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Territory and nest defence in polyandrous pale chanting goshawks: do co-breeders help?

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The behaviour of polyandrous and monogamous pale chanting goshawks *Melierax canorus* was investigated to determine if co-breeders, by defending the territory and nest contents, helped to increase the fitness of polyandrous trios. Polyandrous trios consisted of a female and male breeder, as well as a subordinate co-breeding male. Pale chanting goshawk males performed most of the interspecific territorial maintenance duties, as well as participating in aggressive intraspecific interactions against other males on territory borders. Intraspecific territorial interactions were almost exclusively recorded in high-quality habitat, Karroid Broken Veld, and probably functioned in the defence of foraging habitat and potential mates. In this habitat, males of polyandrous families largely occupied exclusive sections of a territory. It is suggested that the cost of defending territories in Karroid Broken Veld was offset by the co-breeder's contribution to high-risk, intraspecific territorial defence. During the nestling period females of polyandrous trios stayed at nesting sites for longer periods than did monogamous females and all males, enabling these females to guard the nest and act as sentinels. Predation of nestlings was recorded at the nests of monogamous pairs, but not at those of polyandrous trios. Co-breeders did not guard the nesting site but contributed directly to nest defence by either coming to the female's aid when solicited, or attacking potential predators when present at the nesting site. Co-breeders may also have helped indirectly, through activities such as provisioning prey to females that relieved them of their hunting duties. We suggest that the female's nest guarding and the resulting lower nest predation may hold reproductive and fitness benefits for polyandrous breeders.

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Family groups evolve when limitations are placed on breeding opportunities of high quality for sexually mature individuals (Koenig, Pitelka, Carmen, Mumme & Stanback 1992; Emlen 1994). Group living holds no automatic advantages and may even be disadvantageous to an individual (Alexander 1974). However, once a group has formed, individuals may be expected to alter their behaviour to take advantage of the presence of group members and derive benefits from group-living (Emlen 1994). In birds, such benefits may include the early detection and deterrence of predators at nests and of intruders at territory boundaries (Gayou 1986; Rabenold 1990; Mumme 1992). Apart from the fundamental question as to why helpers help and do not disperse, it is necessary to determine if they really contribute significantly to the group, since helping may be no more than an unselected consequence of non-dispersal (Craig & Jamieson 1990; Emlen 1991). If such help does benefit individuals in groups, they can expect to increase their fitness through enhanced survival and reproduction (Emlen & Wrege 1994).

In the pale chanting goshawk (PCG) *Melierax canorus*, predation of eggs or nestlings was the major cause of nest failures in four PCG study areas in South Africa and Namibia (Malan, Crowe, Biggs & Herholdt in press). However, only in one study area (see below) and only in one vegetation type, Karroid Broken Veld, were PCGs found to breed in polyandrous trios. The Karroid Broken Veld supported a very high biomass of otomyinid rodents, *Otomys unisulcatus* and *Parotomys brantsii*, the preferred prey of PCGs, and a suitable hunting habitat incorporating prey visibility and perch availability (Malan & Crowe 1996). Within PCG polyandrous trios, a co-breeding male participated fully in all reproductive activities such as nest construction and prey provisioning to the female and offspring at the nesting site. In addition to co-breeders, non-breeders, either adult or juvenile offspring,

were allowed to delay dispersal in the natal territory, but were not tolerated near the nesting site in the breeding season. Since these offspring continued to interact with their parents into adulthood, PCG groups were referred to as families (Emlen 1994).

The aim of this research was to investigate territory and nest-site defence by breeding PCGs under conditions of monogamy and polyandry, and in habitats of different quality. In this article it is discussed whether co-breeder males, by participating in territory and nest defence, increase the inclusive fitness (Hamilton 1964) of PCGs in polyandrous trios.

Methods

Study area

The study area was located near Calitzdorp (33°32'S, 21°48'E) in the Little Karoo, South Africa. Mean annual precipitation is approximately 200 mm. Three karroid vegetation types occur in the study area, lying in broad parallel bands from Spekboomveld in the north, through Karroid Broken Veld, to Succulent Karoo in the south (Acocks 1988). Open Spekboomveld is an open shrub community comprising 2–5 m high trees and shrubs, Karroid Broken Veld consists of low succulents (< 75 cm) with dwarf trees and shrubs scattered throughout, and Succulent Karoo is open with a sparsely distributed layer of dwarf succulents.

Sampling

A monogamous pair comprises one male and one female breeder (Malan *et al.* in press). A polyandrous trio comprises one female and two male breeders. A breeder is an adult participating in all reproductive activities (Malan *et al.* in press). In the PCG, as with most other raptors (Newton 1979; Faaborg & Bednarz 1990), the female is larger (on average 22% by body mass) than the male (Malan 1995). In the breed-

ing season the dominant female was able to displace the male from prey he brought to the nesting site, as well as from eggs during the incubation period. In a polyandrous trio, a co-breeder is an additional adult male identified by his subordinate status to both the dominant female and male. Dominant males were in all cases larger than co-breeding males, and were able to displace co-breeders from prey and eggs but not *vice versa* (Malan 1995).

During the non-breeding and pre-laying (from first copulation until egg laying) periods of 1988, we studied the territorial behaviour of PCGs in the Karroid Broken Veld and Succulent Karoo vegetation types. Employing instantaneous sampling (Lehner 1979), 86 observation periods totalling 12 368 minutes (mean = 144 ± 73 min) were completed. During the nestling period, the behaviour of all breeding PCGs within a 100 m radius from the nesting site was recorded from a hide overlooking the nesting sites (scan sampling), during 34 eight-hour observation periods (16 320 min). These data were collected for two different polyandrous trios and two monogamous pairs in Karroid Broken Veld (1988 and 1989), and for a monogamous pair each in Succulent Karoo (1988) and Open Spekboomveld (1989). Since breeding raptors spend more time away from the nest during the latter part of the nestling period (Newton 1979), we analysed nest attendance data by employing a one-way analysis of covariance with days after hatching as the independent variable, and minutes per observation period outside the 100 m radius as the dependent variable.

Territorial behaviour

A territorial interaction was defined as an encounter between a territory holder and an intruder (interspecific or intraspecific), which elicited an action or reaction from the focal PCG. We recognized six interaction modes, sequenced in order of increasing aggression according to physical and vocal expression:

Fly diving at — PCG dived at intruder, dives were shallow;

Fly mob — PCG dived repeatedly, deep and directly at intruder;

Fly mob and call — PCG flew mobbed and alarm-called, a quavering *ee-e-e-e-e-e-e* (Maclean 1985);

Fly striking — PCG flew mobbed and physically struck intruder;

Spiral flight and aggressive-call — PCG thermalled in small circles with very fast and shallow wingbeats, with aggressive-calling in a loud fast burst of staccato *kikiki-kikiki-kikiki-kikiki*; and

Cartwheel flight — PCGs locked feet in mid-air and whirled down vertically.

All interactions were recorded during instantaneous and scan sampling during 1988–1989 and *ad hoc* observations during 1988–1992. Interactions were classed as interspecific or intraspecific (between neighbouring PCG families), and occurred either on the border of two territories or within a territory (more than 500 m from territory boundary).

During all observations in the study area, we searched for breeding birds marked with colour rings and patagial tags ($n = 28$) and mapped their positions. We studied the territorial behaviour of the males of two polyandrous trios and observed each male for more than seven hours. Since each male

demonstrated an occupational preference for a section of a territory, we divided each territory into two equally sized sectors along a central axis. During instantaneous sampling, the position of the focal male in each sector was recorded every 60 seconds. For each observation period recorded, males were assigned to a sector according to the majority of minutes spent there (i.e. more than 50% of time).

Predation of nest contents

For each of the 51 visits made to nests during the breeding seasons of 1988–1992, the following data were recorded: the presence/absence of eggs/nestlings, disturbance to nest lining and structure, and the presence of chick remains on the ground below the nest. When previously occupied nests were found to be empty, predation was only considered as a cause of nesting failure if the nest cup or rim had been disturbed, or if offspring remains were found near the nest.

Results

Attendance at the nesting site

During 1988 and 1989, time spent away from the nesting site did not differ significantly between either monogamous males or females from two families in Karroid Broken Veld (GM unpublished data), so data were combined for males and females respectively. During 1988, time spent away from the nesting site did not differ significantly between polyandrous males (ANCOVA; $F = 4.60$; $df = 1$; $p > 0.05$), or between polyandrous males and monogamous males (ANCOVA; $F = 1.07$; $df = 1$; $p < 0.05$), so data were combined for all males. On average, the polyandrous female was away from the nesting site 28% of the time ($n = 480$ minutes), monogamous females 73%, and all males 95% (ANCOVA; $F = 49.1$; $df = 2$; $p < 0.001$). During 1989, on average, the polyandrous female spent 6% of the time ($n = 480$) away from the nesting site, the polyandrous breeder male 45%, the co-breeder male 53%, monogamous females 61% and monogamous males 89% (ANCOVA; $F = 52.8$; $df = 4$; $p < 0.001$).

Predation of nestlings

No predation of eggs was recorded. The frequency of nestling predation did not differ significantly between Open Spekboomveld (19%; $n = 16$), Succulent Karoo (8%; $n = 13$) and Karroid Broken Veld (7%; $n = 73$; $G_2 = 1.9$; $p > 0.05$). Nestling predation was highest during 1988 and 1992, and lowest during 1989 and 1990 (Table 1). During years of intermediate PCG reproduction (1988 and 1992), when 39 families produced 27 broods, seven incidents of predation at the nest were recorded. During years with high reproductive success (1989 and 1990), when 49 families produced 53 broods, only two cases of predation were recorded. During 1991, a year when 29 families produced only three broods, no predation was recorded. Of the 83 breeding attempts recorded over five years (1988–1992), nine (14%) of the 66 nests of monogamous pairs were subject to predation (Table 1). No nests of polyandrous trios were raided by predators. Most cases (89%) of nestling predation were of first broods (or single broods in years when only one brood was raised) and the majority of nestlings (56%; $n = 9$) were preyed upon in the first half of the

Table 1 Instances of predation of pale chanting goshawk nestlings, all from monogamous pairs, in five breeding seasons (1988–1992). OSBV = Open Spekboomveld, KBV = Karroid Broken Veld and SK = Succulent Karoo

Year	Vegetation type	Number of nestlings taken	Age (weeks)	Second successful brood per season	Nest lining/ structure disturbed	Remains on ground (5–7 weeks)
1988	OSBV	2	1	No	Yes	
	OSBV	1	3	No	Yes	
	KBV	1	6	No	No ¹	Yes
1989	KBV	1	6	No	No	Yes
1990	KBV	1	7	Yes	Yes	Yes
1991	No predation					
1992	OSBV	2	5	No	Yes	Yes
	KBV	2	3	No	Yes	
	KBV	2	1	No	Yes	
	SK	2	1	No	Yes	

¹ second chick still in nest

seven week nestling period. Remains of offspring found below nests were all of large nestlings.

Interspecific and intraspecific interactions

Of the interspecific territorial interactions observed during the non-breeding and pre-laying periods, males were involved in

84% ($n = 31$) and were the aggressors in 96% ($n = 26$) of these, whereas females were the aggressors in three out of only five interactions (Table 2).

Apart from two incidents, intraspecific interactions in the non-breeding and pre-laying periods were all between members of the same sex (Table 3). Males were involved in more aggressive interactions, for example spiral and cartwheel flights, and females in less aggressive interactions. Males were also involved in more interactions in total (77%; $n = 17$) than females. Since 20% of the 80 families studied in Karroid Broken Veld were polyandrous trios, coupled to the 22 monogamous pairs studied in Open Spekboomveld (Malan *et al.* in press), the sex ratio was biased in favour of males (118:102). However, even if the observed male:female aggressive interactions frequency is corrected (from 13:4 to 11:4), males were still involved in 73% ($n = 15$) of interactions. Males were involved exclusively in interactions along the borders of territories ($n = 13$), whereas females were also involved in some disputes within territory borders (75%; $n = 4$). Thirteen intraspecific interactions were observed in Karroid Broken Veld, four in Open Spekboomveld and none in Succulent Karoo (Table 3).

Overall, males and females shared equally in defending the nest contents when both sexes were present, although only females were involved in physically striking potential predators (Table 4). Males called in 50% ($n = 12$) of interactions and females in 33% ($n = 15$) ($G_c = 0.23$; $p > 0.05$). PCGs appeared most agitated (e.g. flying with continuous wing-

Table 2 Interspecific interactions recorded for pale chanting goshawks in the non-breeding and pre-laying periods of 1988 and 1989. All intruders were mobbed. KBV = Karroid Broken veld, SK = Succulent Karoo

Aggressor	Vegetation type	Status	Aggressee	No of interactions
<i>Male</i>				
PCG	KBV	Co-breeder	Blackshouldered kite ² <i>Elanus caeruleus</i>	4
PCG	KBV	Polyandrous breeder	Two black crows <i>Corvus capensis</i>	2
PCG	KBV	Co-breeder	Whitenecked raven ² <i>Corvus albicollis</i>	1
PCG	KBV	Co-breeder	Jackal buzzard ² <i>Buteo rufofuscus</i>	3
PCG	SK ¹	Monogamous	Two black crows	4
PCG	SK ¹	Monogamous	Black harrier <i>Circus maurus</i>	1
PCG	SK ¹	Monogamous	Lanner falcon <i>Falco biarmicus</i>	1
PCG	SK	Monogamous	Blackshouldered kite ²	6
PCG	SK	Monogamous	Rock kestrel <i>Falco tinnunculus</i>	1
PCG	SK	Monogamous	Two Egyptian geese <i>Alopochen aegyptiaca</i>	1
PCG	SK	Monogamous	Yellow mongoose <i>Cynictis penicillata</i>	1
Two black crows	SK ¹	Monogamous	PCG	1
<i>Female</i>				
PCG	KBV	Monogamous	Steppe buzzard <i>Buteo buteo</i>	2
PCG	KBV	Polyandrous	Blackshouldered kite ²	1
Two black-shouldered kites	KBV	Polyandrous	PCG	1
Black crow	SK ¹	Monogamous	PCG	1

¹ interactions recorded in SK territory on the border of KBV

² birds pursued to the border of the territory

Table 3 Intraspecific interactions recorded for pale chanting goshawks in the non-breeding and pre-laying periods from 1988 to 1992. See text for explanations of interaction modes. Birds in parenthesis present but did not participate in interaction. KBV = Karroid Broken Veld and OSBV = Open Spekboomveld

Aggressor (vegetation type)	Interact mode	Aggressee	Internal or border interaction	No of interactions
<i>Males</i>				
Co-breeder male (KBV)	Fly mob	Monogamous male	Border	2
Polyandrous breeder male (KBV)	Fly mob	Monogamous male & female	Border	1
Co-breeder male (KBV)	Fly striking	Monogamous male (& female)	Border	1
Polyandrous breeder male (KBV)	Spiral flight and call, cartwheel flight	Monogamous male	Border	1
Monogamous male ¹ (KBV)	Spiral flight and call	Monogamous male	Border	4
Polyandrous males ¹ (KBV)	Spiral flight and call	Monogamous male	Border	1
Monogamous male ¹ (OSBV)	Spiral flight and call	Monogamous male	Border	2
Monogamous male ¹ (OSBV)	Spiral flight and call, cartwheel flight	Monogamous male (& female)	Border	1
<i>Females</i>				
Polyandrous female (KBV)	Fly mob	Non-breeder female (from polyandrous trio)	Internal	1
Monogamous female ¹ (KBV)	Fly mob	Non-breeder female (from monogamous pair)	Internal	1
Monogamous female (KBV)	Fly mob each other	Polyandrous breeder male & female	Border	1
Monogamous female ¹ (OSBV)	Fly mob	Monogamous female	Internal	1

¹ interactions recorded in casual observations

beats) during interactions with gymnogenes (*Polyboroides typus*) and martial eagles (*Polemaetus bellicosus*).

PCGs were able to actively defend their nest contents as demonstrated by the following two incidents. In a particularly aggressive interaction, a polyandrous trio attacked an unidentified intruder on the ground. Although we were unable to observe any tracks, this intruder was terrestrial, less than 75 cm in height as its movements were obstructed by the lower vegetation layer, and probably mammalian as it proceeded at the pace of a fast-walking man. The perched female spotted the intruder approaching down a drainage line towards the nest and gave an alarm call, which brought the two males quickly to the nest. All three birds started calling and diving at the animal continuously, forcing it to follow a circular route around the nest. The same animal, it is presumed, returned to the area of the nest during the same observation period, but was again successfully driven away.

In Succulent Karoo, territorial interspecific interactions were observed at a rate of one every 311 min ($n = 5\,595$ min). In Karroid Broken Veld these interactions were observed once every 599 min by polyandrous breeders ($n = 7\,188$ min). Although monogamous breeders from this vegetation type were only observed for 349 minutes, two interspecific interactions were observed. At nesting sites in Karroid Broken Veld, interspecific interactions were recorded once every 675 min ($n = 12\,145$ min), once in 5 248 min at sites in Succulent Karoo and no interspecific interactions were recorded in 1 440 min at sites in Open Spekboomveld.

Territory occupancy

Twenty-eight marked breeders were observed for 91 breeder-years within their breeding territories, and no marked bird

was ever observed in the territory of another family. One marked breeder was observed for five breeder-years in Open Spekboomveld, six marked breeders for 29 breeder-years in Succulent Karoo, and 21 marked breeders for 57 breeder-years in Karroid Broken Veld. Of those in Karroid Broken Veld, four polyandrous females were studied for 10 breeder-years, three polyandrous breeder males for 10 breeder-years and five co-breeder males for 11 breeder-years.

Clear-cut differences were found in the spatial arrangement of polyandrous males within territories. In one family, the polyandrous breeder male occupied the eastern sector of the territory ($n = 3$ observation periods), whereas the co-breeder male occupied the western sector ($n = 3$) ($G_c = 4.9$; $p < 0.05$). The polyandrous breeder male occupied a higher proportion of quadrats in the east (90%; $n = 474$ min) and the co-breeder male in the west (91%; $n = 579$ min). Another family's polyandrous breeder male occupied the northern sector of the territory ($n = 8$ observation periods), whereas the co-breeder male occupied the south ($n = 3$) and north ($n = 2$) ($G_c = 5.4$; $p < 0.05$). The polyandrous breeder male occupied quadrats at a higher proportion in the north (84%; $n = 607$ min) and the co-breeder male in the south (64%; $n = 758$ min).

Discussion

Territory defence

In general, helpers within a group of social birds usually have a positive impact on each individual's inclusive fitness (Emlen 1990). Helping may, however, have no impact at all, or may even disrupt reproductive and survival activities (Stacey & Koenig 1990; Du Plessis 1991). Defence against potential predators of young may be achieved more successfully by groups containing helpers (Bekoff & Wells 1982; Stacey &

Table 4 Interspecific and intraspecific interactions recorded at nesting sites of pale chanting goshawk in the breeding seasons of 1988–1989. See text for explanations of interaction modes. KBV = Karroid Broken Veld, SK = Succulent Karoo

Aggressor (vegetation type)	Interaction mode	Aggressee
<i>All breeders attack</i>		
Co-breeder male and female (KBV)	Fly mob (and rob)	Booted eagle (3 ×) <i>Hieraaetus pennatus</i>
Monogamous male and female (KBV)	Fly mob and call	Martial eagle ¹ (3 ×) <i>Polemaetus bellicosus</i>
Polyandrous males and female (KBV)	Fly diving at	Booted eagle (2 ×)
Polyandrous males and female (KBV)	Fly mob and call	Terrestrial predator (2 ×)
<i>Female attack, male(s) present</i>		
Monogamous female (KBV)	Fly mob	Jackal buzzard ¹
Monogamous female (SK)	Fly striking and call	Yellow mongoose <i>Cynictis penicillata</i>
Polyandrous female (KBV)	Fly diving at	PCG female
<i>Male attack, female present</i>		
Polyandrous breeder male (KBV)	Fly mob and call	Gymnogene ¹ <i>Polyboroides typus</i>
Monogamous male (KBV)	Fly mob	Lanner falcon
Monogamous male (KBV)	Fly mob and call	Jackal buzzard ¹
Monogamous male (KBV)	Fly mob and call	Steppe buzzard
<i>Female attack, male not present</i>		
Monogamous female (KBV)	Fly striking	Yellow mongoose (2 ×)
Monogamous female (KBV)	Fly striking and call	Yellow mongoose
Monogamous female (KBV)	Fly mob	Jackal buzzard ¹

¹ birds pursued to the border of the territory

Ligon 1987). Groups with helpers that participate in territorial defence may also be more successful in defending such territories (Gayou 1986).

In the PCG, there was first of all a need to defend territories against interspecific intruders. The chasing of predominantly rodent-eating raptors such as blackshouldered kites (*Elanus caeruleus*) and jackal buzzards (*Buteo rufofuscus*) to the borders of territories in these vegetation types may have occurred because these species share the PCG's diet (GM, personal observation). Blackshouldered kites also bred in the study area, whereas Egyptian geese (*Alopochen aegyptiacus*) frequently utilized nests after occupation by PCGs (GM, personal observation). Interspecific interactions were recorded in more or less equal proportions in Succulent Karoo and Karroid Broken Veld. Intraspecific interactions, however, were recorded almost exclusively in Karroid Broken Veld. It therefore appears that not only resources such as prey and nesting habitat, but also the possibility of establishing a territory and breeding, was of particular importance to PCGs. There was thus not only potential benefits to be gained from residing in high-quality Karroid Broken Veld, but also a cost as this habitat had to be defended, not only against interspecifics, but in particular against intraspecifics.

For territorial PCGs, males predominantly defended the territory against interspecific intruders. Against intraspecifics, territorial males were also involved in the highest frequency of interactions. Interactions between territorial males were particularly aggressive, involving among other things, spiral and cartwheel flights (Simmons & Mendelsohn 1993). Spiral and cartwheel flights by raptors involve a high risk factor as birds sometimes injure themselves as they grapple in mid-air and crash into the vegetation below, and fatalities are known in some cases (Simmons & Mendelsohn 1993). Males were thus engaging in high-risk territorial interactions and the defence of resources and mates in Karroid Broken Veld.

A further significant result was the occupation by polyandrous males of different sections of their respective territories. Because the territories of polyandrous trios were not larger than those of monogamous pairs (Malan 1995), the key question was: does the co-breeder help by defending a subsection of high-quality territories (Craig 1984; Gayou 1986)?

A co-breeding male actively defending a subsection of a territory in Karroid Broken Veld may have helped by halving the interaction frequency per individual male. In doing so, co-breeders may have helped by lowering the risks of defending territories in this sought after vegetation type. We hypothesize that the cost of defending territories in Karroid Broken Veld was offset by the co-breeder's contribution to interspecific, and specifically intraspecific territorial defence.

Potential nest predators

Since predation at PCG nests was never observed directly, it is not known which predator species were responsible. Yellow mongooses (*Cynictis penicillata*) were frequently and violently chased from near nest trees, but are not known to climb trees or to prey heavily on birds (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. Since signs of struggle were found in the nests, often with traces of blood on the nest lining, some nestlings and/or parents probably resisted predation. Remains of larger nestlings discovered below nests could have been the result of either nestlings accidentally falling out of the nest and then being eaten, or their being flushed out of the nest during the predation act itself. At some nests ($n = 5$; GM unpublished data) nestlings or eggs disappeared without any obvious damage to the nest itself. While these losses could have been the result of factors other than predation, avian predators (e.g. martial eagle *Polemaetus bellicosus* or whitenecked ravens *Corvus albicollis*) or snakes (boomslang *Dispholidus typus*) could have been responsible. The majority of incidents of predation occurred in this study during the first three weeks of the nestling period, when females were most attentive (see below). Evidently, some nest predators were sufficiently large and/or skilful to prey on nestlings, despite the defensive efforts of the female.

Because predation was only recorded if both offspring disappeared from the nest (ruling out hunger-induced sibling aggression) and disturbance to nest lining and structure was noted, we may have underestimated predation. Since both high predation years, 1988 and 1992, were preceded by years of below average rainfall (1987 = 103 mm; 1991 = 121 mm;

annual mean = 199 mm), we suggest that potential predators may have switched to 'alternative' prey, such as PCG eggs and nestlings, in years when availability of more traditional prey (assumed to be rodents) was depressed. A similar mechanism has been put forward to explain predation at the nests of arctic waders, which vary annually in response to fluctuations in lemming abundance. Predators such as Arctic foxes (*Alopex lagopus*) switch to wader eggs and nestlings in poor lemming years (Underhill, Prys-Jones, Syroechkovski, Groen, Karpov, Lappo, Van Roomen, Rybkin, Schekkerman, Spiekman & Summers 1993). Nest guarding by PCGs may therefore be in greater demand in years of intermediate (e.g. 1988) and even low prey abundance (Ligon & Ligon 1990), when potential predators switch to alternative prey and PCGs, especially nest-guarding females, are more likely to leave the nesting site to hunt.

Nest-site defence

During the nestling period raptors generally practice biparental care; males provide the prey to the female and nestlings, while the females, that are larger, remain at the nesting site and protect the young (Newton 1979; Ward & Kennedy 1996). In PCGs, polyandrous females were more attentive at nesting sites than monogamous females, and since the nests of polyandrous trios were not subjected to predation, the nest-site presence of polyandrous females may have resulted in superior nest defence. If helpers are present at the nesting site, they may contribute to nest defence by either guarding, soliciting help or physically attacking potential predators (McGowan & Woolfenden 1989; Zahavi 1990). In PCGs, it was the female that acted as a sentinel, solicited help and physically attacked potential nest predators. Co-breeders may have helped by assisting in nest defence when solicited by the female. This strategy was clearly demonstrated by one polyandrous trio. Co-breeders also participated in nest defence when present at the nesting site.

To meet the energetic needs of the growing young in the latter parts of the nestling period, raptor females are forced to leave the nesting site to hunt (Newton 1979). The female therefore faces a potential conflict between foraging for the young versus guarding and defending the nestlings (Martin 1992). The nest-site presence of the PCG female may be attributed to the prey abundance and therefore the rate at which prey were provisioned to her, as well as the number of males provisioning that in turn releases females of hunting duties (Newton 1979; Lennartz, Hooper & Harlow 1987; Malan 1995). Females may stay at nesting sites not only to guard the nest contents, but also for other reasons, for example, to accumulate the necessary body reserves to increase their long-term reproductive success (Brown, Dow, Brown & Brown 1978). The nest-guarding behaviour of females may therefore be one more behavioural trait employed by PCGs to increase their reproductive fitness.

We conclude that a co-breeding male, helping to defend the nest contents, contributed directly to the lowering of nest predation in polyandrous trios. Co-breeding males may also have contributed indirectly to the lowering of nest predation by co-provisioning polyandrous females that only left the nesting site for short periods of time. However, because of the potential impact the otomyinid rodent abundance might have on the

prey-provisioning rate of either one or two males, as well as the selection of prey by potential nest predators, the abundance of otomyinid rodents may play a bigger role in ensuring successful reproduction of PCGs than the help provided by the co-breeder *per se*. Nevertheless, we suggest that the participation of subordinate co-breeders in the defence of nest sites may hold fitness benefits, not only for the co-breeder, but also for the dominant breeder. The lower nest predation and the resulting increase in reproductive success of polyandrous trios may hold fitness benefits for all three polyandrous breeders.

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