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Cooperative Hunting and its Relationship to Foraging Success and Prey Size in an Avian Predator

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With 2 figures

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Abstract

Aplomado falcons (*Falco femoralis*) often hunt in pairs when chasing birds; 29 % of 349 hunts observed in eastern Mexico involved mated pairs of falcons simultaneously chasing the same prey animal; and 66 % of 100 hunts of birds were tandem pursuits. Although true cooperative hunting is uncommon in birds of prey, hunts by pairs of Aplomado falcons consistently showed signs of cooperative behavior such as use of a simple coordinative signal, and some division of labor between participating individuals. Pairs were more than twice as successful as solo falcons hunting birds (44 % vs. 19 %), however, there was no evidence that cooperative hunting increased the range of feasible prey sizes. The frequent use of cooperative foraging in this and similar species may relate to necessities of efficient nest defense, and food and nest procurement in savannas inhabited by a diversity of nest-site predators.

Introduction

Despite their reputation as solitary hunters, birds of prey often engage in various types of social foraging behavior. Most commonly, individuals hunt in flocks with little or no coordination among members. This occurs in the western red-legged falcon (*Falco vespertinus*; CRAMP & SIMMONS 1980), Swainson's hawk (*Buteo swainsoni*; BENT 1937), snail kite (*Rhostramus sociabilis*; BROWN & AMADON 1968), and tawny eagle (*Aquila rapax*; CRAMP & SIMMONS 1980), species which feed on invertebrates and small terrestrial vertebrates. Although, foraging efficiency of individuals within such groups may be improved despite their lack of organization (BERTRAM 1978), such flocks may form for reasons unrelated to foraging efficiency. For example, in colonial nesting species like the Eleonora's falcon (*Falco eleonorae*), and sooty falcon (*F. concolor*), foraging flocks form

because these falcons nest communally on small islands or outcrops where good updrafts ensure excellent soaring conditions, and over which (and to which) hordes of migrating passerines must fly (WALTER 1979a, b).

In cooperative foraging two or more individuals hunt together with some degree of coordination. True cooperative foraging, however, is difficult to distinguish from other types of social hunting since groups in which members simultaneously but fortuitously chase the same prey may appear superficially to be coordinated assemblages. If hunts are cooperative ventures then they should show some of the following characteristics: (1) individuals tend to hunt together instead of hunting alone; (2) group members usually select the same prey animals for pursuit; (3) some division of labor occurs during hunts; (4) some signal (or signals) is used to coordinate movements of participants; (5) defendable food is shared among participants; and (6) individuals monitor each other's movements during hunts. Although improved success is not a prerequisite for cooperative foraging (BERTRAM 1978), when cooperative hunting is invariably observed in a species we tend to assume that it is somehow reducing foraging costs (time or energy) by increasing the efficiency of captures.

Evidence for cooperative hunting has been observed in only a few falconiforms. It occurs regularly in the following genera: *Aquila, Haliaetus, Parabuteo, Hieraaetus,* and *Falco* (BROWN & AMADON 1968; CADE 1982). In many species, putative cooperative hunting occurs mainly in the breeding season and is used for capturing elusive prey such as birds (SHERROD et al. 1976; RATCLIFFE 1980; PRUETT-JONES et al. 1981; BIRD & AUBRY 1982; CADE 1982), and lagomorphs (COLLOPY 1983). In falcons, cooperative hunting is limited generally to species that subsist on birds. This behavior is typical of the brown falcon (*F. berigora*, MOONEY in CADE 1982), Luggar falcon (*F. jugger*, SALIM & RIPLEY 1968), Lanner falcon (*F. biarmicus*, MEBS 1959), rednecked falcon (*F. chicquera*, SALIM & RIPLEY

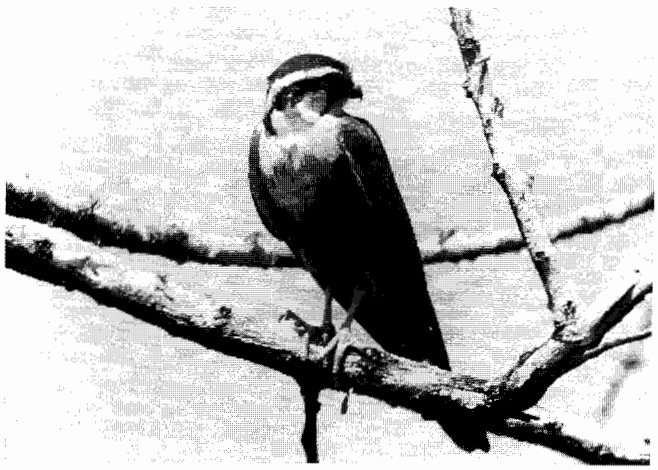

Fig. 1: Adult male Aplomado falcon (*Falco femoralis*). Unlike the more aerial bird-eating falcons such as the peregrine, Aplomado falcons have extremely long tarsi; a characteristic associated with the tendency of this species to pursue prey on foot through ground cover vegetation or tree crowns

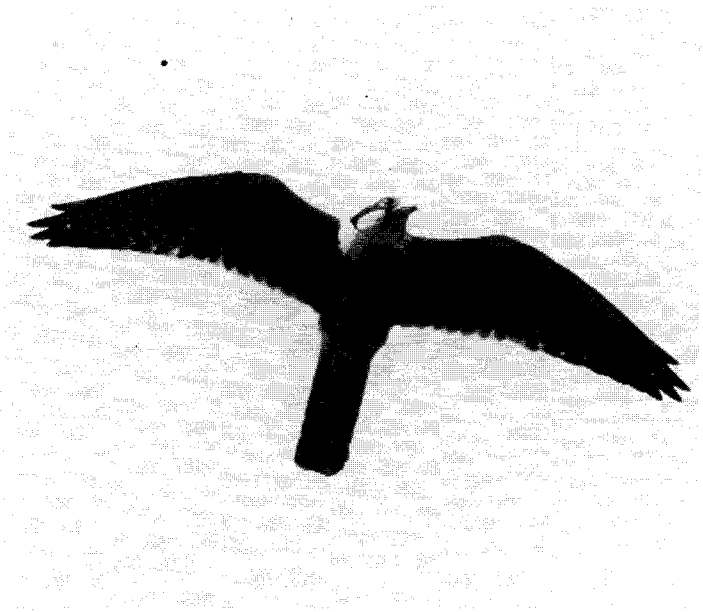

Fig. 2: Adult female Aplomado falcon in flight. The long, flexible tail probably enhances the ability of the species to maneuver quickly when chasing flying prey at high speed through lightly wooded terrain. (Photo by Hal Flanders)

1968), peregrine falcon (*F. peregrinus*, BIRD & AUBRY 1982; CADE 1982; THIOLLAY 1982), and Aplomado falcon (*F. femoralis*, CHERRIE 1916; LIGON 1961).

In 1977 I began a study of the Aplomado falcon (*Falco femoralis*; Fig. 1) in eastern Mexico. One of my objectives was to describe the feeding ecology of this species. Previously, CHERRIE (1916), WETMORE (1926), FRIEDMANN & SMITH (1955), and LIGON (1961) observed that mated pairs of Aplomado falcons often teamed up when capturing small birds and bats. MADER (1981) noticed this same tendency in Venezuelan Aplomado falcons. No data existed, however, that showed how often tandem hunting occurred or how it affected hunting success. Furthermore, the published descriptions contained insufficient detail for determining whether hunts typically were cooperative ventures or simply fortuitous joint pursuits. The purpose of this report, therefore, is to provide a more quantitative description of tandem pursuits by Aplomado falcons. In particular, I suggest that this is a form of cooperative hunting, and discuss its relationship to prey selection and foraging success. In addition, I offer an explanation for the existence of cooperative hunting in other savanna falcons.

Methods

The Aplomado falcon ranges from northern Mesoamerica through South America to Tierra del Fuego. Within this range the species inhabits savannas and desert grasslands (BROWN & AMADON 1968). *Falco femoralis* is intermediate in size between the merlin (*Falco columbarius*), and peregrine (*F. peregrinus*), weighing (in eastern Mexico) 208—305 g (6 males, $\bar{x} = 260$) to 310—500 g (females, $\bar{x} = 407$). Compared to other members of the genus *Falco*, the Aplomado falcon is proportioned

somewhat like an accipiter, since it has long legs, slightly rounded wing tips, and a long, flexible tail (CADE 1982; Figs. 1, 2). Although Aplomado falcons feed mainly on small birds such as doves, quail, grackles, cuckoos, and small fringillids (WETMORE 1965; HECTOR 1985); the species also captures bats (LIGON 1961), rodents (STRECKER 1930), lizards (BENDIRE 1887), frogs (HAVERSCHMIDT 1968), and numerous insects (BENDIRE 1887; BROOKS 1933; HECTOR 1985).

During March—June 1977—1979 I observed Aplomado falcons at nesting territories in northern and central Veracruz, northern Chiapas, western Campeche, and western Tabasco, Mexico between 17—23° N, and 91—99° Long. Here, Aplomado falcons inhabit cattle pastures containing scattered palms (*Sabal mexicana*), oaks (*Quercus oleoides*), acacias, (*Acacia farnesiana*), *Enterolobium cyclocarpum*, *Tabebuia rosea*, and *Crescentia cujete*. Tree densities at nest sites, estimated using the quarter method (COTTAM & CURTIS 1956), ranged from 18.9—25.0 trees/40 ha (HECTOR 1981).

I observed the falcons from exposed positions within 50—100 m of nest trees. Most observation periods lasted 6—7 h and began near sunrise or mid-day. Hunts were described in narrative style using cassette recorders or notepads. Each hunt was classified using the following descriptive variables: number of pursuers, pursuit effort (gliding, slow-flapping, rapid-flapping), hunting mode (direct horizontal pursuit, climbing attack, hovering flight, pursuit on foot), hunting outcome, sex of pursuer, captor sex, time of day, prey type (insect or bird), prey species, prey disposition (eaten, cached or fed to offspring), and pursuit distance.

In most cases outcomes of hunts were easily determined since hunts usually occurred within 1 km of nesting territories in relatively open terrain. Outcomes of only 8 hunts were not determined. It was more difficult, however, to determine prey type, especially for distant, unsuccessful flights. Consequently in 77 of 350 flights with known outcome I could not tell whether falcons were chasing an insect or a bird. Although most of these flights had characteristics of typical bird pursuits, I did not add them to any category. In my presentation of success rates, exclusion of flights for which prey type, number of pursuers or outcome is unknown makes the sample sizes for hunt categories seem incompatible. Careful inspection of Table 1, however, should clarify how each ratio was obtained.

Unidentified prey were assigned weights of known prey species of similar size. I estimated weights of identified prey using three sources: my own reference collection of eastern Mexican prey species, specimens of the Texas A & M Cooperative Wildlife Collections, and references such as COTTAM & TREFETHEN (1968), JOHNSON (1968), LEOPOLD (1972) and HOWELL (1972). A more detailed description of my prey identification methods as well a list of typical prey and their weights is presented in HECTOR (1985).

Prey weights were transformed to natural logarithms then analyzed parametrically using unpaired t tests. Table 2 presents antilogs of the logarithmic means (the "geometric means"), and of the logarithmic confidence limits of prey weights. The smaller categories of prey weights were also compared using the Mann-Whitney test. In no case did the parametric and non-parametric (Mann-Whitney) test disagree.

Results

Nearly all observations were made of nesting falcons. I observed hunting behavior at 18 sites; however, 90 % of observations came from only 6 sites. I saw 357 hunts in 323 h. Within this sample there were 184 captures; 146 during nestling or fledgling stages.

Solitary Hunting Behavior

Aplomado falcons usually perched in tree-tops until prey appeared. Sudden attacks were launched when prey came within 500—1,000 m. Falcons slowly glided after insect prey such as beetles, moths, cicadas, and locusts. Birds, however, were attacked in rapid, full-powered flight. Insects and birds were usually captured in mid-air; however, falcons quickly gave chase on foot when prey animals hid in vegetation of ground cover or tree crowns. Aplomado falcons were remarkably swift, agile, and persistent when pursuing on foot, often crashing into intervening vegetation while running down prey.

Table 1: Outcomes of observed hunting flights (captures/attempts) N actually equals 358, but 8 flights with undetermined outcomes have been excluded

Prey type	Number of pursuers			
	Unknown	One	Two	Totals
Unknown	—	0/43	3/34	3/77
Insects	—	142/170	1/2	143/172
Birds	1/1	7/34	30/66	38/101
Totals	1/1	149/247	34/102	184/350

Cooperative Hunting Behavior

Two falcons chased the same prey individual in 29 % (102/349) of observed hunts, and in 66 % (66/100) of bird hunts (Table 1). In the sample of tandem pursuits, 65 % (66/102) were bird hunts and only 2 % (2/102) were insect hunts. Prey type was not determined in 34 tandem hunts. It is likely that all of these attacks were directed at birds. Each was a lengthy, high-speed chase, and insect flights tended to be brief, and slow.

When searching for prey, falcons usually perched near one another, often in the same tree. Pairs of falcons tended to pursue airborne birds along horizontal, parallel paths. In contrast, when attacking perched birds, one falcon would approach first then hover above the prey until the second falcon arrived. Usually the males initiated such attacks. When a male dashed off after distant prey, the female, though at times caught looking in the opposite direction, would often immediately fly in the direction taken by the male. If the female delayed her departure, however, the male would repeatedly give a sharp "chip" or "cheep" sound. The female often attacked shortly after first issuance of this vocalization.

When attacking prey in trees, females tended to fly close to the ground then ascend abruptly into the inner branches. At that point, prey species such as mourning doves (*Zenaida macroura*), white-winged doves (*Z. asiatica*), and ground-doves (*Columbina* spp.), quickly took flight. The male falcons then dove and attempted mid-air captures. In ensuing chases, females left cover and followed the fleeing prey while males attacked with repeated dives and ascents.

Prey such as fringillids, cuculids, and icterids tended to remain in cover. Female falcons pursued these animals largely by running and hopping through the more congested parts of tree crowns. The male falcons, hovering overhead, attacked whenever the prey birds attempted to leave trees. At other times, both falcons initially entered cover. Pursuits of birds in trees often lasted several minutes and traveled from tree to tree — the prey bird attempting a short flight each time the male falcon moved to an unfavorable position or briefly perched nearby.

Pairs of Aplomado falcons hunted ground-oriented birds like the bobwhite (*Colinus virginianus*), groove-billed ani (*Crotophaga sulcirostris*), squirrel cuckoo (*Piaya cayana*), and eastern meadowlark (*Sturnella magna*) in similar fashion with males hovering overhead while females chased prey through ground vegetation.

During spring migration, falcons attacked migrating flocks of white-winged doves, and mourning doves. The falcons would ascend rapidly from lookout posts then fly directly at flocks still 3—4 km away and 50—200 m above the ground. In most cases, dove flocks did not alter course and scatter until falcons closed to within 50 m. Both falcons then pursued the same individual on a slanting or vertically descending path. Often these chases would level off near the ground with the female following immediately behind the dove, and the male flying overhead to begin a series of dives and ascents.

In chases where the prey attempted to hide in vegetation or outfly the falcons along a more-or-less horizontal course, male falcons would take the higher position, either hovering above hidden prey or repeatedly diving on birds in flight. Females tended to pursue directly behind the prey.

Table 2: Geometric means of weights (g) of prey categories.
Prey with undetermined sex of captor or number of pursuers have been omitted

Pursuit category	N	$\bar{x}$	95 % confidence intervals[a]	$p > t^b$
Birds and Insects				
Sex of captor				
Male prey	84	2.24	1.97—2.62	0.3
Female prey	84	2.59	2.03—3.30	
	168			
Number of pursuers				
Solitary pursuits	149	1.33	1.32—1.34	0.001
Tandem pursuits	31	55.60	48.15—64.18	
	180			
Birds only				
Sex of captor				
Male prey	14	34.98	23.67—51.70	0.002
Female prey	13	86.15	57.93—128.11	
	27			
Number of pursuers				
Solitary pursuits	7	55.52	25.26—122.02	0.2
Tandem pursuits	30	62.02	48.00—80.15	
	37			
Male prey only				
Solitary pursuits	6	41.12	17.16—98.53	0.5
Tandem pursuits	8	30.99	20.19—47.56	
	14			
Tandem hunts only				
Male prey	8	30.99	20.19—47.56	0.003
Female prey	12	81.49	54.85—121.05	
	20			

[a] Antilogs of logarithmic confidence limits;
[b] unpaired t-test comparison of means.

Adult falcons shared carcasses of birds when nestlings were not being fed. Insect prey were not shared. Usually females fed first then allowed males to feed. At other times both falcons simultaneously tore pieces of meat from carcasses held by the female. The female of one pair would even offer small bits of meat to her mate following successful hunts.

Success of Cooperative Hunts

Although tandem hunting falcons captured prey in 33 % (34/102) of attempts, solo hunting falcons captured prey in 60 % (149/247) of attempts (Table 1). This sample, however, includes both insects and birds, and insects are captured more easily than birds. When only bird hunts are considered, percentages of successful attacks change to 21 % (7/34) for solo hunts and 45 % (30/66) for tandem hunts ($\chi^2 = 5.95$, $df = 1$, $.01 < p < .025$). As mentioned in the Methods section, it is likely that all 77 flights with undetermined prey type were bird hunts. If so then capture percentages would change to 9 % (7/77) for solo bird hunts, and 33 % (33/100) for tandem bird hunts.

Correlates of Prey Size

Falcons captured larger prey in cooperative hunts than in solo hunts ($p < .001$; Table 2). This difference, however, is not significant when only avian prey ($p = .2$), or avian prey of males ($p = .5$) is considered (Table 2).

With insects included in the sample, there is no significant difference between prey weights for male and female falcons ($p = .3$; Table 2). The evidence strongly suggests, however, that females captured larger birds than males ($p = .002$). This was also true of prey captured in tandem pursuits ($p = .003$).

Discussion

To some degree, pursuits of birds by mated pairs of Aplomado falcons showed the six signs of cooperative hunting listed in the Introduction. Although male falcons did hunt solitarily, they tended to remain with females instead of foraging alone; two falcons chased the same prey animal when pursuing flocks; females and males tended to adopt distinct roles in hunts; a simple call seemed to promote joint pursuit of common prey; food was shared by adults; and there was some indication (in patterns of departure by hunting birds from perches, and in the timing of the hunting vocalization) that birds were monitoring each others' movements during hunts. My data show that tandem hunting improved foraging success (captures vs. attempts) of Aplomado falcons hunting birds. This of course is not a requisite characteristic of cooperative foraging nor of social foraging in general, but one we tend to expect when predators habitually "teamup".

The fact that tandem pursuits improve hunting success and show characteristics of cooperative foraging, however, does not suggest that cooperative foraging occurs in the Aplomado falcon. Although most falcons hunt solitarily when nesting (BALGOOYEN 1976; FOX 1977; OSBORNE 1981; CADE 1982; THIOLLAY 1982; HUSTLER 1983), availability of prey and vantage points near nests seems to promote tandem hunting in species which normally follow the typical falcon

pattern (BIRD & AUBRY 1982; TRELEAVEN 1980). Five types of observations, however, suggest that cooperative hunting in Aplomado falcons is not just a fortuitous response to prey availability, but an inherent tendency in this species.

First, mated pairs of this species appear to hunt together and share food year-round (LIGON 1961; HECTOR unpubl.). In this regard, my observation of a female feeding her mate is significant since until recently this kind of sociable, intrapair behavior had not been reported in any falconiform bird. OLWAGEN (1984) has recently observed captive female rednecked falcons (*F. chicquera*) doing the same thing. Perhaps not coincidentally, *Falco chicquera* also frequently hunts in pairs (SALIM & RIPLEY 1968).

Second, both sexes apparently vocalize ("chip") to instigate participation by their mates in hunting activities. This vocalization is nearly equivalent to the "eechip" call of the larger falcons (CADE 1982), since it is used in nest site displays, and feeding interactions. Aplomado falcons also give this call in the midst of cooperative nest defense and territorial encounters. In every context, the "chip" call attracts the attention of a second falcon to some activity requiring or benefitting from its participation.

Third, different pairs consistently showed the same division of labor in hunts.

Fourth, older nestlings and recently-fledged siblings showed signs of cooperative or at least food-sharing behavior. Older nestlings stood with wings closed and passively accepted food from the female. In other falcons, nestlings typically grab food from adults and compete aggressively for sole possession of it (TINBERGEN 1958; CADE 1982; SHERROD 1983). MADER (1975) reports that young Harris hawks (*Parabuteo unicinctus*), another social hunter, also feed with little aggression. Recently-fledged Aplomado falcons also hunt together.

And fifth, Aplomado falcons apparently hunt in pairs in most parts of the species' range (CHERRIE 1916; WETMORE 1926; FRIEDMANN & SMITH 1950, 1955; LIGON 1961; MADER 1981).

Captor Sex and Prey Size

Studies by STORER (1966), MUELLER & BERGER (1970), SNYDER & WILEY (1976), and NEWTON & MARQUISS (1982) show that females capture larger prey than males in many of the more sexually dimorphic birds of prey. For example, male sharp-shinned hawks (*Accipiter striatus*) and Coopers hawks (*A. cooperii*) average 58 % and 67 % of the weights of their respective females, yet capture birds only 62 % and 74 % as large as the prey of females (STORER 1966). By comparison, male Aplomado falcons weigh approximately 64 % of the weight of females but captured prey averaging 41 % as large as prey of the females.

If "reversed" sexual dimorphism is due to selective forces favoring reduced intraspecific (intrasexual) competition (SELANDER 1966; NEWTON 1979) or increased provisioning abilities of solitarily foraging adults (WHITE & CADE 1971; SNYDER & WILEY 1976; ANDERSSON & NORBERG 1981), then it is curious that sexual dimorphism in body size and prey size would still be pronounced in Aplomado falcons. Cooperative hunting would seemingly favor a uniform body size for males and females. This is because the smaller males may be exposed to

greater risk of injury, or simply have difficulty assisting in the capture of the typical prey of their larger partners. This situation would apply, however, only to predators which cooperatively subdue prey. Aplomado falcons only pursue prey cooperatively. In cooperative hunters which do not cooperatively subdue prey, sexual size dimorphism could be favored because it allows a hunting pair to be more versatile than a monomorphic pair in terms of feasible prey sizes and prey types, and circumstances under which prey can be captured. Furthermore, sexual dimorphism in prey size selection, and aerodynamic attributes may promote more efficient division of labor during hunts (ANDERSSON & NORBERG 1981; CADE 1982).

Cooperative Foraging in Other Falcons

The "cooperative-hunting falcons" (*F. femoralis, F. chicquera, F. berigora, F. jugger,* and *F. biarmicus*) are small to medium-sized (200—900 g) falcons that inhabit open to semi-open savanna, desert scrub, or desert grassland (BROWN & AMADON 1968; CADE 1982). They feed on a variety of quarry (insects, birds, reptiles, rodents) including many ground-oriented species. All are agile afoot and readily pursue prey through ground cover. All readily enter cover and flush prey for a partner waiting overhead. All depend to some degree on the stick platforms of other birds for nest sites. And all inhabit sub-tropical to tropical regions where larger raptors and corvids are abundant (MEBS 1959; SALIM & RIPLEY 1968; OSBORNE 1981; HECTOR 1985; MOONEY in CADE 1982).

Compared to other falcons, these species may derive special benefits from cooperative foraging. Most importantly, they inhabit terrain with numerous scattered hiding places — tree crowns, shrubs, or patches of denser ground cover. Falcons such as the peregrine capture nearly all prey in mid-air, and quickly give up on quarry which has hidden in vegetation (CADE 1982). The cooperative-hunting falcons, however, show features such as great agility afoot, breakage-resistant feathers, and long tails which equip them for withstanding collisions with brush, and moving rapidly on foot (CADE 1982). Cooperative hunting may be an additional adaptation for this type of terrain and quarry, since a coordinated attack by two pursuers provides an effective solution to the problem of blocking aerial escape routes for volant prey while simultaneously chasing them through patches of cover.

In addition, coordinated attacks by mated pairs might also improve efficiency of nest defense and nest usurption activities. Falcons do not build their own stick nests (BROWN & AMADON 1968; CADE 1982). Consequently, falcons which do not utilize ledges or cavities, must either find abandoned stick platforms, or forcibly take over recently constructed platforms. In either case, they must be able to defend their nests from larger birds of prey, and corvids. Falcons harassing brown jays (*Psilorhinus morio*), or caracaras (*Polyborus plancus*), for example, used the same attack strategies normally directed at avian prey. Falcons also gave the "chip" vocalization in the midst of agonistic encounters.

Cooperative behavior may improve the efficiency of nest defense and foraging in similar ways. Two falcons working together may more easily intimidate a larger intruder, limit escape routes of prey, or herd and drive predators from the vicinity of eggs and young. During cooperative hunts, the presence of

two falcons may provide greater protection to each individual against larger kleptoparasitic raptors. In addition, the higher success rates of cooperative hunts may reduce the time required to provision young and leave more time for nest defense.

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Literature Cited

ANDERSSON, M., & R. A. NORBERG, 1981: Evolution of reversed sexual size dimorphism and role partitioning among predatory birds. Biol. J. Linnean Soc. **15,** 105—130.

BALGOOYEN, T. G., 1976: Behavior and ecology of the American kestrel (*Falco sparverius* L.) in the Sierra Nevada of California. Univ. Calif. Publ. Zool. **103.**

BENDIRE, C. E., 1887: Life histories of North American birds. U. S. Natl. Mus. Special Bull. **1.**

BENT, A. C., 1937: Life Histories of North American Birds of prey. U. S. Natl. Mus. Bull. **170.**

BERTRAM, B. C. R., 1978: Living in groups: predators and prey. In: Behavioural Ecology, an Evolutionary Approach. (KREBS, J. R., & N. B. DAVIES, eds.) Blackwell Sci. Publ., Oxford, pp. 64—96.

BIRD, D. M., & Y. AUBRY, 1982: Reproductive and hunting behavior in peregrine falcons, *Falco peregrinus,* in Southern Quebec. Can. Field-Nat. **96,** sp. 167—171.

BROOKS, A., 1933: Some notes on the birds of Brownsville, Texas. Auk **50,** 59—63.

BROWN, L. H., & D. AMADON, 1968: Eagles, Hawks and Falcons of the World. McGraw-Hill, New York.

CADE, T. J., 1982: The Falcons of the World. Comstock/Cornell Univ. Press, Ithaca.

CHERRIE, G. K., 1916: A contribution to the ornithology of the Orinoco Region. Mus. Brooklyn Inst. Arts Sci., Sci. Bull. **2,** 133—374.

COLLOPY, M. W., 1983: Foraging behavior and success of golden eagles. Auk **100,** 747—749.

COTTAM, C., & J. B. TREFETHEN, 1968: Whitewings. Van Rostrand Co., Princeton.

COTTAM, G., & J. T. CURTIS, 1956: The use of distance measures in phytosociological sampling. Ecology **37,** 451—460.

CRAMP, S., & K. E. L. SIMMONS (eds.), 1980: Handbook of the Birds of Europe, the Middle East and North Africa. The Birds of the Western Palearctic. Vol. II. Hawks to Bustards. Oxford Univ. Press, Oxford.

FOX, N., 1977: The biology of the New Zealand falcon (*Falco novaeseelandiae* Gmelin 1788). Ph. D. Diss. Univ. Canterbury.

FRIEDMANN, H., & F. D. SMITH, 1950: A contribution to the ornithology of Northeastern Venezuela. Proc. U. S. Nat. Mus. **100,** 411—538.

— —, & — —, 1955: A further contribution to the ornithology of Northeastern Venezuela. Proc. U. S. Nat. Mus. **104,** 463—524.

HAVERSCHMIDT, F., 1968: Birds of Surinam. Oliver and Boyd, London.

HECTOR, D. P., 1981: The habitat, diet, and foraging behavior of the Aplomado falcon, *Falco femoralis* (Temminck). M. Sc. Thesis. Oklahoma Coop. Wildl. Res. Unit, Oklahoma State Univ., Stillwater.

— —, 1985: The diet of the Aplomado falcon (*Falco femoralis*) in Eastern Mexico. Condor **87,** 336—342.

HOWELL, T. R., 1972: Birds of the lowland pine savanna of Northeastern Nicaragua. Condor **74,** 316—340.

HUSTLER, K., 1983: Breeding biology of the greater kestrel. Ostrich **54,** 129—140.
JOHNSON, O. W., 1968: Some morphological features of avian kidneys. Auk **85,** 216—228.
LEOPOLD, A. S., 1972: Wildlife of Mexico: the Game Birds and Mammals. Univ. Calif. Press, Berkeley.
LIGON, J. S., 1961: New Mexico Birds and where to find them. Univ. New Mexico Press, Albuquerque.
MADER, W. J., 1975: Biology of the Harris' Hawk in southern Arizona. Living Bird **14,** 59—85.
— —, 1981: Notes on nesting raptors in the llanos of Venezuela. Condor **83,** 48—51.
MEBS, T., 1959: Beitrag zur Biologie des Feldeggsfalken (*Falco biarmicus feldeggi*). Vogelwelt **80,** 142—149.
MUELLER, H. C., & D. D. BERGER, 1970: Prey preferences in the sharp-shinned hawk. Auk **87,** 452—457.
NEWTON, I., 1979: Population Ecology of Raptors. T. & A. D. Poyser, Berkhamsted.
— —, & M. MARQUISS, 1982: Food, predation and breeding season in the sparrowhawk (*Accipiter nisus*). J. Zool. **197,** 221—240.
OLWAGEN, C. D., 1984: Breeding behavior of the rednecked falcon in captivity. Proc. 2nd. Symp. African Predatory Birds. (MENDELSOHN, J. M., & C. W. SAPSFORD, eds.) Natal Bird Club, Durban, pp. 23—30.
OSBORNE, T. O., 1981: Ecology of the red-necked falcon *Falco chicquera* in Zambia. Ibis **123,** 289—297.
PRUETT-JONES, S., C. M. WHITE, & W. R. DEVINE, 1981: Breeding of the peregrine falcon in Victoria, Australia. Emu **80,** 253—269.
RATCLIFFE, D., 1980: The Peregrine Falcon. T. & D. Poyser, Carlton.
SALIM, A., & S. D. RIPLEY, 1968: Handbook of the birds of India and Pakistan. Oxford Univ. Press, New York.
SELANDER, R. K., 1966: Sexual dimorphism and differential niche utilization in birds. Condor **68,** 113—151.
SHERROD, S. K., 1983: Behavior of Fledging Peregrines. Peregrine Fund, Inc. Ithaca.
— —, C. M. WHITE, & F. S. WILLIAMSON, 1976: Biology of the bald eagle on Amchitka Island, Alaska. Living Bird **15,** 143—182.
SNYDER, N. F. R., & J. W. WILEY, 1976: Sexual Size Dimorphism in Hawks and Owls of North America. A. O. U. Monogr. 20.
STORER, R. W., 1966: Sexual dimorphism and food habits in three North American accipiters. Auk **83,** 423—436.
STRECKER, J. K., 1930: Field notes on western Texas birds. Contr. Baylor Univ. Mus. 22, 1—14.
THIOLLAY, J.-M., 1982: Les ressources alimentaires, facteur limitant la reproduction d'une population insulaire de faucons peleris, *Falco peregrinus brookei.* Alauda **50,** 1—44.
TINBERGEN, N., 1958: Curious Naturalists. Country Life Books, London.
TRELEAVEN, R., 1980: High and low intensity hunting in raptors. Tierpsychol. **54,** 339—345.
WALTER, H., 1979a: Eleonora's Falcon; Adaptations to Prey and Habitat in a Social Raptor. Univ. Chicago Press, Chicago.
— —, 1979b: The sooty falcon (*Falco concolor*) in Oman: Results of a breeding survey, 1978. J. Oman Studies **5,** 9—59.
WETMORE, A., 1926: Observations on the birds of Argentina, Paraguay, Uruguay, and Chile. U. S. Nat. Mus. Bull. **133.**
— —, 1965: The birds of the Republic of Panama. Smithson. Misc. Coll. **150.**
WHITE, C. M., & T. J. CADE, 1971: Cliff-nesting raptors and ravens along the Colville River in Arctic Alaska. Living Bird **10,** 107—150.

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