SOLITARY AND SOCIAL HUNTING IN PALE CHANTING GOSHAWK (*MELIERAX CANORUS*) FAMILIES: WHY USE BOTH STRATEGIES?

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ABSTRACT.—I observed Pale Chanting Goshawks (*Melierax canorus*)using solitary and social hunting strategies. Most goshawks hunted predominantly alone, but if an individual was unable to flush and catch a cornered rodent from a shrub, other family members joined in a social hunt. Goshawks perched near or on the tops of shrubs and repeatedly struck at rodents until they were caught. Other family members did not pursue the goshawk that caught prey, even if it did not make the initial hunt. During social hunts, there was no evidence of a dominance hierarchy in families when they were not hunting. I found hunting success of individual goshawks to be low (11–12%) for both solitary and social hunts. Only large rodents were caught during social hunts, whereas smaller vertebrates (lizards and birds), and invertebrates, were caught during solitary hunts. It appeared that dominant breeders did not kleptoparasitize or dominate subordinate family members during social hunts to maximize their individual hunting success. Juveniles were significantly less successful than adults in capturing rodent prey, but may have increased their foraging efficiency and survival by participating in social hunts. Dominant Pale Chanting Goshawks that allowed offspring to partake in social hunts may, therefore, behave selfishly to increase their inclusive fitness.

KEY WORDS: *Pale Chanting Goshawk*; Melierax canorus; *social hunting; juvenile survival; prey size; energy intake.*

Caza individual y social de *Melierax canorus*: por que utilizar ambas estrategias?

RESUMEN.—Observe a *Melierax canorus* utilizar estrategias de caza individual y social. La mayoría de los azores cazan principalmente en forma individual, pero si un individuo no es capaz de capturar a un roedor acorralado en un rastrojo, otros miembros de la familia se pueden unir en una cacería social. Los miembros restantes de la familia no persiguen al azor que ha capturado la presa. Durante la cacería social, no hubo evidencia de dominancia jerárquica la cual existe cuando no estan cazando. Encontré que el éxito individual de caza fué menor al 11–12% en ambas modalidades individual y social. Los grandes roedores fueron capturados sólo en cacerías sociales, mientras que los vertebrados mas pequenos (lagartijas y aves), así como tambien los invertebrados fueron capturados durante la caza individual. Sugiero que los reproductores dominantes no practican el kleptoparasitismo o domiman a miembros subordinados de la familia durante la caza social con el fin de maximizar el éxito de la caza individual. Los juveniles fueron menos exitosos que los adultos en capturar roedores pero pudieron haber aumentado su eficiencia de forrajeo y sobreviviencia al participar en la caza social. Los dominantes *Melierax canorus* que permitieron a sus hijos participar en la caza social pudieron haber actuado en forma autosuficiente con el fin de aumentar su vigor.

[Traducción de César Márquez]

Predators can use various hunting strategies to increase their individual foraging success. They can hunt alone or in association with related or unrelated conspecifics, or even with heterospecifics (Packer and Ruttan 1988, Ellis et al. 1993). In such hunting associations, they can pursue strategies ranging from active participation, where all individuals participate fully and benefit from social hunts, to kleptoparasitism (Hector 1986, Scheel and Packer 1991, Heinsohn and Packer 1995, Steele and Hockey 1995). Predators may adopt one or more of these strategies if their individual hunting success is low or if prey is large and difficult to catch (Packer and Ruttan 1988). The optimal combination of strategies should

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maximize their net energy return (Hansen 1986, Bednarz 1988).

The Pale Chanting Goshawk (*Melierax canorus*) is a large, common raptor that inhabits the arid regions of southern Africa. In one study in the Little Karoo, South Africa, Pale Chanting Goshawks were found to live in family groups consisting of a breeding unit of either a polyandrous trio (a pair plus an additional cobreeding male) or a monogamous pair, with or without nonbreeders (up to two) and juveniles (up to four) (Malan et al. 1996). Cobreeders participated fully in reproductive activities, including copulations, but nonbreeders were actively excluded from the nesting area during the breeding season. Whereas polyandrous trios were recorded only in broken veld, delayed dispersal by nonbreeders and juveniles was the norm in all vegetation types. A dominance hierarchy existed in families with the female breeder on top followed by the male breeder and cobreeder and then the nonbreeders and juveniles (Malan and Jenkins 1996). Although the Pale Chanting Goshawk is a generalist feeder, relatively large rodent prey (45–124 g, *Otomys unisulcatus, Parotomys brantsii, and Rhabdomys pumilio*) that forage near vegetation or in the open make up most of the biomass in its diet (Malan and Crowe 1996). Other prey taxa include a range of other vertebrates as well as invertebrates. Pale Chanting Goshawks are obligate perch hunters and hunt from natural (trees or shrubs) or artificial (fence posts and telephone poles) perches from which they gently swoop to the ground (Malan and Crowe 1997).

This study tests the hypothesis that Pale Chanting Goshawks use solitary and social hunting to maximize their individual hunting success in capturing large and difficult to catch rodent prey. I observed the methods used by Pale Chanting Goshawks during social hunts, as well as the size of the prey caught during solitary and social hunts. Secondly, the solitary and social hunting strategies of large families ($\bar{x} = 5.5$ goshawks) in one habitat were compared with small families ($\bar{x} = 3.4$) in another habitat. Thirdly, I compared the hunting tactics of juvenile Pale Chanting Goshawks with those of adults as well as foraging fledglings, still dependent on their parents for food.

STUDY AREA AND METHODS

The 146 km² study area was located near Calitzdorp (Little Karoo, 33°32′S, 21°48′E) in South Africa. It receives an average annual rainfall of 20 cm and the topography is generally flat. It is utilized for extensive Ostrich (*Struthio camelus*) farming.

Two semi-arid vegetation types occurred in the study area, broken veld (Karroid Broken Veld vegetation type, Acocks 1988) in the north and dwarf shrubland (Succulent Karoo) in the south. Broken veld consisted of small trees and shrubs (1–3 m high) scattered in a matrix of low shrubs. Dwarf shrubland consisted of a sparse layer of prostrate succulents and herbs. In dwarf shrubland, Pale Chanting Goshawks only occupied areas with a high availability of perches (mostly fenceposts) whereas broken veld with its abundant trees and shrubs was probably saturated with Pale Chanting Goshawk families (Malan 1995).

I defined hunts as flights by goshawks from perches to attack prey on the ground or in the air. During each hunt, I aged the participating goshawk(s) as follows: adults, juveniles or goshawks in immature plumage, and fledglings or offspring still fed by their parents for up to 80 d after leaving nests (Malan 1995). For adults, hunting data of breeders and nonbreeders were combined. Three hunt outcomes were recognized: successful hunts or hunts that ended when goshawks landed on the ground and caught prey, unsuccessful hunts or hunts that ended when goshawks landed on the ground but failed to catch prey, and abandoned hunts or hunts that ended when goshawks flew down from perches and, upon reaching the point of impact, briefly hovered about 1 m above potential prey, then flew off without the prey. Hunting of termites was not analyzed because they were not chased (Malan and Crowe 1996).

Using instantaneous sampling (Lehner 1979), I followed a focal Pale Chanting Goshawk by vehicle and recorded aspects of its hunting behavior every 60 sec. During each observation period, the focal goshawk was followed from 60–300 min and, when it was out of sight, the observation period was terminated. The hunting behavior of all other family members within 100 m of the focal goshawk was also recorded. The study was conducted from February 1988–March 1989, but the hunting behavior of mated adults was only studied in the nonbreeding and prelaying (from first copulation until egg-laying) periods. The hunting behavior of goshawks was also recorded during casual observations during the summer breeding seasons of 1989–95. Solitary and social hunts were recorded during 64 observation periods (total observation time = 11 139 min, $\bar{x} = 174$ min, SD = 67 min), and solitary hunts during an additional 17 observation periods (2074 min; $\bar{x} = 123$, SD = 54 min). The hunting behavior of 15 adults were studied for 57 observation periods (9398 min), five juveniles for 16 observation periods (2651 min), and two fledglings for eight observation periods (1164 min). Capture rates per hour were calculated for each observation period and compared between observations periods for single and social hunts, goshawk age classes, and hunt outcomes.

A solitary hunt is defined as only the focal Pale Chanting Goshawk hunting. A social hunt involved either the focal goshawk hunting and being joined on the ground by family members, or the focal goshawk joining family members in a hunt. I termed these hunts "social" because family members hunted together in a nonaggressive and cooperative manner. A social hunt was successful

Table 1.　A comparison of solitary and social striking rates (per hour) by adult, juvenile, and feldgling Pale Chanting Goshawks. During successful hunts, prey was caught. During unsuccessful hunts, goshawks landed on the ground but failed to catch prey. During abandoned hunts, goshawks briefly hovered about 1 m above potential prey but flew off without prey.

	ADULTS	JUVENILES	FLEDGLINGS	KRUSKAL-WALLIS	df
Solitary hunts					
Successful	0.15 ± 0.24[1]	0.07 ± 0.13	0.04 ± 0.10	2.66 ns	2
Unsuccessful	1.00 ± 1.05	1.74 ± 1.02	1.35 ± 1.45	8.49*	2
Abandoned	0.12 ± 0.24	0.21 ± 0.26	0.11 ± 0.31	4.24 ns	2
All solitary hunts	1.26 ± 1.13	2.02 ± 1.21	1.49 ± 1.69	6.99*	2
Social hunts					
Successful	0.04 ± 0.11	0.01 ± 0.06	0.00	1.51 ns	2
Unsuccessful	0.08 ± 0.19	0.02 ± 0.07	0.00	3.24 ns	2
Abandoned	0.05 ± 0.13	0.00	0.00	3.90 ns	2
All social hunts	0.17 ± 0.28	0.03 ± 0.09	0.00	6.01*	2

[1] = mean $\pm$ 1 SD.
* = $P < 0.05$.

if any of the participating Pale Chanting Goshawks caught prey. Due to my small sample size, only social hunts involving two goshawks were analyzed. In all social hunts analyzed, only adult Pale Chanting Goshawks joined the focal adult or juvenile.

Pale Chanting Goshawk families are strictly territorial and unrelated conspecifics were not tolerated within territories (Malan and Jenkins 1996). Pale Chanting Goshawks thus always hunted in association with family members. This association was compared between the significantly larger polyandrous families in broken veld ($\bar{x}$ = 5.5 goshawks) and smaller monogamous families in dwarf shrubland ($\bar{x}$ = 3.4; Malan 1995). The presence of family members within a 100 m radius of the focal animal was compared between three families each from broken veld and dwarf shrubland. For each observation period, I calculated the proportion of time spent alone or in close proximity with one or more family members, either adults, juveniles, or fledglings. Data from 21 focal individuals were analyzed for 63 observation periods(10 055 min; $\bar{x}$ = 160, SD = 66 min) and arcsine transformed to improve normality (Zar 1984).

RESULTS

Prey was attacked on the ground in 99% (N = 397) of all hunts. When prey was pursued on the ground, it was chased actively, very often with wings aloft and flapping. If vertebrate prey, such as an otomyinid rodent, was cornered under a shrub and a family member joined the focal goshawk on the ground, the Pale Chanting Goshawks would surround the shrub and/or perch on top. Individuals would then repeatedly strike at the rodent by jumping into the shrub (flush-and-ambush strategy; Bednarz 1988). In four hunts, all unsuccessful,

a Pale Chanting Goshawk attacked a bird from a perch and actively chased the bird in horizontal flapping flight.

The frequency of successful solitary hunts by adults in dwarf shrubland (14%; N = 86) was not significantly different from the frequency of successful solitary hunts in broken veld (10%, N = 107, Log-likelihood Ratio with Yates correction: G_c = 0.31, P > 0.50). The frequency of successful social hunts by adults also did not differ significantly between broken veld (25%, N = 8) and dwarf shrubland (21%, N = 14; G_c = 0.12, P > 0.70). The rates per hour that adults participated in successful, unsuccessful, or abandoned solitary hunts did not differ significantly (t-test, P > 0.05,) between large and small families. Likewise, the rates per hour that adults participated in successful, unsuccessful, or abandoned social hunts did not differ significantly (t-test, P > 0.05,) between large and small families. My sample size prevented a comparison between the hunting rates of successful, unsuccessful, or abandoned hunts for both juveniles and fledglings from large and small families.

When the solitary and social striking rates of all age classes were considered, the ratio of solitary to social hunts by adults was significantly less than for juveniles and fledglings (Table 1). Juveniles (4%, N = 100) and fledglings (4%, N = 25) were equally successful in solitary hunts, but were significantly less successful than adults (11%, N = 193; G_c =

Table 2. Percent time per observation period Pale Chanting Goshawks hunted within 100 m of other family members in large ($\bar{x} = 5.5$ goshawks) and small families ($\bar{x} = 3.4$).

NUMBER PRESENT	SMALL FAMILIES $n = 3$	LARGE FAMILIES $n = 3$	F	df
Zero	84 ± 44	85 ± 54	0.01 ns	1, 46
One	15 ± 44	11 ± 38	0.36 ns	1, 46
Two	0 ± 4	1 ± 4	2.62 ns	1, 46
Three	0 ± 0	1 ± 6	4.23*	1, 46
Four	0 ± 0	0 ± 3	2.04 ns	1, 46

* = $P < 0.05$.

4.23, $P < 0.05$). Juveniles engaged in social hunts (2%, $N = 102$) significantly less often than adults (10%, $N = 215$, $G_c = 6.75$, $P < 0.01$), whereas fledglings did not participate in social hunts at all. During social hunts, once prey was caught, goshawks flew off with the item and they were not pursued by the remaining family members. Adults caught prey during social hunts in 23% ($N = 22$) of hunts. The adult that initiated the social hunt caught the prey in 20% ($N = 10$) of instances, whereas the focal adult that joined the hunt caught the prey in 27% ($N = 12$) of instances ($G_c = 0.05$, $P > 0.75$). The frequency of success of the solitary hunts by adults (11%, $N = 193$) did not differ significantly from their success in social hunts (23%, $N = 22$, $G_c = 1.40$, $P > 0.10$). Juveniles participated in two social hunts, joining the hunt in both instances, and in one of these hunts, the juvenile was successful. During casual observations, juveniles that participated in social hunts caught rodent prey in four instances.

During all successful hunts only vertebrates (rodents, lizards and birds) were caught. Hunts for

Table 3. Percent time per observation period adult, juvenile, and fledgling Pale Chanting Goshawks spent within 100 m radius of other family members.

NUMBER PRESENT	ADULTS	JUVENILES	FLEDG- LINGS	F	df
Zero	85 ± 41	99 ± 13	99 ± 16	7.30**	2, 69
One	13 ± 38	1 ± 13	1 ± 16	7.07**	2, 69
Two	0 ± 16	0	0	2.18 ns	2, 69
Three	0 ± 10	0	0	0.97 ns	2, 69
Four	0 ± 6	0	0	0.49 ns	2, 69

** = $P < 0.01$.

arthropods were probably so quick, and in the lower vegetation layer, that they were not seen. During solitary hunts, fledglings caught one lizard (*Sauria* spp.), juveniles caught three lizards and one bird, and adults caught 18 rodents (86%), two lizards and one bird. During social hunts, only rodents were caught with adults capturing five rodents and one juvenile catching one rodent.

When the association of family members between large and small families was investigated, adults of large families spent significantly more time in close proximity (<100 m) to three family members than did adults from small families (Table 2). The proportion of time spent alone ($\bar{x} = 99$, SD = 13%) or in close proximity to one family member ($\bar{x} = 1\%$, SD = 13%, ANOVA, all $P > 0.05$) did not differ significantly between juveniles of large and small families. Adults, compared to juveniles and fledglings, spent significantly less time alone and significantly more time in close proximity to one family member (Table 3).

DISCUSSION

Despite the potential advantages associated with hunting in groups, such as an increase in individual hunting success and energy return (Bednarz 1988), Pale Chanting Goshawks still predominantly hunt alone. The average hunting success of individual adult goshawks in social hunts was only 11.5%, half of the 23% success of social hunts in which two goshawks participated. Nevertheless, it was similar to the 11% hunting success of individuals in solitary hunts.

Why would Pale Chanting Goshawks follow two hunting strategies that contribute the same to an individual's hunting success? For social hunting to be a viable option, the individual benefits of this hunting strategy must equal or exceed that of hunting singly (Hansen 1986). First, such benefit could only result if prey captured in family pursuits is, on average, larger than that caught in solitary pursuits (Steele and Hockey 1995). Pale Chanting Goshawks preyed mostly on relatively large otomyinid rodents (mean body mass = 124 g), as well as the smaller *Rhabdomys pumilio* (mean body mass = 45 g) (Malan and Crowe 1996). In broken veld and dwarf shrubland, these rodents contributed 87% or 22 682 g of biomass and 68% or 249 individuals to the vertebrate diet. Pale Chanting Goshawks also preyed on smaller mammals, small birds, hatchling tortoises, small snakes and lizards, as well as sunspiders, harvester termites, grasshop-

pers and beetles (Malan and Crowe 1996). The average mass of rodents caught in the two vegetation types was 90 ± 40 (± 1 SD) g, birds 70 ± 34 g, and reptiles 12 ± 9 g (Malan and Crowe 1996). Thus, because only rodents were captured in social hunts, the average size of prey captured in this way was indeed larger than those caught in solitary hunts. In terms of hunting socially, it was also the prey biomass obtained during these hunts, and not only the relative success or hunting technique used, that was important to each individual. Although the hunting success in solitary and social hunts was equal, the energy returns from hunting large animals in social hunts may have surpassed the returns from hunting smaller prey in solitary hunts.

A second reason why Pale Chanting Goshawks may use two hunting strategies is that their individual hunting success in catching vertebrate prey in solitary hunts is low. Solitary adult hunting success of 11% was substantially lower than the mean of 59% (range = 31–72%) for 11 raptor species that hunt ground-dwelling prey (Toland 1986). It is even lower than the 19–33% success ($\bar{x} = 27\%$) for raptors that hunt other birds in the air, a technique generally thought to be less successful than searching for prey on the ground (Toland 1986). The low success of Pale Chanting Goshawks highlights the difficulty they experience in catching vertebrate prey in a shrub-rich substrate. Since solitary hunters have low success of catching large vertebrate prey, Pale Chanting Goshawks may adopt a social hunting strategy to supplement their solitary hunting and thus increase their overall hunting success.

In spite of the apparent benefits of hunting socially, adult Pale Chanting Goshawks did not habitually hunt together. Adults spent only 15% of time within 100 m of family members, compared with 71% of the time that Harris' Hawks (*Parabuteo unicinctus*) spent within 50 m of group members (Bednarz 1988). Pale Chanting Goshawks could, however, visually monitor each other's movements by perching on the highest available perch. The flapping wing motions during a pursuit may act as a signal to other family members that a hunt is in progress. If the prey animal was cornered, a solitary Pale Chanting Goshawk probably cannot act as a hunter and a beater, and would thus fail in its solitary attack strategy. If the hunting goshawk could attract family members, however, it would have some chance of obtaining the prey. The hunting behavior of the initiator and the goshawks that

subsequently join hunts, therefore, appear to be selfish. If individuals behaved selfishly during social hunts, then why did dominant Pale Chanting Goshawks not attempt to increase their hunting success by kleptoparasitizing subordinate family members and why was there no aggressive behavior observed between family members during a social hunt? Pale Chanting Goshawks do kleptoparasitize Booted Eagles (*Hieraaetus pennatus*) with rodent prey (unpubl. data) and at nesting sites, subordinate cobreeding Pale Chanting Goshawks do transfer prey to the dominant female and male breeder, but not vice versa (Malan and Jenkins 1996). Packer and Ruttan (1988) predicted that if single prey items are hunted, but not shared amongst participants, group members will always cooperate fully in hunts. Dominant Pale Chanting Goshawk breeders may not kleptoparasitize subordinate members because the initial benefit (suckers payoff, Axelrod and Hamilton 1981) of hunting prey not to be shared may result in defection by subordinates, with a subsequent decrease in the rate of social hunts. Likewise, if dominant breeders exert their dominance on subordinate members upon arrival at cornered prey, prey may escape and again no benefits can be gained by the goshawks participating. By displaying no obvious aggression towards each other during social hunts, not perceived to be a common trait among raptors (Faaborg and Bednarz 1990), each family member may increase its individual hunting success.

Given the increase in hunting success when combining social and solitary hunting, one would expect not only the hunting success per Pale Chanting Goshawk in bigger families to be greater, but also individuals from bigger families would be expected to spend more time hunting socially. Surprisingly few differences were found between the hunting strategies of large and small families (5.5 vs. 3.4 goshawks). Emlen (1994) suggested that the benefits of social activities such as social hunting may be secondarily derived after families formed because goshawks were constrained through a factor such as a lack of territorial space, from dispersing, and breeding in pairs. Even if the benefits of social hunting are secondarily derived, I suggest that hunting in families may hold fitness benefits for participants.

First, the participation by rapacious juveniles in social hunts may hold additional benefits associated with hunting relatively large prey that are not shared by family members (Stacey and Ligon

1987). Prior to independence, young raptors experience a high mortality rate (Newton 1995), partly because of their low foraging efficiency (Heinsohn 1991). If they are raised in a social family and delay dispersal from that family, the benefits of philopatry may include participation in social hunts (Heinsohn et al. 1988). Juveniles were involved in social hunts, albeit at a very low rate (0.03/hr). Furthermore, they were only able to catch lizards (estimated mass 10 g; Malan and Crowe 1996) in solitary hunts, but caught rodents in social hunts. The benefits of hunting relatively large rodent prey may increase their foraging efficiency and survival during the critical 12–16 mo of their life. If this was the case, it is difficult to explain why these juveniles engaged in social hunts significantly less often than adults did. The fact that juveniles only occupied a segment of the territory in close proximity to the nesting site (unpubl. data), may have made them less able to detect family members hunting in other segments of the territory.

Second, breeders may also gain fitness benefits from hunting with their offspring. The success from hunting socially, measured in terms of survival fitness, may be higher than if determined directly from the hunting success of individuals in the family (Packer and Ruttan 1988, Koenig and Mumme 1990). The act of allowing other family members to partake in social hunts may thus benefit the individual that cornered the prey indirectly, as the loss in direct fitness is compensated by a gain in indirect fitness. Individual Pale Chanting Goshawks that allowed other family members to partake in social hunts may be therefore behaving selfishly to increase their inclusive fitness.

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