their hosts. Proc. West. Foundation Vertebr. Zool. 2: 225–302.

———, ———, & S. I. ROTHSTEIN. 1977. A further contribution to the knowledge of the host relations of the parasitic cowbirds. Smithsonian Contrib. Zool. 235: 1–75.

GOLDWASSER, S. 1978. Distribution, reproductive success and impact of brood parasitism by Brown-headed Cowbirds on Least Bell's Vireo. Rep., California Dep. Fish & Game, Project SWY-R10, Job IV-1.5.1.

———, D. GOINES, & S. R. WILBUR. 1980. The Least Bell's Vireo in California: a de facto endangered race. Am. Birds 34: 742–745.

GRZYBOWSKI, J. A. 1985. Population and nesting ecology of the Black-capped Vireo (*Vireo atricapillus*): II. Nesting ecology of the Black-capped Vireo. U.S. Fish Wildl. Serv. Rep.

———, R. B. CLAPP, & J. T. MARSHALL JR. 1986. History and current status of the Black-capped Vireo in Oklahoma. Am. Birds 40: 151–161.

HASSEL, M. P., & R. M. MAY. 1974. Aggregation of predators and insect parasites and its effects on stability. J. Anim. Ecol. 43: 567–594.

MAY, R. M., & S. K. ROBINSON. 1985. Population dynamics of avian brood parasitism. Am. Nat. 126: 475–494.

ROTHSTEIN, S. I., J. VERNER, & E. STEVENS. 1980. Range expansion and diurnal changes in dispersion of the Brown-headed Cowbird in the Sierra Nevada. Auk 97: 253–267.

SEDGWICK, J. A., & F. L. KNOPF. 1988. A high incidence of Brown-headed Cowbird parasitism of Willow Flycatchers. Condor 90: 253–256.

SOUTHERN, W. E. 1958. Nesting of the Red-eyed Vireo in the Douglas Lake region, Michigan, part 2. Jack Pine Warbler 36: 185–207.

WILEY, J. W. 1982. Ecology of avian brood parasitism at an early interfacing of host and parasite populations. Ph.D. dissertation, Coral Gables, Florida, Univ. Miami.

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## A Comparison of Two Methods of Estimating Breeding Group Size in Harris' Hawks

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Accurate estimates of the size of social units or breeding groups are central to studies of cooperative breeding in birds and a variety of methods are used in conjunction with color-banding to census group members (Brown 1987). The particular methods used depend largely on how species respond to the presence of humans. Scrub Jays (*Aphelocoma coerulescens*) and Arabian Babblers (*Turdoides squamiceps*), for example, can habituate to the presence of humans; consequently, group sizes can be accurately estimated by simply walking through territories and counting marked individuals (Woolfenden and Fitzpatrick 1984, Carlisle and Zahavi 1986). In other species, group size is estimated by watching the nest and counting individuals from a distance at which birds are not disturbed (e.g. Dow 1977). Some species, however, are extremely wary of humans and remain alarmed when humans are near the nest. Accurate estimates of group size in these species are obtained by observing nests from blinds or other concealed positions (e.g. Ridpath 1972, Craig 1980, Koenig and Mumme 1987).

The Harris' Hawk (*Parabuteo unicinctus*) breeds in groups of >2 throughout its range in the southwestern United States (Mader 1975a, Griffin 1976, Bednarz 1987). Interest in the Harris' Hawk increased dramatically after Mader (1975a) reported helpers at nests (e.g. Griffin 1976, Whaley 1979). Recent studies have focused on the cooperative breeding behavior of this species (Mader 1979, Bednarz 1987, Bednarz and Ligon 1988, Dawson 1988).

Harris' Hawks are extremely wary of humans near the nest and respond to humans by soaring over the nest and giving alarm-calls (Mader 1975b, Whaley 1979), or by fleeing the nest area altogether (Bednarz 1986). Estimates of the size of breeding groups of Harris' Hawks generally are made by counting the number of hawks seen while walking through the nest area, or during visits to the nest for other purposes (Mader 1975b, Whaley 1979, Bednarz 1987). An assumption of this method is that all group members respond to human intruders in such a way that they can be observed and counted. The validity of this assumption has never been established.

We studied breeding Harris' Hawks in Arizona and used two methods to estimate group size at each nest. We compared estimates obtained by counting hawks while visiting the nest with estimates made while observing social behavior from a blind at the nest. We also recorded the behavioral responses of Harris' Hawks to a human approaching the nest.

We studied Harris' Hawks in Pinal County, Arizona, for 3 seasons (January to August, 1984–1986). Vegetation in the study area is in the Paloverde-cactimixed scrub series of the Sonoran Desert (Turner and Brown 1982). We banded 362 Harris' Hawks with unique combinations of 3 colored leg bands and a

TABLE 1. Estimates of the size of breeding groups of Harris' Hawks in Arizona based on observations at the nest (Lists) and number seen while walking through the nest area (Counts), 1984–1986 ($n$ = 53 nests).

| | Lists | | Counts | |
|---|---|---|---|---|
| No. in group | No. of groups | Percentage of all groups | No. of groups | Percentage of all groups |
| 2 | 9 | 17.0 | 23 | 43.6 |
| 3 | 17 | 32.1 | 22 | 41.5 |
| 4 | 12 | 22.6 | 5 | 9.4 |
| 5 | 8 | 15.1 | 2 | 3.7 |
| 6 | 5 | 9.4 | 1 | 1.9 |
| 7 | 2 | 3.8 | 0 | — |
| Mean | 3.8 | | 2.8 | |
| Range | 2–7 | | 2–6 | |

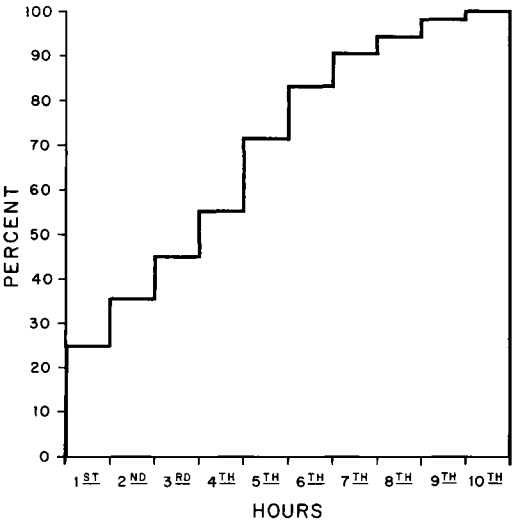


Fig. 1. Cumulative percentage of breeding groups of Harris' Hawks in which maximum group size was observed during 10 h of observation from blinds, 1984–1986, in Arizona.

numbered metal band. Hawks were trapped with balchatri traps (Berger and Mueller 1959) and nestlings were color-banded when they were 35–48 days old. All hawks were marked in 81.1% of the groups ($n$ = 53); one unmarked hawk was present in 15.1% of the groups; and two unmarked hawks were present in 3.8% of the groups (percentages based on estimates obtained by observing hawks from blinds).

We noted areas frequented by groups before nesting. Later we located nests by searching each area every 2 weeks until the nest was found. We estimated the size of the group present at each nest in two ways. First, we visited each nest a minimum of six times and counted the number of hawks seen on each visit. We used the maximum number of hawks seen during a visit, or the maximum number that could be interpreted from observations of different birds (based on age-related differences in plumage or color-bands) on different visits, to estimate group size. We refer to these estimates as "counts." Second, we observed breeding behavior of hawks from elevated, fully enclosed blinds placed from 3–10 m of nests. Hawks generally accepted the presence of blinds in the nest area and returned to the nest shortly after the blind was constructed (mean return time = 13.8 min, $n$ = 64 blind setups). We observed each nest for 10–413 h, and identified the hawks that came into the nest area by their color-bands. We estimated group size by listing the hawks observed in the nest area and refer to these estimates as "lists."

We recorded the responses of nesting hawks to a human at some nests ($n$ = 34) by observing hawks from a blind as a person walked into the nest area. We used all-occurrence sampling (Altmann 1974), and binoculars, a spotting scope, stopwatches, tape recorders, and an ethogram code that represented defense behaviors (e.g. alarm-calling and soaring) to observe and record responses. The nests contained nestlings ranging from 5 to 23 days of age. Breeding status of group members was evaluated from observations of egg laying, copulatory behavior, and participation in nesting duties (Dawson 1988). We classified hawks as adults or immatures based on differences between adult plumage (attained at ca. 1 yr) and immature plumage (Brown and Amadon 1968).

The number of hawks listed while observing groups from blinds was higher than that counted during visits to the nest for 64.1% of 53 nests studied. Estimates of group size clearly depended on the method used (Table 1; Chi-square contingency test for independence: $\chi^2$= 17.91, df = 5, $P$ = 0.003). Group size was underestimated by counts in 58.8% of groups of 3, 83.3% of groups of 4, 87.5% of groups of 5, and 100% of groups of 6 and 7. The frequency of occurrence of groups of 2 and 3 was higher for counts than lists because many groups of 4–7 were underestimated during counts as groups of 2 or 3.

We found that maximum group sizes often were not recorded within the first hour of observation from blinds (Fig. 1). Helpers sometimes perched in the vicinity of nests (150–300 m away) for long periods, but visited the nest infrequently (Dawson 1988). Consequently, only groups of 2 were accurately censused within the first hour of observation. Maximum group sizes were recorded for most groups between 4 and 7 h of observation (Fig. 1). We observed 15 groups for >10 h ($\bar{x}$ = 41 h, range = 26–413 h) and we did not record additional members after 10 h of observation for these groups.

The responses of hawks to humans at 34 nests (74 human approaches) varied among group members

and was related to breeding status and age (Table 2). The most intense responses were alarm-calling from perches within 50 m of the nest and soaring low over the nest. These activities usually were performed by breeders, and occasionally by adult helpers (Table 2). Immature helpers, however, rarely defended the nest area (Table 2). At the other extreme, helpers (particularly immature helpers) often left the nest area as soon as they detected an approaching human (Table 2). Hawks that left the nest area usually flew below the tree level in a direction opposite the approaching human and did not return while the human remained near the nest. These hawks generally were missed during counts (82.4% of 74 approaches/counts).

We believe that estimates of the size of breeding groups of Harris' Hawks obtained by counting hawks during visits to the nest are unreliable. Of the groups we studied, >50% were underestimated by counts because helpers were often not observed during visits. By listing hawks during observations of nesting behavior, we recorded a larger average group size and higher frequencies of groups of >3 than reported previously for Harris' Hawk (Mader 1975a, Griffin 1976, Whaley 1979, Bednarz 1987). In Arizona, Mader (1975b) counted 2 and 3 adults at 54% and 46%, respectively, of 50 nests, and Whaley (1979) counted 2, 3, and 4 adults at 54%, 41%, and 5%, respectively, of 227 nests. Many ecological factors could affect the size of groups over time, but during our counts we recorded percentages of groups of 2 and 3 that were similar to those reported by Mader (1975b) and Whaley (1979).

Bednarz (1986, 1987) also used the number of hawks counted during repeated visits to the nest (a minimum of 5 visits) to estimate the size of Harris' Hawk breeding groups in New Mexico. Some visits included time spent at the nest weighing or banding nestlings. Harris' Hawks in New Mexico appeared to be more shy of humans than those we observed, and group members frequently fled the nest area as soon as a human approached (Bednarz 1986). The tendency to flee from humans would exacerbate the problems associated with the count method. However, differences in vegetation structure between the shrublands of southeastern New Mexico and the Paloverde-cacti-mixed scrub series in Arizona (i.e. the former is more open than the latter) may have increased the likelihood of seeing hawks that flew away (Bednarz pers. comm.). Bednarz (pers. comm.) could not compare estimates based on counts and lists because the hawks he studied would not return to the nest even when a blind was placed >100 m away. Thus, the extent of bias in estimates of the size of Harris' Hawk groups in New Mexico is unknown, but the extreme wariness of hawks to humans (Bednarz 1986) suggests that group sizes may have been underestimated.

Underestimation of group size can potentially cause errors in analyses or interpretation of social behavior. For example, if we used estimates based on counts to compare the productivity of pairs vs. groups, the analysis would be meaningless because >60% of the "pairs" were actually groups of 3 or more. Also, group members that were missed during counts may be misidentified as nonmembers if observed near the nest at other times. This confusion may account for some reports of harmonious interactions between nesting hawks and trespassing "nonmembers" (e.g. Mader 1975a).

TABLE 2. Responses (percentage of observations) of Harris' Hawks to a human approaching the nest area, 1984–1986, Arizona. If hawks performed >1 behavior during an approach, the most conspicuous behavior is listed. Sample sizes are in parentheses.

| | | Helpers | |
|---|---|---|---|
| Behavior | Breeders[a] (144) | Adult (80) | Immature (73) |
| Perch ≤150 m from nest | 28.5 | 0.0 | 0.0 |
| Soar ≤100 m over nest | 41.7 | 10.0 | 0.0 |
| Soar >100 m over nest | 15.9 | 15.0 | 4.1 |
| Perch >150 m from nest | 9.7 | 20.0 | 12.3 |
| Soar >200 m from nest | 3.5 | 22.5 | 15.1 |
| Leave nest area | 0.7 | 32.5 | 68.5 |

[a] All breeders were adults.

We believe that accurate estimates of group size in the Harris' Hawk can be obtained by watching nests from blinds and listing color-banded hawks observed in the nest area. The possibility of overestimating group size by listing nonmembers as part of a group is unlikely because Harris' Hawks actively exclude conspecific trespassers from the nest area (Dawson 1988). It is possible that group sizes could be underestimated if several group members are not marked, or if all helpers do not visit the nest during the observation period. We suggest that observing the nest for at least 10 h will minimize the latter possibility.

Another important advantage of estimating group size by lists is that the criteria used to establish membership in a breeding group can include behaviors that are related directly to reproduction. If a hawk feeds nestlings, brings food to the nest or to another group member, or participates in group hunts, there can be little doubt about its group affiliation. All of the hawks we listed as members participated in one or more of these activities. Responses of hawks to humans, the sole criterion for group membership during counts, varies widely among individuals and requires subjective evaluation before group affiliations can be assigned (e.g. Mader 1975b, Bednarz 1986).

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LITERATURE CITED

ALTMAN, J. 1974. Observational study of behavior: sampling methods. Behavior 49: 227–265.

BEDNARZ, J. C. 1986. The behavioral ecology of the cooperatively breeding Harris' Hawk in southeastern New Mexico. Ph.D. dissertation, Albuquerque, Univ. New Mexico.

———. 1987. Pair and group reproductive success, polyandry, and cooperative breeding in Harris' Hawks. Auk 104: 393–404.

———, & J. D. LIGON. 1988. A study of the ecological bases of cooperative breeding in the Harris' Hawk. Ecology 69: 1176–1187.

BERGER, D. D., & H. C. MUELLER. 1959. The bal-chatri: a trap for banding birds of prey. Bird-Banding 30: 18–26.

BROWN, J. R. 1987. Helping and cooperative breeding in birds. Princeton, New Jersey, Princeton Univ. Press.

BROWN, L. H., & D. AMADON. 1968. Eagles, hawks and falcons of the world. London, Country Life Books.

CARLISLE, T. R., & A. ZAHAVI. 1986. Helping at the nest, allofeeding and social status in immature Arabian Babblers. Behav. Ecol. Sociobiol. 18: 339–351.

CRAIG, J. L. 1980. Pair and group breeding behavior of a communal gallinule, the Pukeko, *Porphyrio p. melanotus*. Anim. Behav. 28: 593–603.

DAWSON, J. W. 1988. The cooperative breeding system of the Harris' Hawk in Arizona. M.S. thesis, Tucson, Univ. Arizona.

DOW, D. D. 1977. Reproductive behavior of the Noisy Miner, a communally breeding honeyeater. Living Bird 16: 163–185.

GRIFFIN, C. R. 1976. A preliminary comparison of Texas and Arizona Harris' Hawk (*Parabuteo unicinctus*) populations. Raptor Res. 10: 50–54.

KOENIG, W. D., & R. L. MUMME. 1987. Cooperatively breeding Acorn Woodpecker. Monogr. Popul. Biol. 24. Princeton, New Jersey, Princeton Univ. Press.

MADER, W. J. 1975a. Biology of the Harris' Hawk in southern Arizona. Living Bird 14: 59–85.

———. 1975b. Extra adults at Harris' Hawk nests. Condor 77: 482–485.

———. 1979. Breeding behavior of a polyandrous trio of Harris' Hawks in southern Arizona. Auk 96: 776–778.

RIDPATH, M. G. 1972. The Tasmanian Native Hen, *Tribonyx mortierii*: I. Patterns of behavior. CSIRO Wildl. Res. 17: 1–51.

TURNER, R. A., & D. E. BROWN. 1982. Tropical-subtropical desertlands. Pp. 181–221 *in* Biotic communities of the American southwest—United States and Mexico. Special issue: desert plants 4 (D. E. Brown, Ed.). Superior, Arizona, Boyce Thompson Southwestern Arboretum.

WHALEY, W. H. 1979. The ecology and status of the Harris' Hawk (*Parabuteo unicinctus*) in Arizona. M.S. thesis, Tucson, Univ. Arizona.

WOOLFENDEN, G. E., & J. W. FITZPATRICK. 1984. The Florida Scrub Jay. Monogr. Popul. Biol. 20. Princeton, New Jersey, Princeton Univ. Press.

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## Breeding Opportunities, Foraging Rates, and Parental Care in White-winged Crossbills

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There has been much research on factors that promote interspecific differences in the relative contribution of the sexes to parental care (Trivers 1972, Maynard Smith 1977, Ridley 1978, Wells 1981), but there has been less work on intraspecific variation in parental care (e.g. Keenleyside 1983, Beissinger and Snyder 1987). I demonstrate that (1) when White-winged Crossbills (*Loxia leucoptera*) have immediate breeding opportunities and energy intake rates are sufficient to permit one parent to care for the fledglings, only the male feeds them (presumably because the female deserts and renests), but (2) when crossbills have no immediate breeding opportunities and lower intake rates, both parents care for the fledglings.

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