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Authors: Coulson, Jennifer O., and Coulson, Thomas D.

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Commentary

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REEXAMINING COOPERATIVE HUNTING IN HARRIS'S HAWK (*PARABUTEO UNICINCTUS*): LARGE PREY OR CHALLENGING HABITATS?

Jennifer O. Coulson[1,3] and Thomas D. Coulson[2]

[1]*Department of Ecology and Evolutionary Biology, Tulane University, 6823 St. Charles Avenue, New Orleans, Louisiana 70118, USA; and*
[2]*64340 Fogg Lane, Pearl River, Louisiana, 70452, USA*

In group-living carnivores, cooperative hunting may be a cause or a consequence of cooperative breeding. Harris's Hawk (*Parabuteo unicinctus*), a raptor that hunts and nests in cooperative groups of 3 to 7 hawks (Mader 1975a, b; Bednarz 1987; Dawson and Mannan 1989), provides an opportunity to examine benefits and possible causes of sociality because its cooperation is facultative and the species is relatively well studied. Attempts to demonstrate factors that promoted the evolution of cooperative breeding in Harris's Hawks have mostly been unsuccessful. For example, the reproductive performance of groups did not differ from that of pairs (Mader 1975b, Bednarz 1987). And, for the most part, researchers did not find differences in the habitat quality or the resources available in territories occupied by groups versus pairs (Bednarz and Ligon 1988, Dawson and Mannan 1991b). However, Bednarz (1988) demonstrated net energetic benefits for hunting parties of 5 or 6 hawks and proposed that cooperative hunting led to social living in Harris's Hawk. Here, we support and extend this argument with a reinterpretation of data from the published literature, including an overlooked finding of significance. We hypothesize that one benefit of cooperative hunting is to increase success in habitats that make the prey difficult to catch (e.g., a high density of hiding places). We think that this benefit could be as important as capturing and overwhelming large prey, a benefit proposed by Bednarz (1988). We propose the "challenging habitats hypothesis" (CHH), similar to an idea proposed by Dawson (1988), as an additional or alternative explanation for the maintenance and, possibly, the evolution of cooperative hunting in Harris's Hawk. As falconers, we developed this hypothesis after many years of hunting with single and cooperative groups of 2 to 8 Harris's Hawks in a variety of habitats. We hope to rekindle scientific inquiry into cooperation in this species.

In cooperatively breeding birds, helpers are usually offspring that delay natal dispersal. Factors proposed to explain delayed dispersal include a lack of suitable breeding territories and other ecological constraints such as a lack of available mates (Selander 1964, Emlen 1982); increased probability of survival and of inheriting the natal territory (Stacey and Ligon 1987, 1991); and high-survival, *K*-selected life-history traits, and low turnover of territories (Brown 1974, Ricklefs 1974, Arnold and Owens 1998). Kin selection may maintain helping in relatives, whereas helping in non-kin is maintained by reciprocity, intraspecific mutualism, or manipulation (Trivers 1971; Clutton-Brock 2002, 2009). These hypotheses are not mutually exclusive, and some or all probably help explain cooperative breeding in many cases (Hatchwell and Komdeur 2000, Pen and Weissing 2000).

The Facultative Nature of Cooperation in Harris's Hawks

Harris's Hawk is a raptor native to the Americas, including the southwestern United States, that facultatively breeds and hunts in social groups (Dwyer and Bednarz 2011). It is found primarily in semiarid to arid scrubland and takes a variety of prey, including cottontails (*Sylvilagus* spp.), jackrabbits (*Lepus* spp.), rodents, (e.g., *Neotoma* spp., *Spermophilus* spp., and *Ammospermophilus* spp.), quail (*Callipepla* spp. and *Colinus virginianus*), and lizards. When and where it is cooperative, this hawk's social structure includes a cooperative breeding system with monogamy, polyandry and polygyny, helpers, delayed dispersal of young, a dominance hierarchy, and cooperative hunting (Mader 1975b, 1979; Bednarz 1987, 1988; Dawson and Mannan 1991a, b).

The degree of sociality exhibited varies both within and across the U.S. breeding range (Bednarz 1987, Coulson and Coulson 1995). The frequency of cooperative breeding is highest in Arizona, followed closely by New Mexico, whereas in Texas most nests are attended by pairs. Groups attended 53% of 341 Arizona nests (range: 46–84%; Mader 1975b, Whaley 1986, Dawson and Mannan 1991a), 51% of 61 New Mexico nests, and 8.6% of 35 Texas nests (range: 5–12.5%; Griffin 1976, Brannon 1980, Bednarz 1987). Patterns for social unit size show similar trends; mean social unit

[3]Present address: 64340 Fogg Lane, Pearl River, Louisiana 70452, USA. E-mail: jacoulson@aol.com

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sizes were 3.8 hawks in Arizona (Dawson and Mannan 1989), 2.7 hawks in New Mexico (Bednarz 1987), and 2.05 hawks in Texas (Griffin 1976).

The occurrence and seasonality of cooperative hunting varies within and among U.S. subpopulations (Bednarz 1987, Coulson and Coulson 1995, Dawson 1998). In Arizona, groups are largest and hunt together year round, whereas in New Mexico, groups are intermediate in size and hunt cooperatively mostly during the non-breeding season. Groups are rare in Texas, and although studies at nests did not detect group hunting (Griffin 1976, Brannon 1980), it sometimes occurs (Coulson and Coulson 1995). Neither cooperative hunting nor cooperative breeding has been documented in Central or South America (Dwyer and Bednarz 2011), but see Santander et al. (2011). We find this variation difficult to explain and suggest that ecological factors that affect foraging efficiency are responsible for the flexible occurrence of cooperative hunting.

Proposed Explanations for Cooperation in Harris's Hawks

Group living in Harris's Hawks could be explained by the benefits of either cooperative breeding or cooperative hunting. Studies designed to examine the benefits of cooperative breeding in Harris's Hawk have been mostly unsuccessful, and predictions from the ecological constraints hypothesis were not supported (Bednarz and Ligon 1988). Although offspring probably benefit from delaying dispersal and helping, these benefits have not been documented. Bednarz and Ligon (1988) compared a large number of variables between groups and pairs in hopes of discovering the ecological bases of cooperative breeding. Variables included breeding-unit sizes, 21 habitat characteristics, 889 prey remains, and three indices of prey abundance. The univariate analysis of habitat characteristics succeeded in distinguishing between breeding versus non-breeding habitat but not between the ranges used by groups and pairs. The results did not support the hypothesis that saturation of suitable breeding habitat favored cooperative breeding and, in fact, 12–15% of breeding ranges (n = 28–34) were vacant each year.

Bednarz (1988) proposed cooperative hunting as a force that drives group living in Harris's Hawks on the basis of observations of radiotagged hawks hunting in winter. Hunting success increased with group size, and group size was positively correlated with the rabbit and hare capture rate. Larger groups (5–6 hawks) met daily per capita energy requirements, but smaller groups (2–4 hawks) did not. The most common observed group size (mean = 4.8 hawks, mode = 5 hawks) during winter corresponded with what was expected to meet daily per capita energy requirements. When the observed group size matches the expected, this has been considered support for cooperative hunting as a cause of sociality (Caraco and Wolf 1975).

Cooperative hunting probably provides multiple benefits to Harris's Hawks. Four non–mutually exclusive hypotheses have previously been proposed to explain these benefits. (1) The large prey hypothesis (LPH) posits that cooperative hunting allows groups to successfully and safely overpower large prey—the prey type mainly available in winter (Bednarz 1988, Bednarz and Ligon 1988). (2) The limited-hunting-time hypothesis proposes that groups are more successful than pairs at capturing crepuscular prey species (cottontails and woodrats), because there is a limited window of time when the activity patterns of predators and prey overlap (Bednarz and Ligon 1988, Faaborg and Bednarz 1990). (3) The carcass-guarding hypothesis posits that groups are better at guarding the carcasses of prey species too large for a hawk to carry (Bednarz 1988, Dwyer and Bednarz 2011). The group defends the carcass from pirating attempts by other raptors and scavengers until it is completely consumed. (4) The increased-survival-of-offspring hypothesis proposes that group hunting increases the survival of offspring that delay dispersal (Bednarz and Ligon 1988, Dawson and Mannan 1991a, Stacey and Ligon 1991). Young hawks and their parents might experience enhanced survival prospects and increase fitness, respectively, during the transition from dependency to self-sufficient hunting because the group shares kills while the young master their hunting skills. Indeed, these benefits might extend throughout the delayed-dispersal period (Stacey and Ligon 1991), which ranges from postfledging to 3 years (Dawson and Mannan 1991a). This idea is attractive because it is consistent with the benefits-of-philopatry hypothesis (Stacey and Ligon 1991, Ligon 1999).

We offer the CHH as another possible explanation for the enhanced hunting success of groups. We propose that groups are more successful than singles and pairs when the habitat presents difficult hunting conditions that help hide or shelter the prey. Evidence exists to support both the CHH and the LPH. We will build our case for the CHH and then discuss the LPH and what additional evidence might support one hypothesis or the other. In Bednarz and Ligon's (1988) breeding-habitat study, one index of prey abundance differed significantly across years and seasons between groups and pairs: the density of woodrat middens was significantly higher in the territories of groups (1.5–2.7 times greater, depending on the sampling period). The authors suggested that this finding was unimportant because woodrats comprised a minor fraction of the diet (3% of the biomass) during the breeding season. They considered this variable as an index of prey abundance and did not entertain other possibilities.

We argue that the density of woodrat middens is directly related to the difficulty of capture for many types of prey and helps explain the occurrence of cooperative hunting in southeastern New Mexico. The midden and associated burrow provide the woodrat protection from avian predators (Reichman and Smith 1990). Other vertebrates also use woodrat middens for shelter, including other rodents, cottontails, and diurnal lizards (Macêdo and Mares 1988), all prey of Harris's Hawk. We have frequently observed cottontails, rodents, quail, and lizards taking refuge in woodrat middens when pursued by captive Harris's Hawks.

There are many advantages to cooperative hunting in challenging habitats. The prey detection rate is probably higher (Dawson 1998). Hawks attacking from multiple directions (Bednarz 1988) have a better chance of overtaking the prey before it reaches the safety of a woodrat midden. When the group executes multiple, successive stoops (Bednarz 1988), the prey often cannot evade the hawks without abandoning its primary escape route. Once diverted, the group's persistence may force it to make a mistake. Alternatively, prey may become fatigued as the chase is prolonged (Bednarz 1988). Even if the prey animal reaches the midden, the pursuit may not be over. Occasionally, a hawk may succeed in flushing prey (Bednarz 1988) from the midden, and others guarding the exits may resume pursuit.

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Dawson (1988) predicted but did not test the idea that breeding-group sizes would be positively related to the complexity of the understory structure in the Sonoran Desert. He found that hawks hunting in groups were more successful than singles, and he speculated that a complex understory favored cooperative hunting in Arizona. However, Bednarz and Ligon (1988) tested multiple variables related to vegetative density and structure in New Mexico and found no difference in the ranges occupied by groups versus pairs. Potentially, results of their study might be interpreted as cause for rejection of the CHH.

The CHH is based on the assumption that Harris's Hawks are risk sensitive (i.e., that their foraging preferences respond to the mean and variance of food reward; Caraco et al. 1980) and that habitats vary in quality, presenting a continuum of easy (low variance) to challenging (high variance) hunting conditions. As the degree of challenge increases, the habitat quality declines in several aspects (e.g., prey detection and capture become more difficult). This is offset for groups by the increased feeding rate and the reduced variation in feeding rate that arise from cooperative hunting tactics and food sharing (Bednarz 1988). As the challenging nature of the habitat increases, more hunting partners may be required to be successful. We suggest that only larger groups will meet per capita energy demands in the most challenging habitats. When breeding habitat is not saturated, a pair should occupy an easy territory if one is available. If only challenging territories are available, group breeding may be a better strategy than attempting to breed independently.

A potentially confounding aspect of the CHH is the likelihood that challenging habitats harbor more prey because of the increase in habitat complexity and/or hiding places. The woodrat midden data (Bednarz and Ligon 1988) may indicate that groups held ranges with greater prey abundance. Perhaps groups form to take advantage of somewhat higher prey densities in complex habitats.

Habitat has influenced the occurrence of cooperative hunting in several mammalian predators. Cooperative hunting in one population of Common Chimpanzees (*Pan troglodytes*) but not in another occurred because of differences in foraging efficiency of groups versus individuals in their respective habitats (Boesch 1994). This efficiency was explained by forest height and corresponding differences in prey responses to predators. The more difficult the hunting conditions became, the more likely chimpanzees were to cooperate (Boesch and Boesch-Achermann 2000). The frequency of cooperative hunting varies among Lion (*Panthera leo*) populations and, in one study, was related to habitat, food dispersion, and seasonal climate (Stander 1992). In the wet season, when prey was abundant, groups and single lionesses easily met daily energy needs. Cooperative hunting became important to survival during the 8-month-long dry season, when prey was sparsely and widely distributed in small groups across open, flat terrain. Hunting success was best predicted by a model that incorporated hunting strategy (cooperative or not), group size, prey species, timing (day–night), habitat types, and an interaction of timing and habitat (Stander and Albon 1993). In an analysis using data from many populations, cooperative hunting in male Lions was more prevalent in open plains than in closed, wooded areas (Funston et al. 1998). Habitat, rather than African Buffalo (*Syncerus caffer*) or Spotted Hyena (*Crocuta crocuta*) density, or hyena:lion ratios, explained the frequency of cooperation. Habitat was directly related to foraging success: males had a lower capture rate in plains than in woods, unless they cooperated.

Implicit in the LPH is the idea that Harris's Hawks avoid hunting grown cottontails and jackrabbits, unless they are in a group, because of the risks involved (see Bednarz 1988, Bednarz and Ligon 1988). We concur that both are large from the perspective of feeding a group. However, we argue that there is a difference between the two in terms of the risk involved. A jackrabbit's mass is more than 3× that of a cottontail (Bednarz 1988). A single male Harris's Hawk (body mass about one-third smaller than the female) flown in falconry can easily hold and subdue a cottontail. However, although many females and some males can overpower jackrabbits by themselves, extra hawks are helpful and sometimes absolutely needed to take down large prey. Considering causes of death for 258 falconry Harris's Hawks, 3.9% were killed by their prey, including 5 deaths by jackrabbits (Coulson and Coulson 2012). No deaths were caused by cottontails. We believe that groups are unnecessary for overpowering adult cottontails, but that groups would be more successful in capturing cottontails when the habitat presents additional demands. If adult jackrabbits are important prey during the non-breeding season, these mortality data support the LPH. In winter, lagomorphs (n = 26 identified to species) met 88.8% of the combined daily maintenance needs of the average group (4.8 hawks), and jackrabbits comprised a substantial portion (55.9%; Bednarz 1988).

The LPH and CHH yield different predictions about the occurrence of cooperative hunting geographically and seasonally. Under the LPH, cooperative hunting should occur mostly in regions in which relatively large prey must be taken for hawks to survive throughout the year. The CHH predicts that cooperative hunting should be rare in structurally simple habitats but fairly common in structurally complex habitats that provide abundant shelter for prey animals. The seasonal occurrence of group hunting in New Mexico could be consistent with the CHH if, during the breeding season, the abundance of young, naive mammalian and avian prey and lizards compensates for the challenging aspects of the habitat.

Recommendations for Testing Cooperation Hypotheses

Investigations into the relationships between hunting success and group size should incorporate both benefits (b) and costs (c; Creel 1997, 2001; Packer and Caro 1997). The best currency to use is the net rate of food intake ($b - c$) modeled in units of energy (kJ). Bednarz (1988) estimated average energetic maintenance costs based on the combined winter activity budget of all hawks in his study. An alternative, and possibly better, approach would be to estimate energy costs on the basis of the activity budget of individuals within different group sizes.

One test of the CHH and LPH would be to examine the latitudinal and longitudinal frequency of cooperative hunting. Is its frequency positively correlated with challenging habitats, a dependence on relatively large prey species, or other ecological factors? More study is needed, particularly in Mexico, Central America, and South America. The introduction of lagomorphs (*Oryctolagus cuniculus* and *Lepus europaeus*) to South America might provide an opportunity to test the LPH, via their presence and removal,

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because these large species have sometimes been important prey (Figueroa R. and González-Acuña 2006, Santander et al. 2011).

Several approaches could be used to test predictions of the CHH. We present ones that reduce the influence of confounding variables that might affect hunting success (e.g., prey density and individual attributes such as athleticism and experience). In a pre–post habitat treatment, wild groups of various sizes could be monitored to compare net hunting benefits in either easy or challenging habitats. These habitats could then be experimentally manipulated to convert them to more challenging or easier habitats by adding brush piles and/or removing high perches (more challenging), or adding high perches and/or removing brush or shrubs (less challenging), and/or blocking holes used for prey escape. The treatment must be sufficient to produce a measurable response, but not so drastic that the hawks and prey immediately abandon the range. The logistics of such a large-scale project with adequate replication would be difficult. Another approach would be to train hawks using modified falconry techniques and monitor net hunting benefits for different hunting-unit sizes in easy and challenging habitats with similar prey densities. The amount of meat consumed and energy expended during hunts would be easier to measure in trained subjects (Blem 2007). Tests of the CHH should consider all common prey species. Identifying prey species and numbers would be easier because trained hawks could be fitted with cameras, and pellets would be easier to retrieve.

Variables that identify challenging habitats must be selected carefully. For example, in the Bednarz and Ligon (1988) study, woodrat middens were not considered a habitat variable. In falconry, habitat conditions that necessitate cooperative hunting include those with high densities of any thorny, woody vegetation ≥1.2 m in height, large prickly pear (*Opuntia* spp.) or cholla (*Cylindropuntia* spp.) cacti, woodrat middens, holes and woody vegetation, and woody shrubs ≥1.5 m in height (e.g., Creosote Bush [*Larrea tridentata*]) with few dominant perches.

The LPH could be further tested by comparing the diet of individuals, pairs, and groups during the breeding season versus winter and along latitudinal and longitudinal gradients. Avoiding sampling biases could be challenging (Marti et al. 2007). Prey deliveries to nests would not necessarily reflect what the hunters are eating. Using direct observation, Bednarz (1988) was not always able to identify smaller prey items. Net energetic benefits for different hunting-unit sizes, including singles, could also be compared in winter, and species-specific prey-inflicted injury rates should be measured. Approaches for the latter might include the use of wild or trained hawks.

Whether the benefits of cooperative hunting or breeding led to social living in Harris's Hawks is by no means settled. Previous work indicates that future investigations into the benefits of cooperative breeding should focus on survival rates of young and their subsequent reproductive success. If survival rates are higher for delayed dispersers, how much of this increased survival is because of group hunting benefits? And what ecological or geographic factors favor helping over dispersal?

In some parts of the United States, Harris's Hawk reproduction follows a boom-or-bust pattern that tracks prey populations (Dwyer and Bednarz 2011). In bust years, hawks forgo breeding. If some populations are food-limited, is the observed helping–dispersal pattern consistent with the environmental constraints and benefits of philopatry hypotheses? Are dispersal from the natal range and first breeding favored in high-prey years and helping in low-prey years (Emlen 1984; see Bednarz and Ligon 1988)?

All the hypotheses presented herein warrant further investigation. If the incidence of cooperative breeding and hunting in Harris's Hawk increases along a longitudinal or latitudinal gradient, a study comparing the net benefits of these behaviors geographically is likely to reveal important associations with ecological variables. For example, the net rate of intake for individuals hunting in different unit sizes might be compared in different locations and seasons. Are benefits of cooperative breeding and/or hunting greatest in relation to some habitat or geographic gradient? Even in a relatively well-studied social species like Harris's Hawk, there is clearly much work to do.

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