Perch availability and ground cover: factors that may constitute suitable hunting conditions for pale chanting goshawk families

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We investigated the impact of perch height and abundance, and the cover for prey, on the hunting tactics of perch-hunting pale chanting goshawks (*Melierax canorus*). Although pale chanting goshawks demonstrate a clear preference for perching on the highest available perches, the availability of perches is of more importance than height because these birds hunt almost exclusively from perches, move regularly between them, and an increased number of perches increases the area of habitat accessible for effective hunting. In Succulent Karoo, pale chanting goshawks occupied areas where perch density (16 natural and 122 artificial/25 ha) was significantly higher than in unoccupied areas (8 natural and 12 artificial/25 ha). The high proportion of cover formed by natural perches (trees and shrubs; 36%) and the low proportion of open ground (42%) resulted in Closed Spekboomveld being unsuitable for pale chanting goshawks, relative to the adjacent Open Spekboomveld that supported goshawks by offering a less restricted view of the ground and prey (perch cover 18% and open ground 49%). In Karroid Broken Veld, the combination of perch availability (3 026/25 ha) and open ground (62%) may provide the most suitable conditions for hunting rodent prey near cover or in the open. We suggest that such habitat may also provide a pathway, through fitness benefits gained, in the development of delayed dispersal and cooperative breeding in pale chanting goshawk families.

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Suitable hunting habitat for pause-travel raptors consists of not only high prey abundance, but also ecological factors that influence the accessibility of prey such as perch height and abundance, and view of the ground (Yosef 1992). If perch availability is inadequate, the habitat may be difficult to exploit (Preston 1990; Widen 1994), even if prey are abundant. Therefore, the foraging success of raptors may be related not only to the prey biomass, but also to detectability of prey in vegetation, that is, prey visibility, and thus the suitability of the hunting conditions (Bechard 1982; Simmons 1989). Furthermore, in more suitable hunting conditions the fitness benefits to be gained from residing in such a high-quality habitat may play a pivotal evolutionary role in the development of delayed dispersal and cooperative breeding in bird groups (Koenig & Pitelka 1981; Bednarz & Ligon 1988; Koenig, Pitelka, Carmen, Mumme & Stanback 1992; Komdeur 1992; Emlen 1994).

Since the pale chanting goshawk (PCG) (*Melierax canorus*) searches for terrestrial prey from perches (Steyn 1982), hunting opportunities may influence its life history traits (Yosef 1992). It lives in low-rainfall, semi-desert southern Africa, where perches are scarce, and arid savanna, where perches are relatively plentiful (Steyn 1982). PCGs not only perch habitually on the tops of trees and shrubs, but also use artificial perches, such as telephone poles and fenceposts (Maclean 1985). Although they are opportunistic hunters and take a broad range of prey, based on biomass, PCGs prey mostly on large otomyinid rodents, *Otomys unisulcatus* and *Parotomys brantsii*, as well as the smaller *Rhabdomys pumilio* (Malan & Crowe 1996). PCGs breed either in monogamous pairs or in polyandrous trios (Malan, Crowe, Biggs & Herholdt in press). During this study, polyandrous trios were recorded in Karroid Broken Veld in 20% of the families (*n* = 80), but in none of the families observed in other vegetation types. Furthermore, offspring delay dispersal from their natal territories for an average of two years, but are not allowed near the nesting site during the breeding season. The largest number of families

with non-breeders was recorded in Karroid Broken Veld (56%; *n* = 80), significantly more than other vegetation types (35%; *n* = 37) (Malan 1995).

In this study we tested the hypothesis that suitable hunting conditions for PCGs comprise both a sufficient number of perches and high prey visibility. We examined the importance of perch height and abundance, and aspects of vegetation structure such as the proportions of open ground and cover. We also speculate on how the suitability of hunting conditions may contribute to the fitness of individuals and the formation of PCG families.

Methods

Study area

The study area is located near Calitzdorp (33°32'S, 21°48'E) in the Little Karoo, South Africa. It is 146 km² in extent and receives a mean annual rainfall of 199 mm (*n* = 116 years: Anon. 1993). The study area is utilized extensively for ostrich (*Struthio camelus*) farming and, occasionally, for cattle and horse grazing. The topography is generally flat and soils are shallow and rich in plant nutrients (Ellis & Lambrechts 1986).

Three karroid vegetation types (Acocks 1988) occur in the study area, lying in parallel bands from the Succulent Karoo vegetation type in the south, through Karroid Broken Veld, to Spekboomveld in the north. Succulent Karoo comprises a sparse layer of prostrate succulents and herbs. In Karroid Broken Veld, small trees and medium-high (1–3 m) shrubs are scattered in a matrix of low shrubs. Spekboomveld can be divided into Closed and Open forms. Open Spekboomveld is dominated by trees and tall shrubs, but includes medium-high and low shrubs, whereas Closed Spekboomveld consists of a dense, continuous cover of trees and tall shrubs (2–5 m high), particularly the tree-succulent *Portulacaria afra*. PCGs did not occur in Closed Spekboomveld and only occupied parts of Succulent Karoo, whereas Open Spekboomveld and Karroid

Broken Veld were considered to be saturated with families (Malan 1995).

Families

A PCG family is defined as a social association comprising either a breeding monogamous pair or a polyandrous trio, with or without non-breeders (up to two individuals) and juveniles (up to four individuals). In polyandrous trios, a male and female breed with an additional co-breeding male that participates fully in reproductive activities, including copulations (Malan *et al.* in press). Juveniles are immature offspring less than one year old that delay dispersal from their natal territories. Non-breeders are offspring more than one year of age, either moulting into or in adult plumage, that also delay dispersal (Malan 1995).

Perch preference

To study perch height preference in relation to the relative availability of perches, we analysed perch use and availability for four selected families (A–D), each territory presenting its own combination of natural and artificial perches. The study area was divided into 25 ha quadrats (500 × 500 m). For each family, we calculated the mean density of perches available per height class (see below), determined from quadrats sampled within each territory (A = 18 quadrats; B = 68; C = 16; D = 18). For five observation periods from family A (1 168 min), 10 for B (1 281 min), four for C (1 465 min) and five for D (1 114 min), we calculated the mean percentage minutes perched on different height class perches. Percentages were employed to adjust for differences in the duration of observation periods.

Perch hunting

Two assumptions were made concerning the hunting tactics of a perch-based hunter: (a) the bird searches a circular area under each perch; and (b) the radius of the search area increases with an increase in perch height (Fitzpatrick 1980; Andersson 1981; Tye 1989; Sonerud 1992). Perch area was defined as the circular area surrounding each perch that could be scanned by a PCG from the top of a perch. To calculate such an area, the following formula was used: $Y = 10^{1.29} \times X^{0.37}$ where Y = mean horizontal striking distance (see below) and X = perch height (Figure 1a). This formula was obtained from the significant regression between horizontal striking distance and perch height (see Results). The horizontal striking distance was the distance in meters from the base of the perch to the site of impact. The perch area of all perches combined made up the utilizable hunting area per unit surface area and, if the utilizable area was less than the surface area, 'dead ground' or unusable hunting area resulted (Yosef & Grubb 1992).

By employing instantaneous sampling (Lehner 1979), we recorded perch height (measured to the nearest meter), horizontal striking distance, the strike outcome, detection and giving-up times, and quadrats visited per hour for a population of PCGs. Detection time was defined as the time, in minutes, that a PCG perched before launching a strike (see below), whereas giving-up time was the time a bird perched before moving to an alternate perch. Data were analysed for 69 separate observation periods (11 355 min; mean = 165 ± 65 min)
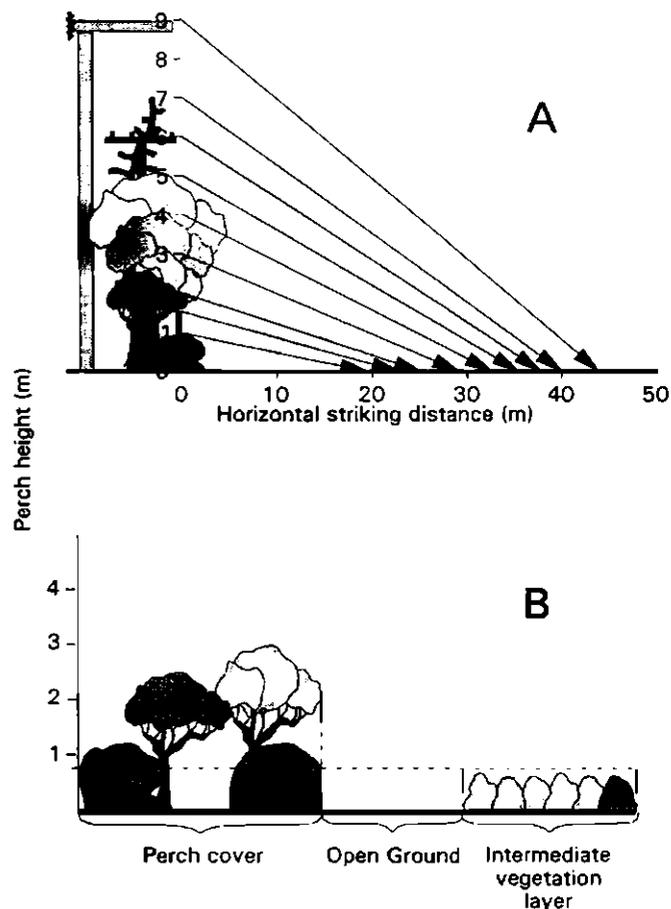

Figure 1 Schematic presentation of two habitat structure indices. (A) The horizontal striking distance, calculated for each perch height, was employed as a radius to calculate a circular area, or perch area, within which a pale chanting goshawk may search for prey from each perch. (B) The proportion of perch cover (of all plants taller than 0.75 m), open ground and the intermediate vegetation layer. Note that the spatial distribution of trees and shrubs are presented 'unnaturally' as clumped.

from the non-breeding periods in 1988. A strike was defined as a PCG flying from a perch to prey on the ground. Three striking outcomes were recognized: the PCG alighted on the ground, (a) either successfully catching the prey (successful strike); or (b) missing the prey (unsuccessful strike); or (c) the bird flew down from the perch and, on reaching the point of impact, briefly hovered (for a second or two) 1 m above the potential prey, and flew off (abandoned strike). To study the relationship between perch height and striking distance, simple linear regressions and tests for the presence of positive or negative correlations were performed (BMDP-1R; Dixon, Brown, Engelman & Jennrich 1990). Data were log-transformed to correct for the decrease in the capacity to detect prey with an increase in perch height (Andersson 1981).

Habitat parameters

For 20 quadrats in Closed Spekboomveld, 11 in Open Spekboomveld, 90 in Karroid Broken Veld, and five in Succulent Karoo, we counted, for each height class, all natural perches (see below) within a 50 m diameter circular plot at the centre of the 25 ha quadrat. Natural perch values were

extrapolated to estimate the number per 25 ha quadrat. For quadrats with low natural perch numbers, three in Karroid Broken Veld and 102 in Succulent Karoo, we counted the total number of natural perches. A natural perch was defined as a plant, alive or dead, taller than 75 cm. The sturdy trees and shrubs of the karroid vegetation types resulted in natural perches that were able to support the weight of perching PCGs (GM personal observation). The height classes were: 0.76–1.5 m; 1.5–2.5; 2.5–3.5; 3.5–4.5; 4.5–5.5; 5.5–6.5 and 6.5–7.5 m. Artificial perches used by PCGs included fence posts (1.5 m in height), telephone poles (6 m), a planted hedge of alien Sisal 'trees' (*Agave sisalana*) (6–7 m) and wooden power pylons (9 m). In each quadrat sampled, we measured the length of the fence and inter-fence post distance (particular to each fence), and then calculated the number of fence posts per quadrat. In addition, we counted the number of telephone poles and power pylons per quadrat.

To determine the proportion of cover in each height class, the height of the vegetation at one meter intervals was measured for 50 m in a straight line (starting from the centre of the quadrat), and the proportion of open ground and perch cover was calculated (Figure 1b). Open ground was defined as cover less than 15 cm tall, since prey such as rodents could probably be seen through the vegetation. Perch cover was defined as the cover directly below each perch (all cover > 75 cm tall) that obstructed the view of possible prey underneath.

Data for natural and artificial perches for each height class were combined to calculate the number of perches per quadrat. Each perch height was then scored with regard to perch area. To calculate a total perch area value per 25 ha quadrat, the mean perch height for each class was multiplied by the number of perches in that class, and the values for all perch height classes summed. Overlap between perch areas of neighbouring, individual perches was not taken into account. Data on ecological variables are presented as numbers per quadrat and referred to as densities per 25 ha.

The proportion of open ground and perch cover, relative density of natural, artificial and all perches, and perch area per quadrat were compared between: a) vegetation types; and b) occupied and unoccupied quadrats in Succulent Karoo. A logarithmic transformation, $\log(x+1)$ was employed to normalize the data in an analysis of variance (ANOVA), and pairwise t tests with Bonferroni-adjusted significant levels were performed. Means were back-transformed and 95% confidence intervals (asymmetrical) calculated (Zar 1984).

Results

Perch preference

Perch-to-ground hunting was employed in 97% ($n = 397$) of strikes recorded. In their territory, family A perched a mean proportion of 64% of the time per quadrat on 6–7 m high Sisal trees and only 29% on 1–2 m high natural perches and fence posts (Figure 2). Where these were available, mean perching time on telephone poles and power pylons was more than 50% for families B and C, with lower proportions on lower perches. The polyandrous family D preferred 2–3 m high natural perches and fence posts, and largely ignored 1 m high natural perches. This family occupied a territory that contained no high (6–9 m) artificial perches.
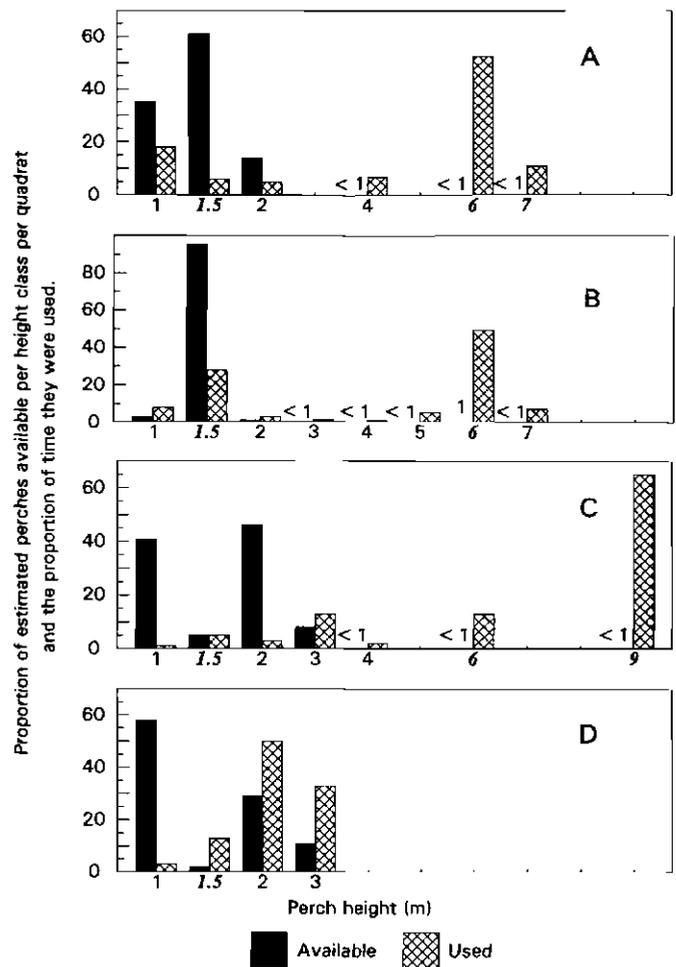

Figure 2 Pairwise comparison of perch availability and usage (% of all in minutes) for four families of pale chanting goshawks, the territory of each family presenting its own combination of artificial (*in italics and bold*) and natural perches. Data were from two monogamous families in Succulent Karoo (A–B), and two polyandrous families in Karroid Broken Veld (C–D). Apart from natural perches, family A had fence posts (1.5 m) and Sisal trees (6 & 7 m) in their territory, family B fence posts and telephone poles (6 m), family C fence posts, telephone poles and power pylons (9 m), and family D only fence posts.

Perch hunting

For adults, no significant correlation was found between perch height and horizontal striking distance for successful strikes ($r = 0.43$; $n = 19$; $p = 0.70$) and abandoned strikes ($r = 0.12$; $n = 26$; $p = 0.56$), whereas a weak, significant relationship existed for unsuccessful strikes ($r = 0.28$; $n = 122$; $p = 0.002$). However, the slopes or intercepts did not differ significantly between the above three strike outcomes (ANOVA; $F = 1.13$; $p > 0.05$) and data were combined and produced a significant regression for all strikes ($r = 0.29$; $n = 167$; $p < 0.001$). For juveniles, no significant relationship existed between perch height and horizontal striking distance for successful strikes ($r = 0.05$; $n = 5$; $p = 0.94$) and abandoned strikes ($r = 0.39$; $n = 12$; $p = 0.22$), whereas a significant relationship existed for unsuccessful strikes ($r = 0.39$; $n = 109$; $p < 0.001$). Again, slopes or intercepts did not differ significantly between the above three strike outcomes (ANOVA; $F = 1.18$; $p > 0.05$) and therefore data were combined and pro-

duced a significant regression for all strikes ($r = 0.38$; $n = 126$; $p < 0.001$). However, slopes or intercepts did not differ significantly between adults and juveniles for strike outcomes combined (ANOVA; $F = 1.21$; $p > 0.05$), and all strike data were combined and produced a significant regression ($r = 0.34$; $n = 293$; $p < 0.001$). The simple regression equation ($Y = 10^{1.29} \times X^{0.37}$) was then employed to calculate a mean horizontal striking distance from each perch height (Figure 1a).

In the comparison between horizontal striking distances of polyandrous families in Karroid Broken Veld and monogamous groups in Succulent Karoo, striking distances from 1 m high perches did not differ significantly (20 vs. 27 m respectively, $df = 19$; $t = -0.84$; $p > 0.05$), nor did striking distances from 2 m high perches (21 vs. 28 m; $df = 26$; $t = 1.10$; $p > 0.05$), from 6 m high perches (30 vs. 36 m; $df = 49$; $t = -0.94$; $p > 0.05$), nor detection times (6.3 vs. 5.0 min; $df = 167$; $t = 0.40$; $p > 0.05$).

The slopes or intercepts of correlations between perch heights and giving-up times did not differ significantly for adults and juveniles (ANOVA; $F = 0.660$; $p > 0.05$) and therefore data were combined and produced a non-significant regression ($r = 0.11$; $n = 298$; $p = 0.06$). There were no significant differences between perch height and time to prey detection for adults and juveniles (ANOVA; $F = 0.585$; $p > 0.05$), but in combination they produced a weak, significant regression ($r = 0.16$; $n = 293$; $p = 0.008$). There were no significant differences between horizontal striking distances and time to prey detection for adults and juveniles (ANOVA; $F = 1.573$; $p > 0.05$), but in combination they produced a weak,

significant regression ($r = 0.22$; $n = 293$; $p < 0.001$).

Each hour, polyandrous families in Karroid Broken Veld visited significantly fewer quadrats (mean = 1.83; 95% confidence limits = 1.46–2.26) than monogamous families in Succulent Karoo (2.41; 1.87–3.03; $df = 56$; $t = 2.15$, $p < 0.05$). Adults in both vegetation types visited significantly more quadrats per hour (2.18; 1.84–2.55) than juveniles (1.19; 0.98–1.42; $df = 73$; $t = 3.53$; $p < 0.001$). The times per hour that polyandrous families in Karroid Broken Veld gave up and moved to a different perch did not differ significantly (mean = 5.5; 95% confidence limits = 4.5–6.6) from that of monogamous families in Succulent Karoo (4.8; 3.9–5.7; $df = 296$; $p > 0.05$).

Habitat parameters

The proportions of open ground, perch cover and perch categories differed significantly between all vegetation types (Table 1). The total perch area:surface area ratio ranged from 67:1 in Closed Spekboomveld to 1:1 in Succulent Karoo. The density of natural perches was significantly and positively correlated with perch area ($r = 0.96$; $n = 231$; $p < 0.001$) and perch cover ($r = 0.81$; $n = 231$; $p < 0.001$), and significantly and negatively correlated with the proportion of open ground ($r = -0.54$; $n = 231$; $p < 0.001$). Perch cover was significantly and negatively correlated with the proportion of open ground ($r = -0.63$; $n = 231$; $p < 0.001$).

In occupied and unoccupied quadrats in Succulent Karoo, the densities of natural and artificial perches were significantly higher in occupied quadrats, with the total perch

Table 1 Results of a comparison of mean values of habitat variables between different vegetation types occupied and unoccupied by pale chanting goshawks. Means not significantly different are linked with underscoring

	Closed Spekboomveld	Open Spekboomveld	Karroid Broken Veld	Succulent Karoo	F^1
	Unoccupied	Occupied	Occupied	Occupied in parts	
% Open ground	42[2] (39–45)	49 (45–54)	62 (60–64)	72 (69–75)	52.36***
% Perch cover	36 (31–41)	18 (22–14)	4 (3–5)	0	225.95***
No. of natural perches	7655 (6741–8693)	7395 (6424–8513)	2376 (1739–3246)	14 (11–18)	321.03***
No. of artificial perches	15 (63–3)	78 (11–528)	23 (12–43)	79 (45–135)	3.90**
No. of all perches	7815 (6889–8866)	7726 (6795–8784)	3026 (2428–3771)	183 (128–261)	88.99***
Total perch area (ha)	1670 (1460–1920)	1400 (1240–1570)	450 (400–620)	20 (10–40)	65.2***
Total perch area: surface area ratio	67:1	56:1	18:1	1:1	
No. of quadrats	20	11	93	107	

** = $P < 0.01$; *** = $P < 0.001$

[1] ANOVA with logarithmic transformations

[2] means and 95% confidence limits

area:surface area ratio at 1.6:1 compared with 0.1:1 for unoccupied quadrats (Table 2).

Discussion

Perch height versus availability

Among perch-hunting raptors, the suitability of the hunting conditions is reflected in factors such as perch height and abundance, vegetation density and prey visibility (Fitzpatrick 1980; Bechard 1982; Simmons 1989; Preston 1990; Sonerud 1992; Yosef 1992; Widen 1994). When hunting, many perch-hunting predators search in a pause-travel mode, because they cannot search efficiently for prey while moving (Tye 1989). The time that they pause depends in part on the size of the area that can be searched, whereas the area scanned may depend on the height of the perch and the structure of the surrounding vegetation (Sonerud 1992; Yosef 1992).

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, it can be predicted that horizontal strike distances, detection times and giving-up times will increase with perch height (Fitzpatrick 1980; Andersson 1981; Tye 1989; Sonerud 1992). As for other mammal-eating raptors, for example 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. Raptors perching on higher perches were therefore able to hunt further from their perches and thereby increase the likelihood of catching ground-dwelling prey. However, for 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, possibly at random and opportunistically and, apart from the hunting conditions, may depend on other factors such as age, experience and hunger. This finding, together with the weak correlations reported between detection time and perch height, and detection time and striking distance, suggests that perch height played a lesser role in the probability of detecting prey. The advantage of the bigger area that can be searched from a higher perch is probably offset by the further distance the PCG has to fly to catch the prey, which increases the likelihood of the advancing bird being detected (Andersson 1981). Furthermore, perches from all height classes were not available (e.g. 4–5 and 7–8 m). Perches in the 4–5 m height classes might be suitable, but since so few are available, birds may be compelled to occupy higher perches.

The clear-cut preference for higher perches, especially by family B, is therefore surprising given that the height of perches was probably not related to foraging success. However, no distinction could be made between a PCG actively perch-hunting and perching for another reason. The height of perches, such as telephone poles and power pylons, may play an important role in other behaviour such as scanning for hunting family members, scanning for intraspecific and interspecific intruders, advertising a territory holder's presence and occupancy, and resting (Yosef 1992). It may even function to escape the heat associated with low perches (Wiley & Richards 1982). Artificial perches such as fence posts, when compared to trees or shrubs, may be easier to sit on as they

Table 2 Comparison of mean values of habitat variables between quadrats occupied and unoccupied by pale chanting goshawks within Succulent Karoo. Means (95% confidence limits) and *t* tests with logarithmic transformation

	Occupied	Unoccupied	*t*
% Open ground	73 (69–76)	71 (65–79)	0.39ns
% Perch cover	0	0	
No. of natural perches	16 (13–22)	8 (3–17)	2.31*
No. of artificial perches	122 (70–213)	12 (2–53)	3.42***
No. of all perches	265 (196–359)	40 (12–131)	4.53***
Perch area (ha)	40.5 (55.8–29.3)	2.5 (17.2–0.4)	4.99***
Total perch area: surface area ratio	1.6:1	0.1:1	
No. of quadrats	86	21	

ns = not significant; * = *P* < 0.05; *** = *P* < 0.001

are more stable and offer an unobstructed view of the ground directly beneath them.

The availability of perches may be more important than perch height for several reasons. First, in almost all (97%) hunts recorded, a perch was used to search for prey and from which to launch attacks. Second, the relatively short giving-up times (4.8–5.5/h or once every 11–12.5 min) indicate that birds move to a different perch regularly rather than just sit and wait. In addition, one polyandrous family (D) occupied a territory that had no perches, artificial or natural, higher than 3 m. Furthermore, the spatial distribution of perches may also be an important factor in hunting conditions. Since trees and shrubs (natural perches) are spaced regularly in arid areas (Phillips & Macmahon 1981; Esler & Cowling 1993), and artificial perches in the study area are always in rows, birds had to utilize shorter natural perches in order to hunt over every part of the surface area of the territory. This might explain why family B (Figure 1) was utilizing 1.5 m high fence posts proportionally less (28%) than their availability (95%), but 1 m and 2 m natural perches proportionally more (8% and 3%) than what was available (3% and 1%).

Suitable hunting conditions

Succulent Karoo was the only vegetation type in which the mean density of artificial perches per 25 ha quadrat exceeded the density of natural perches. Of these, fence posts contributed by far the largest proportion (99%; 701/708; A and B; Figure 1). In fact, we suggest that PCGs only occupy parts of Succulent Karoo because birds were largely dependent on the availability of artificial hunting perches. That some areas in Succulent Karoo have more fence posts than others may be the result of particular farming practices. Parts of Succulent Karoo were divided into numerous small, ostrich breeding camps that were fenced, very often with two fences 2 m apart to separate the aggressive males, which in turn provided ample fence-post perches for PCGs. The total perch area:surface area ratios of occupied and unoccupied quadrats suggests that the amount of 'dead ground' clearly separated suitable

and unsuitable areas. With fence posts placed 1.7–1.9 m apart (Malan 1995), and a mean horizontal striking distance of 23 m from a fence post, a perching PCG would face 12 unnecessary poles on either side of its perch. For example, if on average 120 fence posts were available per quadrat and they were all positioned in a linear fence, a PCG perching in succession on every twenty-fifth pole, utilizing only five poles, will view almost all perch area. By not subtracting this overlap, the calculated Succulent Karoo total perch area:surface area ratio may have been overestimated. Dead ground may therefore exist, and the ratio of 1.6:1 for occupied Succulent Karoo may in fact be even lower than 1:1. This bias was not relevant in other vegetation types since the high density of natural perches (2 376–7 655 perches per 25 ha), and the regular spacing of natural perches (Esler & Cowling 1993), inevitably caused overlap as reflected by the high ratios of 18–67:1. The perch area of all perches combined therefore 'covered' the surface area 18 to 67 times. The low availability of perches per given area in Succulent Karoo thus rendered sections unsuitable. Taking into account that prey (otomyinid) densities did not differ significantly between the occupied and unoccupied Succulent Karoo (Malan 1995), at least in occupied areas the availability of perches provided PCGs access to prey within a major part of the total surface area.

At the other extreme, in densely vegetated Spekboomveld, the proportion of perch cover increased two-fold from 18% in Open Spekboomveld (occupied by PCGs) to 36% in Closed Spekboomveld (unoccupied by PCGs), whereas the mean density of natural perches per quadrat did not differ significantly (Table 1). In addition, the proportion of open ground in Open Spekboomveld (49%) was significantly higher than in Closed Spekboomveld (42%). These results indicate that tree and shrub canopies were broader in Closed Spekboomveld. Given that otomyinid biomass estimates differed significantly between Closed and Open Spekboomveld (Malan 1995), why were there no PCGs resident in Closed Spekboomveld? With trees and shrubs so close together (one every 29–37 m²), a perching PCG may have a very limited view of the ground and prey, and the proportion of open ground that can be scanned becomes severely restricted. We therefore suggest that prey visibility distinguished Open Spekboomveld from Closed Spekboomveld. Secondly, with such a high proportion of ground cover and densely structured vegetation in Closed Spekboomveld, a rodent will have ample cover into which to escape. A striking PCG may also have structural limitations in flying at, and pursuing, a fleeing animal on the ground.

In Spekboomveld, prey visibility and, in Succulent Karoo, perch availability played important roles in the ecological make-up of the hunting conditions for the PCG. However, the variables that most clearly explain the above factors (i.e. density of natural perches, perch area, and proportions of open ground and perch cover) were not independent of each other. Therefore, suitable hunting conditions, by definition, should incorporate both prey visibility and perch availability. First we hypothesize that such conditions must contain adequate perch density, but not at such densities as to obstruct the view of open ground. Therefore, a total perch area:surface area ratio of at least 1:1 should pertain. Thus, since only natural perches are regularly spaced, parts of Succulent Karoo with its very low density of natural perches cannot provide suitable

hunting conditions. Karroid Broken Veld (a ratio of 18:1; 2 376 natural perches/25 ha or a tree or shrub every 105 m²) is more suitable than Open Spekboomveld (56:1 and 7 395 natural perches/25 ha). Second, we hypothesize that suitable hunting conditions must contain a low proportion of perch cover so as not to obstruct the view of terrestrial prey. Given that perch cover increases with the density of natural perches, the most acceptable perch cover is probably found in Succulent Karoo (0%) and Karroid Broken Veld (3–5%). Third, we hypothesize that for a perch-hunting PCG to view terrestrial prey, suitable hunting conditions must contain a high proportion of open ground. Given the negative correlation between the proportion of open ground and the density of natural perches, Succulent Karoo and Karroid Broken Veld, with their low perch density, again probably contain suitable proportions of open ground (72% and 60–64%). Karroid Broken Veld and parts of the Succulent Karoo therefore appear to harbour the most suitable hunting conditions.

Nevertheless, although the density of natural perches and proportions of perch cover and open ground differed significantly between Succulent Karoo and Karroid Broken Veld, only one difference in hunting tactics could be detected. Because of lower perch availability in Succulent Karoo, birds observed flew further between perches, and travelled longer distances (mean = 935–1 515 m/h) than in Karroid Broken Veld (730–1 130 m/h). Thus, hunting in this vegetation type was probably energetically more expensive. However, because the density of natural perches was higher in Open Spekboomveld than Karroid Broken Veld, did birds in Open Spekboomveld not fly even shorter distances between perches?

The only documented foraging benefit in Karroid Broken Veld is that PCGs were taking higher proportions (91–93%) of the three dominant prey species (*O. unisulcatus* and *P. brantsii* ± 124 g; *R. pumilio* ± 45 g) than birds in Open Spekboomveld (88%) and Succulent Karoo (63%) (Malan & Crowe 1996). The remainder of the diet consisted of smaller vertebrates (small birds, hatchling tortoises, small snakes and lizards) as well as invertebrates (sunspiders, harvester termites, grasshoppers and beetles). If birds hunting in Karroid Broken Veld receives a higher energetic return per unit effort, foraging in this vegetation type may ultimately increase their reproductive and survival fitness (Emlen & Wrege 1994; Bednarz 1988). Furthermore, the hunting conditions may function not in isolation, but in conjunction with the refuge strategies and habitat requirements of the dominant prey species. *O. unisulcatus* and *R. pumilio* inhabit areas with a high vegetation cover and therefore forage near and travel between vegetation patches, whereas *P. brantsii* lives in *heuweltjies* in open ground (Bond, Ferguson & Forsyth 1980; Vermeulen & Nel 1988; Milton, Dean & Kerley 1992; Malan 1995). The combination of prey visibility and perch availability that Karroid Broken Veld presents may thus facilitate the catchability of large rodent prey that either forage near plant cover or in the open.

We hypothesize that for non-breeders and inexperienced perch-hunting juveniles the probability of survival is higher in Karroid Broken Veld that offers an opportunity to view and catch a large rodent prey. We suggest that co-breeders partake in polyandrous trios probably because their reproductive fit-

ness would still be higher, even if they share reproduction, than if they disperse to, occupy and breed in an area that incorporates less suitable hunting conditions.

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