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COOPERATIVE HUNTING OF JACKDAWS BY THE LANNER FALCON *(FALCO BIARMICUS)*

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ABSTRACT.—Cooperative hunting has been recorded for several subspecies of Lanner Falcon (*Falco biarmicus*). On average, the success rate for pairs is higher than for single birds. During 1988–90, I collected data on the success of five Lanner Falcon pairs that cooperatively hunted Jackdaws (*Corvus monedula*) in western Sicily. Fifty-three percent of attacks were aimed at larger groups of Jackdaws. Males made most of the initial attacks (74%) but prey captures were mainly made by females (87%). Pairs tended not to share prey and used visual contact to coordinate chases. Most attacks were by partial surprise (60.8%), followed by nonsurprise (21.6%), and surprise attacks (17.6%). Surprise attacks tended to involve small flocks of Jackdaws, whereas partial surprise tended to involve large flocks.

KEY WORDS: *Lanner Falcon*; Falco biarmicus; *cooperative hunting*; *Sicily*; *Jackdaw*; *prey group size.*

Caza cooperativa de *Corvus monedula* por *Falco biarmicus*

RESUMEN.—La caza cooperativa de *Falco biarmicus* ha sido registrada para varias subespecies a lo largo de su distribución. En promedio la tasa de éxito por pareja es mas alta que la individual. Durante 1988–90 recolecté datos sobre el éxito de la caza cooperativa de *Corvus monedula* de cinco parejas en el oeste de Sicilia. Cincuenta y tres porciento de los ataques fueron dirigidos a grandes grupos de *Corvus monedula.* Los machos efectuaron los ataques iniciales (74%) pero la captura de presas fue efectuada por las hembras (87%). Las parejas tendían a no compartir la presa y utilizaron contactos visuales para coordinar las persecusiones (60.8%), seguidas de ataques sin sorpresa (21.6%), y ataques sorpresivos (17.6%). Los ataques por sorpresa involucraron pequeñas parvadas de *Corvus monedula,* mientras que los parcialmente sorpresivos involucraron parvadas mas grandes.

[Traducción de César Márquez]

Cooperative hunting is a social foraging behavior where predators coordinate their movements to increase efficiency of capture (Ellis et al. 1993). Prey may be shared among members according to social organization, prey size and individual functional role (Bednarz 1988, Ellis et al. 1993). Pair hunting is cooperative when participants perform separate roles. In certain species and under certain circumstances, cooperative hunting is more successful than solitary foraging (Hector 1986, Thiollay 1988, Yosef 1991, Ellis et al. 1993).

Cooperative hunting in the genus *Falco* seems to be restricted to bird-eating species, such as Lanner Falcons (*Falco biarmicus*), Aplomado Falcons (*F. femoralis*), and Red-headed Falcons (*F. chicquera*), which inhabit semi-open savannas and desert and Mediterranean scrub (Mebs 1959, Osborne 1981, Hector 1986). Southern Mediterranean Peregrine Falcons (*F. peregrinus brookei*) hunt cooperatively in areas where prey density is low (Thiollay 1988).

Cooperative hunting in Lanner Falcons has been recorded for several subspecies throughout the species' geographic range (Cramp and Simmons 1980, Tarboton and Allan 1984, Leonardi et al. 1992). Lanner Falcon pairs pursue swift flying prey (e.g., swifts [*Apus* spp.]) along parallel paths (Mirabelli 1982, Bijlsma 1990). They hunt flocks of gregarious small birds (e.g., swallows [*Hirundo* spp.]) working together with repeated stoops upon the same individual (Mirabelli 1982). In contrast, for larger perched prey (e.g., shorebirds and pigeons [*Columba* sp.]), one falcon flushes the quarry while it is taken by the mate (Mebs 1959, Massa et al. 1991, Yosef 1988). Partners have distinct roles. Males usually attack and direct prey toward females (Yosef 1991) and females tend to pursue large prey (Brossett 1961, Tree 1963, Kemp 1993). Success

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rates when hunting in pairs (20–25%) are higher than that of single birds hunting alone (15–40%) (Bijlsma 1990, Yosef 1991, Kemp 1993).

This paper describes my observations of cooperative hunting in Lanner Falcons nesting in western Sicily. In this region, pairs frequently attack colonial nesting Jackdaws (*Corvus monedula*). This provided an opportunity to compare success rates among attacks on different sized flocks, as it related to sex of pursuers and attack strategies utilized.

STUDY AREA

I studied Lanner Falcons on the island of Sicily in the central Mediterranean. I observed five pairs during the breeding season: two breeding pairs near the northern periphery of the Sicilian distribution and three pairs in a southern area where the species was studied previously by Mascara (1986).

The climate of the northern study area is temperate-wet with 600–800 mm of rainfall and an average annual temperature of 12–14°C. The southern study area has a subarid climate (<600 mm of rainfall and temperature >16°C) (Instituto Geografico De Agostini 1987).

Land use in the study areas was predominately farming and pasture. Cereal farming and pasturelands covered by olive (*Olea europaea*) and prickly pear (*Opuntia ficus-indica*) cultivation dominated northern open spaces. The southern study area was largely in a wheat monoculture with interposing spots of xeric Mediterranean vegetation and small *Eucalyptus* plantations. Within both study areas, lanners nested on clay-sand and calcareous cliffs with heights of 50–1150 m (Massa et al. 1991).

METHODS

I visited breeding sites 21 times during two prereproductive periods (November–January 1988–90). Each breeding site was visited 10 times for 55 total H. I watched Lanner Falcons hunting in pairs from 200–600 m with 8 × 40 and 10 × 40 binoculars. Age and sex of observed falcons was recorded for each sighting according to criteria in Cramp and Simmons (1980) and Porter et al. (1981).

Attacks were defined as very rapid flights or stoops toward one or more clearly observed prey (an individual or group of specific prey species) (Cresswell 1994, 1996). First attacks were defined as the first, fast approach by falcons toward potential prey. During each attack, I recorded the following data: position and sex of each falcon at the start of the attack, size of the prey flock, and type of attack strategy. I placed attack strategies into three categories: surprise attacks, partial surprise attacks, and nonsurprise attacks. In surprise attacks, Lanner Falcons first approached close to Jackdaws from behind rock cliffs. In partial surprise attacks, one of the two attacking falcons was visible to prey while the other falcon attacked by surprise. In partial surprise attacks, two perched falcons would depart at different times (Yosef 1991, Kemp 1993). In nonsurprise attacks, both falcons were visible at the onset of attacks, then they tried to encircle Jackdaw flocks (Cresswell 1994, 1996). In nonsurprise attacks, one falcon stooped on prey after soaring while the other attempted to flush prey (Mebs 1959, Massa et al. 1991, Kemp 1993, Jenkins 1995).

I observed Lanner Falcons cooperatively hunting both Rock Pigeons (*Columba livia*) and Jackdaw flocks near their nests. Both prey species nest on cliffs 100–300 m from Lanner Falcon nests (Sodhi et al. 1990, Suhonen et al. 1994). For evaluating the importance of cooperative hunting, I only investigated hunts of Jackdaws. Preliminary observations indicated that single female Lanner Falcons initiated nearly all pursuits of pigeons. Also, <5% of the total attempts on pigeons ($N = 32$) were performed by males. Cooperative hunting, and necessarily, participation by males, was more common in hunts of Jackdaws. In addition, Jackdaws consistently comprised a large percentage of dietary biomass for lanners in Sicily (Massa et al. 1991, Leonardi et al. 1992, Leonardi 1994) Finally, Jackdaws responded to attacking falcons with intricate forms of mobbing behavior. This provided an opportunity to investigate interactions between cooperative hunting and antipredator defense behavior (Kenward 1978, Caraco et al. 1980, Turner and Pitcher 1986, Cresswell 1994).

The number of Jackdaws present was estimated daily by counting the maximum number of birds seen simultaneously. Jackdaw colonies typically contained 20–70 individuals. During an attack, I estimated the size of each flock attacked by assuming the members to be all birds within 25 m of each other (Cresswell 1994, 1996). At times entire colonies behaved as a single flock. Under these circumstances, I counted the number of individuals in the group first attacked (Kenward 1978). For statistical comparisons, I placed Jackdaw flocks into three size categories according to previous studies of predation on prey groups (Kenward 1978, Cresswell 1994, 1996): 2–10, 11–30 and 31–50 individuals. I assessed the validity of the above flock size classes for this study through preliminary observations of flocking reactions measured for single and paired Lanner Falcons (Leonardi 1991, Leonardi unpubl. data).

I compared *F*-frequencies of hunting strategies and success rates among different flock sizes and strategies using chi-squared tests and *G*-tests (Zar 1984). I used Cochran's corrected chi-square test for differences between males and females using a 2 × 2 contingency table (Zar 1984).

RESULTS

In 52 cooperative hunts, I detected no vocalizations which might have functioned to coordinate pursuits. Females alone ate 70% of prey captured in cooperative hunts (captures $N = 10$). In only 2 of 16 cases (12%), males fed on prey captured in cooperative hunts after the departure of females. Although Lanner Falcons preferred to attack larger flocks (Table 1; $\chi^2 = 12.33$, df = 2; $P < 0.001$), hunting success was inversely proportional to flock size ($G = 10.7$, df = 2; $P < 0.005$).

Female Lanner Falcons initiated attacks less often than did males (26% vs. 74%). Although males preferred to pursue larger prey (87% of 52 pur-

Table 1. Distribution of Lanner Falcon attacks on flocks of Jackdaw by cooperative hunting in Sicily.

	JACKDAW FLOCK SIZE CLASS		
	2–10	11–30	31–50
Attempts	10	14	27
Kills	2	5	9
Total	12	19	36
Captures (%)	20	35.7	33.3

suits) and larger flocks more often than did females (Table 2; $G = 13.9$; df = 2; $P < 0.001$), male hunting success rates tended to be lower than those of females (Table 2; $\chi^2 = 2.86$, df = 2; $P < 0.10$).

Lanners attacked Jackdaws by partial surprise (60.8%) much more frequently than they did by nonsurprise (21.6%) and surprise attacks (17.6%) ($N = 52$). Although degree of surprise is one of the most important factors in improving the success of raptor attacks, lanners used this technique in only nine of 52 attempts. Also, open attacks give time for antipredatory behavior by prey. Nevertheless, partial surprise was used significantly more often ($\chi^2 = 17.40$, df = 2; $P < 0.001$). In addition, lanner pairs captured more prey using nonsurprise attacks (Table 3; $\chi^2 = 11.90$, df = 2; $P < 0.01$).

Cooperative hunting techniques were not uniformly distributed among prey flock classes. Hunting success in relation to prey flock size was significant for partial surprise on larger groups (22%; Table 3; $P < 0.01$) and nonsurprise attacks on medium flocks (27%; $\chi^2 = 14.40$, df = 2; $P < 0.01$).

DISCUSSION

Evidence of coordinative signaling among hunting predators is indicative that hunts are cooperative (Hector 1986, Ellis et al. 1993). Male Aplomado Falcons initiate attacks and then vocalize a "chip" call (Keddy-Hector pers. comm.). Although I detected no vocalizations among hunting lanners, Thomsett (1987) reported that pairs of lanners hunting bats gave chupping calls. Mebs (1959), however, failed to mention any calls given by cooperative hunting lanners in Sicily. Participants in hunts, however, can coordinate pursuits without vocal signals. Massa et al. (1991) suggested that partners monitor their movements by visual contact. Predators should avoid vocalizations during surprise attacks, which would reveal their presence. In partial surprise attacks, flying Lanner Falcon males from outside the colony area would suddenly stoop on Jackdaws.

Table 2. Capture success (%) from first attacks of Lanner Falcons cooperatively hunting flocks of Jackdaws in Sicily.

	JACKDAW FLOCK SIZE CLASS			
	2–10	11–30	31–50	Total
Males				
First attack	2	12	24	38
Kills	0	1	1	2
Captures (%)	0	0.08	0.04	
Females				
First attack	8	2	3	13
Kills	2	5	7	14
Captures (%)	0.25	2.5	2.3	

Prey capture percentage of this study was lower (31%) than that observed for other lanner subspecies (50%; Yosef 1991, Kemp 1993) and Aplomado Falcons (45%; Hector 1986). Sicilian lanners pursued small- and medium-sized prey with solitary hunting strategies and used cooperative hunting for large-size prey like Jackdaws. Nevertheless, this low percentage may have been due to Jackdaw antipredator behavior. Large Jackdaw flocks frequently used mobbing (43%, $N = 58$) against lanners. This active defense, combined with the dilution effect of individuals in a flock, can improve predator avoidance by prey. The dilution effect is an advantage because individuals are less likely to be taken by predators when in a flock (Turner and Pitcher 1986). Morgan and Godin (1985) reported that the rate of predator attack per individual prey is inversely proportional to group size.

Although examples of role reversal are known (Mebs 1959, Mirabelli 1982, Massa et al. 1991), the

Table 3. Percent hunting successes (kills/attempts; total of 52 attempts, 16 kills) by Lanner Falcons hunting cooperatively on flocks of Jackdaws in Sicily.

	JACKDAW FLOCK SIZE CLASS		
ATTACK TYPE	2–10	11–30	31–50
Partial surprise	0	6	22
Surprise	11	11	0
Nonsurprise	9	27	9

male success rate of <1% was irrelevant in comparison to the 50% reported. This was probably because of the strong reversed sexual dimorphism (RSD) of this species and its tendency not to share prey. In other words, females physically dominated males during hunts and feedings. RSD may also account for divergences in hunting and prey choice. Males of *F. b. feldeggi* weigh 69% that of females and capture prey which average 45% the size of the female's prey (Leonardi et al. 1992). It is likely that RSD favors cooperative hunting, since it allows the hunting of a wide range of prey and also the use of different hunting strategies.

Data on flock size choice showed that lanners prefer to attack larger groups. In previous studies of flocking behavior and hunting, hunting success has been shown to be inversely proportional to flock size (Kenward 1978, Turner and Pitcher 1986, Cresswell 1994, Krause and Godin 1995). Krause and Godin (1995) suggested that flock conspicuousness, rather than flock size per se, influenced predator choice. Flock conspicuousness lends to repeated attacks in a single chase, thereby increasing success (Krause and Godin 1995). In Jackdaws, antipredator defense is based on the group's conspicuousness (which determines the encounter rate) and on the total number of individuals in the group (dilution effect; Turner and Pitcher 1986). In my study, the effect of group conspicuousness on rates of encounter with falcons may have been immaterial because Jackdaws lived so close to nesting lanners (Pitcher 1986, Krause and Godin 1995).

As in my study, partial surprise was the strategy most commonly used by cooperative hunting Lanner Falcons in South Africa (Kemp 1993, Jenkins 1995). Sicilian lanners frequently use this strategy (60.8%) in capturing Jackdaws only. In South Africa, nonsurprise attacks were aimed at small prey (Kemp 1993, Jenkins 1995). Previous Sicilian studies described nonsurprise attacks as frequent cooperative techniques used against larger prey (Mebs 1959, Massa et al. 1991). My data indicated a subordinate use of this strategy in comparison with the partial surprise attack. Inversely, lanners using nonsurprise attacks had good hunting success rates. This technique was probably used because it involved energetically inexpensive soaring and resulted in relatively high hunting success (Jenkins 1995).

The surprise attack was reported as the most important factor in Peregrine Falcon and Merlin (*Falco columbarius*) hunting success when pursuing small flocks of birds (Cresswell 1996). In this study, surprise attacks were less successful than were other strategies (17.6%) and were employed mostly for attacks of pigeons. In South Africa, surprise attacks from fast, low coursing flight were principally aimed at small birds and doves (*Streptopelia* spp.; Kemp 1993). In my study in Sicily, surprise attacks on Jackdaws caused intense confusion inside flocks. This confusion, and the dilution effect, produced an abatement effect; Lanner Falcons had difficulty attacking the group repeatedly, decreasing capture chances (Leonardi 1991, Turner and Pitcher 1986, Krause and Godin 1995).

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