

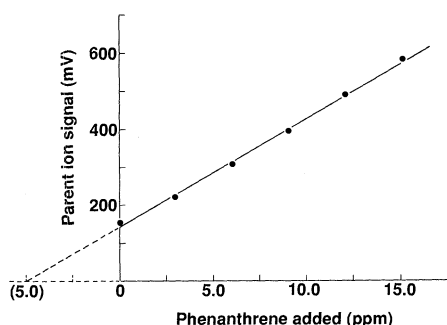


Fig. 4. The ion intensity for mass 178 of the Murchison #1 inside sample spiked with various amounts of a known phenanthrene solution ($30 \text{ ng } \mu\text{l}^{-1}$). Extrapolation to an ion intensity = 0 yields a phenanthrene concentration in the unspiked sample of $5 \text{ } \mu\text{g g}^{-1}$ or 5 ppm.

chondrite Clovis (Fig. 3f) shows no PAH components (17) and it should be just as susceptible to terrestrial contamination as the carbonaceous chondrites. Another possible explanation for the presence of more alkylated PAHs is that these C2 meteorites were heated more extensively than others sometime throughout their history, since the high extent of alkylation of PAHs has been attributed to the thermal cracking of the "organic polymer" (3, 18).

For quantitation we spiked the Murchison #1 inside sample with various amounts of phenanthrene. Figure 4 plots the phenanthrene parent ion peak heights versus the amount of phenanthrene added to the sample. The linearity is excellent. The calculated concentration of phenanthrene for the unspiked Murchison meteorite sample is 5.0 parts per million (ppm). Pering and Ponnampuruma (12) previously reported that Murchison contains 3 to 5 ppm of phenanthrene.

The relative abundances of different PAHs are not determined because of different ionization efficiencies. However, from the relative ion intensities in different spectra we found that the concentration of PAHs is in the order of Ivuna > Murchison $\approx$ Haripura $\approx$ Mighei $\approx$ Murray > Allende. This sequence is similar to the order of the carbon content of the various carbonaceous chondrites (11). We can assume that the desorption efficiencies are similar for the various carbonaceous chondrites and conclude that Ivuna contains roughly 15 to 20 ppm of phenanthrene/anthracene. The other C2 chondrites have abundances similar to Murchison. Allende has ≈ 0.5 ppm of phenanthrene/anthracene. This is close to the detection limit (with a signal-to-noise ratio of 2) of our system, which is calculated to be about 0.3 ppm, corresponding to 2 fmol per laser shot. Ordinary noncarbonaceous chondrites, like Clovis (and the Chinese meteorite Jilin, which we also analyzed), are devoid

of PAHs, at least at the sensitivity of our system.

One CO_2 laser shot desorbs PAHs from approximately $1 \text{ } \mu\text{g}$ of a sample and can produce a complete mass spectrum. Thus, we believe that the two-step laser methodology has particular promise as a tool in cosmogeochemistry because the technique is well suited to the analysis of samples available only in limited amounts.

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11. The meteorites analyzed were: Ivuna (C1, Tanzania, 1938, 3.9%); Murchison (C2, Australia, 1969, 2.1 to 2.5%); Murray (C2, United States, 1950, 2.8%); Haripura (C2, India, 1921, 4.0%); Mighei (C2, U.S.S.R., 1889, 2.5%); Allende (C3, Mexico, 1969, 0.3%); and Clovis (H3, United States, found 1960-61, 0.2%). The type of meteorite, the date of fall, and the percentage of carbon are given in parentheses and were taken from (1); E. A. King, Jr., E. Schonfeld, K. A. Richardson, J. S. Eldridge, *Science* **163**, 928 (1969); B. Mason, *Handbook of Elemental Abundances in Meteorites* (Gordon & Breach, New York, 1971); J. A. Wood and S. Chang, *The Cosmic History of the Biogenic Elements and Compounds, Special Paper 476* (National Aeronautics and Space Administration, Washington, DC, 1985). Three separate Murchison samples were investigated: an inside and outside portion of the original sample analyzed by K. A. Kvenvolden *et al.*, *Nature (London)* **228**, 923 (1970), and a second inside piece obtained from D. J. Macdougall who also kindly supplied the other meteorites with the exception of Allende which was provided by K. A. Kvenvolden.
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Cooperative Hunting in Harris' Hawks (*Parabuteo unicinctus*)

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Coordinated hunting by several individuals directed toward the capture and sharing of one large prey animal has been documented convincingly only for a few mammalian carnivores. In New Mexico, Harris' hawks formed hunting parties of two to six individuals in the nonbreeding season. This behavior improved capture success and the average energy available per individual and enabled hawks to dispatch prey larger than themselves. These patterns suggest that cooperation is important to understanding the evolution of complex social behavior in higher vertebrates and, specifically, that benefits derived from team hunting are a key factor in the social living of Harris' hawks.

COOPERATIVE HUNTING, WHEN individuals coordinate actions such that the probability of successful capture of one large prey item that is shared among all participants is increased, has been reported almost exclusively for social mammalian carnivores (1). All species that exhib-

it social hunting behavior also live in groups (2), but most investigators have argued that

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factors other than cooperative foraging, such as food dispersion (1) or kinship advantages (3) may be more critical to social living in the species studied to date.

In the class Aves cooperative hunting has been alleged for some bird-eating falcons (4, 5), Harris' hawks (*Parabuteo unicinctus*) (6), and golden eagles (*Aquila chrysaetos*) (7). All these cases involved mated pairs during the nesting season, and observations suggest that "tandem" hunting is rare and mostly not successful (4, 7). In the Aplomado falcon (*Falco femoralis*), tandem hunts were less frequent than solo hunts (29% of hunts observed), but social foraging may have resulted in a greater probability of capturing birds (5). Overall, however, hunts by pairs of Aplomado falcons were less successful (33%) than solo hunts (60%). Here, I describe and discuss the behavior and success of hunting "parties" of two to six Harris' hawks during the nonbreeding season.

My study site is the Los Medanos Raptor Area located 45 km east of Carlsbad, New Mexico (8). Radiotelemetry (9) observations were made from 16 September 1985 to 31 March 1986 and from 4 September 1986 to 11 December 1986 on 15 hawks from eight different social units (two to six individuals). Birds were observed from high vantage points, usually at distances of 400 to 800 m. All eight social units of Harris' hawks consisted of a male and female breeding adult, none to two adult-plumaged aux-

iliaries (1 to 2.5 years of age, reared on currently occupied range), and none to three immature-plumaged hawks reared during the last breeding effort (10).

Continuous observations (11) were maintained on sample birds for a total of 403 hours and 13 minutes. In most cases the entire social party of Harris' hawks could be monitored by following a single instrumented member because of the cohesiveness of the group. The focal individual was with other hawks during 71% of the observations ($n = 14,055$ spot samples). The average number of hawks recorded (within approximately 50 m of the sample individual) during quantitative sampling was 2.49 ($n = 14,055$). This is an underestimate of the actual number of closely associated hawks because some birds often perched out of view and were not recorded. Moreover, other hawks in the social party typically were in visual range (between 50 to 500 m) of the subunit of hawks being monitored.

During the study, 26 confirmed (carcass found) and 4 probable kills of lagomorphs were tallied. The probable captures occurred during continuous monitoring and involved behavior identical to that observed when kills were verified. These unconfirmed captures occurred in circumstances (for example, fog) that made it difficult to pinpoint the location of the carcass.

The mean number of hawks observed at 29 kill sites was 4.4, but some birds perched

low in vegetation were likely missed. Of the 30 kills observed, 22 took place during intensive radio-monitoring observations and eight were incidentally encountered. Identified carcasses included 17 desert cottontails (*Sylvilagus auduboni*) (65.4%) and 9 black-tailed jackrabbits (*Lepus californicus*) (34.6%).

Hunts often begin at morning twilight, with hawks departing from night roosts and perching conspicuously on relatively tall trees or power poles within their home range. As birds detect other family members they aggregate at one perch site. Once assembled, the hunting party splits into smaller subgroups (one to three hawks) that alternately make short flights (100 to 300 m) and land on relatively high perches. In this manner Harris' hawk subgroups "leap-frog" throughout the group's home range, occasionally rejoining and splitting again, while moving in one general direction (Fig. 1). This leapfrog movement is most intense when the hawks seem to be actively searching for prey, and once initiated it usually continues until prey are secured, prey are no longer active (midday), or, if an afternoon hunt, until dark.

Fig. 1. Sequence of movements of Harris' hawk 995 and associates that culminated in a successful capture of a desert cottontail. Only the subunit including the radio-instrumented hawk (995) was continuously monitored, although all five hawks were in visual proximity during the entire session. Perched hawks indicate the number of birds recorded in the subunit at that location. Subunit size remained unchanged from the previous location if no hawks are pictured.

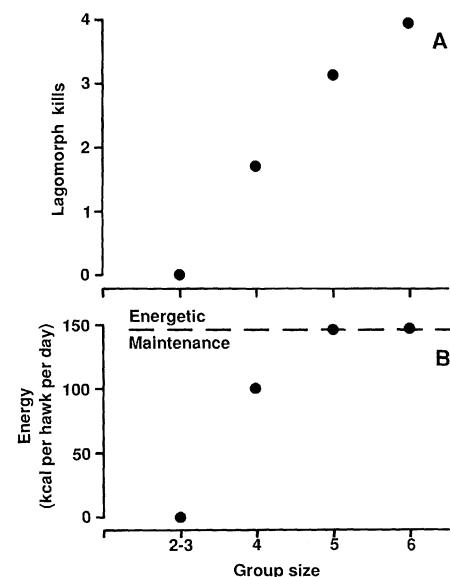
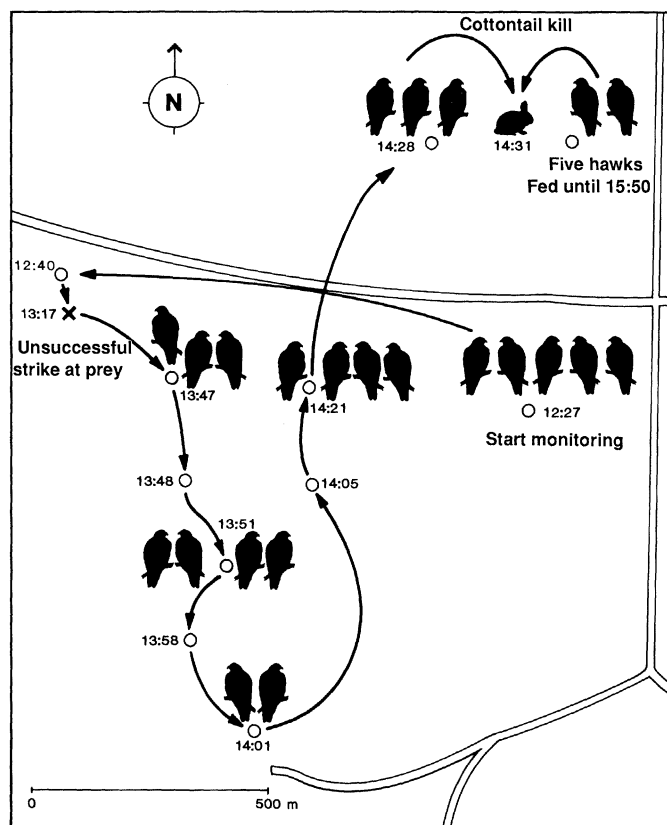


Fig. 2. (A) Capture rate of lagomorphs (lagomorph kills per 50 hours) by various sizes of Harris' hawk hunting parties. Groups of two to three hawks made no kills during 40.42 hours of observation ($n = 2$ groups); groups of four hawks made 1.7 kills per 50 hours, $n = 85.97$ hours ($n = 2$); groups of five hawks made 3.1 kills per 50 hours, $n = 160.23$ hours ($n = 6$); and groups of six hawks made 3.9 kills per 50 hours, $n = 116.60$ hours ($n = 4$). (B) Estimated average energy available to individual hawks in groups of different sizes based on above lagomorph harvest rates. An estimated 100.8 kcal/day were available for individuals in groups of four; 148.1 kcal/day for individuals in groups of five; and 148.6 kcal/day for individuals in groups of six. Estimated energy needed for maintenance (dashed line) was 147.8 kcal/day.

Captures were observed clearly 13 times. The most common tactic may be described as a surprise pounce (seven kills) involving several hawks coming from different directions, and converging on a rabbit away from cover (Fig. 1). Captures occurred quickly, but sometimes involved multiple, short rapid dives by different hawks for several minutes before the prey was dispatched. Surprise pounces included brief episodes of the other two hunting tactics described below.

When a rabbit found temporary refuge or cover, a flush-and-ambush strategy was employed. Here, the hawks surrounded and alertly watched the location where the quarry disappeared while one or possibly two hawks attempted to penetrate the cover. When the rabbit flushed, one or more of the perched birds pounced and made the kill. This tactic yielded cottontails during four of the observed successful hunts. This method is probably used more commonly, but is difficult to see because vegetation obstructed views of hawk activity near the ground.

The final hunting tactic used, "relay attack," was the least common (2 of 13). This technique involved a nearly constant chase of a rabbit for several minutes while the "lead" was alternated among party members. A switch occurred when the lead hawk stooped at the prey and missed, at which point the chase was continued by another member of the party. I recorded one relay chase that continued for at least 800 m and involved more than 20 stoops and hence switches in the lead.

Harris' hawks use a continuum of hunting styles. The tactics described here represent identifiable steps in a spectrum of cooperative hunting behaviors. The techniques were often intermixed and intensity varied in an unpredictable sequence, apparently dependent on the changing circumstances that occurred during pursuit of prey. Certainly the surprise pounce approach often involved brief episodes of flush-and-ambush tactics and relay attacks.

All the hawks observed flying from prey remains had bulging crops, indicating the prey had been shared among members of the hunting party. From a blind, I twice observed all six hawks of one group kill, share, and completely consume a picketed rabbit. In both cases, all individuals of the party fed freely on the carcass until obviously satiated. Likewise, an average of 3.2 hawks fed on five tethered pigeons.

Besides lagomorphs, smaller prey species were taken during cooperative hunting episodes, but observation distances (400 to 800 m) precluded determinations of success. During monitoring of instrumented hawks, I have never seen a solitary bird exhibit hunting-like behavior. I have ob-

served a noninstrumented lone adult Harris' hawk capture a scaled quail (*Callipepla squamata*), indicating that single individuals can hunt successfully. Radiotelemetry observations suggest, however, that solo hunting is rare for members of an established family group.

Is cooperative hunting important? Using estimates of hawk mass, average daily temperature, and proportion of the day hawks are in flight, I calculated the energy maintenance budget for an individual to be 147.8 kcal/day (12). The average energy provided by the cooperatively taken lagomorphs (0.63 kills per day) (13) is 630 kcal/day (14), which accounts for 88.8% of the combined maintenance needs of the average-sized hunting party (4.8 hawks, 709.4 kcal/day). Therefore, the lagomorphs obtained by cooperative efforts must be crucial to the daily energetic budget and fitness of individual Harris' hawks in New Mexico.

Moreover, successful capture of the lagomorph prey is correlated (Kendall's coefficient = 1.0, $P = 0.05$) with group size (Fig. 2A), indicating a performance advantage for larger groups (parties of five to six hawks). Individual benefits, in terms of average energy intake available, from the lagomorph harvest seem to stabilize at a hunting party size of five (Fig. 2B). This corresponds with the most common group size observed during the nonbreeding season (mean = 4.8 hawks, mode = 5). These patterns suggest that the social nature of this species may be related to the adaptive advantages of cooperative hunting.

The probable advantages of team hunting include the use of distraction tactics and the ability to harass the intended prey to exhaustion, increasing its vulnerability. In addition, by confusing and exhausting prey, any defensive capabilities could not be effectively directed at one attacker. This potential advantage of cooperative hunting may be especially important in taking jackrabbits, which are several times larger (2114 g) (14) than individual hawks (male hawks, mean = 678.9 g, $n = 36$; female hawks, mean = 959.4 g, $n = 38$). A final factor favoring group foraging may be the ability to guard and thus completely use all edible portions of the prey (15).

Some argue that in the evolution of social carnivores food dispersion (1) or kin selection (3) may be crucial to the development or maintenance of social groups, simply because group size tends to exceed expectations based on the calculated benefits of cooperative hunting (16). Others (10, 17) have reported results that failed to support several hypotheses proposed to explain group living in Harris' hawks. The data presented here indicate that social unit size

of Harris' hawks in the nonbreeding season approximates the optimum for individuals. I suggest that the benefits of the spectacular and coordinated team hunts implemented by Harris' hawks in southeastern New Mexico are a key factor in the development and maintenance of their societal structure.

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13. All calculations based on 11.5-hour photoperiod.
14. Daily lagomorph harvest = average energy per lagomorph prey (1004.5 kcal) $\times$ mean capture success per day (0.627312); average energy per lagomorph = mean lagomorph mass (1161.7 g) $\times$ portion of edible mass (0.706) $\times$ wet matter energy in kilocalories per gram (1.2247) [see M. V. Stalmaster and J. A. Gessaman, *J. Wildl. Manage.* **46**, 646 (1982)]; and mean lagomorph mass = [cottontail mass (657.9 g; J. C. Bednarz unpublished data) $\times$ occurrence (0.654)] + [jackrabbit mass (2114 g; K. Steenhof, *Raptor Res.* **17**, 15 (1983) $\times$ occurrence (0.346)].
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