direct relationships between group size, density, fitness and territorial quality are examined will one be able to determine the key crucial factor.

CHAPTER 7

HIGH OTOMYINID RODENT BIOMASS AND ASSOCIATED HABITAT PARAMETERS: ECOLOGICAL FACTORS THAT MAY CONSTITUTE HABITAT QUALITY AND PROMOTE REPRODUCTIVE SUCCESS IN THE PALE CHANTING GOSHAWK

Status: sections in this chapter on tortoise predation have been published as part of a more detailed study: MALAN, G. & BRANCH, W.R. 1992. Predation on Tent Tortoise and Leopard Tortoise hatchlings by the Pale Chanting Goshawk in the Little Karoo. *S. Afr. J. Zool* 27:33-35.

SUMMARY

Ecological factors that constitute habitat quality for the Pale Chanting Goshawk (PCG), such as the availability of prey, the habitat structure that is favoured by dominant prey species, and overall prey abundance, were investigated. Based on biomass, PCGs prey mostly on rodents, but also birds, hatchling tortoises, snakes, lizards, sunspiders, harvester termites, grasshoppers, beetles and carrion. Groups in Karroid Broken Veld (KBV) preyed almost exclusively on three rodent species, *Otomys unisulcatus* (42-48%), *Parotomys brantsii* (18-32%) and *Rhabdomys pumilio* (17-27%). A possible relationship was found between reproductive success and otomyinid (*O. unisulcatus* and *P. brantsii*) densities, as well as with rainfall. Reproductive success and otomyinid densities varied temporally and spatially during the five years of the study.

Four ecological factors which primarily influence PCG demography were identified. (1) Heuweltjie densities accounted for 56% of the variation in *P. brantsii* warren densities, and the number of shrubs at height class 76-150 cm accounted for 60% of the variation in the densities of *O. unisulcatus* lodges. KBV contained the highest densities of 76-150 cm high scrubs, albeit not significantly higher than Open Spekboomveld (OSBV). Furthermore, KBV and Succulent Karoo (SK) contained the highest heuweltjie densities. KBV was therefore the only vegetation type that scored well for both factors. (2) A very high otomyinid (*Parotomys brantsii* and *Otomys unisulcatus*) biomass of 347 kg/km^2 can be attained in KBV in some years, compared with 189 kg/km^2 in OSBV and 84 kg/km^2 in SK. Given Calitzdorp's mean annual rainfall of 198.8 mm, these values are remarkable high. Preying on these abundant rodents may have allowed PCGs to double-brood in temperate regions where the length of the breeding summer period is restricted. (3) Diversity and evenness of the three dominant prey species were highest in the diet of polyandrous trios and monogamous pairs in KBV. The ability to diversify in selecting prey may provide a buffer against fluctuations in availability in one or two of these species. (4) By selecting otomyinids, more so in KBV, PCGs were preying on rodents whose average weight of 124 g satisfied the bird's minimum daily requirement of an

estimated 124 g. These four ecological factors may have constitute habitat quality and thus fitness, and therefore influenced the decision of PCGs to delay dispersal and breed cooperatively.

7.1 INTRODUCTION

Habitat quality is one of the primary factors that might promote the evolution of cooperative breeding and delayed dispersal in birds (Lack 1968; Bednarz & Ligon 1988; Stacey & Ligon 1991; Koenig *et al.* 1992; Komdeur 1992). However, the determination of habitat quality is difficult and characteristics such as the diet, indices of prey abundance and different habitat parameters have been employed as surrogate measures (Koenig & Pitelka 1981; Lennartz *et al.* 1987; Bednarz & Ligon 1988; Koenig *et al.* 1992; Komdeur 1992). These factors, through increased reproductive success and lifetime fitness, may influence the decision to delay dispersal and breed cooperatively (Koenig *et al.* 1992; Emlen 1994).

Critical resources that constitute habitat quality, such as food supply, may be subjected to considerable spatial and temporal variation and the stability and predictability of these critical resources within an environment may all favour group living (Emlen 1982; Waser 1988; Stacey & Ligon 1991; Koenig *et al.* 1992). Because of the difficulty in determining habitat quality, various authors have resorted to lifetime reproductive success or, if not available, annual reproductive success, as an indicator of habitat quality (Koenig & Pitelka 1981; Stacey & Ligon 1991).

The Pale Chanting Goshawk is an opportunistic hunter and takes a wide range of taxa, including reptiles (lizards, snakes), insects, birds, mammals and carrion (see Appendix 4). In Namibia, in the first of in two anecdotal studies on the diet of this species, Biggs *et al.* (1984) recorded birds, snakes, carrion, lizards, mammals (mice and shrew) and insects. In the second in the Northern Cape Province, Steyn & Myburgh (1992) recorded birds, lizards, rodents and a snake. The aims of this chapter are firstly to: (1) compare diets of polyandrous PCG trios (only from the KBV) and monogamous pairs in different vegetation types, (2) examine the habitat structure that is associated with dominant prey species, (3) examine the spatial and temporal distribution of prey abundance, (4) examine the relationship between prey abundance and reproductive success, and (5) identify ecological factors that may constitute habitat quality and influence reproductive success.

7.2 METHODS

7.2.1 Pellet and diet analyses

The diet of the PCG was studied by collecting their regurgitated pellets on a monthly basis (within the first week of every month) from April 1988 to February 1989 beneath pre-selected perches. Pellets found beneath perches in a search before the monthly collection started were labelled pre-April, and no predation date could be associated with these prey remains. Pellets were collected from beneath ESKOM poles (wooden power pylon, 9 m in height), telephone poles, various tree roosts and a row of *Agave mericana* 'trees'(Fig. 7.1). Pellets were not collected to within 100 m from territory borders as to avoid sampling the diet of neighbouring groups or other perch hunters (*e.g.* Steppe Buzzard *Buteo buteo*).

Pellets were dissolved in water and the macroscopic remains identified visually. Since diurnal raptors digest bone, whereas nocturnal raptors such as owls do not (Newton 1986), all pellets containing skulls were discarded. Prey remains were identified to the lowest possible taxon level. Where possible, the most commonly represented element, or parts thereof, was used to calculate the minimum number of individuals represented in each sample (Boshoff *et al.* 1990). The upper and lower incisors were used to identify *Otomys unisulcatus* and *Parotomys brantsii*, and upper and lower incisors and molars (12 in total) to identify *Rhabdomys pumilio* (de Graaff 1981). Because of this discrepancy, the numbers estimate for *O. unisulcatus* and *P. brantsii* were probably underestimates in comparison with *R. pumilio*. The number of Solpugidae was calculated by counting the minimum number of dorsal and ventral claws for the two chelicerae combined.

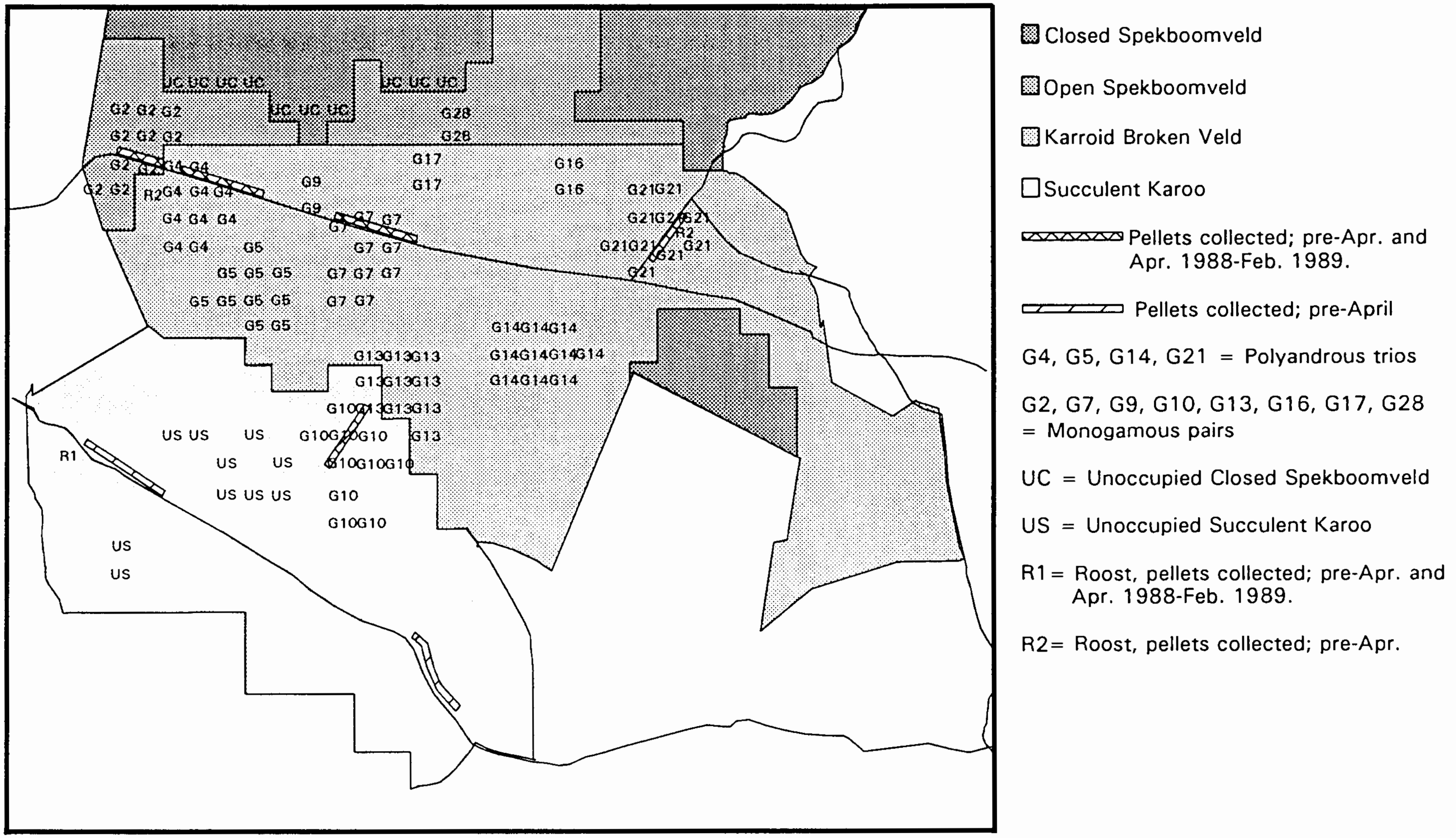

Fig. 7.1 Location of quadrats sampled for rodent densities and habitat parameters in territories of polyandrous trios, monogamous pairs and unoccupied areas. Group numbers correspond to that in Table 3.1, Figs. 3.1-3.5.

To study the relative importance of prey taxa in terms of biomass, I used either published mass records or mass estimates (Avery *et al.* 1985; Watson 1986). For each mammal and bird species, a mean value were calculated, combining the mass of both sexes. For reptiles, excluding tortoises, mass values were obtained from the herpetological collection, Port Elizabeth Museum. The number of tortoises in pellets was determined by the number of scutes retrieved. The presence of *Psammobates tentorius* was determined by: (1) the presence of first vertebral (V1) scutes (characterised by the anterior constriction as the scute is reduced in width where it makes contact with the small nuchal scute) in pellets; (2) the presence in some pellets of more scutes than could be present on a single tortoise (*i.e.* more than five large vertebrals, more than two large abdominals, *etc.*). Scaled reptiles and snakes were separated on the presence of a spinal cord and/or vertebrae in the latter. For insects and spiders, mass values were obtained from W.R.J. Dean (unpubl. records) or by catching and weighing selected species. For bird, reptile, insect and spider taxa with no known mass values, values were assigned according to corresponding size classes.

Since PCGs are only capable of consuming a proportion of larger prey individuals, Brown (1970) estimated, for a PCG, a minimum daily requirement of 15% of mean adult weight, therefore 15% of 862 g or 124 g (n = 68 birds; GM unpubl. data). Although Smeenk (1974) and Watson (1986) argued that, when breeding, this figure should be multiplied to include both partners and even chicks, I used 124 g as a conservative and realistic estimate. This assumption should be treated with caution since an otomyinid is not digestible in total, PCGs may be capable of catching and digesting two otomyinids within a full day, and minimum daily requirements of the reverse dimorphic sexes may differ. I furthermore used the importance value, biomass, in calculating diversity indices (Odum 1971; Zar 1984). The failure to identify several taxa to Order level made it only possible to calculate a Shannon-Wiener index of general diversity according to Class (Zar 1984). However, indices of general diversity and evenness (expressing the observed diversity as a proportion of maximum possible diversity; Zar 1984), were calculated for the three dominant prey species.

Small mammals represented in the diet in low numbers (< 10) were identified by Dr. D.M. Avery, large mammals and birds by Dr. G. Avery, insects and spiders by Drs. A.P. Prins and H.G. Robertson (all from the South African Museum, Cape Town) and reptiles by Dr. W.R. Branch (Port Elizabeth Museum). Taxonomy and mass values follows de Graaff (1981), Smithers (1983), Maclean (1985), Scholtz & Holm (1985) and Branch (1988).

7.2.2 Prey caught and nest site prey provisions

All prey items caught in the non-breeding and pre-laying periods were recorded while studying the behaviour of single PCGs (instantaneous sampling; see Chapter 2), as well as other PCGs within a 100 m from the focal bird. At nest sites (scan sampling; see Chapter 2) all prey items provisioned to the nest were recorded. It was difficult to identify prey species caught and provisioned since: (1) prey were almost always caught in the lower shrub layer (up to 75 cm high) and, if eaten on the ground, the prey itself was not in view, (2) prey items were plucked before being eaten, (3) prey items eaten on a perch or in the nest were, in most instances, turned on their back, and (4) the unobstructive manner and speed with which males delivered prey to the female and nest site. I therefore identified prey provisioned in broad taxa, *e.g.* rodents, birds, snakes *etc.* On all nest visits nests were inspected for prey remains. I consulted the literature for published information and solicited unpublished records of PCG prey items from southern African raptor biologists.

All prey items (pellets, provisions and remains) were divided, according to origin, into status-vegetation type groupings: MpO = Monogamous pair from Open Spekboomveld, PtK = Polyandrous trio from Karroid Broken Veld, MpK = Monogamous pair from Karroid Broken Veld, MpS = Monogamous pair from Succulent Karoo and MpKS = Monogamous pair from Karroid Broken Veld/Succulent Karoo border. The border between KBV and SK is clearly defined (Acocks 1988), and this dividing line ran through the territories of two monogamous pairs. The source of prey could not be attributed to a specific vegetation type, therefore the MpKS grouping.

7.2.3 Prey densities and habitat parameters

Based on the knowledge that *Otomys unisulcatus* and *Parotomys brantsii* were the two dominant prey species in terms of biomass (see section 7.3.1), I collected ecological data on their densities and habitat characteristics that might influence distribution and abundance (Bond *et al.* 1980; du Plessis & Kerley 1991). In order to collect these ecological data, the territories of four polyandrous trios and four monogamous pairs were selected and, for each territory, 10 such quadrats (500x500 m) were selected randomly and studied ecologically. The five territories where pellets were collected were firstly included. These were from a monogamous pair from OSBV (Group 2), from two polyandrous trios (Groups 4 & 21) and a monogamous pair (Group 7) from KBV, and a monogamous pair from SK (Group 10) (Fig 7.1; see also Table 3.1; Fig. 3.2). In addition, I randomly selected two polyandrous trios (Groups 5 & 14) and a monogamous pair from KBV (Groups 13). I also collected similar data for 10 quadrats in Closed Spekboomveld (CSBV), the vegetation type unoccupied by PCGs, and from 10 unoccupied quadrats in SK (Fig. 7.1).

To determine the proportion ground cover in each height class, from the centre of each quadrat in a random direction I placed a 50 m line with knots 1 m apart. Using the point method (Bond *et al.* 1980) the height of the vegetation at each interval was measured and a percentage cover calculated. The height classes were: 0-15 cm (= open ground), 16-75 cm, 76-150 cm, 151-250 cm, 251-350 cm, 351-450 cm, and > 451 cm. Cover less than 15 cm tall was regarded as open, since prey such as rodents could probably be seen through the vegetation. Since OSBV and KBV vegetation types were two-layered, a layer of small plants with dwarf trees and shrubs scattered throughout (Acocks 1988), the 16-75 cm height class was introduced to measure cover of the lower layer.

The density of the Karoo Bush Rat *Otomys unisulcatus* was estimated by counting active Bush Rat lodges (stick nests) while walking a 200x30 m transect, following the plot line for the first 50 m. The value obtained was extrapolated to cover the total surface area of the quadrat. A lodge was recorded active if: (1) an individual of this species was seen running to or from the lodge, (2) if the runways from the lodge were in regular use, and (3) if fresh fecal droppings and left-over bits of their vegetable matter were present in close proximity of the lodge. Since *O. unisulcatus* frequently build their lodges under shrubs (Vermeulen & Nel 1988), I counted all shrubs within a 50 m diameter circular plot, with the centre point at the start of the transect. A shrub was defined as plant taller than 75 cm with side branches reaching ground level.

Brant's Whistling Rat *Parotomys brantsii* lives in small colonies in extensive tunnel systems or warrens in sandy soils (de Graaff 1981), especially in the relatively stoneless soil of Mima-like mounds or heuweltjies (Lovegrove & Siegfried 1986; Cox *et al.* 1987). While walking the 200x30 m transect, the number of heuweltjies, and the number of active and inactive *P. brantsii* warrens on and off heuweltjies was noted. A heuweltjie/warren activity ratio was then calculated. The number of heuweltjies was subsequently counted from aerial photographs (Lovegrove & Siegfried 1989) and the number of active warrens (both on and off heuweltjies) estimated using the activity ratio. Warrens were recorded as active using the same criteria as for *O. unisulcatus*, plus the audible alarm whistle emitted before diving into the warren (de Graaff 1981). Since the subfamily Otomyinae includes both *P. brantsii* and *O. unisulcatus*, an Otomyinid Index was calculated by combining the estimates of *Otomys* and *Parotomys* densities. Data recorded for heuweltjies, *P. brantsii*, *O. unisulcatus* and Otomyinid Index are presented as numbers per quadrat, and although I did not calculate relative densities (*e.g.* 320 warrens/km^2), I refer to results as densities.

The above ecological data were collected during October-December 1989, *i.e.* at the height of the PCG breeding season. During December of the 1991 breeding season, I collected data on *P. brantsii* and *O. unisulcatus* densities in seven territories where I collected data during 1989 (Groups 2, 4, 5, 7, 10, 13, 21; Table 3.1; Fig. 3.4). I also collected data from an additional four territories (Groups 14, 16, 17, 28) (Fig. 7.1). Only two quadrats were sampled, the quadrats containing the nest site or if not breeding, the nest used the previous year, and the quadrat directly south of it.

To determine if PCGs were preying on *O. unisulcatus* and *P. brantsii* in proportion to their abundance, I tested for a positive correlation between the proportion biomass (derived from the pellet analysis) with *O. unisulcatus* lodge and *P. brantsii* warren densities for all groupings except MpS (no density data recorded). To test for differences in habitat variables and indices of rodent densities between the different vegetation types, I performed an analysis of variance (ANOVA) and, if significant, a pairwise $\underline{t}$ test with Bonferroni-adjusted significance levels. Levene's test of homogeneity of variance was preformed to test for differences in variance in *O. unisulcatus* lodge and *P. brantsii* warren densities between polyandrous trios and monogamous pairs in KBV. To test for the possible influence of habitat structure on otomyinid densities, otomyinid density indices were used as dependent variables in correlation analyses and stepwise multiple linear regression analyses with ecological variables as independent variables (BMDP-2R; Dixon *et al.* 1990). A logarithmic transformation, log(x+1) was employed in all statistical analyses to improve the normality of data and to standardise the considerably different scales of variables.

Live bird biomass was calculated by counting all birds while walking 300x50 m transects in three quadrats each in KBV and SK. All birds recorded were grouped into families and a biomass value calculated for each quadrat, using a mean mass value per family.

7.2.4 Reproductive success

For the groups whose otomyinid densities were sampled during 1989 and 1991, I calculated a Reproductive Index as follows; a score of one was attributed if a PCG egg was laid, one if the egg hatched and one if the chick fledged. Therefore, if a group laid two eggs in one breeding season, and both chicks hatched and fledged successfully, then a value of six was scored. If a breeding group was discovered within the six weeks after chicks fledged, and if at least one fledgling was noted but the number of eggs laid or chicks fledged was unknown (n = 11 cases), a four was scored, three for the fledgling and one for the probability that a second egg was laid. This probability was based on the fact that two eggs were laid in 94% (n = 92) of laying attempts in the Calitzdorp study area. To determine if the annual reproductive success reflected the otomyinid density, I tested for a positive correlation between a Reproductive Index and Otomyinid Index. To study the spatial distribution of breeding success for 1989-1992, as a measure of the distribution of otomyinids, I tested for correlation between the Reproductive Index of each group and that of its nearest neighbour, the nearest neighbour being determined by the closest nest. I also tested for a correlation between the annual reproductive success and rainfall.

7.3 RESULTS

7.3.1 Diet

From the 625 pellets analysed, 8 219 prey individuals were identified (Tables 7.1 & 7.2). Insects contributed the highest number of prey individuals (7 646), followed by mammals (390), reptiles (106), spiders (53) and birds (23) (Table 7.2). However, the highest proportion of biomass was contributed by mammals (36 150 g; 91%), followed by birds (1 572 g; 4%), reptiles (1 438 g; 3.6%), insects (286 g; 0.7%) and spiders (265 g; 0.7%). Three rodent species contributed by far the highest proportions biomass to the diet; *Otomys unisulcatus* (43%), *Parotomys brantsii* (29%) and *Rhabdomys pumilio* (15%) (Tables 7.1 & 7.2). The remainder of the mammal sample consists of low numbers of gerbils, shrews and elephant-shrews. The dominant bird species were Cape Turtle Dove *Streptopelia capicola* and mousebird *Colius* spp. Apart from the doves, all birds caught were in the 50 to 100 g size class. Dominant reptile species were hatchling Leopard Tortoises *Geochelone pardalis* and Tent Tortoises *Psammobates tentorius*, and Karoo Sand Snakes *Psammophis notostictus*. Harvester termites, grasshoppers and sunspiders were the dominant

Table 7.1 Taxa, the minimum number of individuals and estimated biomass (underlined) from pellet collected at the Calitzdorp study area, April 1988 to February 1989. MpO = Pair-Open Spekboomveld, PtK = Polyandrous trio-Karroid Broken Veld, MpK = Monogamous pair-Karroid Broken veld, MpKS = monogamous pair-Karroid Broken Veld/Succulent Karoo, and MpS = Monogamous pair-Succulent Karoo. TOT = Total. Totals were rounded off and Classes sorted from the highest to lowest biomass contributions. Mass values in brackets represents values higher than the estimated minimum daily requirement of 124 g (see text for further explanation).

Prey taxa	MASS	MpO	PtK	MpK	MpKS	MpS	TOT	BIOMASS
No. of pellets		201	103	84	148	89	625	
MAMMALIA								
Bush Karoo Rat *Otomys unisulcatus*	123.9	81	24	20	9	4	138	17098
Brant's Whistling Rat *Parotomys brantsii*	124.0	3	9	15	53	12	92	11408
Striped Mouse *Rhabdomys pumilio*	44.5	28	37	23	28	15	131	5830
Vlei Rat *Otomys irroratus*	118.0	3		1			4	473
Smith's Rock Elephant-shrew *Elephantulus rupestris*	65.2	3	2	1			6	391
Littledale's Whistling Rat *Parotomys littledalei*	124.0	2					2	248
Hare *Lepus* sp. (2305)	124.0					2	2	248
Round-eared Elephant-shrew *Macroscelides proboscideus*	38.2		1		5		6	229
Hairy-footed Gerbil *Gerbillurus paeba*	25.4			1	3		4	102
Short-tailed Gerbil *Desmodillus auricularis*	52.3					1	1	52
Pouched Mouse *Saccostomus campestris*	45.4			1			1	45
Reddish-grey Musk Shrew *Crocidura cyanea*	9.0	1	1				2	18
Lesser Dwarf Shrew *Suncus varilla*	6.5					1	1	7
AVES								
Bird spp.	81.0			1	3	3	7	567
Cape Turtle Dove *Streptopelia capicola* (153)	124.0					2	2	248
Mousebird *Colius* sp.	49.9	2	1			1	4	200
Feral Pigeon *Columba livia* (350)	124.0					1	1	124
Common Quail *Coturnix coturnix*	97.1					1	1	97
Bird sp1.	81.0			1			1	81
Bird sp2.	81.0	1					1	81
Cape Sparrow *Passer melanurus*	25.7					2	2	51
Cape Weaver *Ploceus capensis*	44.7					1	1	45
Whitethrouted Canary *Serinus albogularis*	27.3					1	1	27
Masked Weaver *Ploceus velatus*	26.0					1	1	26
Lark Alaudidae	25.0					1	1	25

Table 7.1 Continued

	MASS	MpO	PtK	MpK	MpKS	MpS	TOT	BIO-MASS
REPTILIA								
Leopard Tortoise *Geochelone pardalis*	36.5	7	1		3	1	12	438
Scaled reptile Squamata	10.0	6	6	3	7	10	32	320
Karoo Sand Snake *Psammophis notostictus*	20.0	3		1	2	4	10	200
Tent Tortoise *Psammobates tentorius*	5.0	7	4	2	18	5	36	180
Snake Serpentes	20.0		1		4	2	7	140
Mole Snake (juvenile) *Pseudaspis cana*	20.0	2			4		6	120
Sand Snake *Psammophis* sp.	20.0	1					1	20
Lizard *Cordylus* sp.	10.0					1	1	10
Skink *Mabuya* sp.	10.0	1					1	10
INSECTA								
Harvester termite *Hodothermes mossambicus* or *Microhodotermes viator* (Hodotermitidae)	0.02	1035	617	216	3114	2549	7568	151
Grasshopper Orthoptera spp.	2.00	4	1	2	23	12	42	84
Beetle Scarabaeidae	1.50	4		2			6	9
Beetle Tenebrionidae sp3.	1.50	2			2		4	6
Criket *Iryllus birnaculatus*	1.50				3		3	5
Ground Beetle *Anthia* sp.	5.00	1					1	5
Ground beetle *Caminara chlorostichum*	5.00				1		1	5
Tapping beetle Tentyriinae	1.50		1			2	3	5
Beetle Tenebrionidae sp1.	1.50				2		2	3
Beetle Tenebrionidae sp4.	1.50				1		1	3
Locust Acrididae	1.40				2		2	3
Beetle Tenebrionidae sp2.	1.50				1		1	2
Leaf Beetle Chrysomelidae sp1.	1.50				1		1	2
Leaf Beetle Chrysomelidae sp2.	1.50				1		1	2
Snoutbeetle Curculionidae	1.50				1		1	2
Beetle (leaf chafer) *Sparrmannia* sp	1.20		1				1	1
Grasshopper (small sp) Orthoptera sp.	1.40					1	1	1
Sunbug Cicadidae	1.00			1			1	1
Bee (small) Hymenoptera sp1.	0.02			1			1	0
Formicine ant *Anoplolepis steingroeveri*	0.02		1				1	0
Formicine Ant *Camponotus fulvopilosus*	0.02	1				1	2	0
Formicine Ant Formicidae	0.02				1		1	0
Wasp Hymenoptera sp2.	0.02				1		1	0
ARACHNIDA								
Sunspider Solpugidae sp2.	5	15	7	4	14	2	42	210
Sunspider Solpugidae sp1.	5	3	1		2	2	8	40
Thin tailed scorpion *Opisthophthalmus* sp.	5				2		2	10
Scorpion Scorpionidae sp.	5			1			1	5
CHILOPODA								
Centipede Chilopoda	2					1	1	2

arthropods. A wide range of the larger beetles were caught, mainly from the families Scarabaeidae, Tenebrionidae and Carabidae. Prey items identified from prey remains and direct observations showed that not only medium size birds were preyed on, but also large items such as African Wild Cat *Felis lybica* (Table 7.3).

Table 7.2 For each Class and the three dominant prey species, totals of the minimum number of individuals and estimated biomass (underlined) from pellet collected from the Calitzdorp study area, April 1988 to February 1989. MpO = Monogamous pair-Open Spekboomveld, PtK = Polyandrous trio-Karroid Broken Veld, MpK = Monogamous pair-Karroid Broken veld, MpKS = Monogamous pair-Karroid Broken Veld/Succulent Karoo, and MpS = Monogamous pair-Succulent Karoo. TOT = Total.

Prey taxa	MpO	PtK	MpK	MpKS	MpS	TOT (%)	BIOMASS (%)
MAMMALIA							
Bush Karoo Rat *Otomys unisulcatus*	81	24	20	9	4	138 (1.7)	17098 (43.1)
Brant's Whistling Rat *Parotomys brantsii*	3	9	15	53	12	92 (1.1)	11408 (28.7)
Striped Mouse *Rhabdomys pumilio*	28	37	23	28	15	131 (1.6)	5830 (14.7)
Total - Numbers	121	74	62	98	35	390 (4.8)	
Total - Biomass	12461	5914	5617	9200	2958		36150 (91.0)
AVES							
Total - Numbers	3	1	2	3	14	23 (0.3)	
Total - Biomass	181	50	162	243	936		1572 (4.0)
REPTILIA							
Total - Numbers	27	12	6	38	23	106 (1.3)	
Total - Biomass	481	137	60	470	292		1438 (3.6)
INSECTA							
Total - Numbers	1084	621	222	3154	2565	7646 (93.0)	
Total - Biomass	44	17	12	134	79		286 (0.7)
ARACHNIDA							
Total - Numbers	18	8	5	18	4	53 (0.6)	
Total - Biomass	90	40	25	90	20		265 (0.7)
CHILOPODA					1	1 (< 0.1)	2 (< 0.1)
Grand total - Numbers	1253	726	297	3311	2642	8219	
Grand total - Biomass	13257	6158	5876	10137	4287		39713

Scutes of 12 Leopard Tortoises were found in the pellets, mostly in OSBV (Table 7.1). Hatchlings measure 40-50 mm and weigh 23-50 g (Branch 1988). Most Leopard Tortoise prey were hatchlings with no evidence of growth on the scutes. However, at least two sets of tortoise scutes had growth rings, indicating that they came from juveniles up to 12 months of age. Under natural conditions tortoise growth is slow during the first year and hatchlings weight may have only increased to 50-80 g after 12 months (Patterson *et al.* 1989). This is possibly reaching the upper limit of prey size taken by PCGs, as ossification of the hatchling shell will have increased its protection.

Table 7.3 Species and number of individuals identified from prey remains collected from Pale Chanting Goshawk nests, and bird species caught during direct observation (1988-1992). OSBV = Open Spekboomveld, KBV = Karroid Broken Veld, SK = Succulent Karoo.

Prey species	Mass g	Number	Vegetation type
PREY REMAINS			
Helmeted Guineafowl *Numida meleagris*	1352	1	OSBV
Cape Hare *Lepus capensis* (juveniles)	1633	3	KBV
African Wild Cat *Felis lybica*	4300	1	KBV
Agama *Agama* sp.		1	KBV
BIRDS CAUGHT			
Southern Tchagra *Tchagra tchagra*	45	1	OSBV
Longbilled Lark *Mirifra curvirostris*	22	1	SK
Karoo Robin *Erythropygia coryphaeus*	20	1	SK
Fiscal Flychatcher *Sigelus silens*	26	1	SK

The remains of 36 Tent Tortoises were recovered from the pellets (Table 7.1). No pellet was positively determined to contain the remains of more than two tortoises. The scutes ranged in length from 5-8 mm and were from hatchlings (Malan & Branch 1992). Although no hatchling weights have been recorded for this species, hatchlings of the closely related Geometric Tortoise *Psammobates geometricus* weigh approximately 6-8 g, and measure 35-40 mm (*P. tentorius* hatchlings measures 25-30 mm; Branch 1988). It is thus probable that Tent Tortoise hatchlings will weigh approximately 5 g and that predation occurs soon after hatching.

7.3.2 Prey selection

Direct observations during the non-breeding period revealed that groups in KBV were preying almost exclusively on small mammals, whereas monogamous pairs in SK were taking a wider range of taxa, including birds and termites (Table 7.4). Small mammals were the dominant prey delivered to the nests 88% (56/64) of polyandrous trios and monogamous pairs in KBV, with the remainder consisting of lizards, snakes and a shrew (Table 7.5). Again, in SK, monogamous pairs were provisioning a wider range of taxa.

Table 7.4 Prey taxa caught by Pale Chanting Goshawks in the non-breeding and pre-laying periods of 1988 in different vegetation types.

Vegetation type	Small mammals	Lizard	Bird	Termites[1]
Polyandrous trios-Karroid Broken Veld	22	3	0	1
Monogamous pair-Karroid Broken Veld	2	0	0	0
Monogamous pairs-Succulent Karoo	17	1	3	13
Total	41	4	3	14

1 Times a PCG flew down to the ground to eat termites

Table 7.5 Prey taxa provisioned to nest sites by two polyandrous trios and four monogamous pairs during 1988 and 1989. OSBV = Open Spekboomveld, KBV = Karroid Broken Veld, SK = Succulent Karoo.

Status, group and year	Vegetation type	Rodent	Lizard	Snake	Bird	Shrew
Polyandrous trio-Okkies 1988	KBV	13	3	0	0	1
Polyandrous trio-Zwartkop 1989	KBV	26	2	0	0	0
Monogamous pair-Cutting 1988	KBV	10	1	1	0	0
Monogamous pair-BaasF 1989	KBV	7	0	0	0	0
Monogamous pair-Erenst 1989	OSBV	6	1	1	0	0
Monogamous pair-Badsaf 1988	SK	6	4	6	3	1
Total		68	11	8	3	2

According to the pellet analysis, polyandrous trios (PtK) (96%), monogamous pairs (MpK) from KBV, and monogamous pairs from OSBV (MpO) (94%) and KBV/SK border (MpKS) (90.8%) (95.6%) preyed almost exclusively on mammals (Fig. 7.2). However, monogamous pairs in SK (MpS) preyed less on mammals (69%) and on a higher proportion of birds (21.9%) compared with the 0.8-2.8% birds of other groupings. Reptiles and insects were also caught in higher proportions by MpS (6.8; 1.9%) and MpKS (4.6; 1.3%) (Fig. 7.2). Spiders were caught in relative uniform proportions, ranging from 0.9% (MpKS) to 0.4% (MpK). The Class diversity indices were the lowest for PtK and the highest for MpS (Table 7.6).

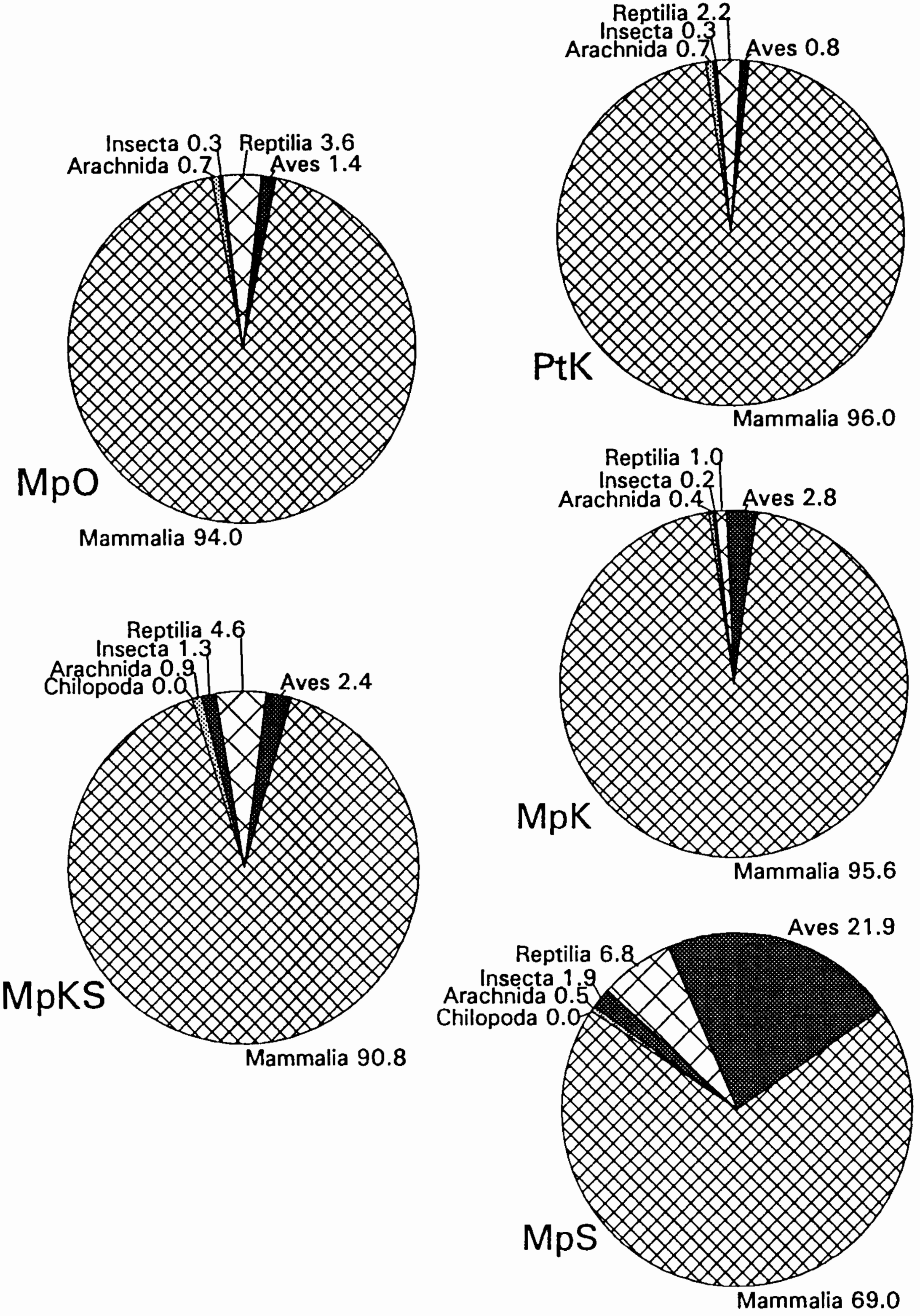

Fig. 7.2 Relative proportions of prey selected according to class by Pale Chanting Goshawks according to Class for monogamopus pairs from the Open Spekboomveld (MpO), polyandrous trios (PtK) and monogamous pairs (MpK) in the Karroid Broken Veld, monogamous pairs on the Karroid Broken Veld/Succulent Karoo (MpKS) border and monogamous pairs from the Succulent Karoo (MpS).

Table 7.6 Indices of general diversity and evenness, with biomass as an importance value, according to Class and three dominant prey species for different status-vegetation type groupings. MpO = Monogamous Pair-Open Spekboomveld, PtK = Polyandrous trio-Karroid Broken Veld, MpK = Monogamous pair-Karroid Broken veld, MpKS = monogamous pair-Karroid Broken Veld/Succulent Karoo, and MpS = Monogamous pair-Succulent Karoo.

Indices	MpO	PtK	MpK	MpKS	MpS
Class diversity	0.29	0.21	0.23	0.42	0.87
Three dominant prey species					
Species diversity	0.48	1.02	0.92	0.76	0.98
Evenness	0.43	0.93	0.84	0.69	0.90

Considering the three dominant prey species in the pellet analysis, *O. unisulcatus*, *P. brantsii* and *R. pumilio*, MpO was catching almost exclusively *O. unisulcatus* (76%) with the proportions decreasing towards SK (MpKS 11% and MpS 12%) (Fig. 7.3). The opposite was prevalent for *P. brantsii*, where the highest proportion were caught by MpKS (65%), followed by MpS (35%) and MpK (32%) with proportions decreasing towards MPO (3%). *R. pumilio* was caught in high proportions in KBV (PtK 27% and MpK 17%). For the three species combined, the proportion biomass was the highest for PtK (93%), followed by MpK (91%), MpO and MpKS (88%), and MpS (62%). The species diversity and evenness indices for the above three species were the highest for PtK and the lowest for MpO (Table 7.6).

7.3.3 Prey densities and habitat parameters

Lodge densities for *O. unisulcatus* sampled during 1989 varied considerably, from 294-381 in the centre of KBV to 6 in SK (Table 7.7, Fig. 7.1). Estimated densities of *P. brantsii* warrens ranged from 9 in OSBV and 7 in a territory on the northern boundary of KBV, to 41-160 in the center KBV and SK (Table 7.7, Fig. 7.1). Of the 524 *heuweltjies* sampled, 58% (354/524) contained active *P. brantsii* warrens, whereas 97% (140/145) of warrens not on heuweltjies were active (Table 7.8). In KBV, 69% (270/393) of heuweltjies contained active *P. brantsii* warrens, whereas 95% (97/102) of warrens off heuweltjies were active (Table 7.8).

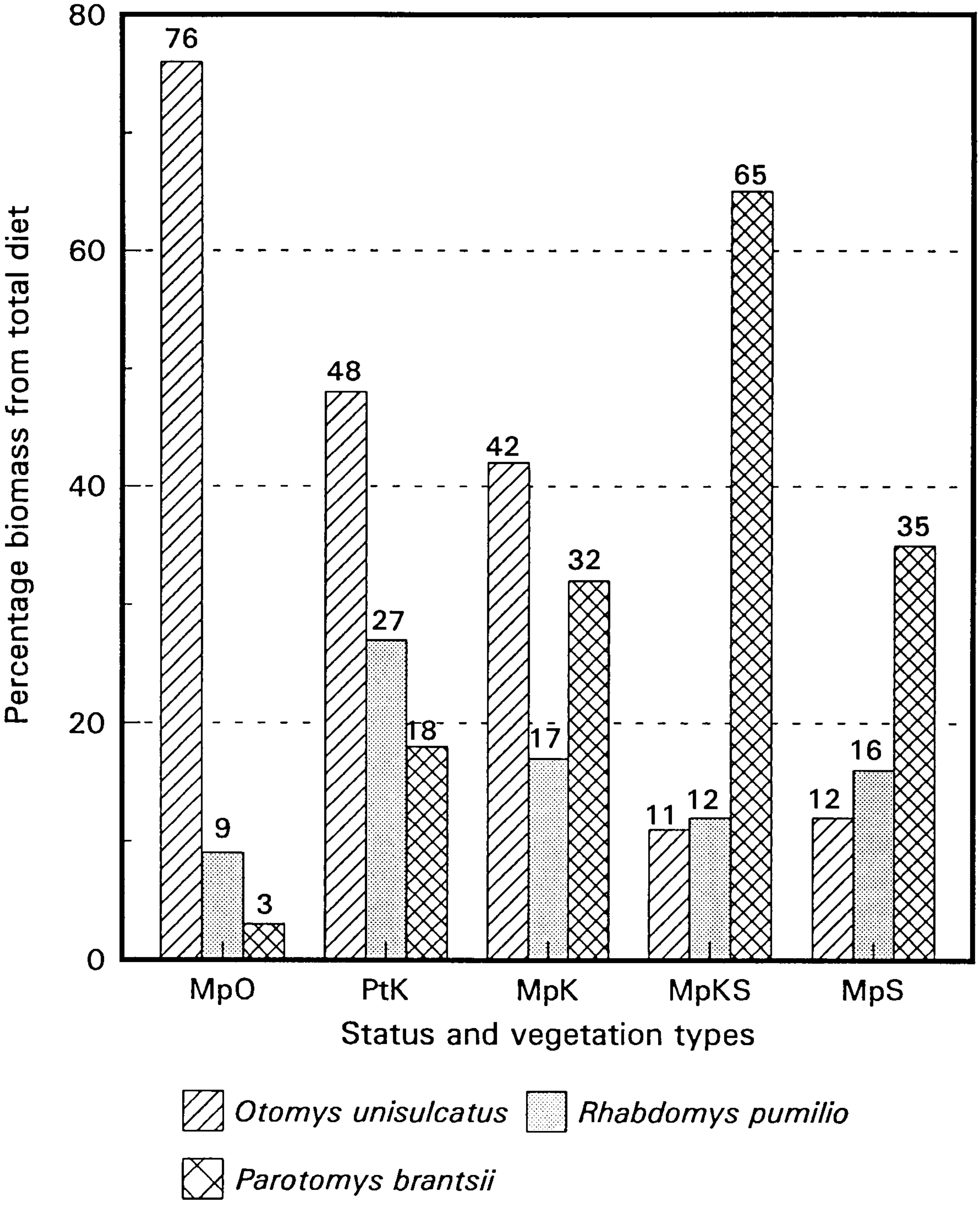

Fig. 7.3 The three most frequently recorded (= biomass) species in Pale Chanting Goshawks pellets for Monogamopus pairs from the Open Spekboomveld (MpO), polyandrous trios (PtK) and monogamous pairs (MpK) in the Karroid Broken Veld, monogamous pairs from the Karroid Broken Veld/Succulent Karoo (MpKS) border and monogamous pairs from the Succulent Karoo (MpS).

Table 7.7 The mean number of *Otomys unisulcatus* lodges and *Parotomys brantsii* warrens per quadrat for different groups in the 1989 and 1991 breeding seasons. Mean and (± 1 standard deviations), Poly trio = polyandrous trio, Mono Pair = monogamous pair (see Fig. 7.1).

Group	Status	*O. unisulcatus*		*P. brantsii*	
		1989	1991	1989	1991
No. quadrats sampled per territory		10	2	10	2
Open Spekboomveld					
G2 = 1stKloof	Mono Pair	181 (127)	31 (44)	9 (12)	0
G28 = BoKuile	Mono Pair		313 (0)		0
Karroid Broken Veld					
G4 = Okkies	Poly trio	294 (169)	63 (0)	41 (48)	0
G21 = Kruisrivier	Poly trio	200 (49)	188 (0)	7 (21)	0
G5 = JohanG	Poly trio	344 (198)	31 (44)	77 (36)	101 (0)
G14 = AndriesK	Poly trio	381 (155)		121 (49)	
G7 = Cutting	Mono Pair	294 (196)	63 (44)	70 (46)	50 (0)
G13 = Bloubosvlei	Mono Pair	113 (101)	31 (44)	160 (33)	0
G9 = DGates	Mono Pair		125 (0)		0
G17 = Kuile	Mono Pair		313 (88)		0
G16 = Secretary	Mono Pair		313 (0)		0
Succulent Karoo					
G10 = Engelskamp	Mono Pair	6 (20)	0	97 (64)	0

Table 7.8 The numbers of heuweltjies recorded, active *Parotomys brantsii* warrens on heuweltjies, inactive and active warrens not on heuweltjies in ten quadrats counted in eight territories and two unoccupied areas (see Fig. 7.1). CSBV = Closed Spekboomveld, OSBV = Open Spekboomveld, KBV = Karroid Broken Veld, SK = Succulent Karoo.

Group	Vegetation type	Heuweltjies	Active warrens on heuweltjies	Inactive warrens not on heuweltjies	Active warrens not on heuweltjies
Unoccupied	CSBV	10	2	0	0
G2 = 1stKloof	OSBV	21	10	4	4
G4 = Okkies	KBV	65	32	4	4
G5 = JohanG	KBV	68	39	17	16
G21 = Kruisrivier	KBV	31	4	0	0
G14 = AndriesK	KBV	93	85	37	37
G7 = Cutting	KBV	50	30	19	17
G13 = Bloubosvlei	KBV	86	80	25	23
G10 = Engelskamp	SK	80	65	30	30
Unoccupied	SK	20	7	9	9
Total		524	354	145	140

The proportion of open ground differed significantly between all vegetation types, except between KBV and SK (Table 7.9). The proportion ground cover and number of shrubs in height classes > 75 cm differed significantly between vegetation types, whereas cover of the lower vegetation layer (16-75 cm) did not. As expected, ground cover and the number of shrubs increased in the upper height classes from the open SK to dense CSBV (Table 7.9). The number of heuweltjies did not differ significantly between KBV and SK, but was significantly lower in OSBV and CSBV. This trend was repeated with the densities of *P. brantsii* warrens, except that they did not differ between CSBV and OSBV. For MpO, PtK, MpK and MpKS the proportion biomass of *O. unisulcatus* recorded in the pellet analysis was not significantly correlated with the recorded lodge densities ($r = 0.50$; $P = 0.50$; $n = 4$), but the proportion of *P. brantsii* biomass was significant correlated with warren densities ($r = 0.996$; $P < 0.01$; $n = 4$). Warren densities for *P. brantsii* were significantly correlated with the density of heuweltjies ($r = 0.75$; $P < 0.001$; $n = 100$). Densities of *O. unisulcatus* did not differ significantly between CSBV and other vegetation types, but were significantly higher in OSBV and KBV compared to SK. The Otomyinid Index was significantly higher in KBV than CSBV and SK (Table 7.9).

In comparisons between polyandrous trios and monogamous pairs in KBV, the densities of heuweltjies and *P. brantsii* warrens were significantly lower, and *O. unisulcatus* lodge densities significantly higher for polyandrous trio quadrats (Table 7.10). However, if these two density estimates were combined (Otomyinid Index), the difference became statistically non-significant. The variance in *O. unisulcatus* lodge and *P. brantsii* warren densities was, in both cases, significantly lower for polyandrous trios *vs* monogamous pairs (Table 7.10).

The significant differences between CSBV, with no PCGs resident, and the bordering OSBV, with PCGs resident, are the higher proportions ground cover in the higher height classes (> 151 cm), less shrubs at 151-250 cm high and the lower number of heuweltjies (Table 7.9). At the other end of the study area, in unoccupied *vs* occupied SK, the only significant differences were the number of shrubs in the 76-250 cm height class (Table 7.11).

Table 7.9 Results of a comparison between rodent densities and proportions ground cover per quadrat for different vegetation types. Means and (± 1 standard deviations). Analysis of variance with logarithmic transformation. CSBV = Closed Spekboomveld, OSPV = Open Spekboomveld, KBV = Karroid Broken Veld, SK = Succulent Karoo, %GC = percentage ground cover.

	CSBV	OSBV	KBV	SK	ANOVA
No. of quadrats	10	10	60	20	
%GC 0-15 cm	44 (6) NS[1] ***[2] ***[3]	49 (6) **[4] ***[5]	62 (12) NS[6]	67 (13)	$P < 0.001$
%GC 16-75 cm	23 (9)	33 (8)	31 (9)	33 (13)	NS
%GC 76-150 cm	6 (2) * * ***	12 (5) *** ***	5 (8) ***	0	$P < 0.001$
%GC 151-250 cm	17 (7) ** *** ***	6 (3) * ***	2 (3) ***	0	$P < 0.001$
%GC 251-350 cm	6 (5) NS NS *	1 (1) NS NS	1 (1) **	0	$P < 0.001$
%GC 351-450 cm	4 (4) ** ** **	0 NS NS	0 NS	0	$P < 0.001$
%GC > 451 cm	1 (2)	0	0	0	
No. shrubs 76-150 cm	1258 (457) NS NS ***	2154 (911) NS ***	2515 (2045) ***	71 (243)	$P < 0.001$
No. shrubs 151-250 cm	2641 (1123) *** * ***	4952 (1265) *** ***	2222 (1937) ***	11 (35)	$P < 0.001$
No. shrubs 251-350 cm	629 (535) NS *** ***	283 (346) NS *	139 (235) ***	0	$P < 0.001$

Table 7.9 Continued	CSBV	OSBV	KBV	SK	ANOVA
Heuweltjies	7 (3) ** *** ***	21 (11) *** ***	96 (36) NS	99 (33)	P < 0.001
Parotomys brantsii warrens	2 (4) NS *** ***	9 (12) ** **	80 (63) NS	82 (59)	P < 0.001
Otomys unisulcatus lodges	75 (77) NS NS NS	181 (127) NS **	271 (173) ***	3 (14)	P < 0.001
Otomyinid Index	77 (76) NS * NS	190 (121) NS NS	350 (178) ***	85 (65)	P < 0.001

Pairwise t tests; NS = Not significant, * = P < 0.05, ** = P < 0.01, *** = P < 0.001; 1 = CSBV *vs* OSBV, 2 = CSBV *vs* KBV, 3 = CSBV *vs* SK, 4 = OSBV *vs* KBV, 5 = OSBV *vs* SK, and 6 = KBV *vs* SK.

Table 7.10 Results of a comparison between rodent densities, proportions ground cover and the number of shrubs for 40 quadrats in polyandrous trio territories and 20 quadrats in monogamous pair territories in Karroid Broken Veld. Means and (± 1 standard deviations), t tests and Levene's tests with logarithmic transformations. %GC = percentage ground cover. NS = Not significant

Variables	Polyandrous Trio	Monogamous Pair	t test	Levene's test
% Open Ground (0-15 cm)	61 (12)	61 (12)	NS	
%GC 16-75 cm	29 (8)	35 (10)	P < 0.05	
%GC 76-150 cm	6 (9)	3 (4)	NS	
%GC 151-250 cm	3 (3)	2 (2)	P < 0.05	
No. Shrubs 76-150 cm	2680 (2229)	2186 (1620)	NS	
No. Shrubs 151-250 cm	2303 (2072)	2060 (1673)	NS	
No. Shrubs 251-350 cm	157 (267)	102 (155)	NS	
Heuweltjies	82 (34)	123 (22)	P < 0.001	
Parotomys brantsii warrens	61 (58)	115 (60)	P < 0.01	P < 0.001
Otomys unisulcatus lodges	305 (163)	203 (178)	P < 0.05	P < 0.001
Otomyinid Index	366 (184)	318 (168)	NS	

Table 7.11 Results of a comparison between rodent densities, proportion ground cover and the number of shrubs between occupied and unoccupied quadrats in the Succulent Karoo during 1989. Means and (± 1 standard deviations), t test with logarithmic transformation. %GC = percentage ground cover, NS = Not significant.

No. of quadrats	Occupied 10	Unoccupied 10	t test
% Open Ground (0-15 cm)	64 (12)	70 (13)	NS
% GC 16-75 cm	36 (12)	30 (14)	NS
% GC 76-150 cm	0	0	
No. of Shrubs 76-150 cm	133 (340)	9 (9)	P < 0.01
No. of Shrubs 151-250 cm	22 (48)	1 (1)	P < 0.001
No. of Shrubs 251-350 cm	0	0	
Heuweltjies	98 (38)	99 (29)	NS
Parotomys brantsii warrens	97 (63)	66 (52)	NS
Otomys unisulcatus lodges	6 (20)	0	NS
Otomyinid Index	104 (73)	66 (52)	NS

Lodge densities for *O. unisulcatus* and warren densities for *P. brantsii* were significantly lower in KBV during 1991 than 1989 (Table 7.12).

For all vegetation types combined during 1989, the *P. brantsii* warren densities was significantly positively correlated with the proportion open ground, and significantly negatively correlated with proportion ground cover above 75 cm (Table 7.13). However, in combination only heuweltjies densities accounted for 56% of the variation in warren densities. Lodge densities for *O. unisulcatus* were significantly positively correlated with ground cover and number of shrubs at height classes 76-350 cm, although only the number of shrubs at height class 76-150 cm accounted for 60% of the variation in *O. unisulcatus* densities. In all vegetation types, the densities of *O. unisulcatus* lodges and *P. brantsii* warrens were not significantly correlated ($r = -0.10$; $P = 0.34$; $n = 100$), nor for KBV ($r = -0.16$; $P = 0.22$; $n = 80$).

Table 7.12 A comparison of *Otomys unisulcatus* lodge and *Parotomys brantsii* warren densities per quadrat for different vegetation type-status groupings during 1989 and 1991. Mean ($\pm$ 1 standard deviations), n = number of quadrats sampled. OSBV = Open Spekboomveld, KBV = Karroid Broken Veld, SK = Succulent Karoo.

	1989	1991	t test
Otomys unisulcatus - OSBV and KBV	258 (170)	144 (127)	P < 0.01
n	70	20	
Parotomys brantsii - KBV and SK	82 (63)	15 (35)	P < 0.01
n	70	20	

Table 7.13 Results of correlation and stepwise multiple regression analyses of *Parotomys brantsii* warren and *Otomys unisulcatus* lodge densities and measures of habitat structure. %GC = percentage ground cover.

Variable	Correlation	[1]Contribution to coefficient of determination in regression analyses
	Parotomys brantsii	
% Open ground (0-15 cm)	0.50 ***[2]	
% GC 16-75 cm	0.08 NS	
% GC 76-150 cm	-0.49 ***	
% GC 151-250 cm	-0.40 ***	
% GC 251-350 cm	-0.50 ***	
% GC 351-450 cm	-0.46 ***	
% GC > 451 cm	-0.31 **	
Heuweltjies	0.75 ***	0.56 (1)[3]
	Otomys unisulcatus	
% Open ground (0-15 cm)	0.11 NS	
% GC 16-75 cm	0.10 NS	
% GC 76-150 cm	0.44 ***	
% GC 151-250 cm	0.23 *	
% GC 251-350 cm	0.05 NS	
% GC > 451 cm	-0.12 NS	
No. Shrubs 76-150 cm	0.77 ***	0.60 (1)
No. Shrubs 151-250 cm	0.73 ***	
No. Shrubs 251-350 cm	0.25 **	

1 with *P. brantsii* or *O. unisulcatus* densities as dependent variable
2 NS = Not significant, * = P < 0.05, ** = P < 0.01, *** = P < 0.001
3 contribution to multiple coefficient of determination and (order of entry into regression model)

In SK and KBV, mean bird biomass per transect (15 000 m^2) did not differ significantly (729 *vs* 568 g; P < 0.50; n = 6; t test).

7.3.4 Reproductive success

For 1989 and 1991 the Reproductive Index was significantly correlated with the Otomyinid Index ($r = 0.40$; $P < 0.001$, $n = 18$), and the Reproductive Index values of each group and its nearest neighbour for 1989-1992 ($r = 0.73$; $P < 0.001$; $n = 106$). The annual reproductive success (1988 = 0.7 young per group, 1989 = 1.6, 1990 = 1.9, 1991 = 0.2, 1992 = 0.9) was significantly correlated with the annual rainfall (1988 = 156.4 mm, 1989 = 297.0, 1990 = 283.7, 1991 = 120.8, 1992 = 259.5) ($r = 0.90$; $P < 0.05$; $n = 5$).

7.4 DISCUSSION

7.4.1 Prey preference

Various problems are associated with the interpretation of prey mass, as opposed to numbers, in depicting the relative importance of each prey taxon. The biomass consumed may be strongly biased if calculated from mean body mass values (Steenhof 1983), since birds of prey may often take juveniles (Simmons *et al.* 1991; tortoises, this study) or individuals with lower than the mean body mass value of the population (Temple 1987). The wide size range of prey items caught by PCGs (0.02-2305 g), however, required an importance value that weighed the mass contribution to the diet, rather than merely the frequency of particular prey items. Compare the size range of prey items caught with 1-15 kg for Martial Eagle *Polemaetus bellicosus* (Boshoff *et al.* 1990), 0.2-13.0 kg for Black Eagle *Aquila verreauxii* (Boshoff *et al.* 1991) or 8.2-83.2 g for the Blackshouldered Kite *Elanus caeruleus* (Mendelsohn 1982). Notwithstanding these constraints, I contend that the results presented here provide a realistic picture of the importance of taxa as well as diversity in the diet of the PCG at Calitzdorp.

When taxa derived from the pellet analysis are compared with prey caught during direct observations, there were no major differences in proportions for mammals, 91% *vs* 86%, or birds, 4% *vs* 6%, but proportion reptiles did differ, 3.6% *vs* 8% (see above, Tables 7.2 & 7.4). In the pellet analysis the more resilient prey remains, *e.g.* mammals, may also be over-represented compared with the more digestible items such as birds and reptiles (Brooker & Ridpath 1980; Simmons *et al.* 1991). When the above results are compared with nest provisions, the selection shifted further towards reptiles. A omission from the prey taxa caught, compared with that provisioned, are the absence of insects and spiders (Table 7.5). This shift may be the result of PCGs selecting larger prey taxa, *e.g.* snakes, to satisfy the growing need for food of chicks and female at the nest. The lack of arthropods in nest site provisions could be attributed to individuals being to small to warrant the time and energy. As has been demonstrated by Collopy (1983), Simmons *et al.* (1991) and this study, only when pellet, prey remains and direct observations are combined can a less biased picture of the diet of a raptor be obtained.

Published and unpublished observations of PCG prey (Appendix 4) are not in close agreement, as far as numbers, biomass distribution and species composition are concerned, with those from the diet analysis at Calitzdorp. Observations from other areas showed that rodents, larks (Alaudidae), snakes (Serpentes) and lizards (Sauria) were preferred and bird taxa such as francolins (Phasianidae), korhaans (Otididae) and owls (Strigiformes) are well represented. It is only in the reptile genera, *Pseudaspis* (mole snake), *Psammophis* (sand snakes), *Mabuya* (typical skinks) and *Cordylus* (girdled lizards), that are equally represented in both samples. The absence of more larger prey items, *e.g.* guineafowl or hares, from the Calitzdorp prey remains could be attributed that in the five years of the study I never observed a guineafowl, and only once Greywing Francolin *Francolinus africanus* and hare. However, Black Korhaan *Eupodotis afra* were numerous, but did not appear in the prey remains. Since the origin (either prey caught or carrion) of remains collected from nests at Calitzdorp are unknown, it is not known if PCGs actually caught juvenile Cape Hare *Lepus capensis* (1633 g) or African Wild Cat *Felis lybica* (4300 g). The carrion records show that PCGs demonstrate a preference for hares and were even able to approach large items, *e.g.* Steenbok *Raphicerus campestris*. Overall, the lack of agreement in prey taxa between published and unpublished observations and Calitzdorp is the result of two factors. The opportunist PCG (Tables 7.1 & 7.2; Appendix 4) will take a few individuals of whatever is available, *e.g.* hatchling tortoises. Secondly, the majority of prey, *e.g.* rodents or arthropods, are small and fall outside the 'interest' field of the general observer. Therefore, only the capture of larger and more spectacular taxa are reported. This result can perhaps be used as a remainder that to compile a prey list from anecdotal observation for an opportunist aerial predator, may prove erroneous. A more realistic list of prey should read as follows: mostly rodents, but also birds (from 25-1352 g), hatchling tortoises, snakes, lizards, sunspiders, harvester termites, grasshoppers, beetles and carrion.

The predation on hatchling tortoises warrants special mention since very little comparative quantitative data are available. Black Eagle and Martial Eagle are known to take the adult and juvenile *G. pardalis* and *P. tentorius* (Boshoff *et al.* 1990; Boshoff *et al.* 1991). On Dassen Island Kelp Gulls *Larus dominicanus* preyed mainly on juvenile Angulate Tortoises *Chersina angulata* and the absence of hatchling shells were attributed to their soft shells which can be torn apart and eaten at the capture site (Branch & Els 1990). In certain areas in California, the Common Raven *Corvus corax* may prey heavily on juvenile Desert Tortoises *Gopherus agassizi* (Anon 1989). As the above are all records of adult or juvenile predation, it is unclear how the variation in size and weight of the shell, and the habits of the various tortoise species render them more vulnerable to different size aerial predators. Compared with the hatchling Tent Tortoise, the larger hatchling Leopard Tortoise will possibly be easier to detect and will certainly provide a higher energy return.

7.4.2 Otomyinid densities and habitat parameters

The two otomyinids, *O. unisulcatus* and *P. brantsii* are: largely sympatric, similar in morphology and body size, diurnal and crepuscular, social and communal, and both occur in the drier regions of southern Africa (Nel 1975; Brown 1987a; de Graaff 1981; Smithers 1983). Litter size is small, 1.8 (n = 9) for *O. unisulcatus* (Brown 1987a), and 2.1 (n = 9) for *P. brantsii* (Smithers 1971). Although both are herbivorous and their diets overlap as a function of food availability, du Plessis *et al.* (1991) suggest their niches are separated on a spatial rather than a trophic basis.

In this study area the majority of *P. brantsii* warrens were situated within heuweltjies (Table 7.8). Heuweltjies are earth mounds, 25-32 m in diameter, 1.25-2.25 m in height and are dispersed in a uniform fashion 41-51 m apart (measured centre to centre) (Cox *et al.* 1987; Lovegrove & Siegfried 1989). The highest heuweltjie density recorded to date in South Africa, is 500/km², 37 km southeast of the study area (Lovegrove & Siegfried 1989), compared with 40-372/km² (mean = 210; Table 7.8; heuweltjies column x 4) for the Calitzdorp study area. They are biological in origin and involve soil translocation and digging activities by either termites or bathyergid mole rats (Cox *et al.* 1987; Milton *et al.* 1992). The stone and soil contents of heuweltjies *vs* the surrounding soil differ as less gravel and pebbles are found in the heuweltjies (Cox *et al.* 1987; Lovegrove & Siegfried 1989). If the habitat requirements of *O. unisulcatus*, and *P. brantsii* are compared, *P. brantsii* prefer deeper soils (77 cm *vs* 48 cm) (du Plessis & Kerley 1991). In the shallow soils (< 40 cm) of the study area (Ellis & Lambrechts 1986), *P. brantsii*, an obligatory burrower, is probably dependent on the deeper, more penetrable soils of heuweltjies. The relationship between heuweltjie and *P. brantsii* densities can therefore be explained by the dependability of *P. brantsii* on the suitable heuweltjie soils.

O. unisulcatus are dependent on shrubs to build their lodges under (Table 7.13; Brown 1987a; Vermeulen & Nel 1988). Shrubs do not only provide lodging sites, but also sticks to build the lodges, food and cover against predators (du Plessis & Kerley 1991; du Plessis *et al.* 1991) At Calitzdorp, the thorny *Carissa haeatocarpa* and *Mattenys polyacantha* are selected, presumably to prevent terrestrial predators such as Black-backed Jackals *Canis mesomelas* from getting to and digging into the nests (Vermeulen & Nel 1988; GM pers. obs.). The lack of a significant correlation between the densities of *O. unisulcatus* and *P. brantsii* agrees with the specific habitat requirements of these two species, preventing them from being in direct spatial competition (du Plessis & Kerley 1991).

PCGs were catching *P. brantsii* individuals in proportion to the warren densities, but not to *O. unisulcatus* lodges. This result could be attributed to two factors. Firstly, PCGs may find it easier to catch *P. brantsii* on or near their warrens that are normally devoid of any vegetation (Palmer 1987; Milton *et al.* 1992; GM pers. obs.). The higher ground cover *per se* and fairly straight paths between adjacent shrubs may minimize the exposure of *O. unisulcatus* to aerial predators (Vermeulen & Nel 1988). Secondly, the relative density of the third dominant prey species, *Rhabdomys pumilio* may influence the prey selection since, like *O. unisulcatus*, *R. pumilio* inhabit areas with a high vegetation cover (Bond *et al.* 1980). Indeed in OSBV and KBV, groupings that were catching proportionally more *O. unisulcatus*, *e.g.* MpO, were catching less *R. pumilio* and *vice versa* (Fig 7.3)).

7.4.3 Otomyinid densities fluctuate

Fluctuating rodent densities are known to influence the reproductive success of avian predators greatly (Mebs 1964; Hagen 1969; Simmons *et al.* 1986). The relationship between Otomyinid and Reproductive Indices strengthen the hypothesis that the PCG's annual reproductive success was dependent on otomyinid densities. Such an assumption should be treated with caution since it does not take into account the breeding status of each group, random environmental factors and the variance of otomyinid densities within territories, and within and between years (Gargett 1990; Koenig *et al.* 1992). In Chapter 3, I concluded that 1988 was an intermediate reproductive year (0.7 young per territorial group; Table 3.6), 1989 and 1990 high reproductive years (1.6 and 1.9), 1991 a low reproductive year (0.2), and 1992 again an intermediate year (0.9). Therefore, following the above hypothesis, the otomyinid numbers increased form 1988 to 1989, reached a peak during 1990, crashed during 1991 and returned to the 1988 'level' during 1992. Furthermore, otomyinid densities and reproductive success (1.6 and 0.2) varied greatly between 1989 and 1991 (Table 7.12). Also compare the reproductive rate of the two years, during 1989 23 groups initiated 32 breeding attempts, whereas during 1991 29 groups only initiated five (Figs. 3.2 & 3.4). The otomyinid population therefore goes through major cycles, a recorded trend for rodents in general (French *et al.* 1976) and *P. brantsii* in specific (Nel & Rautenbach 1975).

However, otomyinid fluctuations do not only have a temporal, but also a spatial component. During 1989, PCGs double-brooded in the centre of KBV, one polyandrous trio fledging four chicks successfully (Fig. 3.2). During 1990, groups from the two surrounding vegetation types that bred close to the border of KBV, also double-brooded (Fig. 3.3). After the apparent otomyinid crash, breeding was localised in the KBV/OSBV border region (Fig. 3.4). There were thus variations in otomyinid densities, nor only in the study area, but also within vegetations types. These variations were however on a large scale and only differed between sections of the study area and not between territories (GM pers. obs.). By 1992, otomyinids recolonised the full length of KBV/OSBV border and western part of the study area, but not the centre of KBV (Fig. 3.5). The significant relationship between the reproductive success of each group and its nearest neighbour for 1989-1992 supports this hypothesis. What causes these changes in abundance in time and space is unclear, but both otomyinids are susceptible to sporadic outbreaks of plague *Yersina pestis* (De Graaff 1981). These dramatic changes may also be associated with changes in the food supply, which again are dependent on the rainfall (Nel 1983). Since rainfall was positively correlated with reproductive success, an inter-relationship existed between rainfall, otomyinid densities and reproductive success. Otomyinid densities may therefore not fluctuate in 'natural' five year cycles (1988 to 1992), but in the semi-arid Calitzdorp study area, abundance may be limited by good rainfall.

7.4.4 Ecological factors that constitute habitat quality

Below I identify four ecological factors that may influence the fitness of PCGs through an increase in reproductive success. I have focused on KBV since, only in this vegetation type, were co-breeders present, and groups contained the largest number of non-breeders and had highest reproductive success (see Chapters 3, 4 & 6).

(1) The first ecological factor which influence PCG demography is habitat associated with high otomyinid densities. For both otomyinids to occur at high densities, a vegetation type must contain a maximum number of shrubs in the 76-150 cm height class, as well as heuweltjies (Table 7.13). KBV contained the highest densities of 76-150 cm high scrubs, albeit not significantly higher than OSBV and CSBV. Furthermore, KBV possessed along with SK, the highest densities of heuweltjies. KBV was therefore the only vegetation type that contained high values for BOTH habitat variables.

Why, during 1989, the significantly lower heuweltjie and *P. brantsii* warren densities in territories of polyandrous trios, but higher *O. unisulcatus* lodge densities in territories of monogamous pairs (Table 7.10), are problematic? The significantly lower proportion of cover in the lower vegetation layer (16-75 cm), coupled with the significant higher *O. unisulcatus* lodge density, may have eased catchability. Whatever caused these differences, otomyinid densities still did not differ between quadrats occupied by polyandrous trios and monogamous pairs. More important than mean otomyinid densities, is the variance in otomyinid densities between quadrats. Since the variance in otomyinid densities was significantly lower in quadrats occupied by polyandrous trios, prey was more evenly distributed. This, in turn, may have resulted in more predictable hunting conditions.

Surprisingly, no significant differences in densities of *O. unisulcatus* lodges and *P. brantsii* warrens were found between OSBV (PCGs present) and CSBV (no PCGs), as well as between occupied and unoccupied quadrats in SK. This result suggests that other factors, *e.g.* the availability of shrubs as perches (SK) or the proportion ground cover limiting the view of potential prey (CSBV), may also influence habitat quality. This hypotheses will be tested in the next chapter.

(2) The second ecological factor is the high otomyinid densities that can be attained during some years, which, in turn, may have allowed PCGs to double-brood. Normally two to

six otomyinids inhabit a single lodge or warren (Brown 1987a; Milton *et al.* 1992). If one conservatively assumes that two individuals inhabit a lodge, then, for *O. unisulcatus* in KBV, the biomass value of 269 kg/km^2 was estimated (0.1239 kg mass x 2 individuals x 271 lodges (Table 7.9) x 4 (1 quadrat = 0.25 km^2)). For *P. brantsii*, at two individuals per warren, the biomass estimate was 79 kg/km^2 (0.124 x 2 x 80 x 4) and for both otomyinids, 347 kg/km^2. Corresponding otomyinid values for CSBV would be 76 kg/km^2, 189 kg/km^2 for OSBV and 84 kg/km^2 for SK. Actual biomass values will be higher since *R. pumilio*, gerbils, shrews, small mammals or other prey taxa mass values were not taken into account.

These very high otomyinid biomass values are more remarkable if Calitzdorp's mean annual rainfall of 198.8 mm is taken into account. In fact, Schulze & McGee (1978) describe the Little Karoo, within which Calitzdorp falls, as an area "in virtually permanent drought". In comparison, Kerley (1990) estimated a mean small mammal biomass value of 32 kg/km^2 for six sites in the southern Karoo (although none in the Little Karoo), all with a similar mean annual rainfall of approximately 200 mm. For desert grasslands in North America with a annual rainfall of 230 mm, French *et al.* (1976) estimated a mean small mammal biomass of 67 kg/km^2. Mean small mammal biomass values for five other sites with higher rainfall ranged from 8-81 kg/km^2 (French *et al.* 1976).

A further advantage of a high otomyinid biomass is that, in temperate regions (see Chapter 3), raptors that prey on often abundant rodents are able to double-brood (Newton 1979; Bednarz 1987a). White-tailed Kite *Elanus leucurus* (Pickwell 1930), American Kestrel *Falco sparverius* (Howell 1932), Harris' Hawk (Bednarz 1987a) and Blackshouldered Kite (Mendelsohn 1989) have been noted. Double-brooding by a raptor in temperate regions is rare since the relatively adverse winter conditions limit the summer breeding period (Newton 1979). PCGs overcame this restriction by overlapping the two breeding cycles (Chapter 3). The very high otomyinid densities at Calitzdorp probably allowed males, mostly from groups in KBV, to provision the female at a rate sufficient to release her from hunting duties and allow her to accumulate the necessary body reserves for a second breeding attempt (Chapters 3-5). With two males provisioning, polyandrous trios were able to undertake more frequent and successful breeding attempts, even for two years in succession (Chapters 3).

(3) The third ecological factor involves a diversification in prey selection, within the framework of the three dominant prey species. Class diversity in the diet was the lowest for polyandrous trios (PtK) and monogamous pairs (MpK) in KBV, since these groups were preying predominantly on small mammals. However, the three dominant prey species were preyed upon at a far higher proportion than other prey taxa, and diversity and evenness of the three dominant prey species were the highest for PtK and MpK. Groups in Karroid Broken Veld were therefore not only selecting a higher biomass within a single taxa (Rodentia), but within this taxon, a higher diversity of the three dominant prey species. The ability to diversify may provide these groups with certain advantages. Differences in annual rodent reproductive cycles and population numbers of each species may buffer PCGs in KBV against fluctuations in the availability of one or two species. This, in turn, may lead to a more stable prey abundance. Of course if they select these species in proportion to their abundance, then diversification is the result of a wider choice, on its own also a benefit.

(4) The fourth ecological factor is the selection of prey species that satisfy your minimum daily prey requirement. The PCG was regarded as a generalist feeder (Brown 1970), but this study revealed that PCGs, at least at Calitzdorp, demonstrated a preference for rodents. In OSBV groups were catching almost exclusively *O. unisulcatus* (76%), in KBV *O. unisulcatus* (42-48%) and *P. brantsii* (18-32%), and in SK, *P. brantsii* (35%). It is an open question if PCGs in KBV and OSBV deliberately ignore alternatively prey such as birds, in favour of rodents. The lack of a significant difference in live bird biomass between KBV and SK, but the large proportion of birds in the diet of SK birds (21.9% *vs* 0.8-2.8%) may point to the fact that PCGs indeed do. Selection is thought to be favoured

when prey are abundant and the difference among prey values is large (Huges 1979), both components that had been identified in this study. Again, there was a further advantage for PCGs in KBV since they had the potential to select from two otomyinids. Furthermore, these otomyinids that, on average, weigh 124 g, may have satisfied the PCG's estimated minimum daily requirement of 124 g. Selecting otomyinids may therefore prove to be cost- and time-effective.

CHAPTER 8

PERCH AVAILABILITY AND PREY VISIBILITY: FACTORS THAT MAY CONSTITUTE HABITAT QUALITY AND PROMOTE SOCIALITY IN THE PALE CHANTING GOSHAWK

SUMMARY

For the Pale Chanting Goshawk (PCG), not only is the abundance of prey important, but also the ecological makeup of its hunting habitat. Factors such as perch availability and prey visibility can improve the potential to hunt within a habitat considerably. Variables that may distinguish good *vs* poor hunting habitat such as perch height and abundance, and proportion of open ground and perch cover were investigated. The PCG qualified as a pause-travel predator since it perched more than ten times per capture. PCGs hunted almost exclusively from perches and demonstrated a clear preference for perching on the highest available perches, often artificial, probably because they were also used for other social purposes such as advertising behaviour. A positive relationship was found between perch height and horizontal striking distance for all striking modes (successful, unsuccessful and abandoned), but not for successful strikes. It is suggested that the number of perches is of more importance than perch height, since with a nine-fold increase in perch height there was only a two-fold increase in striking distance. In Succulent Karoo (SK), PCGs occupied areas, not only with significantly greater number of perches, but more artificial (fence posts) than natural perches (trees and shrubs). Perch availability, therefore, facilitated the occupancy of territories in SK. Alternatively, in Closed Spekboomveld (CSBV), where there are no PCGs, high proportions of perch cover (37%), and low proportions open ground (43%) was probably shunned because of a very limited view of the ground and prey. It was therefore prey visibility that separated CSBV from Open Spekboomveld (OSBV), which PCGs utilise, despite its significantly lower proportions of perch cover (19%) and higher open ground (50%), but not number of perches. No differences in hunting tactics and success of PCGs in KBV and SK could be demonstrated, except that the lower density of perches in SK (means = 433 *vs* 4 402 perches per quadrat) resulted in birds having to fly further when travelling between perches. KBV, with 63% open ground, 6% perch cover and a tree or shrub every 60 m^2, may provide the optimum hunting habitat for this pause-travel predator to select larger rodent prey with equal hunting effort. Prey visibility and perch availability may therefore influence prey selection and hunting tactics, and therefore habitat quality and fitness.

Moreover, not only hunting habitat influences an individual PCG's hunting success, but also the option of coordinated hunting by several group members. A low vertebrate hunting success of 12% for single, and 24% for social hunts, highlighted the difficulty of catching vertebrate prey, *e.g.* rodents. PCGs fulfilled almost all requirements to qualify as cooperative hunters, although only one out of every nine strikes were social. Furthermore, since the individual hunting success, at 12%, was equal for social and single hunts, there may have been no preference given to social hunting. Nevertheless, the fact that, during social hunts, the bird did not make the initial strike was allowed to catch the prey, benefitted the group and qualified the PCG as a cooperative hunter. Since juveniles and adult non-breeders were allowed to partake in cooperative hunts, the skill learned to catch elusive vertebrate prey may increase their survival.

8.1 INTRODUCTION

Habitat quality is one of the ecological factors that may promote the evolution of cooperative breeding and delayed dispersal (Koenig & Pitelka 1981; Bednarz & Ligon 1988; Stacey & Ligon 1991; Koenig *et al.* 1992; Komdeur 1992). Among the factors that constitute high-quality habitat are attributes that may influence their hunting success, *e.g.* perch height and abundance, vegetation density and prey visibility (Fitzpatrick 1980; Simmons 1989; Sonerud 1992; Yosef 1992; Widen 1994). When hunting, many predators search in a pause-travel mode since they cannot search efficiently for prey while moving (Tye 1989). The time that they pause or perch may also depend on the size of the area that can be searched, and prey taken successfully from the perch (Sonerud 1992). The area scanned may, in turn, depend on the height of the perch and structure of the surrounding vegetation (Sonerud 1992; Yosef 1992). For a bird like the PCG, which searches visually for terrestrial prey and hunts from a perch to the ground (Steyn 1982), hunting success may influence territorial utilization and life history traits (Yosef 1992).

Sociality in raptors is rare, probably because of the limiting effect of food and aggressiveness associated with these aerial predators (Faaborg & Bednarz 1990). However, cooperative, coordinated hunting by several individuals in capturing and sharing prey is associated with sociality in the Harris' Hawk, another cooperative-breeding raptor. Bednarz (1988) suggested that the social nature of this species may be related to the adaptive advantages of cooperative hunting. The intrinsic benefit of this foraging strategy, although difficult to distinguish from other types of social hunting (Hector 1986; Ellis *et al.* 1993), may have favoured the evolution of cooperative breeding (Bednarz & Ligon 1988).

The aims of this chapter are to study: (1) PCG hunting habitat such as the importance of perch height and abundance, and vegetation structure, and (2) sociality and cooperative hunting strategies for groupings of different status and vegetation types.

8.2 METHODS

8.2.1 Striking modes

Two assumptions need to be made concerning the hunting tactics of a perch-based hunter: (1) the bird searches a circular area under each perch, *i.e.* perch area, and (2) the radius of the search area increases with an increase in perch height (Fitzpatrick 1980; Andersson 1981; Tye 1989; Sonerud 1992). The perch areas of all perches combined makes up the utilizable area per surface unit (Yosef & Grubb 1992). However, if the utilizable area is less than the surface area, 'dead ground' or unusable area exists. For a perch hunter, a utilizable/surface area ratio of larger than one will provide coverage of the total surface area, and access to the prey base (Yosef & Grubb 1992).

Employing instantaneous sampling during 1988 (Chapter 2), I recorded perch height, horizontal striking distance, the strike mode, detection and giving-up times, and time hunting and walking/sitting on the ground for a population of PCGs. The horizontal striking distance was the distance in metres (rounded off to the nearest 10 m) from the base of the perch to the site of impact. A strike is defined as a PCG flying from a perch to prey on the ground. Three striking modes were recognised. In the first two, the PCG alighted on the ground, either successfully (successful strike) or unsuccessfully (unsuccessful strike) catching the prey. In the third, the bird flew down from the perch and, on reaching the point of impact, briefly hovered (for a second or two) one metre above the potential prey, and flew off (abandoned strike). Perching strategies were divided into those in which the PCG flew to a second perch without attempting a strike (giving-up), and those in which a strike was launched (detection) (Sonerud 1992). Data were analysed for 69 observation periods (11 355 min., mean = 165 ± 65 min.), from the non-breeding and pre-laying periods. Data were collected from first copulation to prior to males starting provisioning females to avoid sampling the increased hunting intensity of males provisioning females. To study the relationship between perch height and striking distances, simple linear regressions and tests for the equality of regression lines were preformed (BMDP-1R;

Dixon *et al.* 1990). Data were log transformed as to correct for the decrease in the capacity in prey detection with an increase in perch height (Andersson 1981).

8.2.2 Single and social hunting

A single strike is defined as only the focal bird striking. A social strike involved either the focal bird striking and being joined in the hunt on the ground by group members, or the focal bird joining group members. A social strike was successful if any of the participating PCGs, including the focal bird, caught prey. Social strikes involving two birds were only recorded during observation periods. Strikes to harvester termite colonies were analysed separately, since prey was not chased, but a PCG ate numerous individuals over several minutes standing at the termites' foraging port (GM pers. obs.). Only observation periods of $\geq$ 60 minutes were analysed, *i.e.* 58 observation periods (10 208 min.; mean = 176 ± 63) where single and social strikes were recorded, and an additional 17 observation periods (2 074 min.; mean = 123 ± 54) for single strikes. Rates per hour were calculated for each observation period and compared between observation periods. To study movement frequency, the number of quadrats (500x500 m) visited per hour were calculated. Data were analysed for adults and juveniles from three polyandrous trios in KBV and three monogamous pairs in SK.

8.2.3 Sociality

To study the association of a PCG with other group members, the presence of all other members within a 100 m radius from the focal animal was recorded. For each observation period, the proportion of time spent alone or in association with one or more birds was calculated, and then I calculated a mean for all observation periods per grouping as to avoid pseudoreplication. Data were analysed for 48 observation periods (7 632 min; mean = 159 ± 63 min.), only for adults of three polyandrous trios in KBV and three monogamous pairs in SK. Lastly, as for data in section 8.2.1, the minutes per hour adults and juveniles spent within 100 m of other group members was calculated.

8.2.4 Habitat parameters

To study perch height preference in relation to its relative abundance, I analysed perch preference and availability for four PCG groups, each territory presenting its own combination of natural and artificial perches. A natural perch was defined as plant, alive or dead, taller than 75 cm. Artificial perches were fence posts (1.5 m in height), telephone (6 m) and ESKOM (9 m wood power pylons) poles. Apart from natural perches, in SK, Group Engelskamp had predominantly fence posts and Sisal trees available, and Group Badsaf had fence posts and telephone poles. In KBV, Group Okkies had fence posts, telephone and ESKOM poles, and Group JohanG only fence posts. Alien Sisal trees *Agave mericana* were included as artificial perches since PCGs perched on the 6-7 m high panicles of these 2 m high fleshy-leafed shrubs. For these groups, for quadrats sampled within each territory, I calculated the mean number of perches available per height class. For five observation periods from Group Engelskamp, 10 for Badsaf, four for Okkies and five for JohanG, I calculated the mean percentage minutes perched on different height class perches.

For 20 quadrats in CSBV, 11 in OSBV, 90 in KBV, and five in SK, I counted, for each height class, all natural perches within a 50 m diameter circular plot from the centre of the quadrat. The height classes were: 76-150 cm, 151-250, 251-350, 351-450, 451-550, 551-650 and 651-750 cm. Natural perch values were extrapolated to estimate the number per quadrat. For quadrats with low natural perch numbers, three in KBV and 102 in SK, I counted the actual number of natural perches. In each quadrat sampled, I measured each fence's length and inter-fence post distance (particular to each fence), and calculated the number of fence posts per quadrat. In addition, I counted the actual number of telephone and ESKOM poles per quadrat.

To determine the proportion ground cover in each height class, from the centre of each quadrat in a random direction I placed a 50 m line with knots 1 m apart. Using the point method (Bond *et al.* 1980) the height of the vegetation at each interval was measured and a proportion open ground (0-15 cm) and perch cover (all cover > 75 cm tall) calculated.

Data for natural and artificial perches for each height class were combined to calculate a number of perches per quadrat. Each perch height was then scored with the circular surface area, the perch area, that could be scanned by a PCG from the top of a perch. The radius of the circle was obtained from the significant regression between horizontal striking distance and perch height (see Section 8.3.3). To calculate a perch area value per quadrat, the perch area for each perch height was multiplied by the number of perches in that height class, and values for all height classes combined.

The proportion open ground and perch cover, relative density of natural, artificial and all perches, and perch area per quadrat were compared between vegetation types, mating systems (polyandrous trios and monogamous pairs in KBV), and occupied and unoccupied quadrats in SK. A logarithmic transformation, log(x+1) was employed in analysis of variance (ANOVA) and t tests with Bonferroni-adjusted significant levels, to improve the normality of the data and to standardise the considerably different scales of variables.

Furthermore, for direct comparison between chapters, the 100 quadrats sampled in Chapter 7 were extracted from the 231 analysed above. I used the variables proportion open ground, proportion perch cover, relative density of natural and artificial perches, and perch area in a stepwise discriminant functions analysis (DFA; BMDP-7M) in a log-log model to determine if one or more of the five ecological variables could be used to distinguish quadrats of the different categories. In the DFA, the jackknifed percentage correct classification was used as a measure of discriminating ability (Lachenbruch & Mickey 1986).

8.3 RESULTS

8.3.1 Sociality and hunting success

Members of groups with polyandrous trio groups from KBV and groups from SK with monogamous pairs spent a mean per observation period of 76% and 77% of their time further than 100 m from other group members (Fig. 8.1). Members of monogamous pairs were recorded only in association with a third member, whereas members of polyandrous trios spent 5% of their time with three to four birds. Adults spent, on average, 17 min per hour with group members, significantly more than the 2 min per hour spent by juveniles (Table 8.1).

Adults made a successful single strike at a rate once every 4 h (0.15/h), whereas juveniles made a successful single strike at every 8.6 h (0.07/h) (Table 8.1). Adults initiated a single strike at a rate of once every 47 min (1.27/h), significantly less often than juveniles (once every 32 min. or 1.94/h). One out of every nine single strikes (12%) by adults was successful compared with one out of 27 (4%) for juveniles. Adult PCGs visited significantly more, twice as many quadrats, per hour than juveniles.

Social strikes involved one bird striking while chasing prey in and among the vegetation, very often with wings aloft and flapping, and being joined on the ground by one or more group members. If a vertebrate prey, *e.g.* an otomyinid rodent, was cornered under a shrub, PCGs would surround the shrub or perch on top it, and individuals would repeatedly strike at it by jumping into the shrub (flush-and-ambush strategy; Bednarz 1988). Of the six successful social strikes observed, in two, the bird that made the initial strike, once a juvenile, was successful. At the Calitzdorp study area, two birds were never observed striking simultaneously at the same prey. Once prey was caught by a PCG, it flew off with the item, and was not pursued aggressively by the remaining members. Adults were involved in a social strike at a rate of once every 3.5 h (0.17/h), one out every four (24%) being successful (Table 8.1). Juveniles were only involved in a social strike at

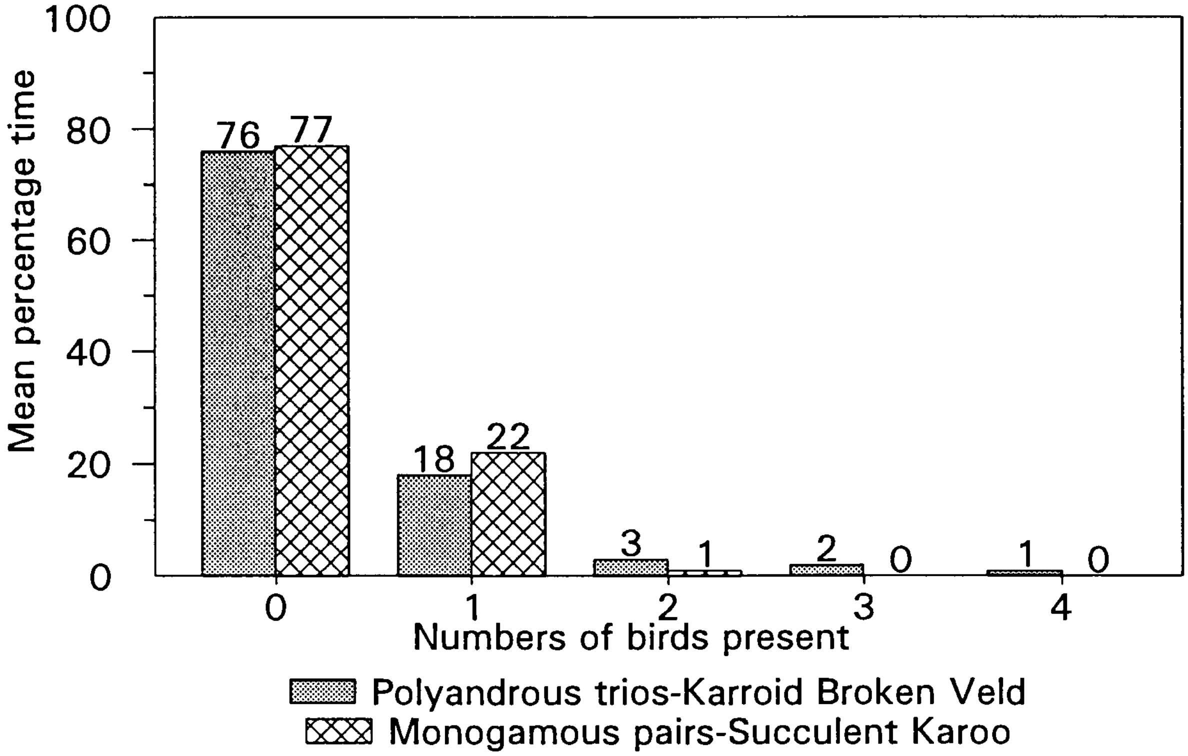

Fig. 8.1 Mean percentage time per observation period Pale Chanting Goshawk adults of polyandrous trios from Karroid Broken Veld and monogamous pairs from Succulent Karoo spent, in the non-breeding period, within 100 m radius of other birds.

Table 8.1 A comparison of single and social striking rates (per hour), giving-up rates (per hour), additional birds present (minutes per hour), and quadrats visited (per hour) per observation period by adult and juvenile Pale Chanting Goshawks. Mean and (± 1 standard deviation).

	Adults	Juveniles	*t* test
Single strikes			
Successful	0.15 (0.24)	0.07 (0.13)	NS
Unsuccessful	0.99 (1.05)	1.68 (1.00)	$P < 0.05$
Abandoned	0.12 (0.24)	0.20 (0.26)	NS
All single strikes	1.27 (1.12)	1.94 (1.22)	$P < 0.04$
Termite strikes	0.03 (0.26)	0.10 (0.33)	NS
Observation periods	58	17	
Social strikes			
Successful	0.04 (0.11)	0.00	NS
Unsuccessful	0.08 (0.19)	0.02 (0.07)	NS
Abandoned	0.05 (0.13)	0.00	NS
All social strikes	0.17 (0.28)	0.02 (0.07)	$P < 0.05$
Giving-up	2.53 (2.17)	2.57 (2.07)	NS
Additional birds	16.89 (18.15)	2.13 (4.20)	$P < 0.01$
Quadrats visited	2.47 (1.49)	1.23 (0.44)	$P < 0.01$
Observation periods	41	17	

a very low rate of or once every 30 h (0.02/h). The overall successful striking rate for single and social strikes was once every 3 h (0.19/h).

Striking rates for the different striking modes were not significantly different between adult polyandrous members from KBV and monogamous members from SK (Table 8.2). In SK, one out of every seven single strikes (15%) was successful, not significantly differed from one out of 10 (10%) in KBV (Chi-square; $P > 0.50$). The success rate of social strikes was 24% in both vegetation types. There was a trend for monogamous birds to be

Table 8.2 For adult Pale Chanting Goshawks from polyandrous trios and monogamous pairs, a comparison of single and social striking rates (per hour), giving-up rates (per hour), additional birds present (minutes per hour), and quadrats visited (per hour) per observation period. Mean and (± 1 standard deviation), t test.

	Monogamous pairs - Succulent Karoo	Polyandrous trios - Karroid Broken Veld	t test
Single strikes			
Successful	0.17 (0.25)	0.14 (0.23)	NS
Unsuccessful	0.89 (0.82)	1.09 (1.23)	NS
Abandoned	0.08 (0.19)	0.17 (0.29)	NS
All single strikes	1.14 (0.92)	1.39 (1.29)	NS
Termite strikes	0.07 (0.36)	0.00	NS
Observation periods	29	29	
Social strikes			
Successful	0.05 (0.13)	0.03 (0.09)	NS
Unsuccessful	0.09 (0.18)	0.08 (0.19)	NS
Abandoned	0.08 (0.17)	0.02 (0.07)	NS
All social strikes	0.22 (0.32)	0.13 (0.24)	NS
Giving-up	2.62 (2.26)	2.44 (2.15)	NS
Additional birds	18.03 (14.57)	15.90 (21.05)	NS
Quadrats visited	2.91 (1.66)	2.02 (1.15)	P < 0.05
Observation periods	19	22	

involved in a higher social striking rate (0.22 *vs* 0.13/h), whereas polyandrous birds concentrated more on single strikes (1.39 *vs* 1.14/h) (Table 8.2), but this trend could not be associated with vegetation types (Chi-square; P > 0.05). Birds in SK visited significantly more quadrats per hour. Termite strikes were recorded at very low rates, once every 20 h (0.03/h) for adults and 6 h (0.10/h) for juveniles, with a trend for adults to hunt more termites in SK (Table 8.2).

8.3.2 Hunting techniques

The perch-to-ground strike was employed in 97% (383/397) of hunts recorded. Once on the ground, prey was either chased actively, or the PCG would motionlessly sit and wait for a prey individual to move within reach (GM pers. obs.). Once within reach, the PCG would jump onto it. In the study area this surprise-pounce technique was used in all successful bird captures. In a further three hunts recorded, all unsuccessful, a bird was attacked from a perch and actively chased in horizontal flight (flapping flight; Cade 1982). A third technique, observed only once, involved a PCG flying directly between perches, briefly hovering 10 m above ground and diving down at a bird, chasing it in horizontal flight. A fourth technique was employed by a female in a large open area devoid of vegetation (perches), but with numerous active *Parotomys brantsii* burrows. She spent 61 minutes walking from burrow to burrow and surprise-pounced six times before capturing an individual.

8.3.3 Perch preference

In their territory, Group Engelskamp perched a mean proportion of 64% of their time on a mean of two, 6-7 m high, Sisal trees per quadrat and only 29% on 1-2 m high natural perches and fence posts (Fig. 8.2). Group Badsaf perched a mean proportion time of 49% on a mean of five, 6 m high, telephone poles per quadrat, as apposed to 28% on 474 fenceposts per quadrat (Fig. 8.2). Group Okkies, with ESKOM and telephone poles in their territory, perched 65% on one, 9 m high, ESKOM pole per quadrat, but only 13% on two telephone poles per quadrat (Fig. 8.2). Furthermore, fence posts (1.5 m) were used proportionally more than 1-2 m high natural perches. Group JohanG, with only 3 m high and lower perches available, preferred 2-3 m high natural perches and fence posts, but largely ignored 1 m high natural perches (Fig. 8.2). The above groups perched respectively 70%, 77%, 83%, and 13% of the time on artificial perches.

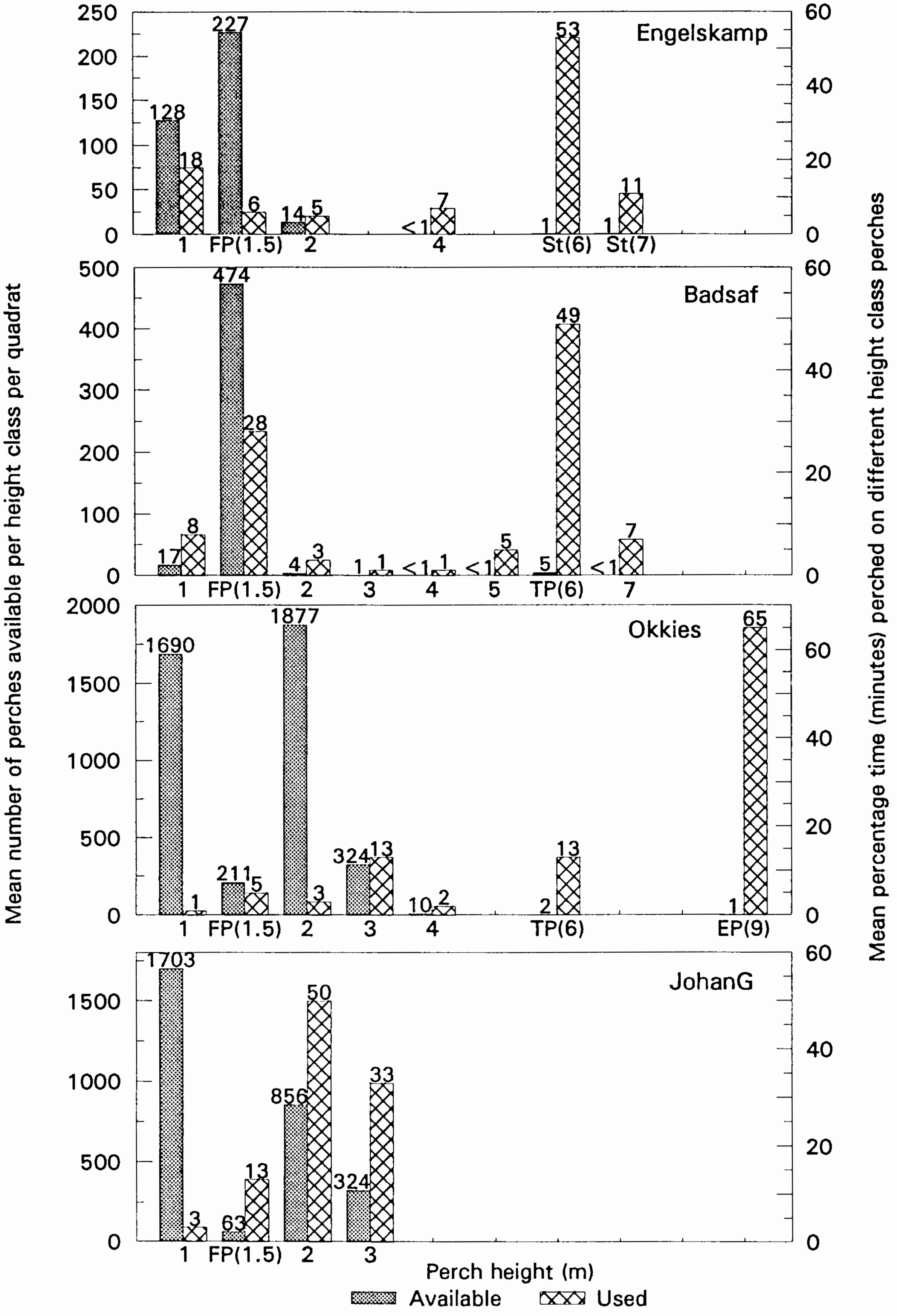

Fig. 8.2 A comparison of perch availability and usage. Apart from natural perches, Group Engelskamp had fence posts (FP=1.5 m) and Sisal trees (St) perches in their teritory, Group Badsaf fence posts and telephone poles (TP=6 m), Group Okkies fence posts, telephone poles and ESKOM poles (EP=9 m), and Group JohanG only fence posts.

8.3.4 Perch height and striking distance

For adults, no significant correlation was found between perch height and horizontal striking distance for successful strikes ($r = 0.43$; $P < 0.10$; $n = 19$), and abandoned strikes ($r = 0.12$; $P > 0.50$; $n = 26$), whereas a significant relationship existed for unsuccessful strikes ($r = 0.28$; $P < 0.05$; $n = 122$). However, the slopes or intercepts did not differ significantly between strike modes (ANOVA; $F = 1.13$; $P > 0.25$), therefore data were combined to produce a significant regression for all strikes ($r = 0.29$; $P < 0.001$; $n = 167$). For juveniles, no significant relationship exist between perch height and horizontal striking distance for successful strikes ($r = 0.05$; $P > 0.90$; $n = 5$) and abandoned strikes ($r = 0.39$; $P > 0.10$; $n = 12$), whereas a significant relationship existed for unsuccessful strikes ($r = 0.39$; $P < 0.001$; $n = 109$). Again, slopes or intercepts did not differ significantly between strike modes (ANOVA; $F = 1.18$; $P > 0.25$), therefore data were combined to produce a significant regression for all strikes ($r = 0.38$; $P < 0.001$; $n = 126$). However, slopes or intercepts did not differ significantly between adults and juveniles for strikes modes combined (ANOVA; $F = 1.21$; $P > 0.25$), and all strike data were combined to produce a significant regression ($r = 0.34$; $P < 0.001$; $n = 293$). The back-transformed formula was a follows: $Y = 10^{1.29} \times X^{0.37}$ where Y = horizontal striking distance and X = perch height. According to the formula, a PCG would strike 20 m from a 1 m high natural perch to 44 m from a 9 m high ESKOM pole (Fig. 8.3).

For strikes of adults and juveniles combined, perch heights were not significantly correlated with detection times ($r = 0.11$; $P < 0.10$; $n = 293$), nor with giving-up times ($r = 0.04$; $P > 0.50$; $n = 448$). However, horizontal striking distances were poorly, but significantly positively correlated with detection times ($r = 0.13$; $P < 0.05$; $n = 293$). The overall perching rate was 4/h (single, social and giving-up rates combined).

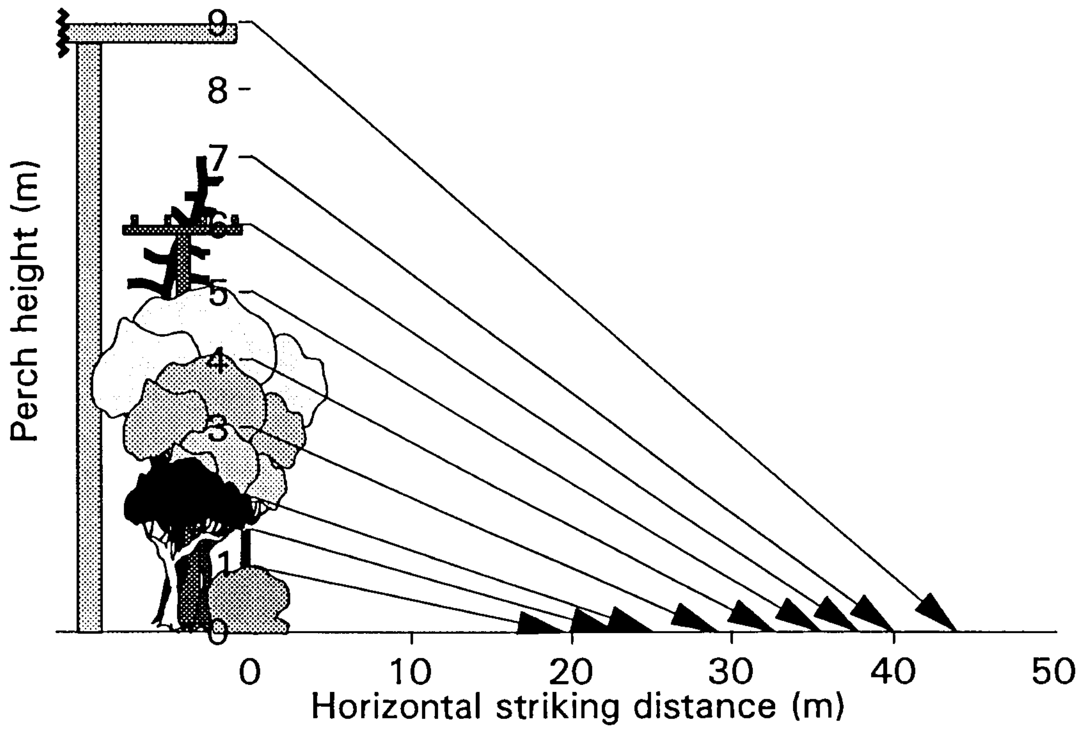

Fig. 8.3 Mean Pale Chanting Goshawk horizontal sriking distances from different perch heights from natural and artificial perches.

In the comparison between horizontal striking distances of polyandrous trios in KBV and monogamous pairs in SK, striking distances from 1 m high perches did not differ significantly (25 *vs* 31 m respectively; $P > 0.05$; $n = 21$; t test), nor did striking distances from 2 m high perches (32 *vs* 25 m; $P > 0.05$; $n = 28$; t test), from 6 m high perches (39 *vs* 43 m; $P > 0.05$; $n = 51$; t test), nor detection times (11 *vs* 12 min; $P > 0.05$; $n = 167$; t test) or giving-up times (11 *vs* 10 min; $P > 0.05$; $n = 298$; t test).

8.3.5 Habitat parameters

The proportion open ground and perch cover differed significantly between all vegetation types (Table 8.3; Fig. 8.4). The mean number of artificial perches only differed significantly between KBV and SK. The perch/surface area ratio at 70:1 was the highest in CSBV, and decreased to 2.8:1 in SK (Table 8.3). In occupied SK, the ratio at 3.04:1, was double that of 1.62:1 for unoccupied quadrats (Table 8.5). The DFA produced a 70-95% correct classification of quadrats in all vegetation types, and natural perches, perch cover and proportion open ground contributed significantly to the discriminant function (Table 8.6). In a comparison between CSBV with no PCGs and OSBV with PCGs, the DFA produced a 80-90% correct classification, but only perch cover contributed significantly to the discriminant function (Table 8.6).

For KBV, a comparison between quadrats occupied by polyandrous trios and monogamous pairs, only perch cover was significantly different and higher for polyandrous trios (Table 8.4). The DFA produced a low (55-70%) correct classification of quadrats and artificial perches, and perch cover contributed significantly to the discriminant function (Table 8.6).

In occupied and unoccupied quadrats in SK, the number of natural perches, artificial perches, all perches and perch area were significantly higher in occupied quadrats (Table 8.5; Fig. 8.4). The DFA produced a 80-90% correct classification, and natural perches contributed significantly to the discriminant function (Table 8.6).

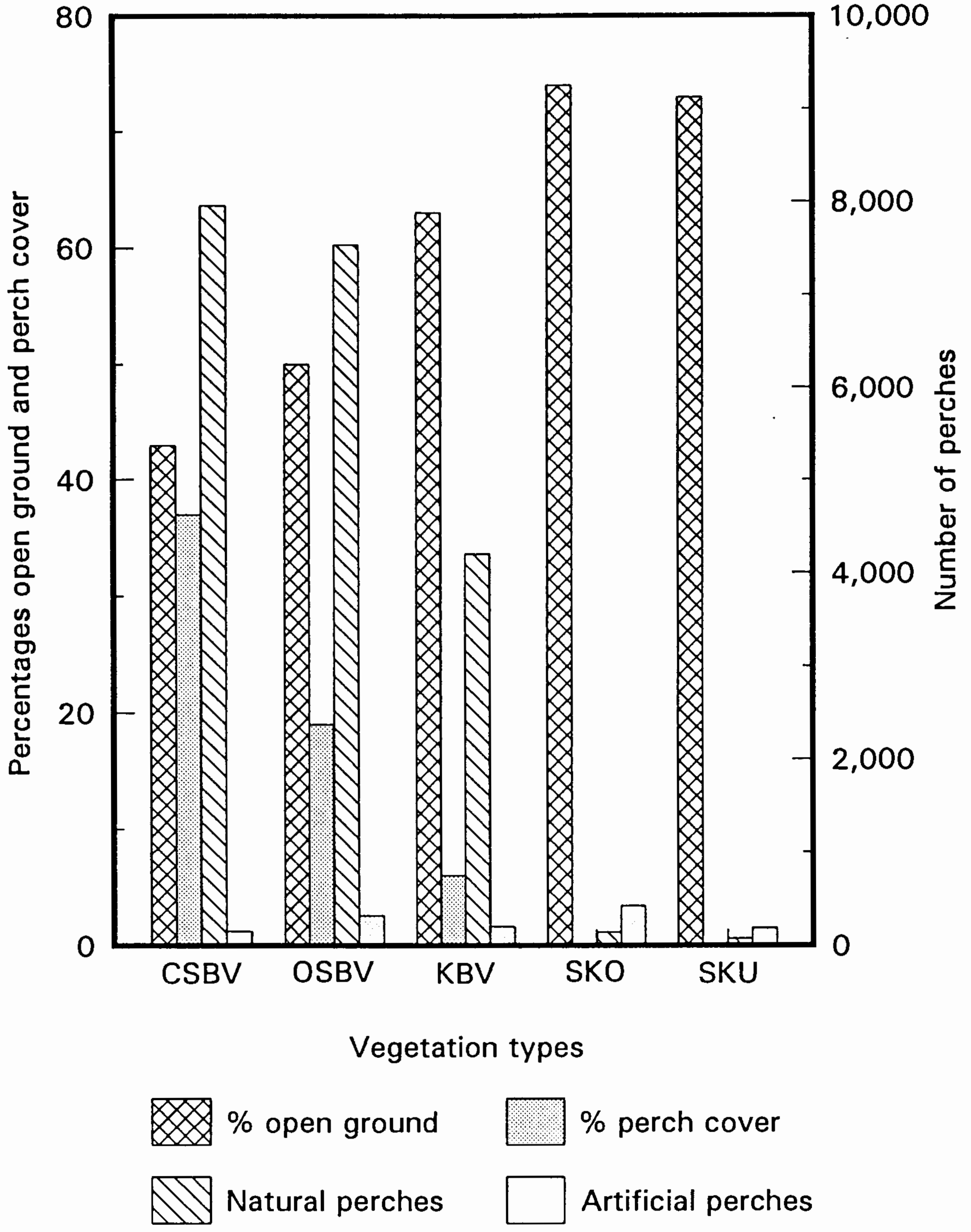

Fig. 8.4 The mean proportions open ground (0-15 cm) and perch cover (> 75 cm), and numbers of natural and artificial perches per quadrat for Closed Spekboomveld (CSBV) (with no Pale Chanting Goshaks; PCGs), Open Spekboomveld, Karroid Broken Veld (KBV), occupeid Succulent Karoo (SKO) and unoccupied Succulent Karoo (SKU).

Table 8.3 Results of a comparison between proportion open ground and perch cover, number of natural, artificial and all (natural and artificial) perches, and perch area for different vegetation types. Means and ($\pm$ 1 standard deviations). Analysis of variance (ANOVA) with logarithmic transformation. CSBV = Closed Spekboomveld, OSBV = Open Spekboomveld, KBV = Karroid Broken Veld and SK = Succulent Karoo.

	CSBV	OSBV	KBV	SK	ANOVA
% Open ground	43 (7) *1 ***2 ***3	50 (7) ***4 ***5	63 (11) ***6	74 (16)	$P < 0.001$
% Perch cover	37 (10) *** *** ***	19 (6) *** ***	6 (5) ***	0 (1)	$P < 0.001$
Natural perches	7954 (2430) NS *** ***	7531 (1457) *** ***	4198 (3523) ***	112 (194)	$P < 0.001$
Artificial perches	155 (199) NS NS NS	323 (279) NS NS	204 (245) *	380 (344)	$P < 0.01$
All perches	8109 (2408) NS *** ***	7854 (1408) *** ***	4402 (3480) **	492 (373)	$P < 0.001$
Perch area (m^2)	1.75x10^7 (0.57x10^7) NS *** ***	1.41x10^7 (0.24x10^7) *** ***	0.72x10^7 (0.57x10^7) ***	0.07x10^7 (0.06x10^7)	$P < 0.001$
Perch area/surface area ratio	70.0:1	56.4:1	28.8:1	2.8:1	
No. of quadrats	20	11	93	107	

NS = Not significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$. 1 = Closed Spekboomveld *vs* Open Spekboomveld, 2 = Closed Spekboomveld *vs* Karroid Broken Veld, 3 = Closed Spekboomveld *vs* Succulent Karoo, 4 = Open Spekboomveld *vs* Karroid Broken Veld, 5 = Open Spekboomveld *vs* Succulent Karoo, and 6 = Karroid Broken Veld *vs* Succulent Karoo

Table 8.4 For Karroid Broken Veld, results of a comparison between proportion open ground and perch cover, natural, artificial and all (natural and artificial) perches, and perch area for polyandrous trios and monogamous pairs. Means and (± 1 standard deviations). t test with logarithmic transformation, NS = not significant.

	Polyandrous trio	Monogamous pair	t test
% Open ground	64 (10)	62 (11)	NS
% Perch cover	7 (5)	5 (5)	$P < 0.05$
Natural perches	4463 (3797)	3692 (2919)	NS
Artificial perches	191 (229)	229 (276)	NS
All perches	4654 (3761)	3920 (2862)	NS
Perch area (m^2)	7.67×10^6 (6.13×10^6)	6.38×10^6 (4.63×10^6)	NS
Perch area/surface area ratio	30.68:1	25.52:1	
No. of quadrats	61	32	

Table 8.5 For Succulent Karoo, results of a comparison between proportion open ground and perch cover, number of perches at different heights, natural, artificial perches and all (natural and artificial) perches, and perch area for quadrats occupied and unoccupied by Pale Chanting Goshawks. Means and (±1 standard deviations), t test with logarithmic transformation, NS = not significant.

	Occupied	Unoccupied	t test
% Open ground	74 (16)	73 (16)	NS
% Perch cover	0.1 (0)	0.1 (1)	NS
Natural perches	147 (157)	77 (308)	$P < 0.05$
Artificial perches	427 (349)	191 (251)	$P < 0.01$
All perches	474 (366)	268 (362)	$P < 0.01$
Perch area (m^2)	7.60×10^5 (5.88×10^5)	4.04×10^5 (5.12×10^5)	$P < 0.01$
Perch area/surface area ratio	3.04:1	1.62:1	
No. of quadrats	86	21	

Table 8.6 Result of stepwise discriminant function analyses with five ecological variable in different vegetation types, Closed Spekboomveld (CSBV) without Pale Chanting Goshawks and Open Spekboomveld (OSBV) with Pale Chanting Goshawks, occupied and unoccupied Succulent Karoo (SK), as well as polyandrous trios and monogamous pairs in the Karroid Broken Veld (KBV). For each category the rank order the variable were entered into the discriminant function are provided. The results of a jackknifed percent correct classification analysis for the above categories are also provided.

STEPWISE DISCRIMINANT ANALYSES

Categories compared	Open ground	Perch cover	Natural perches	Artificial perches	Perch area
All vegetation types					
CSBV *vs* OSBV *vs* KBV *vs* SK	3	2	1		
Spekboomveld					
CSBV (no PCGs) *vs* OSBV (with PCGs)		1			
Karroid Broken Veld					
Polyandrous trios *vs* monogamous pairs		1		2	
Succulent Karoo					
Occupied *vs* unoccupied			1		

JACKKNIFED PERCENT CORRECT CLASSIFICATION

Categories compared (quadrats sampled)	Percent correct				
All vegetation types		CSBV	OSBV	KBV	SK
CSBV (10)	70	7	3	0	0
OSBV (10)	90	1	9	0	0
KBV (60)	77	1	11	46	2
SK (20)	95	0	0	1	19
Spekboomveld		CSBV	OSBV		
CSBV (unoccupied) (10)	90	9	1		
OSBV (unoccupied) (10)	80	2	8		
Karroid Broken Veld		Polyandrous trios	Monogamous pairs		
Polyandrous trios (40)	70	28	12		
Monogamous pairs (20)	55	9	11		
Succulent Karoo		Occupied	Unoccupied		
Occupied (10)	90	9	1		
Unoccupied (10)	80	2	8		

8.4 DISCUSSION

8.4.1 Hunting success

In almost all hunts recorded, a perch was used to search for prey and launch attacks. Although the glides from perch to ground were unhurried, once on the ground, PCGs were fast and agile on their feet (GM pers. obs.). They used their long legs to great effect to jump/run after prey, and to run through and poke into vegetation. In this respect the PCG is probably more of a terrestrial, than aerial hunter. Although attempts to catch a bird in direct flight were unsuccessful in this study, Brown (1970) observed a PCG 'flying down' and catching a Harlequin Quail *Coturnix delegorguei.*

With an overall perching rate of 4/h and successful striking rate of 0.19/h, an adult PCG had to perch 21 times to capture prey successfully. The amount of perching per capture qualifies the PCG as a pause-travel predator that actively searches for prey, as apposed to a sit-and-wait predator (Andersson 1981; Tye 1989). The hunting success of 12-24% for single and social strikes was very low compared with a mean of 59% (range = 31-72%) for 11 raptor species that search for their prey (Toland 1986). It is even lower than the 27% (range = 19-33%) for raptors that attack their avian prey in the air, a technique generally thought to be less successful than searching. However, 12-24% is an underestimate as it does not take into account the 'successful' strikes at termites. Large numbers of termites were taken per strike since in SK, despite a low termite strike rate of once every 8.6 h, 96.5% of prey individuals were termites (2549/2642; Tables 7.1 & 7.2). Feeding on arthropods was probably so quick, and in the lower vegetation layer, that it avoided detection. The low success rate must therefore be seen as a vertebrate success rate for rodents, shrews, lizards and birds, in terms of biomass, the important prey taxa (see Chapter 7). What this low success rate however highlights is the elusive nature and/or the difficulty of catching these vertebrate prey.

8.4.2 Sociality and cooperative hunting

To determine if cooperative hunting may have favoured sociality in the PCG, two questions need to be answered; (1) were PCGs cooperative hunters and (2) if social strikes were twice as successful as single strikes, why were social striking rates lower than single rates? Ellis *et al.* (1993) defined, among others, three social foraging categories for raptors: non-cooperative hunting, cooperative searching and cooperative hunting. PCGs are non-cooperative hunters in that they most often hunted solitarily. The non-cooperative hunting technique where PCGs follow Honey Badgers *Mellivora capensis*, Slender Mongooses *Galerella sanguinea* or Rock Monitors *Varanus exanthematicus* as flushing agents for prey they might disturbed, have been observed in nature reserves (Dean & MacDonald 1979; Paxton 1988; Steyn 1992), but not in the Calitzdorp study area (GM pers. obs.). PCGs also qualified as cooperative searchers, in that they cued in on conspecifics chasing prey on the ground, probably using the aloft and flapping wings of hunting birds as a signal. This, in turn, may have increased the probability of locating prey (Ellis *et al.* 1993).

To qualify as cooperative hunters PCGs should hunt predominantly together, monitor each others movements, pursue a single prey individual in coordinated movements, divide labour of hunting and share prey among participants (Hector 1986). PCGs did not predominantly hunt together, since only one out of every nine strikes was social. In fact, the solitary PCGs spent 23-24% of time in close proximity of group members, compared with 71% for the Harris' Hawk (Bednarz 1988). PCGs could, however, visually monitor each other's movements by perching on the highest available perch and observing other birds striking. The higher social strike rate in SK *vs* KBV may be the result of SK's flatter topography (Chapter 2) and almost absence of high growing natural vegetation, making it easier for individuals to observe others hunting. Once on the ground, birds tried to capture a cornered prey individual in a apparent uncoordinated manner without a division of labour. However, a rodent cornered under a shrub probably did not necessitate highly coordinated movements or any clear division of labour. Birds standing around and on top of the shrub, and jumping at the prey when the opportunity arise, were probably coordinating enough to either capture or flush it out. Lastly, once caught, prey was not shared, although this could be the result of the small size of vertebrate prey in the study area that did not exceed the birds' minimum daily requirement (Chapter 7). Biggs *et al.* (1984) observed three PCGs hunting and feeding on a Helmeted Guineafowl *Numida meleagris*, a bird almost twice the size of a PCG (Maclean 1985).

PCGs therefore fulfill almost all requirements to qualify as cooperative hunters, except that they hunt predominantly as singletons. Since a success rate of 24% for social hunts decreases to 12% per individual with two birds and even further when more birds participating (up to five; GM pers. obs.), the success rate per individual equals or falls below the 12% success rate of single hunts. Per PCG, social and single hunting therefore contribute less to individuals' hunting success. Perhaps the acid test to qualify as a cooperative hunter is expressed by Ellis *et al.* (1993) as "the functional role of the individual, at least some of the time, is not to improve its own changes for capture success but rather to enhance the probability of success by the group". The intention of the PCG making the initial strike may have been selfish, but allowing the another member to catch the prey, certainly was intentional. A system may therefore evolved where each group member, more so dominant birds, valued the group's benefits above that of the individual.

If a striking member could be regarded as a beater for the group (Ellis *et al.* 1993), the PCG qualifies as a cooperative hunter. Cooperative hunting tactics may not be as well developed as in the Harris' Hawk or some bird-eating falcons (Hector 1986; Bednarz 1988; Dawson 1988; Malan 1991), but the cooperation and socialisation learned by these rapacious birds may prove valuable in making the necessary social adaptive changes that accompany cooperative polyandry and delayed dispersal. The intrinsic benefit of this cooperative foraging strategy may therefore indeed have favoured group living and cooperative breeding.

Compared with adults, hunting tactics by juveniles showed some clear-cut differences. While hunting, they remained within a smaller area (quadrat) and struck at a higher rate. By being allowed to cooperate in hunts with adult PCGs, even at a very low rate, juveniles may have learned valuable hunting techniques. Since vertebrate prey is elusive and difficult to catch, the hunting experience for juveniles and adult non-breeders may increase their survival in their first years and ultimately, survival fitness (Heinsohn *et al.* 1988, 1990; Heinsohn 1991; Emlen & Wrege 1994; see also Chapter 9). The hunting skill to be learned and increased survival may have favoured philopatry and influence the decision to delay dispersal (Heinsohn *et al.* 1990).

8.4.3 Perch availability and prey visibility

In Chapter 7, I identified ecological factors, such as high otomyinid rodent biomass and related habitat parameters, that may constitute habitat quality. Habitat quality governed reproductive success which, in turn, may have influenced inclusive fitness and the decision to delay dispersal and breed cooperatively. Of the four vegetation types, only KBV contained high densities of both 76-150 cm high scrubs and heuweltjies, both factors essential in obtaining access to a high *Otomys unisulcatus* and *Parotomys brantsii* densities. However, not only is the absolute otomyinid abundance important, for a pause-travel predator, ecological factors that influence the accessibility of prey such as perch height and abundance, and prey visibility are also critical (Simmons 1989; Yosef 1992; Widen 1994). Even if prey is abundant, if perch availability is inadequate, the habitat may be difficult to exploit (Widen 1994). Simmons (1989) found that for the African Marsh Harrier *Cirus ranivorus*, an aerial hunter, hunting success was not correlated with rodent abundance, but to the relative depth of the vegetation, therefore prey visibility.

Based on the assumptions that a bird searches a circular area under each perch and that the radius of the search area increases with an increase in perch height, several predictions can be made to study the importance of perch height and abundance: (1) horizontal strike distances should increase with an increase in perch height, (2) detection and giving-up time should increase with perch height, (3) the area to be searched should increase with distance from the perch, and (4) birds occupying areas with fewer perches should be forced the move further between perches (Fitzpatrick 1980; Andersson 1981; Tye 1989; Sonerud 1992). As for other mammal-eating raptors, *e.g.* Steppe Buzzards *Buteo buteo*, Rough-legged Buzzards *Buteo lagopus*, Rock Kestrels *Falco tinnunculus* and Hawk Owls *Surnia ulula* (Sonerud 1992), a positive relationship between striking distance and perch height was found for the PCG. However, for the important criterion, successful strikes, there was no relationship between perch height and striking distance. This suggests that successful strikes were performed over a wide range of distances, probably at random and opportunistically. The significant relationship between detection time and striking distance indicates that birds search outwards, starting at perch base. Three factors suggest that perch availability was of more importance than perch height. First, with a nine-fold increase in perch height there was only a two-fold increase in striking distance, although the area to be scanned increased greatly. Second, perch area could not be used to discriminate between vegetation types or occupied and unoccupied areas. Third, because the PCG is a pause-travel predator, by definition, the bird moves to a different perch regularly rather than just sit and wait. Only in SK did the limited number of high artificial perches, *e.g.* telephone poles, not exceed the number of natural perches. Since trees and shrubs (natural perches) are spaced regularly in arid areas (Phillips & Macmahon 1981; Esler & Cowling 1993), and artificial perches are always in rows, birds had to utilise shorter natural perches in order to hunt over territories' surface area. It was therefore surprising to find the PCGs' clear-cut preference for not only for higher perches, but also time spent on these perches (Fig. 8.2). This result must be viewed against the finding that no distinction can be made between a PCG perch-hunting or perching for any other reason. The height of perches, such as telephone and ESKOM poles, may play an important role in other behaviour such as: (1) scanning for hunting group members, (2) scanning for intraspecific and interspecific intruders, (3) advertising a territory holder's presence and occupancy, (4) resting (Yosef 1992), or (5) even to escaping the heat trapped amongst the vegetation (GM pers. obs.).

SK was the only vegetation type in which the mean number of artificial perches per quadrat actually exceeded the number of artificial perches (88%; 380/433). Of these, fence posts contributed the largest proportion (99%; 227/229 and 474/479; Fig. 8.2). The perch/surface area ratio of greater than one further suggests that no dead ground existed in this vegetation type. With fence posts placed 1.7-1.9 m apart (GM unpubl. data), and a mean horizontal striking distance of 23 m from a fence post, a perching PCG would face 12 'dead' poles on either side of its perch. By not deducting this overlap, the calculated SK perch/surface area ratio may have been an overestimate. Dead ground may therefore indeed exist, more so the unoccupied SK with an perch/surface area ratio of 1.62:1 *vs* the 3.04:1 of occupied SK.

This bias was not relevant in other vegetation types since the high number of natural perches (666-10 384/quadrat), and the regularly spacing of natural perches (Esler & Cowling 1993), inevitably caused overlap as reflected by the perch/surface area ratios of 25-70:1. That PCGs were occupying areas in SK with significantly fewer natural than artificial perches may be the result of particular farming practices. Parts of SK, closest to the intensive farming areas and roads (see Chapter 2), were divided into many small Ostrich *Struthio camelus* breeding camps where these birds were fed and watered artificially, and these camps provided ample artificial perches. In addition, artificial perches such as fence posts may be easier to sit on, non-swaying (in the wind) flat wooden surfaces with a clear view of the ground directly beneath.

Taking into account that otomyinid densities in 1989 did not differ significantly between the occupied and unoccupied SK (Table 7.11), at least in occupied areas, the perch availability brought the major part of surface area within striking range. In fact, PCGs were 'artificially' occupying parts of SK since birds in this vegetation type were largely dependent on the availability of artificial hunting perches.

At the other side of the study area, in the densely vegetated Spekboomveld (Acocks 1988), the proportion perch cover increased almost two-fold from 19% in OSBV (PCGs present) to 37% in CSBV (no PCGs), whereas the mean number of natural perches per quadrat (mean densities of 7531-7954 perches/quadrat) did not differ significantly (Table 8.3; Fig. 8.4). This result indicates that tree and shrub canopies were larger in CSBV, appropriately described by Acocks (1988) as a shrub-forest. In addition, the proportion open ground in OSBV (50%) was significantly higher than in CSBV (43%).

Taking into account that, during 1989, otomyinid densities did not differ significantly between CSBV and OSBV (Table 7.8), why where there no PCGs resident in CSBV? Two factors may play a role. First, when perching on an evergreen shrub or flat-top tree, there is a circular area directly underneath and surrounding the perch that is obstructed from view. With trees and shrubs so close together (or a tree or shrub every 31-33 m^2) a perching PCG may have a very limited view of the ground or prey, and the proportion open ground that can be scanned becomes negligible. It appears that, if the proportion perch cover rises above 20% and the proportion open ground drops below 50%, the hunting habitat becomes unsuitable for PCGs. It was therefore prey visibility that separated OSBV from CSBV, a hypothesis which is supported by the results of DFA. Furthermore, with such a high proportion ground cover (67%) and densely structured vegetation, in CSBV, a rodent will have ample cover into which it may escape. A striking PCG may also have structural limitations in pursuing a fleeing animal on the ground.

Optimum PCG hunting habitat at Calitzdorp should be an area that contains maximum prey visibility and perch availability. Areas in SK partly fulfilled prey visibility requirements. However, the ecological factors, prey visibility and perch availability, are not independent of each other. Of the three variables that discriminated between vegetation types, perch cover increased with the number of natural perches, but decreased with proportion open ground (see Chapter 9). Therefore, rather than a maximum, one should search for an optimum combination of these ecological factors.

Although the number of natural perches and proportions of perch cover and open ground differed greatly between SK and KBV, no differences in hunting success and tactics could be detected. What did differ however, was that, for a pause-travel predator, the lower perch availability in SK forced birds to fly further from perch to perch, frequenting more quadrats per time period. Hunting in SK was therefore energetically more expensive. It would therefore appear if perch availability does change PCG's hunting behaviour.

In KBV, only perch cover differed significantly between quadrats occupied by polyandrous trios and monogamous pairs. This result can be attributed to more shrubs in polyandrous trio territories, under which *O. unisulcatus* build their nests (Chapter 7). However, in the DFA the low correct classification of variables that constitute hunting habitat suggests that hunting habitat did not differ. This finding is supported by the lack of clear cut differences found in otomyinid densities and related habitat parameters (Chapter 7). However, compared with the hunting habitat of other vegetation types, the quality of KBV hunting habitat may stem from the fact that the vegetation structure harbours a near optimum for prey visibility and perch availability. With, on average, 63% of ground open and 6% covered by perches, and a density of 4 198 perches/quadrat (or a tree or shrub every 60 m^2), a perch-hunting PCG may have adequate perches at its disposal to view all open ground and vegetation in the territory, and hunt terrestrial prey. Furthermore, differences in hunting success and tactics, as found between KBV and SK, may not be as important as the opportunity the hunting habitat offers to select larger prey, *i.e.* hunting efficiency (Bednarz 1988; Yosef 1992). In spite of the lack of differences in hunting success, during 1988-1989, PCGs in KBV selected a higher biomass and diversity of rodents (Chapter 7). By forfeiting some hunting success in favour of a having the option to select large rodent prey, that either live in the open (*Parotomys brantsii*) or under plant cover (*Otomys unisulcatus* and *Rhabdomys pumilio*), PCGs in KBV may experience higher hunting efficiency by receiving a higher energy return on their hunting effort.

In this chapter I identified a further two factors, again ecologically based, that may have constituted habitat quality for the PCG. In such a high-quality habitat, hunting efficiency may increase prey provisioning, reproductive success and fitness, and ultimately the decision to delay dispersal and breed cooperatively.

CHAPTER 9

HABITAT QUALITY AND ITS DEMOGRAPHIC IMPACT ON DELAYED DISPERSAL AND CO-BREEDING IN A PALE CHANTING GOSHAWK POPULATION DURING A FIVE-YEAR STUDY

SUMMARY

The demographic impact, *e.g.* population stability, recruitment, fidelity and survival, of Pale Chanting Goshawks (PCGs) living in habitats of differing quality was investigated during 1988-1992. Habitat quality was described by two ecological factors, shrub-perch (availability of 76-150 cm high shrubs for *Otomys unisulcatus*, the dominant prey species, and natural perches for PCGs), and heuweltjie-openness (availability of mounds for *Parotomys brantsii*, the second most dominant prey species, and openness to view terrestrial prey). Areas of high-quality Karroid Broken Veld (KBV) vegetation scored well for both factors, but in medium-quality Open Spekboomveld (OSBV) and Succulent Karoo (SK) only one factor featured strongly.

The fluctuations in densities of key prey, the variability of habitat quality, did not appear to influence a PCG's decision to delay dispersal or co-breed. Novice breeders did not succeed in producing more than one offspring, even in years of high otomyinid densities, and breeding experience is therefore essential to reproduce successfully. Furthermore, no PCG group changed status from monogamous pair to polyandrous trio by the addition of a co-breeder to a settled monogamous pair. Therefore potential co-breeders can only obtain a breeding position by forming a coalition with another male. Once settled in polyandrous trios, the reproductive success and inclusive fitness of polyandrous breeders were higher than that of monogamous breeders. The help provided by co-breeders contributed more to this success than otomyinid densities and territory size. There was, however, a cost for breeders residing in KBV.

Although the highest number of offspring was produced in KBV, territoriality limited the number of offspring per group and a significantly larger proportion of non-breeders was probably forced to disperse. Furthermore, since 69% of breeders marked during 1988 were still occupying the same territories during 1992, the population was very stable (CV = 4% in KBV) and breeder recruitment was very low (< 1% per year). It is suggested that, under these circumstances where access for young to high-quality habitat is severely

limited and the population is stable, breeders changed their reproductive strategy to increase offspring's survival and accommodate them into the population. Once offspring delayed dispersal and families were formed, secondary benefits of family living may have developed such as allowing offspring to partake in cooperative hunts, and/or bud-off or inherit a territory.

9.1 INTRODUCTION

The decision to delay dispersal and provide help in your natal territory may be based on a range of ecological, social and demographic benefits and constraints (Koenig *et al.* 1992; Emlen 1994). Which option to follow is based on the assumption that each individual will try to maximise its reproductive and survival fitness (Emlen & Wrege 1994). However, breeder's reproductive success, pivotal in determining reproductive fitness, is often correlated with habitat quality (Brown & Brown 1981; Stacey & Ligon 1987; Komdeur 1992). Apart from being circular, the relationship between habitat quality and reproductive success is confounded by the inter-correlation with other factors such as the presence of helpers and territory size (see Lennartz *et al.* 1987; Koenig *et al.* 1992). Furthermore, if the quality of the habitat differs, and fitness is higher in high-quality habitat, breeders will occupy such territories and access of offspring to free breeding opportunities will be limited (Fitzpatrick & Woolfenden 1986). In addition, if the population is stable, and survival and reproductive success of inhabitants are increased by living in groups, offspring are further restrained in obtaining a breeding opportunity (Woolfenden & Fitzpatrick 1984; Russell & Rowley 1988). Under such demographic pressures, breeders may adjust their reproductive strategy as to increase offspring survival, as well as to assist in obtaining territorial space (Fitzpatrick & Woolfenden 1986).

The aims of this chapter are: (1) to examine, demographic features such as dispersal from the study area, breeder group status changes, study area fidelity, recruitment, survival and the inclusive fitness for disrupted and settled groups in a population of PCGs in habitats of differing quality over a five-year study, (2) to identify the factors that constitute habitat quality, and (3) to examine the interrelationships between the number of males helping, territory size, otomyinid abundance and reproductive success.

9.2 METHODS

9.2.1 Habitat quality

To identify the factors that constitute habitat quality I analysed the availability of the following six ecological variables, identified in Chapters 7 and 8: (1) shrubs 76-150 cm high, (2) heuweltjies, (3) open ground, (4) perch cover, and (5) natural perches (6) and artificial perches. Since the values of the above ecological variables would remain relatively stable between years, they were analysed as the constant aspect of habitat quality and the density estimates of key rodent species, *Otomys unisulcatus* and *Parotomys brantsii* that fluctuated greatly between years, as the variable aspect. For the 100 quadrats (500x500 m) for which data were available (Chapter 7), I used stepwise discriminant functions analysis (DFA; BMDP-7M; Dixon *et al.* 1990) in a log-log model to determine if one or more of the six constant ecological variables could be used to distinguish quadrats of the different categories. The categories were the following: Closed Spekboomveld (CSBV) with no PCGs, Open Spekboomveld (OSBV) with monogamous groups, Karroid Broken Veld (KBV) with monogamous and polyandrous groups, Succulent Karoo occupied (SKO) with monogamous groups, and Succulent Karoo unoccupied (SKU) with PCGs. In the DFA, the jackknifed percentage correct classification was used as a measure of success (Lachenbruch & Mickey 1986). I also performed a factor analysis (BMDP-4M; Dixon *et al.* 1990) to study ecological variable inter-correlations and to group variables into factors.

9.2.2 Males, otomyinids and reproduction in KBV

In KBV, to determine if the presence of two males provisioning at equal rates, otomyinid densities, or territory size had the greatest impact on reproduction, I analysed data from 10 quadrats each from territories of three polyandrous trios (Groups 4, 5 & 14) and two monogamous pairs (Groups 7 & 13). An Otomyinid-Area Index was calculated by firstly combining the density estimates of *P. brantsii* and *O. unisulcatus*. To include territory size, the above value for each quadrat was multiplied by a factor (range 1.0-1.6) as to represent a surface area 1/10 of a territory. I calculated a Reproductive Index as follows: a score of one was attributed if a PCG egg was laid, one if the egg hatched and one if the chick fledged, *e.g.* if a group laid two eggs, and both chicks hatched and fledged successfully, a value of six was scored. I preformed a stepwise multiple linear regression analyses (BMDP-2R; Dixon *et al.* 1990) in a log-log model with Reproductive Index as dependent variable.

9.2.3 Dispersal/disapearance and status change

To determine breeder recruitment and PCG fidelity to the study area, perching PCGs and fledglings were marked as described in Chapter 2. The presence of marked birds was recorded *en route* between nest sites and during 51 visits to nests during the breeding seasons of 1988-1992 (Chapter 3). Marked birds not observed the following breeding season and whose rings were not recovered, were classified as dispersed/disappeared, since it was not known if they died or dispersed from the study area.

The status of breeding groups, either polyandrous or monogamous, was determined by observing marked birds copulating or counting marked or unmarked breeders at nest sites in the breeding season (see Chapter 3). Breeding groups changed status from monogamous pair to polyandrous trio if a breeder joined a monogamous pair or, from polyandrous to monogamous if a breeder departed from a polyandrous trio. A group that dispersed/disappeared left their territory vacant, and a group established when a new group either occupied a vacated territory or set up a territory and defended an area previously occupied by one or more groups. Novices were breeders that bred for the first time in the study area, either adults marked as juveniles or nestlings, or unmarked adults that established in the study area.

9.2.4 Reproductive success and fitness of settled and disrupted groups

Breeding groups were divided into three categories according to the group's history in the study area: (1) groups with no prior history (n = 23), groups that occupied territories in a sector of the study area not previously searched for resident groups (all groups that were discovered the first two years of the study), (2) disrupted groups as novices or groups with a history that changed status (n = 13), and (3) settled groups, with a history, as groups where no status change took place and whose previous breeding experience in the study area disqualified them as novices (n = 81). The reproductive success of settled *vs* disrupted groups was compared, as well as for settled polyandrous and monogamous groups in KBV. Lastly, the reproductive inclusive fitness of settled polyandrous and monogamous groups in KBV was calculated as outlined in Chapter 4.

9.2.5 Dispersal and longevity

All ringing recoveries and retraps of PCGs ringed in southern Africa were obtained from the South African Bird Ringing Unit, University of Cape Town. Longevity, in months, and the distances dispersed, in kilometre, were provided. Records were kept of all mortalities in the Calitzdorp study area.

9.3 RESULTS

9.3.1 Habitat quality

The DFA considered the following variables: proportion open ground, proportion perch cover, relative density of natural and artificial perches, relative density of 76-150 cm high shrub and heuweltjies, and produced between 80-90% correct classification for the different categories (Table 9.1). The variables that contributed significantly to the discriminant function, and therefore distinguished quadrats of the different categories, were in rank order natural perches, densities of heuweltjies and 76-150 cm high shrubs (Table 9.2).

All variables were inter-correlated, except artificial perches (Table 9.3). Particularly high correlations were found between natural perches, and 76-150 cm high shrubs (r = 0.98), and perch cover (r = 0.72). Perch cover, natural perches and 76-150 cm high shrubs were significantly negatively correlated to proportion open ground and heuweltjies. In the factor analysis, variables were grouped into two factors (Table 9.2; Fig. 9.1). In the first factor,

Table 9.1 The results of a jackknifed percent correct classification analysis for the following categories: CSBV = Closed Spekboomveld, OSBV = Open Spekboomveld, KBV = Karroid Broken Veld, SKO = Succulent Karoo occupied and SKU = Succulent Karoo unoccupied.

Categories (quadrats sampled)	Percent correct	CSBV (10)	OSBV (10)	KBV (60)	SKO (10)	SKU (10)
CSBV	90	9	1	0	0	0
OSBV	80	1	8	1	0	0
KBV	87	0	6	52	2	0
SKO	80	0	0	1	8	1
SKU	90	0	0	0	1	9
Total	86	10	15	54	11	10

Table 9.2 Results of a factor analysis with sorted factor loadings and significant stepwise discriminant functions analysis for ecological variables sampled in 100 quadrats in Closed Spekboomveld, Open Spekboomveld, Karroid Broken Veld, Succulent Karoo occupied and Succulent Karoo unoccupied.

Variables	Factor analysis		[1] Stepwise discriminant analysis
	Factor 1	Factor 2	
Heuweltjies	0.898	0.000	2
Open ground	0.858	0.000	
Perch cover	-0.732	0.563	
Shrub 76-150 cm	0.000	0.972	3
Natural perches	-0.316	0.939	1
Artificial perches	0.000	0.000	

[1] rank in order discriminant analysis

Table 9.3 Results of correlation matrix with variables of measures of habitat quality. NS = not significant; * = $p < 0.05$; *** = $p < 0.001$

Variables	Open ground	Shrub 76-150 cm	Heuweltjies	Perch cover	Natural perches
Shrub 76-150 cm	-0.23*				
Heuweltjies	0.58***	-0.21*			
Perch cover	-0.56***	0.64***	-0.67***		
Natural perches	-0.33***	0.98***	-0.33***	0.72***	
Artificial perches	0.03 NS	-0.03 NS	0.00 NS	-0.02 NS	-0.03 NS

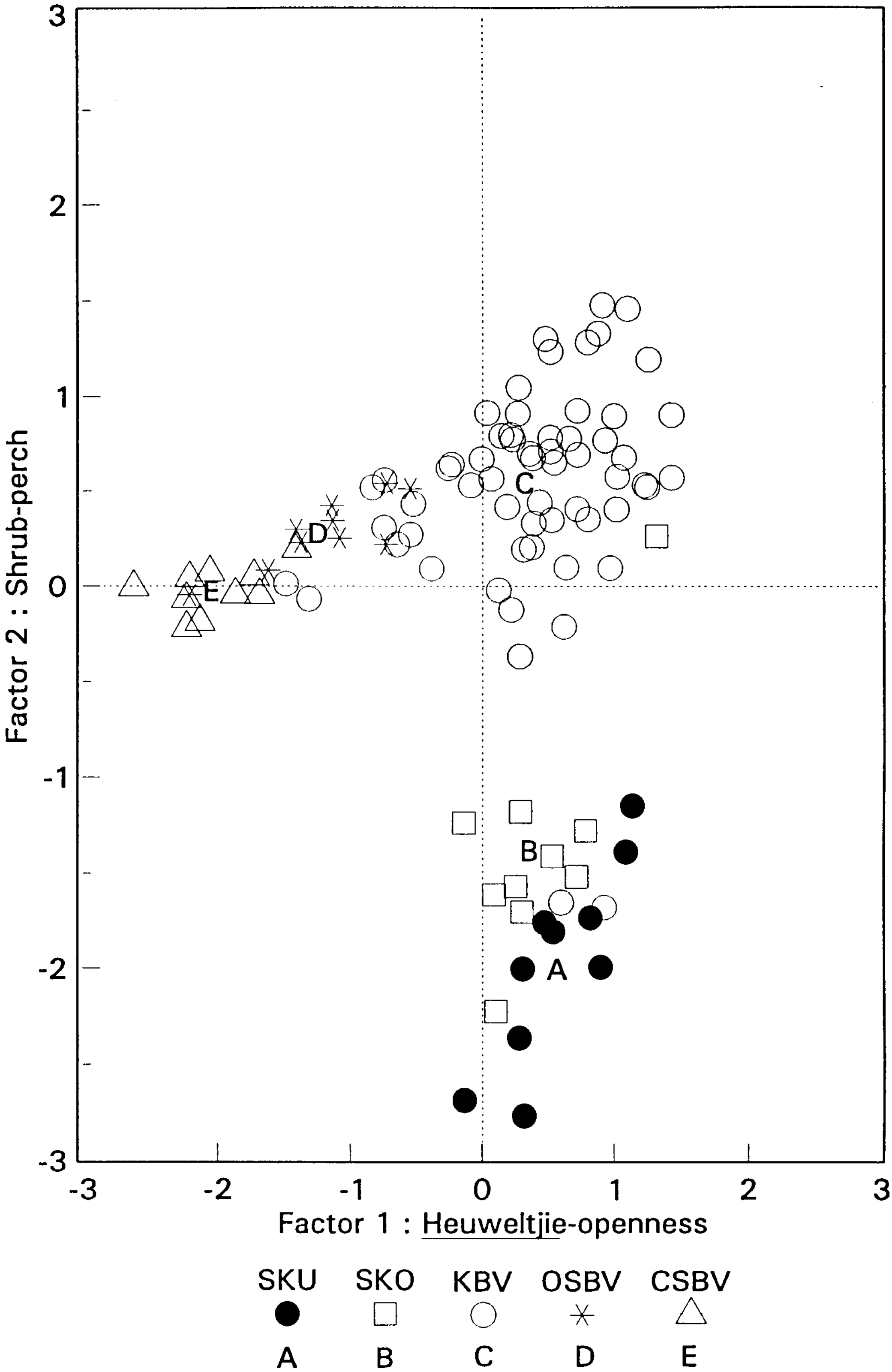

Fig. 9.1 Results of factor analysis, for unoccupied Succulent Karoo (SKU), occupied Succulent Karoo (SKO), Karroid Broken Veld (KBV), Open Spekboomveld (OSBV) and Closed Spekboomveld (CSBV).

proportion open ground, heuweltjies and perch cover (negatively) were most heavily weighed was termed 'heuweltjie-openness'. In the second factor, 76-150 cm high shrubs, natural perches and perch cover were most heavily weighed and it was termed 'shrub-perch'.

9.3.2 Males, otomyinids and reproduction in KBV

In KBV during 1989, the number of breeding males was significantly positively correlated with Reproductive Index and Otomyinid-area Index (Table 9.4). Both variables contributed significantly to the coefficient of determination in the regression analysis, the number of males more than Otomyinid-area Index, although accumulatively they only explained 37% of variation in reproduction.

Table 9.4 Results of correlation and stepwise multiple regression analyses for polyandrous trios and monogamous pairs in Karroid Broken Veld between Otomyinid-area Index (otomyinid density per given area), Reproductive Index (number of eggs laid, chicks hatched and fledgling fledged) and breeding males per group. NS = not significant; ** = $p < 0.01$; *** = $p < 0.001$

Variables	Reproductive Index	Males	Contribution to coefficient of determination in regression analysis
Males	0.50***		0.25 (1)
Otomyinid-area Index	-0.06 NS	0.49***	0.12 (2)

9.3.3 Polyandrous trio and non-breeder abundance

Of the 31 groups that were studied from 1988-1992, polyandrous trios were only recorded in KBV (Table 9.5). Of the group years recorded in KBV, 20% (16/80) of groups were polyandrous trios. During 1988, three polyandrous trios (3/7; 43%) were present in KBV, four during 1989 (4/16; 25%) and 1990 (4/17; 24%), two during 1991 (2/20; 10%) and one during 1992 (1/20; 5%).

Table 9.5 Pale Chanting Goshawk monogamous pairs and polyandrous trios **in bold and underlined** studied at Calitzdorp from 1988 to 1992, vegetation types they nested in, the number of offspring fledged and non-breeders (in brackets) per group. Values for non-breeders in brackets, the number of values indicate the number of non-breeders (*e.g.* U U = two birds) and the values itself the age of the birds, U = unknown age, N = known age but observed in later years, 1 = one year old, 2 = two years old, *etc.*

Vegetation type No.	Group name	1988	1989	1990	1991	1992
Open Spekboomveld						
1	Nellis		1 (U U)	2	0 (1)	0
2	1stKloof	0 (U U)	1 (2 U)	3 (1)	0	0
3	2ndKloof			1	0	
18	KweekK		1			
19	Unknown			1 (1)	0	2
20	Erenst		1	0	0	0
28	BoKuile			2	1	2 (U)
Karroid Broken Veld						
4	Okkies	**1 (N U)**	**4 (N U)**	**3 (U)**	**0 (1 5)**	0 (U)
5	JohanG	**0 (1)**	**2**	**2 (N)**	0 (1 2)	0 (U)
6	Ridge			4	0	0
7	Cutting	1 (U)	2	2 (1)	0	**0**
8	Kraal	2 (U)	2 (U)	2	0 (2 2)	2
9	DGates			**1**	**0**	1
11	Vlakte		1	1(N)	0 (2)	2
12	Zwartkop	**2**	**3 (U)**	**4**	0 (1)	
13	Bloubosvlei	0 (U)	2 (U)	2 (1 1)	0 (U)	0 (U)
14	AndriesK		**2 (U)**	0 (U U)	0	0
15	TarRoad		2 (U)	2	0	2 (U)
16	Secretary		2 (U)	3 (U U)	0 (U U)	2 (U U)
17	Kuile		1		1	0 (1 U)
21	Kruisrivier	**1 (U)**	0	2	1 (U)	0 (U U)
22	Rietfontein		1	2	0	0
23	Vleirivier		2 (U)	2 (1)	0 (U)	2 (U U)
24	BaasF		2 (U)	2	0 (1 U)	2
25	Saayman		**1**	1 (U)	0 (U)	2
29	Pickniks				0	2 (U)
30	BoOkkies					1
31	ErnieF				2	2 (1 U)
Succulent Karoo						
10	Engelskamp	0	2	3 (N)	0 (2 2)	0
26	Badsaf	1	2 (U)	1 (N)	0 (1)	0 (4)
27	Remhog	0	1	1	0 (U)	2

In all vegetation types, the number of non-breeders per group did not differ significantly between years (mean = 0.67; range = 0.61-0.82; P > 0.05; ANOVA; n = 117), nor between polyandrous trios and monogamous pairs in KBV (mean = 0.76; range = 0.63-

0.10; P > 0.05; ANOVA; n = 80) (Table 9.5). The proportion of groups with non-breeders in OSBV (7/22) and SK (6/15) did not differ significantly and were combined (Chi-square; P < 0.05). Fifty-six percent of groups (45/80) in KBV had non-breeders, significantly more than the 35% of groups in OSBV and SK (13/37) (Chi-square; P < 0.05). In KBV, 56% of both polyandrous and monogamous groups had non-breeders in their groups (9/16 and 36/64 respectively).

9.3.4 Breeder group status change

Seven groups changed status between breeding seasons (Figs. 9.4-9.6). From three polyandrous trios, the beta dispersed/disappeared (Group 14, 1990; Groups 5 & 12, 1991). Thus, no alpha males from polyandrous trios (where at least one male was marked), dispersed or disappeared. From a further two polyandrous trios one of two unmarked males dispersed/disappeared (Group 25, 1990; Group 9, 1991). In one polyandrous trio (Group 4, 1992), both marked males dispersed/disappeared and were replaced by an unmarked male. In one monogamous pair (Group 7, 1992), the marked male dispersed/disappeared and was replaced by two unmarked males. No breeder group thus changed status from monogamous pair to polyandrous trio by the addition of a single male.

For a further two groups, status changes were either human-induced, or occurred within the nesting period. A polyandrous trio that was removed for genetic analysis during March 1989 (Group 21, 1989), and their son, a 1987 fledgling, paired with an unmarked female, a 1988 fledgling (judged from eye colour). I marked her, but on my return to the study area in October 1989, the male was paired with a marked non-breeder female from Group 13, a 1987 fledgling. In the second group (Group 24, 1989), two males were present during the nest building phase, but a week before laying the landowner (pers. comm.) reported two PCGs interacting. On my arrival only one male was present, as for the rest of the nesting period.

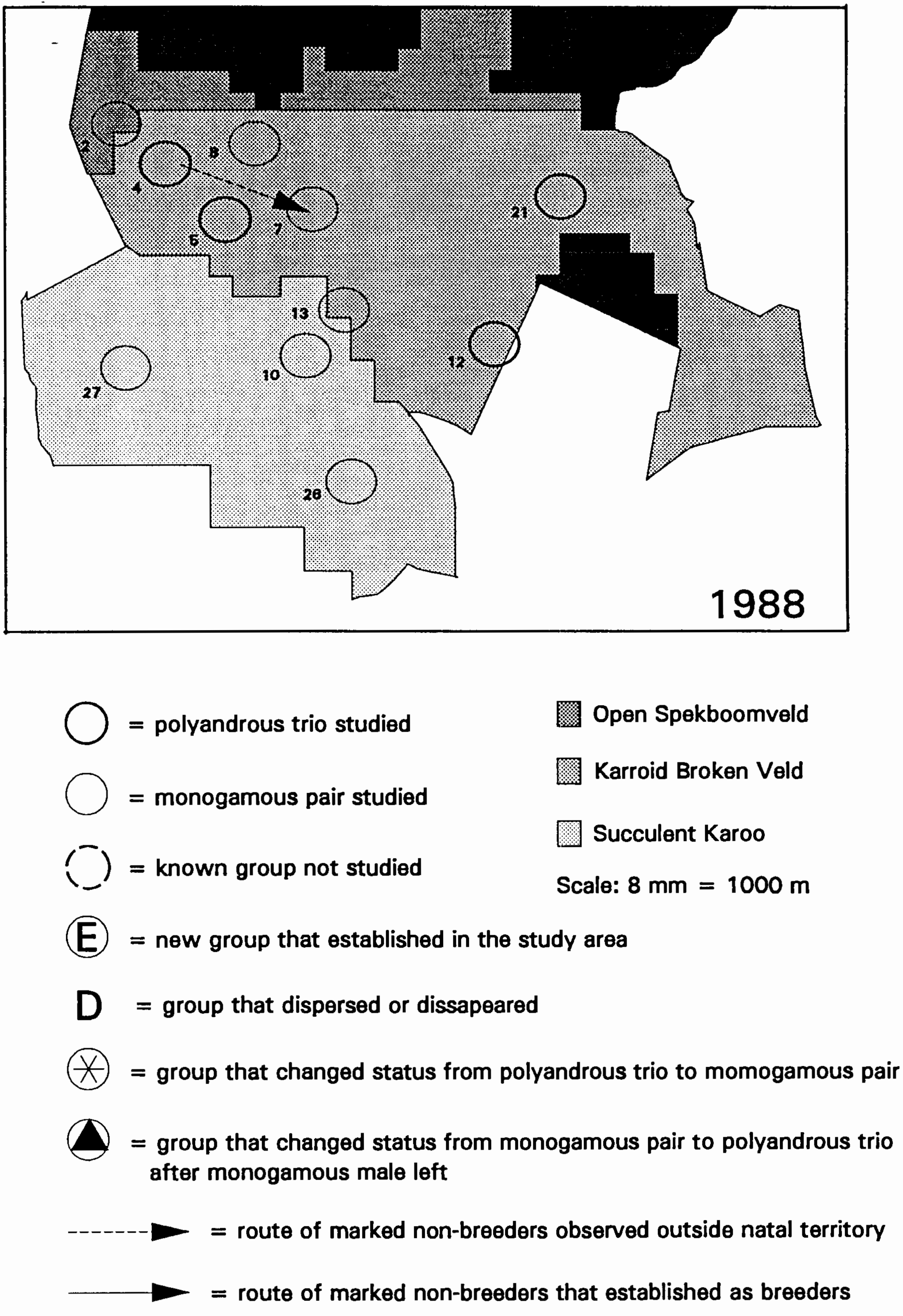

Fig. 9.2 Groups studied at Calitzdorp during 1988.

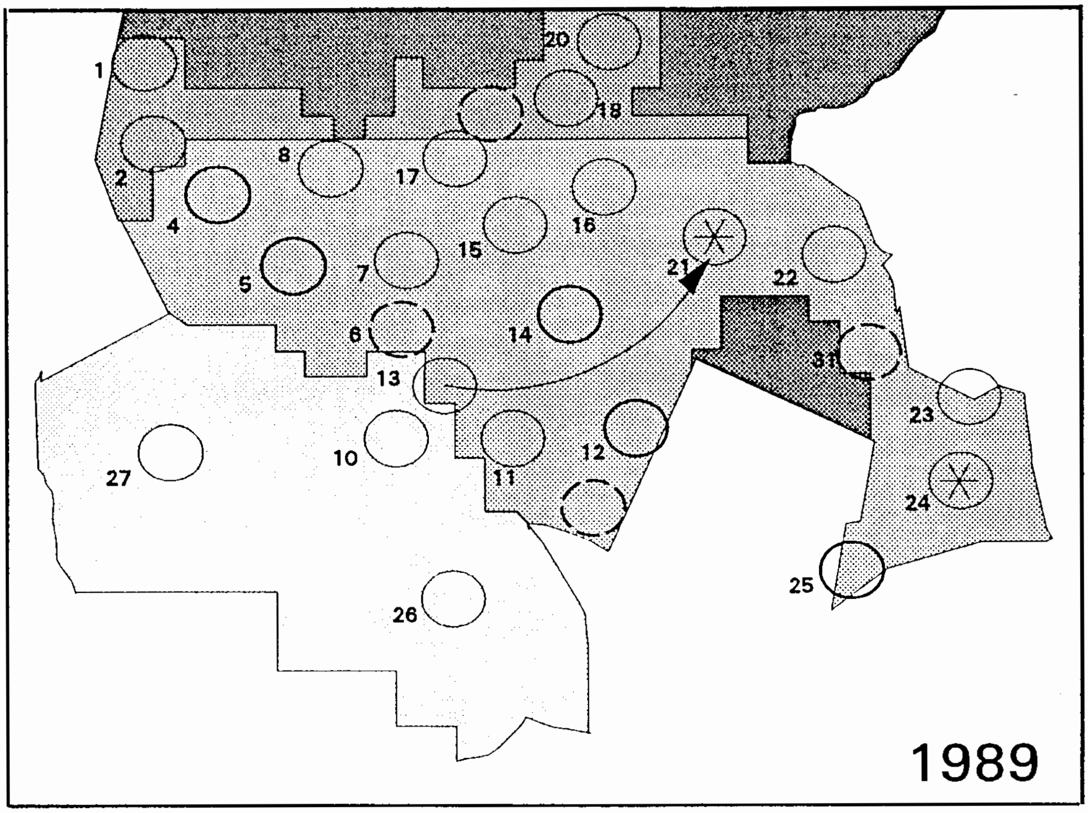

Fig. 9.3 For 1989, polyandrous trio (Group 24) removed for genetic analysis, non-breeder son and non-breeder female from Group 13 pair; Group 24 two males present during nest building but only left one when eggs are laid.

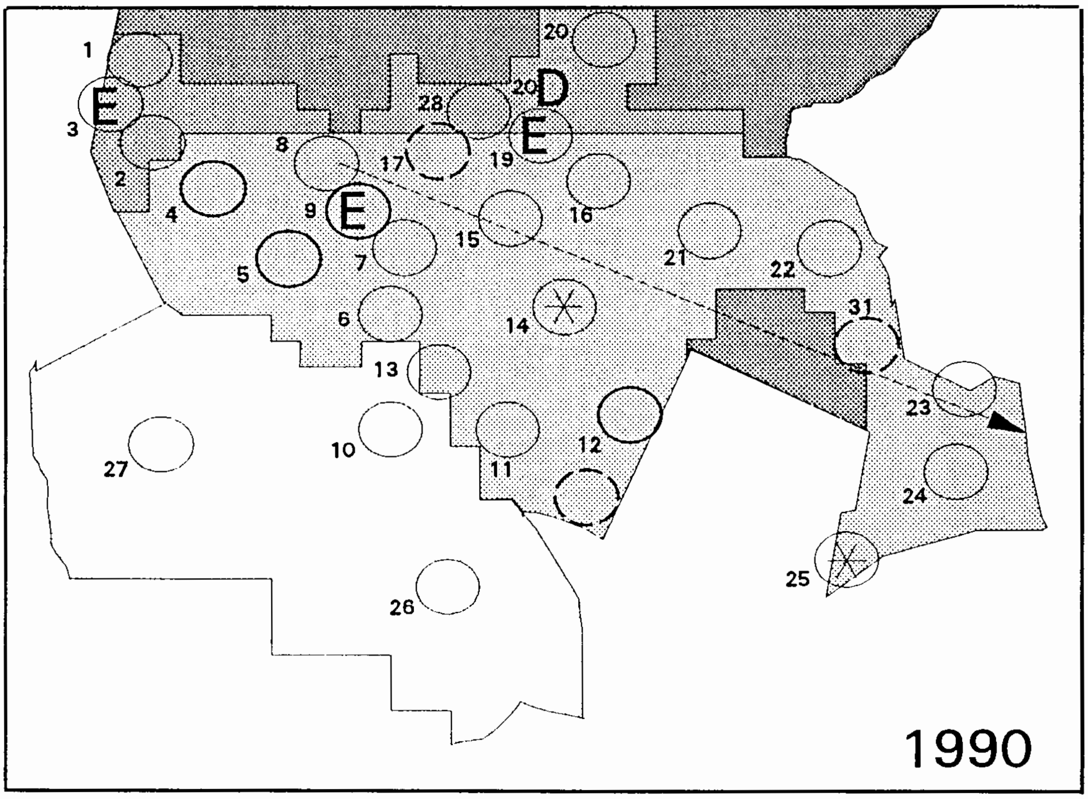

Fig. 9.4 For 1990, three new groups establish (Groups 3, 9 & 19), one a polyandrous trio (Group 9); two groups change status from polyandrous trio to monogamous pair (Groups 14 & 25); and Group 20 (monogamous pair) dispersed.

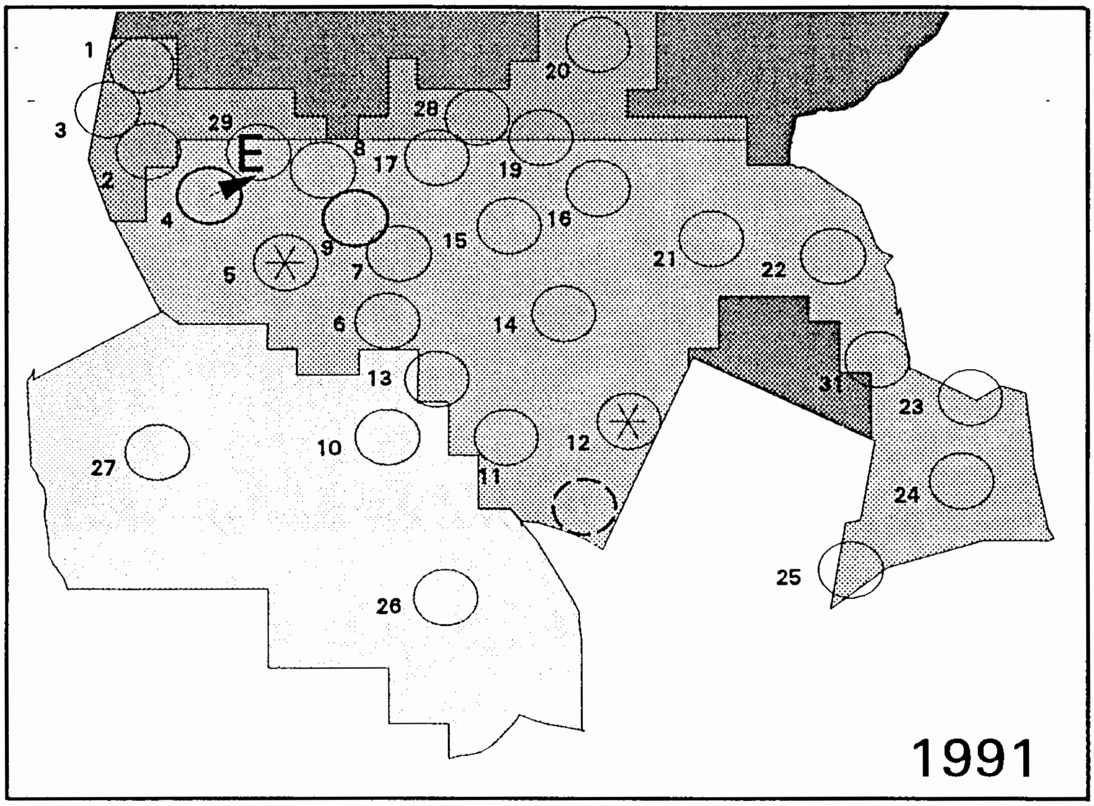

Fig. 9.5 For 1991, Groups 5 & 12 change status from polyandrous trio to monogamous pair; and Group 29 establish in the study area, a monogamous pair, the male an offspring from Group 4.

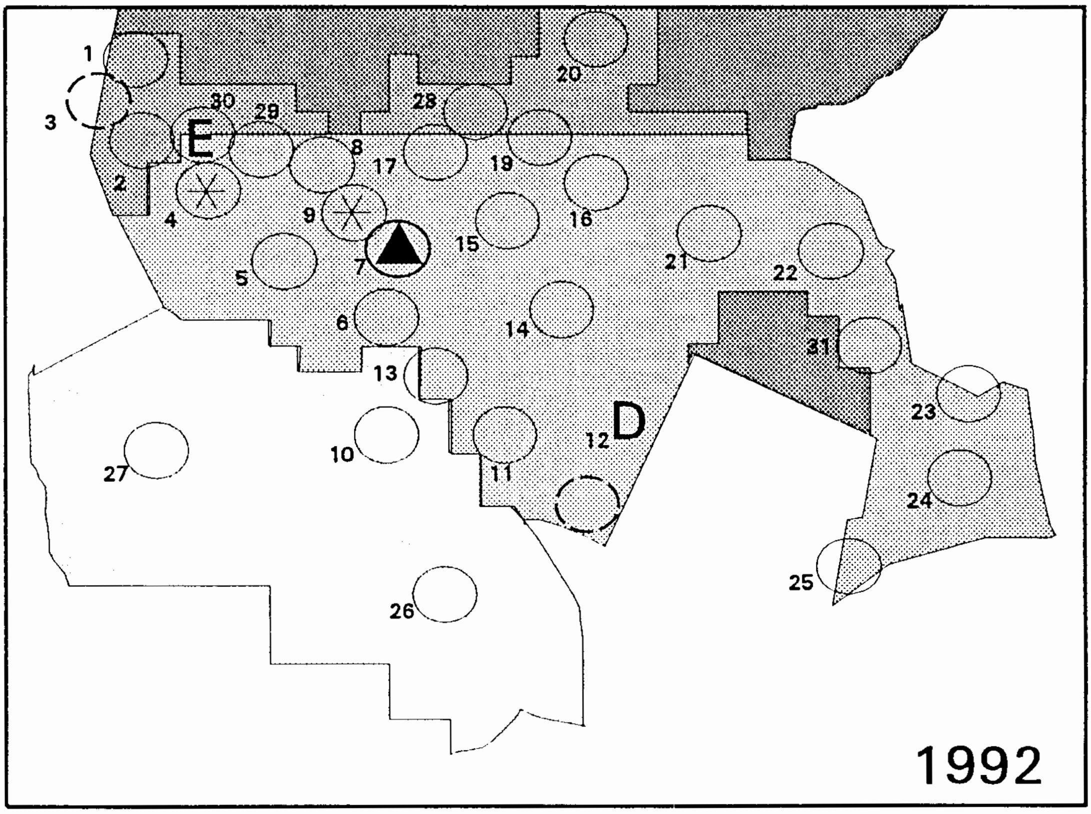

Fig. 9.6 For 1992, two polyandrous groups change status to monogamous pairs (Groups 4 & 9), but two marked males from Group 4 are replaced by an unmarked male; the marked male of Group 7 is replaced by two unmarked males; Group 12 (momogamous pair) disperse; and Group 30 establish.

9.3.5 Group dispersal/disappearance and establishment

For the four years (1989-1992) when I searched for all groups (including those not studied), the population stability at Calitzdorp was high. Per vegetation type, in KBV the coefficient of variation was 4% (mean = 20 ± 0.816 groups), in OSBV, 18% (mean = 5.25 ± 0.95), and in SK no group changes took place (3 groups).

Five new groups established in the study area, two monogamous pairs and one polyandrous trio during 1990, and one monogamous pair during 1991 and 1992. During 1990, Group 3 established in the remaining drainage line between Groups 1 & 2 (Fig. 9.4). Group 9, a polyandrous trio, established among Groups 5, 7 & 8, in fact their 1990 nest site was on the spot where the territories of the three groups previously converged (Fig. 9.4). Group 19 largely established in the territory that was left vacant after Group 20 dispersed/disappeared (Fig. 9.4). During 1991 Group 29, the male a marked son of Group 4 (1989 fledgling), established between and onto sections of the territories of Groups 4 & 8 (Fig. 9.5). When Group 4 changed status and the polyandrous males dispersed/disappeared, Group 30 established in the vacant section of the territory (Fig. 9.6). During 20 group years in OSBV, three groups established and one dispersed/disappeared, in 80 group years in KBV three established and one dispersed/disappeared, and in 15 group years in SK no changes took place.

9.3.6 Settled and disrupted groups

The reproductive success of settled groups in all vegetation types, as well as in KBV, was significantly higher than that of disrupted groups (either novices or groups with breeders replaced) (Table 9.7). Novice groups in KBV, produced on average, 0.5 offspring (range = 0-1; n = 4) and disrupted groups, 0.3 offspring (range = 0-1; n = 7). In OSBV, two novice groups produced, respectively, one offspring each. The first of two groups which I knew had no breeding experience, Group 21, was the only group that fledged no offspring during 1989, a high reproductive year. The second, Group 29, did not breed during 1991, although it was a low reproductive year. One of the novice groups that established was accompanied by a non-breeder (Table 9.6; Fig. 9.4, Group 19).

Table 9.6 Settled and disrupted Pale Chanting Goshawk monogamous and polyandrous groups **in bold**, studied at Calitzdorp from 1988 to 1992, vegetation types they nested in, the number of offspring fledged and non-breeders (in brackets) per group. Disrupted groups are either *novices* or *groups where one or two breeders were replaced*. Groups with no prior history are deleted. Values for non-breeders in brackets, the number of values indicate the number of non-breeders (*e.g.* U U = two birds) and the values itself the age of the birds, U = unknown age, N = known age but observed in later years, 1 = one year old, 2 = two years old, *etc.*

Vegetation type No.	Group name	1988	1989	1990	1991	1992
Open Spekboomveld						
1	Nellis			2	0 (1)	0
2	1stKloof		1 (2 U)	3 (1)	0	0
3	2ndKloof			*1*	0	
18	KweekK					
19	Unknown			*1 (1)*	0	2
20	Erenst			0	0	0
28	BoKuile			2	1	2 (U)
Karroid Broken Veld						
4	Okkies		**4 (N U)**	**3 (U)**	**0 (1 5)**	*0 (U)*
5	JohanG		**2**	**2 (N)**	*0 (1 2)*	0 (U)
6	Ridge			4	0	0
7	Cutting		2	2 (1)	0	*0*
8	Kraal		2 (U)	2	0 (2 2)	2
9	DGates			*1*	**0**	*1*
11	Vlakte			1(N)	0 (2)	2
12	Zwartkop		**3 (U)**	**4**	*0 (1)*	
13	Bloubosvlei		2 (U)	2 (1 1)	0 (U)	0 (U)
14	AndriesK			*0 (U U)*	0	0
15	TarRoad			2	0	2 (U)
16	Secretary			3 (U U)	0 (U U)	2 (U U)
17	Kuile				1	0 (1 U)
21	Kruisrivier		*0*	2	1 (U)	0 (U U)
22	Rietfontein			2	0	0
23	Vleirivier			2 (1)	0 (U)	2 (U U)
24	BaasF			2	0 (1 U)	2
25	Saayman			*1 (U)*	0 (U)	2
29	Pickniks				*0*	2 (U)
30	BoOkkies					*1*
31	ErnieF				2	2 (1 U)
Succulent Karoo						
10	Engelskamp		2	3 (N)	0 (2 2)	0
26	Badsaf		2 (U)	1 (N)	0 (1)	0 (4)
27	Remhog		1	1	0 (U)	2

Table 9.7 A comparison of the reproductive success of settled and disrupted groups in all vegetation types and KBV, as well as between settled polyandrous trios and monogamous pairs in KBV. NS = not significant; ** = $p < 0.01$; *** = $p < 0.001$

Variables			*t* test
All vegetation types	Settled	Disrupted	
Chicks fledged	1.17 (1.17)	0.46 (0.52)	$P < 0.05$
Non-breeder per group	0.65 (0.76)	0.62 (0.77)	NS
(n)	(81)	(13)	
Karroid Broken Veld	Settled	Disrupted	
Chicks fledged	1.32 (1.22)	0.36 (0.51)	$P < 0.05$
Non-breeder per group	0.76 (0.81)	0.64 (0.81)	NS
(n)	(53)	(11)	
Karroid Broken Veld	Settled polyandrous trios	Settled monogamous pairs	
Chicks fledged	2.25 (1.58)	1.17 (1.09)	$P < 0.05$
Non-breeder per group	0.88 (0.84)	0.73 (0.81)	NS
(n)	(8)	(45)	

The reproductive success of settled groups in OSBV (0.81 ± 1.05 offspring), KBV (1.32 ± 1.22) and SK (1.00 ± 1.04) did not differ significantly ($P > 0.05$; ANOVA; $n = 92$). In KBV, settled polyandrous trios produced significantly more and almost double the number of offspring than settled monogamous pairs (Table 9.7). Females achieved higher fitness when co-breeding, and alpha males higher inclusive fitness by co-breeding, or breeding independently with a full sib (Table 9.8). Beta males produced fewer offspring equivalents if co-breeding with an unrelated alpha male, more when co-breeding with a full sib but the highest if, as full sibs, they breed independently. Beta males co-breeding with a full sib also produced more offspring equivalents (= 0.75) than did monogamous breeders (= 0.59).

Table 9.8 The number of offspring equivalents produced in the Karroid Broken Veld by settled polyandrous and monogamous males and females, calculated out of the female's, and alpha and beta male's perspectives. The males are either not related or full sibs, and the paternity split is 68:32 in favour of the alpha male.

	Polyandrous trios	Monogamous pairs
No. of group years	8	54
No. of young	18	53
Offspring per group	2.25	1.17
FEMALE'S PERSPECTIVE		
Independent breeding	0.59	(0.5x1.17)
Co-breeding	1.13	(0.5x2.25)
ALPHA MALE'S PERSPECTIVE AND PATERNITY SPLIT 68:32		
Males not related		
Independent breeding	0.59	(0.5x1.17)
Co-breeding	0.77	0.5(0.68x2.25)
Males full sibs		
Independent breeding	0.88	(0.5x1.17)+0.5(0.5x1.17)
Co-breeding	0.95	(0.68x1.13)+0.5(0.32x1.13)
BETA MALE'S PERSPECTIVE AND PATERNITY SPLIT 32:68		
Males not related		
Independent breeding	0.59	(0.5x1.17)
Co-breeding	0.36	0.5(0.32x2.25)
Males full sibs		
Independent breeding	0.88	(0.5x1.17)+0.5(0.5x1.17)
Co-breeding	0.75	(0.32x1.13)+0.5(0.68x1.13)

The number of non-breeders per group did not differ between settled and disrupted groups in all vegetation types and KBV, nor between settled polyandrous trios and monogamous pairs in KBV (Table 9.7).

9.3.7 Study area fidelity

Excluding the polyandrous trio removed, breeders were marked for 39% (96/247) of breeder years. Of the 25 breeders marked, 84% (21) were still present in their territories in 1992. Of the breeders marked during 1988, 69% (9/13) were still present in their territories during 1992.

Over the five-year study, co-breeders delayed dispersal for 1-4 years (mean = 2.1; n = 7 groups), three males delaying dispersal for only one year. These values represent an underestimate since none of the polyandrous trios actually established and dispersed/disappeared during the study period. Marked non-breeders delayed dispersal for an average of 1.3 years in OSBV (range = 1-2; n = 4), 1.5 in KBV (range = 1-5; n = 16), and 2.3 in SK (range = 1-4; n = 4) (Table 9.5).

Discarding 23 fledglings marked in late 1992 whose dispersal/disappearance could not be recorded, 62% (62/100) of chicks that fledged during 1988-1991 were marked. Of the 73 fledglings, juveniles and non-breeders marked in the study area from 1988-1991, 67% (49/73) was not observed the following years. The proportion of marked birds not observed again in OSBV (6/10) and SK (4/9) did not differ significantly and were combined (Chi-square; $P < 0.05$). Of the birds marked in KBV, 70% (38/54) were not observed again, significantly more than the 35% (10/29) in OSBV and SK (Chi-square; $P < 0.01$).

9.3.8 Breeder recruitment

Only three marked non-breeders established as breeders, two after the polyandrous trio was removed (see Section 9.3.3), and a non-breeder son of Group 4 (1989 fledgling) with an unmarked female in a territory extending partly onto the territory of his parents (Fig. 9.5; from Group 4 to 29). I included the first two since other vacancies may have been created by unnatural causes, *e.g.* poisoning. Of PCGs that established as breeders, only 21% (3/14) were marked. Therefore, of the 73 fledglings, juveniles and non-breeders that were marked during 1988-91, only 4% (3/73) established as breeders. Overall breeder recruitment, *i.e.* the establishment of individuals as breeders was 9% in OSBV (4/44), 6%

in KBV (10/173) and zero in SK. Calculated over five years, these values were 2% in OSBV and 1% in KBV.

9.3.9 Dispersal and survival

The 28 breeders that were marked during the study period were observed for 86.5 breeder years within their breeding territories, and no breeder was ever seen in a known territory of another group (see Chapter 5). In KBV, two non-breeding adult females were observed outside their natal territory. During 1988, the first was observed twice in a territory once removed from hers (Fig. 9.2). The second was observed on the border of the study area (Fig. 9.4), some distance from her natal territory.

Of 64 marked fledglings, juveniles, non-breeders and breeders that dispersed/disappeared, three were recovered from outside the study area. A juvenile found dead, dispersed 99 km in 12 months and a second, also a juvenile found dead, dispersed 397 km in only four months. The third, delayed dispersal for one year, then dispersed and was shot 32 months later, 20 km from her natal territory.

Three PCGs, marked as fledglings, were recovered dead from within the study area. The first was found dead 44 months later near the nest site, cause of death unknown. Another two was a road-kill within three months after fledging, in both cases the nest sites where within 100 from a public road. A further two dead birds were found, a carcass laying below a tree and a wing of an adult female in territory of Group 12 (1992).

PCGs that weigh on average 862 g (Chapter 7), have a life expectancy of 16 years (192 months) (Lindstedt & Calder 1976). To date, four PCGs have been found to live for longer than eight years (96 months) and have lived 107, 112, 138 and 182 months respectively.

9.4 DISCUSSION

9.4.1 Habitat quality

For PCGs at the Calitzdorp study area, habitat quality was described by two ecological factors, shrub-perch and heuweltjie-openness (Table 9.2, Fig. 9.1). Shrub-perch provided 76-150 cm high shrubs for the dominant prey species *Otomys unisulcatus*, to build their stick lodges under (Vermeulen & Nel 1988), as well as natural perches for this pause-travel predator. As the density of shrub-perch declined from KBV to occupied Succulent Karoo (SKO) and unoccupied Succulent Karoo (SKU), habitat quality decreased (Fig. 9.1). In fact, quality also decreased as one moved into the denser, more woody OSBV and CSBV. For the second factor, heuweltjie-openness, heuweltjies provided the suitable soil conditions for the burrower and second dominant prey species, *Parotomys brantsii*. It also provided openness, essential for perching PCGs to view terrestrial prey. As heuweltjie-openness declined from KBV towards OSBV and CSBV, habitat quality decreased (Fig. 9.1).

In KBV, shrub-perch and heuweltjie-openness coincided in an optimum combination, and provided PCGs with a high-quality habitat, a habitat not only associated with high otomyinid biomass, as well as optimum hunting habitat. The habitat quality in OSBV was judged as medium quality since there was less heuweltjie-openness, therefore potentially fewer *P. brantsii* and less 'openness'. In CSBV (no PCGs), the habitat was unsuitable since very few heuweltjies occur, and the vegetation is so dense (or openness limited) that it probably restricted perch hunting. Alternatively, KBV and SK were clearly separated on the absence of shrub-perch in SK. SK was judged as medium quality because of lower densities of *O. unisulcatus* and abundance of natural perches. Although the presence of artificial perches was not statistically meaningful (in both discriminant function and factor analyses), it was biological meaningful since perches provided PCGs in SK with hunting platforms in areas that would otherwise be unsuitable. The occupied SK was therefore of medium quality and unoccupied SK, unsuitable since it did not provide adequate artificial and/or natural perches.

Whereas natural and artificial perches, 67-150 cm high shrubs, heuweltjies, and proportion open ground and perch cover were all constant variables, the study area's prey abundance, more specifically the otomyinid densities, were variable. Otomyinid densities recorded and estimated, were intermediate during 1988, high during 1989 and 1990, 1991 low, and in 1992 again intermediate, and the reproductive success followed this trend (Chapter 7). Moreover, the density of otomyinids was higher in KBV, than OSBV and SK, therefore promoting higher quality habitat. Habitat quality thus consisted of effectively constant and a variable elements.

Since polyandrous trios were present only in KBV, it is only in this vegetation type that status changes took place. However, groups changed status in the same territories or parts thereof. The ecological differences, although statistically meaningful, found between otomyinid densities, associated habitat parameters and hunting habitat of polyandrous trio and monogamous pair territories, were therefore probably superficial and related to differences between territories (see Chapters 7 & 8; see also Bednarz & Ligon 1988). Since territories could be utilised interchangeably, territories in KBV can therefore be regarded as of equal quality.

9.4.2 Non-breeder demography

As might be expected, the highest number of non-breeders per group was found in high-quality KBV, as well as the highest number of groups with non-breeders. Moreover, between years, the number of non-breeders did not differ as the variable element of habitat quality changed. This variable aspect of habitat quality therefore not only influenced the decision to delayed dispersal, but also other factors such as the restriction of two non-breeders per natal territory. Since 35-70% of marked fledglings were not observed again, it appeared that mortality was high among young PCGs. Mortality of young raptors is known to be very high, ranging from 50-83% in the first year to 30-47% in the second (see references in Newton 1979). Starvation may be major cause of mortality among PCG juveniles, given their 4% vertebrate hunting success rate of (Chapter 8), but predation, disease (Newton 1979) and unnatural causes, *e.g.* shooting, poisoning, roadkills, *etc.*, may also play a role.

Since all marked birds reported from outside the study area were found dead, dispersal by an inexperienced juvenile may also increase the probability of death. However, the chances of finding dead marked birds may differ depending on the distribution of mortality factors within the population. For juvenile PCGs, the first fitness benefit to be gained from delaying dispersal is enhanced survivorship, a benefit of philopatry (Stacey & Ligon 1987, 1991; Emlen & Wrege 1994). Such a benefit is the skill learned in hunting difficult to catch vertebrate prey (see Chapter 8). However, the decision to hunt cooperatively and share in prey did not only rest with non-breeders, but breeders, since they as dominant breeders had to make a conscious decision to allow non-breeders to share in the returns of cooperative hunting (Ellis *et al.* 1993). The intrinsic benefit gained from cooperative hunting and the predicted increase in survival may have evolved after non-breeders delayed dispersal and, as such, may be a secondary benefit of family living.

A further finding was that marked non-breeders observed outside their natal territories (n = 2), or marked non-breeders that established as breeders (n = 3), all did so within their natal KBV vegetation type. Five studies have now shown that offspring from high-quality territories will not disperse to a habitat of lower quality, but only habitat of equal or higher quality since they can afford to be more selective (Stacey & Ligon 1987; Rabenold 1990; Koenig *et al.* 1992; Komdeur 1992; Emlen & Wrege 1994; this study). Birds from high-quality habitat can, because of the fitness advantages it offers, wait longer and therefore have a higher probability of acquiring a vacancy in high-quality habitat (Stacey & Ligon 1987; Waser 1988).

9.4.3 Novice co-breeder demography

Since co-breeders only occurred in high-quality KBV, there was an obvious relationship between co-breeding and habitat quality. Moreover, a polyandrous trio established during 1991, and a group changed status to polyandrous (with two 'new' males) during 1992, when the otomyinid densities and reproduction were respectively low and intermediate. The variable element of habitat quality, as such, did not impact on the decision to co-breed. Obtaining a breeding vacancy in KBV did not automatically result in reproductive success. It is difficult to establish if first-time breeders required any special breeding skill or were they simply inexperienced breeders. In some raptor populations examined, individuals breeding for the first time produced fewer young than experienced breeders, whereas in others they did not (Newton 1979). The fact that one novice group established with a non-breeder suggested that either groups with breeding experience may establish, or that non-breeder sibs may follow breeders into their newly acquired territory. If breeding experience is a critical prerequisite to successful reproduction, then high-quality habitat would at least offer a greater probability for gaining such experience.

Non-breeders were prevented from helping at the nest site (Chapter 3), therefore no breeding experience could be attained. Furthermore, since no monogamous pair changed status to a polyandrous trio, the option to enter the breeding population as a fully cooperative helper, was apparently not open. To enter the breeding population, two options were therefore left, either establish as a monogamous breeder, or as in the Galapagos Hawk *Buteo galapagoensis*, form a coalition with another male (Faaborg *et al.* 1980; Koenig 1981; Faaborg 1986). Given that only two out of seven groups, that established were polyandrous trios, it does not appear if the coalition itself comprised any bargaining power (Stacey & Ligon 1987; Heinsohn *et al.* 1990). Moreover, if co-breeders were always sibs, to form a coalition, potential breeder males must associate beforehand, and such an association could only be forged if PCGs were living in families. After all, not only did PCG offspring from different clutches from the same year or different years recognise each other as sibs, but non-breeders from different age classes delayed dispersal together. Thus forming of a coalition and polyandrous trio may be a benefit of philopatry, a secondary benefit of PCGs living in families.

9.4.4 Settled co-breeder demography

In cases where groups changed status, the 'disturbance' appeared to disrupt reproduction. It is an open question if the loss of a second provisioning male caused, the now monogamous female, to cease breeding due to a lack of extra provisioning. Whatever the reason for the inability to produce more than one offspring per group, either as novices, or after changing status, settled groups were reproductively far more successful than disrupted groups. Moreover, in KBV, polyandrous breeders achieved a much greater inclusive fitness than did monogamous pairs (Tables 9.7 & 9.8). This success was due largely to help provided by fully-cooperating beta males. In fact, it contributed more to the reproductive success of polyandrous groups than densities of dominant prey and territory size.

If such benefits are to be gained from helping, why then did co-breeding beta males disperse from breeding groups? Again the variable element, or actual reproduction, in high-quality habitat seemed to play a lesser role, since one marked beta male dispersed during 1990, two during 1991 and one during 1992. It therefore appeared that, once co-breeders gained breeding and reproduced successfully, a different set of circumstances caused co-breeders to disperse from polyandrous trios. Whatever the reason, if co-breeders would obtain a breeding vacancy as a monogamous male in habitat of equal quality, the inclusive fitness of the ex beta males would be higher than if they remained co-breeders in polyandrous trios (independent breeding; Table 9.8).

9.4.5 Breeder demography

At Calitzdorp, in spite of large fluctuations in prey abundance and breeding rates, the PCG population was remarkable stable. The population stability, on average, bettered the 8% coefficient of variation measured over 14 years in the Florida Scrub Jay *Aphelocoma* *coerulescens*, described by Fitzpatrick & Woolfenden (1986) as unequaled in land-living birds. When group members dispersed or established, changes took place in KBV and to a lesser degree, OSBV. One would expect changes in otomyinid densities to influence birds in medium-quality more than high-quality habitat. For example, in the Acorn Woodpecker *Melanerpes formicivorus*, while the number of available food storage holes greatly influenced habitat quality, in years of low crop production, large numbers of birds left their territories, more so territories with fewer storing holes (Stacey & Ligon 1987; Koenig & Stacey 1990). This raises the question, were there any costs involved in residing in high-quality habitat?

First, PCGs may have been able to survive in low otomyinid years by being less selective feeders, and switching to a more diverse diet. Birds in SK, preying on a more diverse diet in years of intermediate and high otomyinid densities (1988-1989; Chapter 7), may therefore be impacted less by varying otomyinid densities. Second, given the high and often aggressive interspecific and intraspecific interaction frequency in KBV and also OSBV (Chapter 5), and that from these two vegetation types PCGs dispersed/disappeared, it would appear that living in high-quality habitat presents some risks for PCG males defending territories and their mates. Were breeders actively displaced from their territories, or did breeders passively vacate territories? A further possibility is that breeders may have died of unnatural causes, such as from feeding on poisoned meat placed for Black-backed Jackals *Canis mesomelas* (GM pers. comm.).

There was however a further, more important, cost of residing in high-quality habitat. Since the highest number of offspring were produced in KBV, but territoriality limited the number of offspring per group, a larger proportion of non-breeders was probably forced to disperse. Furthermore, PCGs have a life expectancy of 16 years and 69% of breeders marked during 1988 were still occupying the same territories during 1992. The population was therefore very stable, access to territorial space of suitable quality was limited and breeder recruitment very low. Under such circumstances where access for young to gain breeding opportunities was limited, one can expect breeders to change their reproductive strategy as to accommodate their offspring into the population (Fitzpatrick & Woolfenden 1986). Given the apparent high mortality of non-breeders, perhaps one should also judge the fitness of breeders on their ability to accommodate non-breeders. Indeed, non-breeders present in natal territories may be a further index of reproductive success. The temporary reduction in reproductive success of disrupted groups may therefore be of less significance than the survival of non-breeders.

As a first reproductive strategy to accommodate their offspring, I suggest that breeders allowed offspring to delay dispersal and partake and share in the returns of social hunting. It would incur some cost, losing the occasional vertebrate prey item, but it would increase the survival of their offspring. Once non-breeders were accommodated into groups, they could inherit a territory, more so a natal territory of high quality (Woolfenden & Fitzpatrick 1984; Stacey & Ligon 1987). This actually happened when I removed the polyandrous trio and the non-breeding son successfully occupied and defended the territory.

A further reproductive strategy is budding-off from the natal territory (*sensu* Woolfenden & Fitzpatrick 1984). The marked son of polyandrous trio (Group 4; Fig. 9.5), established during 1991, at the end of his first year, by defending a separate territory bordering partly on his natal territory and partly on a neighbouring territory (Group 29; Fig. 9.5). During 1992, interactions between him and the neighbouring male were observed, but not towards the male that replaced his father(s) (GM unpubl. data). Although it is an open question if the polyandrous group facilitated the budding-off, it certainly presented the offspring with a breeding opportunity with minimal cost to parents.

Living in habitats of differing quality in a stable population presented breeders and their offspring with a range of benefits and constraints. Non-breeders benefitted by gaining improved survivorship, but were constrained by the low proportion of sibs that were allowed to delay dispersal. Co-breeders were constrained by the lack of breeding experience and options to gain such experience, but benefitted once they reproduced in a polyandrous group. Breeders benefitted from reproduction, but were constrained by population stability, apparently high mortality of juveniles and the lack of territorial space for their offspring. The constraints and benefits PCGs encounter *en route* from juvenile to monogamous breeder will be discussed in the Summary and Syntheses.

SECTION 3

SUMMARY AND SYNTHESIS

10.1 SUMMARY OF FINDINGS

The aims of this study were to investigate and review a range of demographic and ecological factors that may predispose Pale Chanting Goshawks (PCG) to delay dispersal and breed cooperatively. The social system and ecological variables that may constitute habitat quality were investigated in three vegetation types, Karroid Broken Veld (KBV), Open Spekboomveld (OSBV) and Succulent Karoo (SK) at the main Calitzdorp study area. PCG breeding biology was studied for 117 group years (11-29 groups) over five breeding seasons from 1988-1992.

The key results of this study are the following:

1. Delayed dispersal by offspring was recorded in all vegetation types and non-breeders were not allowed near nest sites during breeding seasons. Cooperative polyandry was recorded only in KBV, and the males of one polyandrous trio analysed genetically (DNA fingerprinting) were first order relatives. Both males shared one female and, although subordinate to alpha males, beta males participated equally in the critical reproductive activity of prey provisioning. Given the constraint of breeding in a temperate region, with its restricted summer period, and being able to lay a maximum of two eggs, the occurrence of two males enabled polyandrous trios to undertake more frequent and successful breeding attempts. The help provided by beta males contributed more to this success than did otomyinid rodent densities and territory size.
2. PCGs living in KBV preyed on more otomyinids (*Otomys unisulcatus* and *Parotomys brantsii*) than those occupying other vegetation types, and a positive relationship was found between reproductive success and otomyinid density. The quality of KBV was judged as high since it was the only vegetation type which supported: (1) a very high otomyinid biomass (347 kg/km^2 compared to 189 kg/km^2 in OSBV and 84 kg/km^2 in SK), (2) desirable habitat parameters, such as heuweltjies and 75-150 cm high shrubs (associated with otomyinids), (3) a hunting habitat with an optimum combination of high prey

visibility and perch availability that allowed this pause-travel, perch-based predator to secure large otomyinid prey to satisfy its daily nutritional requirements.

3. The roadcount (2.1 km/bird) and estimated PCG densities (0.71-1.01 km^2/bird) in KBV and OSBV are among the highest single-species raptor densities in the Afrotropics, a further indication of the excellence of this PCG habitat.

4. The PCG population was stable and space for territories was limited. This lack of territorial space affected breeders (no space for all their offspring), co-breeders (no space to breed) and non-breeders (no space for all offspring to delay dispersal). Since the number of offspring per group was limited to two by this extrinsic constraint, and groups in high-quality habitat produced more offspring, it is suggested that breeders, as a reproductive strategy, tolerated offspring in their natal territories. The survival of these offspring was further facilitated by allowing cooperative hunting with breeders. Furthermore, breeder recruitment was low and, to accommodate their offspring into the breeding population, breeders could facilitate the acquisition of a territory by assisting their offspring in wresting some territorial space away from a neighbouring group. By delaying dispersal non-breeders may also eventually inherit the territory if breeders die or disperse.

5. Sexually immature non-breeders delayed dispersal since they benefitted from higher survival in high-quality habitat. However, non-breeders were prevented from gaining any breeding experience. Therefore, sexually mature non-breeders probably dispersed when the cost in fitness of delayed dispersal became too high.

6. Novice groups did not succeed in producing more than one offspring, even in years of high otomyinid densities, whereas experienced breeders produced more than one offspring per season. Therefore, breeding experience was essential to be successful reproductively. Co-breeders in KBV delayed dispersal since their fitness as co-breeders was probably higher than fitness due to dispersing to a breeding vacancy in habitat of lower quality. Alternatively, since no co-breeders were present in habitats of lower quality, their fitness as co-breeders was probably less than the probable fitness of breeding monogamously in the first breeding vacancy in low-quality habitat. It is therefore suggested that co-breeders

father few, if any, offspring since, if they did, their fitness would increase and co-breeding would become an option in habitat of lower quality.

7. Settled or experienced polyandrous trios were highly successful reproductively, apparently to the extent where the fitness of co-breeders exceeded that of monogamous breeders. I suggest that co-breeders dispersed after a few years as soon as their experience attained as a breeder, *e.g.* provisioning prey to the females and nestlings at nest sites and territorial defense, allowed them to attain a breeding position in habitat of equal quality.

10.2 SYNTHESIS: THE EVOLUTION OF FAMILY-LIVING IN THE PALE CHANTING GOSHAWK

10.2.1 Introduction

Families are formed when offspring delay dispersal and associate with one or both parents (Emlen 1994). At Calitzdorp, non-breeding Pale Chanting Goshawks (PCGs) delayed dispersal and, in some groups in Karroid Broken Veld (KBV), male PCGs associated with other male sibs and co-bred in polyandrous trios. Living in groups holds no automatic benefits to individuals (Alexander 1974), but social systems are shaped by a range of social and ecological benefits and constraints (Koenig & Pitelka 1981; Stacey & Ligon 1987, 1991; Koenig *et al.* 1992; Emlen 1994). The greater the interplay there is between these benefits and constraints, the higher the demographic pressure, and the further the social system may evolve from single nesting monogamous pairs with non-breeders to plural nesting (Fitzpatrick & Woolfenden 1986).

10.2.2 Benefits and constraints

Habitat quality at the Calitzdorp study area has been defined by two factors, shrub-perch and heuweltjie-openness. Breeders occupying a territory in high-quality KBV had the highest reproductive success, both in relation to PCGs from other vegetation types at Calitzdorp and populations elsewhere. Other attributes of PCGs which bred in KBV included double-brooding, large PCG groups, the highest frequency of groups with non-breeders and some of the highest raptor densities in the Afrotropics (Fig. 10.1). The quality of KBV was further highlighted by the finding that almost all instances of intraspecific territoriality were recorded in this vegetation type. Therefore, compared with other study areas, groups from KBV were less constrained ecologically. What was a constraint however was the lack of territorial space for breeders and non-breeders alike. As has been demonstrated by the delayed dispersal threshold model of Koenig *et al.* (1992), and the empirical study of Komdeur (1992), only when there is a distinct relationship between habitat quality (and the accompanying reproductive and survival fitness), and a lack of territorial space, that the stage is set for young to remain with their parents (Fig. 10.1). Once they form groups, inhabitants may adapt to advantages of living with other individuals and various secondary benefits of family living may develop, *e.g.* helping close relatives, searching for breeding vacancies from natal territories or inheriting a territory (see Emlen 1994).

10.2.3 Why do breeders adjust their reproductive strategy?

Mortality of PCG juveniles appeared to be high, and breeders in high-quality habitat, although they produced the largest number of offspring, were constrained by the lack of space and were thus limited in the number of offspring per territory (Table 10.1). Therefore, rather than to expel or stop feeding offspring, as birds of prey normally do (Brown 1970; de Vries 1973; Newton 1986), a logical reproductive strategy would be to tolerate offspring on the natal territory (Fig. 10.1). At the least, the more offspring that disperse, the better the changes are for some of the remaining birds to survive, obtain a breeding opportunity and breed, especially so in high-quality habitat. However, juvenile survival will increase even further if breeders could improve the survival of their offspring by allowing them extended right of residence.

To increase non-breeder survival further, breeders may, as a reproductive strategy, allow non-breeders to partake and feed exclusively on prey they catch during cooperative hunts. Since even the vertebrae hunting success of experienced breeders was low, the critical

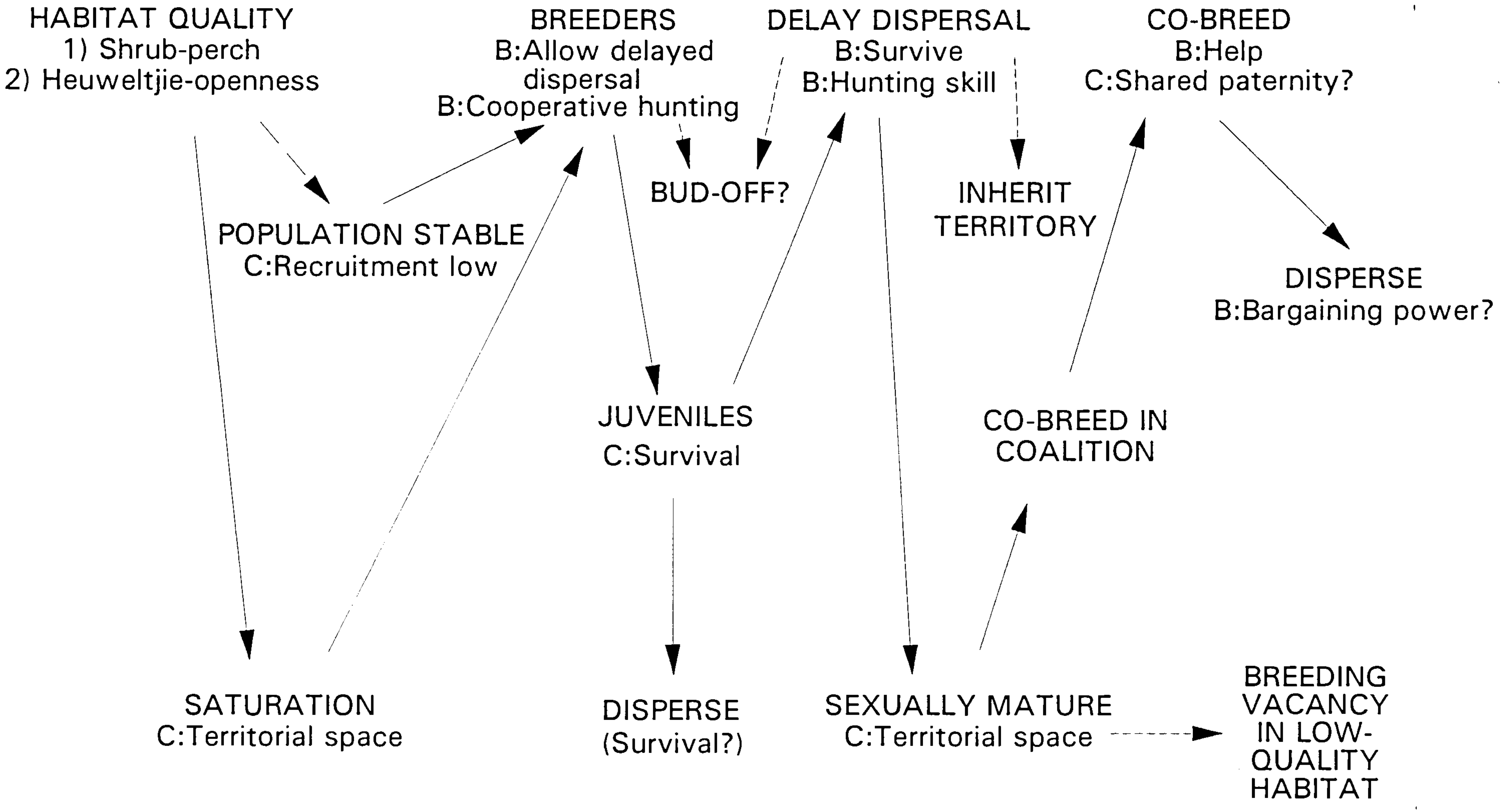

Fig. 10.1 A flow-diagram presenting the different constriants (C) and benefits (B) that breeders, juveniles and co-breeders ecounter as the result of living in high-quality habitat that was near saturation.

survival factor was the ability to catch prey, not merely having a high abundance of prey. For individual breeders, the occasional loss of a prey item in a hunt they initiated was a small price to pay for the increased survival of their offspring through an advancement in their hunting technique. Once non-breeders survived, breeders faced an additional constraint in that the population was stable and breeder recruitment low and the probability of establishing their offspring in the breeding population therefore marginal (Fig. 10.1). The population stability itself may be, at least in part, the result of living in habitats of higher quality. A further reproductive strategy would thus be to promote the introduction of your own offspring into the population actively, *e.g.* by facilitating them to bud-off (Woolfenden & Fitzpatrick 1984). Having your offspring delaying dispersal in their natal territory holds a secondary benefit in that they may inherit the territory if breeder parents die or disperse.

10.2.4 Why do sexually immature non-breeders delay dispersal?

The first constraint non-breeder PCGs, and particularly juveniles, faced was that of survival. Their changes of survival must have been higher in higher-quality natal habitat since it allowed higher hunter efficiency and a diverse selection of larger prey. The benefit of learning how to hunt vertebrate prey during cooperative hunts further enhanced their survival, since even the hunting success of vertebrate prey by experienced adults was low (12%; see also Toland 1986) (Fig. 10.1). As was expected, more groups with non-breeders were found in high- *vs* medium-quality habitat, since survival fitness gains were larger (Table 10.1). However, since not all non-breeders could delay dispersal due to the lack of territorial space, it is unknown how the number of non-breeders per group was controlled. Perhaps, the 'best' chicks from a given breeding attempt could displace the 'worst' from previous years.

Table 10.1 Life history traits of monogamous and polyandrous Pale Chanting Goshawk groups in different quality habitats. For polyandrous trios, males are fulls sibs and paternity split 68:32 (or 100:0 in brackets) in favour of alpha males. Fitness of breeders in Open Spekboomveld and Succulent Karoo calculated as for monogamous breeders in Karroid Broken Veld. CSBV = Closed Spekboomveld, OSBV = Open Spekboomveld, KBV = Karroid Broken Veld, SKO = Succulent Karoo occupied and SKU = Succulent Karoo unoccupied.

Vegetation types	CSBV	OSBV	KBV	SKO	SKU
HABITAT QUILITY	Unsuitable	Medium	High	Medium	Unsuitable
PCGS PRESENT	No	Yes	Yes	Yes	No
GROUP SIZE					
Monogamous pair		3.27	3.81	3.40	
Polyandrous trio			5.38		
CO-BREEDERS PRESENT		No	Yes	No	
ALL STUDIED GROUPS					
REPRODUCTIVE SUCCESS					
Monogamous pair		0.82	1.08	0.87	
Polyandrous trio			1.63		
INCLUSIVE FITNESS					
Monogamous pair					
Female/Male		0.41	0.54	0.44	
Polyandrous trio					
Female			0.82		
Alpha male			0.69 (0.82)		
Beta male			0.54 (0.41)		
SETTLED GROUPS					
REPRODUCTIVE SUCCESS					
Monogamous pair		0.81	1.17	1.00	
Polyandrous trio			2.25		
INCLUSIVE FITNESS					
Monogamous pair					
Female/Male		0.41	0.59	0.50	
Polyandrous trio					
Female			1.13		
Alpha male			0.95 (1.13)		
Beta male			0.75 (0.57)		
NON-BREEDERS PRESENT		Yes	Yes	Yes	
NON-BREEDERS PER GROUP					
Monogamous pair		0.46	0.73	0.53	
Polyandrous trio			0.75		
GROUPS WITH NON-BREEDERS					
Monogamous pair		7/22 (32%)	9/16 (56%)	7/15 (47%)	
Polyandrous trio			36/64 (56%)		
MARKED OFFSPRING NOT OBSERVED AGAIN		6/10 (60%)	38/54 (70%)	4/9 (44%)	

10.2.5 Why do sexually mature non-breeders disperse?

Once non-breeders reached sexual maturity, they faced the extrinsic constraint that there was no space available to establish their own territory and breed (Fig. 10.1). I do not know the age at which PCG non-breeders become reproductively active, but two groups containing only two-year old males at least laid eggs that hatched. I suggest that the majority of non-breeders dispersed after a year since the cost of dispersal, *i.e.* the fitness loss due to dispersing and breeding in a territorial vacancy in habitat of poorer quality, was less than the cost of delayed dispersal, *i.e.* the reproductive success associated with missed breeding opportunities (Koenig *et al.* 1992; Emlen 1994). Why non-breeders were not allowed to help at the nest is an open question, as helping may have a positive impact on reproduction (Emlen 1990). Helping may, however, have no impact at all, or may even disrupt breeding attempts (Brown & Brown 1990; du Plessis 1991).

10.2.6 Why do co-breeders delay dispersal?

To reproduce successfully in high-quality habitat, sexually mature non-breeders faced two options, co-breed or disperse (Fig. 10.1). Since the formation of a polyandrous trio by the joining of an established monogamous pair by a co-breeder was not recorded in the study period, the only option left was to establish in a coalition with another male (Koenig 1981), as in the Galapagos Hawk *Buteo galapagoensis* (Faaborg *et al.* 1980; Faaborg 1986). It was not known if dominant alpha males had any breeding experience or if the high reproductive success of these birds was simply the result of dominance *per se*.

Why co-breeding occurred, and why it occurred only in high-quality KBV habitat, can only be answered if one assumes that territories would be filled in rank order of quality and one then compares the fitness of a co-breeder with the fitness of a bird that disperses and breeds in a territorial vacancy in habitat of poorer quality. I suggest that co-breeders delayed dispersal in high-quality habitat, even if they fathered no offspring (indirect fitness = 0.41 offspring equivalents; Table 10.1), since their reproductive fitness would probably still be higher than if they had dispersed to a territorial vacancy. If co-breeders did father offspring and achieved some direct fitness benefits, not only their inclusive fitness would increase, but it would also favour co-breeding, even in habitats of lower quality. I further hypothesise that no co-breeders were found in medium-quality habitat since the co-breeding threshold was crossed, *i.e.* the fitness of a co-breeder would be lower than the fitness of a bird that disperse and breeds in a territorial vacancy in habitat of even poorer quality. At what level of habitat quality the first territorial vacancies were to be found is an open question, but in the Claratal study area territories, or parts thereof, were abandoned (Biggs *et al.* 1984). Here monogamous pairs produced on average 0.40 offspring per group, below that of groups in medium-quality habitats at Calitzdorp (Table 10.1).

Another factor to consider is that four other studies (see Emlen 1994), and evidence from this study have shown that offspring from high-quality habitats can be more selective in acquiring a breeding vacancy. There may be a relationship between the ability to find such a vacancy and quality of habitat from which the bird disperses. Non-breeders that disperse from high-quality habitat might be in better body condition and in possession of better survival skills, that enable them not only to wait longer, but to search further than birds from low-quality habitats. If so, it would decrease the cost of delayed dispersal. It would also allow dominant breeders to adjust paternity skew to allow co-breeders greater reproductive fitness. In short, it is the dominant breeders that really benefit form allowing co-breeders into the breeding group.

10.2.7 Why do experienced co-breeders disperse?

In high-quality habitat, reproductive success was high, groups bred almost every year (even twice in some years), and breeding experience could therefore be attained. As soon as co-breeders gained breeding experience, the help provided by beta males became an intrinsic benefit since settled polyandrous trios produced twice as many offspring as did monogamous pairs (Table 10.1). Even if experienced co-breeders fathered no offspring, their inclusive reproductive fitness would be 0.57 offspring equivalents, only slightly less than that of monogamous breeders (= 0.59). Under such circumstances, one would expect all PCGs to breed in polyandrous groups because of the higher reproductive fitness per individual. Why then did co-breeders disperse from polyandrous trios?

As reproductive success of settled or experienced polyandrous trios increased, so did the cost of co-breeding, *i.e.* the suspected fitness loss of a beta male, provisioning at the same rate as a the alpha male, but copulating at a lower frequency and probably out of the fertility period (Chapter 4). For example if a polyandrous trio produced on average 2.00 offspring, with no paternity skew the beta male, as a sib of the alpha male, would achieve 0.75 offspring equivalents. However, if the beta males fathered no offspring, he achieves 0.50 offspring equivalents and the cost of co-breeding is 0.25. Alternatively, if a polyandrous trio produced 3.00 offspring, the cost would be 0.38 offspring equivalents (1.13-0.75). Nevertheless, co-breeding beta males acquired a range of essential reproductive skills such as female attendance in the pre-laying period, copulation, nest construction, prey provisioning and territorial defense, *i.e.* skills not obtainable by non-breeders. Co-breeders were therefore equipped with 'bargaining power' (Fig. 10.1), and I suggest that such an individual would have a better chance of establishing himself as an independent breeder than a less fit individual. I hypothesise that, if the intrinsic benefit of bargaining power exceeds the cost of co-breeding, the beta male would disperse and compete for a monogamous breeding position in a habitat of equal quality. After all, if both sibs would breed independently in high-quality habitat their fitness (see Tables 4.13 & 9.8), because of indirect fitness benefits, will always be higher than that of monogamous breeders.

10.2.8 Conclusion

The quality of the habitat at Calitzdorp, especially of KBV, provided high fitness benefits to resident PCGs. Since high-quality KBV was sought after, as reflected by the interaction frequency in this vegetation type, the lack of territorial space constrained inhabitants. This extrinsic constraint forced breeders to adjust their reproductive strategy and their offspring to delay dispersal. Once families were formed, a range of secondary benefits evolved. These included higher survival of juveniles, the possibility of budding-off or inheriting a territory, and gaining experience by helping as an breeder. Whereas the intrinsic benefit of family living in the Harris' Hawk is cooperative hunting large prey, and the lack of territorial space on islands was the extrinsic constraint which favoured group formation in the Galapagos Hawk (Faaborg & Bednarz 1990), in the PCG, ecological factors that contributed to the quality of habitat provided the proximate impetus, and the resulting saturation, as an extrinsic constraint, the ultimate impetus in developing family living.

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APPENDIX 1. AN ETHOGRAM FOR PALE CHANTING GOSHAWKS

All behavioural acts recorded while employing instantaneous and scan sampling were divided into three groups based on the substratum in use, either air, a perch or the ground. All behavioural acts are therefore preceded by either Fly, Perch or Ground. In the description below, each act is preceded by its computer code and followed by a brief description of the behavioural act. Acts with fewer than 10 recordings are noted rarely observed. Acts are ordered into alphabetical order.

FLY

FA: Fly Abandon Strike. Pale Chanting Goshawk (PCG), slowly and silently, with shallow wingbeats fly down from perch to prey, but on reaching the prey or where the prey was supposed to be, the PCG briefly hovers 1 m above the ground, abandon the strike and flies off.

FB: Fly Being Mobbed. PCG flying and being dived at by conspecific.

FC: Fly Circling Same Height. PCG gliding with outstretched wings in lose circles, not gaining or loosing height.

FD: Fly Direct. PCG flies direct from point A and B, with rapid shallow wingbeats interspersed with glides, PCG flying not more than 50 m above the ground.

FE: Fly With Nest Lining. PCG flying with nest lining, material carried in the bill or foot.

FF: Fly Mobbing. PCG flying and diving at other raptor(s). Dives are shallow but steep.

FG: Fly Aggressive Hovering. PCG thermals, flying in small circles with very fast and shallow wingbeats (wings almost vibrating), this behaviour always accompanied by aggressive calling. This behavioural act was only observed to be preformed by males high in the air, and often above the boundary of their territories.

FH: Fly Physically Striking. PCG fly and dive at other raptor, physically striking the bird with a foot. No obvious injuries (bleeding or bird disabled) were inflicted by these attacks. Rarely observed.

FI: Fly With Stick. PCG flying with stick, carried in the bill or foot.

FJ: Fly With Prey, Being Mobbed. PCG flying with prey and being mobbed by conspecific.

FK: Fly Ground Striking. PCG flies direct, catches prey by grabbing it off the ground without alighting. Rarely observed.

FL: Fly Locking Talons. This behavioral act followed on FG (Fly Aggressive Hovering), with the two males diving at each other, locking talons and cartwheeling down to the ground, either breaking free before impact or birds crashing into vegetation. Rarely observed.

FM: Fly Diving. PCG fly and dive at conspecific. Dives are fewer and not as steep as FF (Fly Mobbing).

FN: Fly Nuptial Display. Female flies slowly with exaggerated wingbeats, interspersed with gliding and wings held in a 'V' position, legs not held against but away from the body (possibly as air-brakes?). Male fly behind and above female, repeatedly diving down at the female, passing over her back and swooping upwards in an undulating path. Males also displayed at nest sites in the breeding season by slowly flying towards the nest with exaggerated wingbeats interspersed with 'V' gliding, legs outstretched, very often with a stick in the bill or foot.

FO: Fly Robbing Prey. PCG fly and chase other raptor carrying prey, trying to rob it. Only observed interspecifically.

FP: Fly With Prey. PCG fly with prey, either it the foot (larger prey *e.g.* rodent) or bill (smaller prey *e.g.* lizard).

FQ: Fly Being Mobbed. PCG flying and being dive at by either a PCG or other raptor species.

FR: Fly Chasing Bird. PCG flying, actively chasing bird in open air. Rarely observed.

FS: Fly Stoop-Glide. Wings held half open, PCG stoop-glides, often reaching high speeds, from a great height to a perch. Observed mostly after FT (Fly Thermalling) or FC (Fly Circling Same Height).

FT: Fly Thermalling. PCG gliding with outstretched wings in lose circles, gaining height, PCG regularly thermalled to the periphery of human vision.

FV: Fly Diving At. A shallow playful dive preformed by the PCG male, diving at the perching female, usually after prey was passed to the female or copulation.

FY: Fly Dropping Prey. PCG parent passes prey to fledgling by dropping it in mid air. Rarely observed.

FZ: Fly Hovering. PCG flies direct, checks and hovers in mid air, looks down. Rarely observed.

GROUND

GA: Ground Water. PCG standing in water (soil dam). Rarely observed.

GB: Ground Feeding Bird. PCG feeding on bird on the ground.

GC: Ground Chasing Prey. PCG running, jumping over and between vegetation with outstretched wings, chase prey on ground.

GD: Ground Feeding On Roadkill Snake. PCG feeding on snake killed by passing vehicle. Rarely observed.

GE: Ground Feeding Snake. PCG feeding on snake killed by itself.

GF: Ground Feeding Rodent. PCG feeding on rodent.

GG: Ground Aggressive. Polyandrous males sits in close proximity to each other, wings are moved fast, outwards (not more than 2 cm) and back (almost vibrating against the body). Always accompanied by calling.

GH: Ground Holding Prey. PCG sitting on the ground, not feeding and holding onto prey with a foot.

GI: Ground Alert. PCG standing on the ground, alert, looking around. Usually observed after an unsuccessful strike and before bird flies off.

GJ: Ground Water's Edge. PCG standing near (< 5 m) water (soil dam or trough). Rarely observed.

GK: Ground Passing Prey. Prey is passed on the ground from one bird to another, *e.g.* male to female, observed in the breeding season.

GL: Ground Cleaning Bill And Talons. Only observed after PCG finished feeding, first cleaning each talon with bill and then wiping the bill clean on ground.

GM: Ground Mantle Prey. PCG mantles over prey on the ground, facing aggressor, prey held in feet, wings open and feathers on back and breast held aloft, usually accompanied by calling, interaction between breeding adults or fledgling and adult.

GO: Ground Contact Copulating. Male mounts female, the tail of each bird is displayed laterally and the two cloacae come into juxtaposition.

GP: Ground Preening PCG preens, not actively looking around.

GR: Ground Feeding Reptile. PCG feeding on reptile (skink, lizard or agama) other than a snake.

GS: Ground Striking/Searching. PCG, slowly and silently, with shallow wingbeats fly down from perch to prey. On striking the ground the PCG run-jumps after prey, usually with wing held aloft and/or flapping. PCGs often jumped into shrubs up to 30 cm high, striking forward with feet, usually with wing held aloft and/or flapping.

GT: Ground Feeding Termites. PCG sits on the ground near the entrance of a termite colony and feeds on the termites by pecking them off the ground.

GU: Ground Pulling On Prey. Prey is in transfer from one bird to another, *e.g.* male to female, in the breeding season. Both birds are holding onto the prey, trying the pull it from each others feet. Usually accompanied by calling.

GV: Ground Feeding Fledgling. PCG feeding fledgling on the ground, observed in the first few days after the fledgling has left the nest, but is still not hunting independently.

GW: Ground Walking. PCG walks with long strides and a slightly swaying motion, usually looking for termites.

GX: Ground Copulating Attempt. Male mounts female, but as soon as the tail of the male moves downwards, the female by shaking her body and often stepping aside, stops the process.

GY: Ground Try To Fly Off With Snake. PCG tries to fly off with a roadkill snake, snake to heavy to lift off the ground. Rarely observed.

PERCH

PA: Perch Alert. PCG perched, body upright, alert, looking around. It was impossible to distinguish between a PCG hunting (visually searching), watching for intraspecific and interspecific intruders or resting, and these possible different behavioural acts were therefore lumped into one heading.

PB: Perch Feeding Bird. PCG perched and feeding on bird.

PC: Perch Contact Copulating. Male mounts perching female, the tail of each bird is displayed laterally and the two cloacae come into juxtaposition.

PCN: Perch Clean Nest. PCG female removes intestines of prey (normally rodent) from the nest cup after chick(s) were fed, flies off the nest tree/shrub and drops it onto a shrub specifically used for this purpose.

PE: Perch Incubating. PCG sits on eggs.

PF: Perch Feeding Rodent. PCG perched and feeding on rodent.

PFB: Perch Feeding Chick A Bird. PCG feeding chick a bird.

PFD: Perch Flap Dancing. A PCG nestling about to fledge, extend its wings and with rapid shallow wingbeats, flap around the nest, rising a few centimeters above the nest with each jump, presumably exercising its wings (Newton 1986).

PFF: Perch Feeding Chick A Rodent. PCG feeding chick a rodent.

PFR: Perch Feeding Chick A Reptile. PCG feeding chick a reptile.

PFS: Perch Feeding Snake. PCG perched and feeding on a snake.

PG: Perch Aggressive. Polyandrous males perches in close proximity to each other, birds calling, wings vibrating against the body.

PGG: Perch Aggressive Female. PCG calls to interspecific intruder, wings vibrating against the body. Rarely observed.

PH: Perch Holding Prey. PCG perched, holding prey, usually with only one foot, but not feeding.

PI: Perch Physically Striking. PCG perching, and being struck by a diving conspecific.

PJ: Perch Displace Incubating Bird Off Eggs. Alpha male displaces beta male (calling) from the eggs by gently nudging it with the shoulder. Rarely observed.

PK: Perch Passing Prey. PCG passes prey, with foot or bill to foot or bill, to conspecific.

PL: Perch Cleaning Bill And Talons. As in GL (Ground Cleaning Bill And Talons), bill cleaned on perch, usually on the sharp edge of pole or branch.

PM: Perch Being Mobbed. PCG perching, and being mobbed by PCG of the same group. Rarely observed.

PMM: Perch Being Dived At. PCG perching and being dived at by PCG from another group or other raptor species.

PN: Perch Nest Building. PCG, usually male, builds nest by placing stick in place.

PNL: Perch Chick Feeding On Nest Lining. Chick in nest feeding on nest lining (dung, goat hair, sheep wool or hessian) after not being fed for eight hours (length of observation period). Rarely observed.

PO: Perch Thermoregulating. PCG perched, panting, wings slightly dropped and held away from the body, only observed in very hot weather. Rarely observed.

PP: Perch Preening. PCG perched and preening, not actively looking around.

PPH: Perch Mantle Prey. PCG mantles over prey on a perch, facing aggressor, prey held in feet, wings open and feathers on back and breast held aloft, usually accompanied by calling, interaction between breeding adults or fledgling and adult.

PPP: Perch Pulling On Prey. Prey is in transfer from one bird to another, *e.g.* male to female, in the breeding season. Both birds are holding onto the prey, trying the pull it from each others feet. Usually accompanied by calling.

PQ: Perch Changing Incubating Position. PCG sitting on eggs, stands up, turns around and sits down again.

PR: Perch Feeding Reptile. PCG feeding on reptile (skink, lizard or agama) other than a snake.

PS: Perch Holding Stick. PCG perched, holding stick in foot or bill.

PSC: Perch Shading Chick. On warm days with chick(s) to big to cover effectively, PCG stands in nest cup, positioning itself between the sun and the chick(s), often dropping wings.

PSN: Perch Feeding Chick A Snake. PCG feeding chick a snake.

PT: Perch With Wings Raised. PCG perched in rain with one wing raised above it body, turning the wing into the rain and repeating the action with the other wing.

PU: Perch Copulating Attempt. Male mounts perched female but as soon as the tail of the male moves downwards, the female by shaking her body and often stepping aside, stop the process.

PV: Perch Being Dived At. A shallow playful dive preformed by the PCG male, diving at the perching female, usually after prey was passed to the female or copulation.

PW: Perch Water. PCG perched in or on the edge of the water (soil dam or trough) and drinking. Rarely observed.

PX: Perch Holding Nest Lining. PCG perched, holding nest lining in foot or bill, not actively building.

PY: Perch Lining Cup Of Nest. PCG lining nest cup with miscellaneous items (see Malan 1992).

PZ: Perch Brooding Chicks. PCG sitting on chicks.

APPENDIX 2. BEHAVIOURAL GROUPINGS, NON-BREEDING AND PRE-LAY PERIODS FOR THE PALE CHANTING GOSHAWK

Only behavioural acts recorded in the non-breeding and pre-lay periods (first copulation till egg laying) were included. Behavioural acts were grouped into the following behavioural groupings: PERCH ALERT, PERCH PREENING, FLY DIRECT, FLY THERMALLING, FORAGING BEHAVIOUR, AGGRESSION - INTERGROUP AND INTERSPECIFIC, AGGRESSION - INTRAGROUP, and REPRODUCTIVE BEHAVIOUR.

PERCH ALERT
PA: Perch Alert.
PO: Perch Thermoregulating.

PERCH PREENING
GP: Ground Preening.
GL: Ground Cleaning Bill And Talons.
PL: Perch Cleaning Bill And Talons.
PP: Perch Preening.
PT: Perch With Wings Raised.

FLY DIRECT
FD: Fly Direct.

FLY THERMALLING
FC: Fly Circling Same Height.
FS: Fly Stoop-Glide.
FT: Fly Thermalling.

FORAGING BEHAVIOUR
FA: Fly Abandon Strike.
FK: Fly Ground Striking.
FP: Fly With Prey.
FR: Fly Chasing Bird.
FY: Fly Dropping Prey.
GA: Ground Water.
GB: Ground Feeding Bird.
GF: Ground Feeding Rodent.
GH: Ground Holding Prey.
GI: Ground Alert.
GJ: Ground Water's Edge.
GK: Ground Passing Prey.
GR: Ground Feeding Reptile.
GS: Ground Striking/Searching.
GT: Ground Feeding Termites.
GW: Ground Walking.
PB: Perch Feeding Bird.
PF: Perch Feeding Rodent.
PH: Perch Holding Prey.
PR: Perch Feeding Reptile.
PW: Perch Water.

AGGRESSION, INTERGROUP AND INTERSPECIFIC
FQ: Fly Being Mobbed.
PMM: Perch Being Mobbed.
FL: Fly Locking Talons.

AGGRESSION, INTRAGROUP
FF: Fly-Mobbing.
PG: Perch Aggressive.

REPRODUCTIVE BEHAVIOUR
FE: Fly With Nest Lining.
FI: Fly With Stick.
FN: Fly Nuptial Display.
FV: Fly Diving At.
GO: Ground Contact Copulating.
PC: Perch Contact Copulating.
PK: Perch Passing Prey.
PN: Perch Nest Building.
PS: Perch Holding Stick.
PU: Perch Copulating Attempt.
PV: Perch Being Dived At.

APPENDIX 3. BEHAVIOURAL GROUPINGS, INCUBATION AND NESTLING PERIODS FOR THE PALE CHANTING GOSHAWK

Only behavioural acts recorded in the incubation and nestling periods were included. Behavioural acts were grouped into the following behavioural groupings: FEEDING SELF, FEEDING CHICK(S), FORAGING BEHAVIOUR AT NEST SITE, AGGRESSION INTERSPECIFIC, AGGRESSION INTRAGROUP, FLY THERMALLING, NEST ACTIVITIES, and REPRODUCTIVE BEHAVIOUR.

FEEDING SELF

GD: Ground Feeding On Roadkill Snake.
GE: Ground Feeding Snake.
GF: Ground Feeding Rodent.
GM: Ground Mantle Prey.
GR: Ground Feeding Reptile.
GT: Ground Feeding Termites.
PB: Perch Feeding Bird.
PF: Perch Feeding Rodent.
PFS: Perch Feeding Snake.
PNL: Perch Chick Feeding On Nest Lining.
PPH: Perch Mantle Prey.
PR: Perch Feeding Reptile.

FEEDING CHICK(S)

GV: Ground Feeding Fledgling.
PFB: Perch Feeding Chick A Bird.
PFF: Perch Feeding Chick A Rodent.
PFR: Perch Feeding Chick A Reptile.
PSN: Perch Feeding Chick A Snake.

FORAGING BEHAVIOUR AT NEST SITE

FA: Fly Abandon Strike.
FP: Fly With Prey.
FR: Fly Chasing Bird.
FZ: Fly Hovering.
GH: Ground Holding Prey.
GK: Ground Passing Prey.
GS: Ground Striking/Searching.
GU: Ground Pulling On Prey.
GW: Ground Walking.
GY: Ground Try To Fly Off With Roadkill.
PH: Perch Holding Prey.
PK: Perch Passing Prey.
PPP: Perch Pulling On Prey.

AGGRESSION, INTERSPECIFIC

FF: Fly Mobbing.
FH: Fly Physically Striking.
FO: Fly Robbing Prey.

AGGRESSION, INTRAGROUP

FB: Fly Being Mobbed.
FM: Fly Diving.
PG: Perch Aggressive.
GG: Ground Aggressive.

FLY THERMALLING
FS: Fly Stoop-Glide.
FC: Fly-Circling Same Height.
FT: Fly Thermalling.
FD: Fly Direct.

NEST ACTIVITIES
FI: Fly With Stick.
FE: Fly With Nest Lining.
PCN: Perch Clean Nest.
PN: Perch Nest Building.
PX: Perch Holding Nest Lining.
PY: Perch Lining Cup Of Nest.

REPRODUCTIVE BEHAVIOUR
GO: Ground Contact Copulating.
GX: Ground Copulating Attempt.
PC: Perch Copulating.
PU: Perch Copulating Attempt.
FV: Fly Diving At.
FN: Fly Nuptial Display.

Appendix 4. Published and unpublished records of Pale Chanting Goshawk prey in southern Africa. KGNP = Kalahari Gemsbok National Park

Prey species	Number	Locality	Reference
AVES			
Swainson's Francolin *Francolinus swainsoni*	1	Transvaal	Tarboton & Allan 1984
Crested Francolin *Francolinus sephaena*	1	Transvaal	Tarboton & Allan 1984
Redbilled Francolin *Francolinus adspersus*	1	Namibia	Bradfield 1932
	1	Namibia	Biggs *et al.* 1984
Francolin *Francolinus* spp.	2	Namibia	Biggs *et al.* 1984
	1	Transvaal	Tarboton & Allan 1984
Helmeted Guineafowl *Numida meleagris*	2	Namibia	Biggs *et al.* 1984
	3	Rooipoort	T.M. Crowe pers. comm.
	1	Rooipoort	GM pers. obs.
Moorhen *Gallinula chloropus*	1	Beaufort West	Winterbottom 1962
Blue Korhaan *Eupodotis caerulescens*	1	Cradock	Collett 1984
Redcrested Korhaan *Eupodotis ruficrista*	1	Transvaal	Tarboton & Allan 1984
Black Korhaan *Eupodotis afra*	1	Namibia	Biggs *et al.* 1984
Crowned Plover *Vanellus coronatus*	1	Transvaal	Mendelsohn 1976
Doublebanded Courser *Rhinoptilus africanus*	1	Namibia	Biggs *et al.* 1984
Namaqua Sandgrouse *Pterocles namaqua*	2	Namibia	Biggs *et al.* 1984
	1		Yates 1991
Barn Owl *Tyto alba*	1	KGNP	J.J. Herholdt pers. comm.
Whitefaced Owl *Otus leucotis*	2	KGNP	Herholdt 1992
Spotted Eagle Owl *Bubo africanus*	2	KGNP	J.J. Herholdt pers. comm.
	1	KGNP	C. Haagner pers. comm.
Hornbill *Tockus* sp.	1	Namibia	Biggs *et al.* 1984
Larks (fledglings) Alaudidae	12	Brandvlei	Steyn & Myburgh 1992
South African Cliff Swallow *Hirundo spilodera*		Graaff-Reinet	Taylor 1942
Sociable Weaver *Philetairus socius*		KGNP	Maclean 1973
Birds	4	Namibia	Biggs *et al.* 1984
	3	Brandvlei	Steyn & Myburgh 1992
Total	48		

REPTILIA			
Mole Snake *Pseudaspis cana*	4	Namibia	Biggs *et al.* 1984
Stripe-bellied Sandsnake *Psammophis subtaeniatus*	1	Namibia	Biggs *et al.* 1984
Snakes (Serpentes)	9	Namibia	Biggs *et al.* 1984
	1	Brandvlei	Steyn & Myburgh 1992
Lizards (Sauria)	2	Namibia	Biggs *et al.* 1984
(mostly agamas, 1 skink)	8	Brandvlei	Steyn & Myburgh 1992
Cape Skink *Mabuya capensis*	1	Namibia	Biggs *et al.* 1984
Yellow-throated Plated Lizard *Gerrhosaurus flavigularis*	2	Namibia	Biggs *et al.* 1984
Karoo Girdled Lizard *Cordylus polyzonus*	1	Namibia	Biggs *et al.* 1984
Agamas (Agamidae)	1	Namibia	Biggs *et al.* 1984
Ground Agama *Agama aculeata*	1	Namibia	Biggs *et al.* 1984
Total	31		
MAMMALIA			
Elephantulus sp.	1	Namibia	Biggs *et al.* 1984
Rodent	7	Namibia	Biggs *et al.* 1984
	1	Transvaal	Tarboton & Allan 1984
mostly Striped Mouse, *Rhabdomys pumilio*	7	Brandvlei	Steyn & Myburgh 1992
	3	Cape Province	D.G. Allan pers comm.
Total	19		
CARRION			
Hares *Lepus* sp.	1	Namibia	Winterbottom 1965
	6	Namibia	Biggs *et al.* 1984
	2	Ceres Karoo	Malan 1988
	1	Namibia	T. Tree pers. comm.
	1	Robertson	GM pers. obs.
Bateared Fox *Otocyon megalotis*	1	Namibia	Biggs *et al.* 1984
Lamb (newborn) *Ovis aries*	1	Nieuwoudtville	P. Steyn pers. comm.
Steenbok (roadkill) *Raphicerus campestris*	1	Prins Albert	D.G. Allan pers. comm.
Spotted Eagle Owl *Bubo africanus*	2	KGNP	A.C. Kemp pers comm.
Dikkop *Burhinus capensis*	1	Namibia	Biggs *et al.* 1984
Total	17		

INSECTA			
Termites		Philipstown	Hare 1932
-		Namibia	Biggs *et al.* 1984
AMPHIBIA			
Common Platanna *Xenopus laevis*	1	Philipstown	Hare 1932