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Age-specific Productivity and Nest Site Characteristics of Cooper's Hawks (Accipiter cooperii)

Abstract

Nesting Cooper's Hawks (*Accipiter cooperii*) were studied in northeastern Oregon. Second-year (SY) males did not breed, but 22 percent of the breeding females were SY's. Mean clutch size ($P = 0.012$) and mean number of young fledged per pair that laid eggs ($P < 0.10$) were lower for SY females than for adult (after second year [ASY]) females; however, an equal percentage of the eggs (excluding a collected sample egg) yielded fledged young for each age class. Stepwise discriminant analysis suggested differences in structural characteristics of the nest site habitat for ASY and SY females, i.e., SY female nest sites were associated with younger successional stages than ASY female nest sites. Nests of both age groups were built in trees with high crown volume, but ASY females utilized mistletoe (*Arceuthobium* sp.) for nest structures more frequently ($P < 0.01$) than SY females.

Introduction

Age of breeding individuals affects many aspects of reproductive performance of several bird species including raptors. Nesting habitat use, mate selection, laying date, clutch size, and breeding success can be affected by age and experience (Coulson and White 1958, Greenwood *et al.* 1979, Middleton 1979, Newton 1979). Individuals breeding for the first time seem to have lowered reproductive success. Younger breeding females generally lay smaller clutches and raise fewer offspring than older individuals.

Most raptors do not begin breeding in juvenal plumage and require varying periods of time to acquire adult plumage. Breeding of raptors in juvenal plumage may be evidence of favorable breeding conditions or higher numbers of unoccupied territories (Newton 1979). Henny *et al.* (1973) found a breeding SY female Red-shouldered Hawk (*Buteo lineatus*) nesting successfully when the overall breeding density was lowest on a study area in central Maryland. Cooper's Hawks (*Accipiter cooperii*) retain juvenal plumage for one year and generally do not breed the first year (Reynolds and Wight 1978). The present study examines productivity and nest site characteristics of breeding ASY and SY Cooper's Hawks in northeastern Oregon.

Study Area and Methods

Study Area

The study area was located within and around Wallowa-Whitman National Forest of northeastern Oregon between 45° and 46° North Latitude at elevations between 500 m and 1600 m. The Wallowa-Whitman National Forest is in the Blue Mountains province of Oregon and consists primarily of montane forest with moderate to steep relief. A detailed description of the physiognomy of this province and climatic conditions of the various forest types are given by Franklin and Dyrness (1973). Hall (1973) recognized several climax forest plant communities in this area: ponderosa pine (*Pinus ponderosa*), lodgepole pine (*P. contorta*), grand fir (*Abies grandis*), subalpine fire(*A. lasiocarpa*), and mixed conifer stands, e.g., ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), grand fir, and western larch (*Larix occidentalis*). Many stands are on a gradient between these community types. Vegetation on natural open areas consists of grass and forb species. A mosaic of forest stands of various age classes and species composition is present in the region.

Vegetation Sampling

Nests at undisturbed sites which had been located between 1975 and 1979 were sampled in 1978 and 1979. Vegetation was sampled within 0.08 ha circular plots centered at the nest tree. Vertical distribution of tree crown volume was measured by the technique of Mawson *et al.* (1976) and the program HTVOL. Each tree within the plot was considered in relation to 15 possible crown shapes and relegated to the one it fitted best. The dimensions of these shapes were measured using a clinometer and a steel tape. The HTVOL program calculated total crown volume within 3 m height classes up to 30 m to develop a crown profile for each plot. Diameter at breast height (DBH) and species were recorded for each tree in the plot. All plants greater than 0.3 m and less than 3 m tall were measured as shrubs. Shrub crown volume was calculated by fitting shrubs or groups of shrubs into the smallest possible cube and measuring the dimensions of that cube. Shrub and tree crown volumes were combined to develop a total crown profile for each plot.

The following nest tree characteristics were recorded: species, condition (alive, dead), DBH, and crown height. The following nest characteristics were measured: height, nest substrate, and canopy coverage at the nest (measured with a spherical densiometer).

Productivity

Clutch size and number of bandable young (3-4 weeks old) were recorded. When possible, one egg was removed from each nest for analysis of pesticide contamination. Productivity for each age group was determined by using only nests at which clutch size and number of 3-4 week old young were known and where an egg was removed from the clutch.

Age Determination

Breeding individuals were trapped and banded at nest sites just before or immediately after fledging of the young. Age was determined by differences in plumage. Birds were placed into two age classes: SY birds were one year old and retained juvenal plumage, and ASY birds were two years or older with adult plumage. Initial molting of juvenal plumage and replacement by darker adult plumage were evident during the incubation period and continued through the breeding season.

Analysis

Tree crown profiles and stand composition variables at nest sites were tested for differences between age groups by using multivariate techniques. A stepwise discriminant analysis was used to select those variables most important in discriminating between nest sites of each age group. A canonical analysis on nest site variables was used to identify those variables which were the most powerful discriminators of each age group's nest site characteristics (Morrison 1967).

We tested differences in clutch size and numbers of young fledged among years using a Kruskall-Wallis one-way ANOVA. We tested differences in clutch size, number of young fledged, and fledging success between age groups using a Wilcoxon rank sum test (Conover 1971). Computer analyses utilized the Statistical Analysis System (SAS; Helwig and Councils 1979) and the Statistical Package for the Social Sciences (SPSS; Nie *et al.* 1975).

Results

Age and Productivity

Forty-five occupied Cooper's Hawk nests were observed. Of the 37 breeding females which were aged, 8 (22 percent) were in SY plumage. The percentage of the breeding population consisting of SY females is much higher than the previously reported 6 percent by Reynolds and Wight (1978) and Meng (1951), but similar to the 20 percent reported by Hennessy (1978). Henny and Wight (1972) inferred that 30-37 percent of the Cooper's Hawk population in the eastern United States consisted of SY's during the breeding season. Assuming a similar proportion for our study area, the observed 22 percent SY breeding females suggests that perhaps about half of the SY females were nesting. Only 15 of 45 breeding males were aged but all were in adult plumage. The absence of breeding SY males was also observed by Reynolds and Wight (1978) in Oregon and Meng (1951) in New York. In 1979, one SY male was caught foraging within 50 m of a nest, but it was not known if this was the male of that breeding pair.

There were no differences among years in mean clutch size ($P > 0.44$) or for mean number of young fledged per pair that laid eggs ($P > 0.83$). Therefore, productivity data were combined from the four years to examine age differences.

Mean clutch size for SY females was significantly lower than mean clutch size for ASY females ($P = 0.012$, Table 1). ASY females laid a higher proportion of four or five egg clutches whereas most SY female clutches had three or four eggs. As expected, mean number of young fledged per pair that laid eggs was also lower for SY females ($P < 0.10$). The percentage of eggs laid (after one egg removed) that yielded fledged young (fledging success) was comparable for both age groups ($P > 0.38$,

TABLE 1. Comparison of clutch size in SY and ASY female Cooper's Hawks.

Female age	N	Nests by clutch size 1	2	3	4	5	Clutch size[1] $\bar{x} \pm SD$
SY	8	0	1	4	3	0	3.25 ± 0.70
ASY	20	0	0	3	10	7	4.20 ± 0.69

[1]Before egg removal.

Table 2). However, the systematic removal of an egg from each nest probably increased fledging success of remaining eggs for both age classes, e.g., 19 successful ASY female nests (with one egg removed) fledged an average of 2.63 (82 percent of remaining eggs) whereas 8 successful ASY female nests (with no eggs removed) fledged an average of 3.00 (71 percent of eggs laid).

The percentage of nest attempts successful in fledging at least one young was slightly higher for ASY females than SY females (Table 2); however, the unadjusted estimates are biased high because most nests were not found on the day of clutch initiation (Steenhof and Kochert 1982). Nests that failed early could be missed, especially when nests were located by sign (prey remains) and adult activity which increased as the nesting season progressed. The percentage of nests successful was indeed lower for each age class when based on the Mayfield Exposure Day method (for details see Steenhof and Kochert 1982), but age class values were not statistically different ($P > 0.05$).

Overall, after an adjustment for the sample egg collected (assuming 71 percent of eggs in successful nests yielded fledglings) and the undetected loss of nests (based on Mayfield's approach), we estimated that 2.64 young were fledged per ASY female that laid eggs, and 1.73 young per SY female. Newton et al. (1981) reported SY European Sparrowhawks (*Accipiter nisus*) also laid smaller clutches (4.20) than older females (4.60) and fledged fewer young per nesting attempt (1.55 [SY] vs. 2.27 [third year] or 2.35 [older] famales).

TABLE 2. Comparison of productivity between SY and ASY female Cooper's Hawks (nests with a sample egg collected).

Female age	N	Young fledged $\bar{x} \pm SD$	Fledging success[1] $\bar{x} \pm SD$	Percent nests successful[2]
SY	8	1.75 ± 1.0	0.78 ± 0.37	87.5 (75.0)
ASY	20	2.50 ± 1.1	0.78 ± 0.30	95.0 (88.1)

[1] $\bar{x}$ young fledged/$\bar{x}$ clutch size - 1.

[2] Unadjusted data, ( ) adjusted by Mayfield Exposure Day method as detailed in Steenhof and Kochert (1982), with 61 day exposure period.

Age and Nest Site Characteristics

Crown profiles from mean crown volume values were developed for each age group (Fig. 1). Nest sites of SY females had greater crown volumes from 0 to 6 m, but smaller crown volumes from 12 to 21 m than did sites of ASY females; volumes for other strata were similar for each age group. This indicates a greater proportion of small trees or shrubs in nest sites of SY females. This trend in vegetative structure is further illustrated by the frequencies of trees in various size classes (Table 3). SY females nested in stands of younger successional stages or stands which had undergone recent selective overstory removal. Vegetative structure of nest sites used by SY females more closely resembled those nest sites used by Sharp-shinned Hawks (*Accipiter striatus*) which also utilize stands of early successional growth stages (Moore and Henny 1983).

Crown volume in the ten 3-m strata, frequency of each tree size class, basal area, and stem density were used in a stepwise discriminant analysis to test for differences between age groups in vegetative structure of nest sites. The stepwise discriminant identified those variables most important in discriminating between groups in a step-

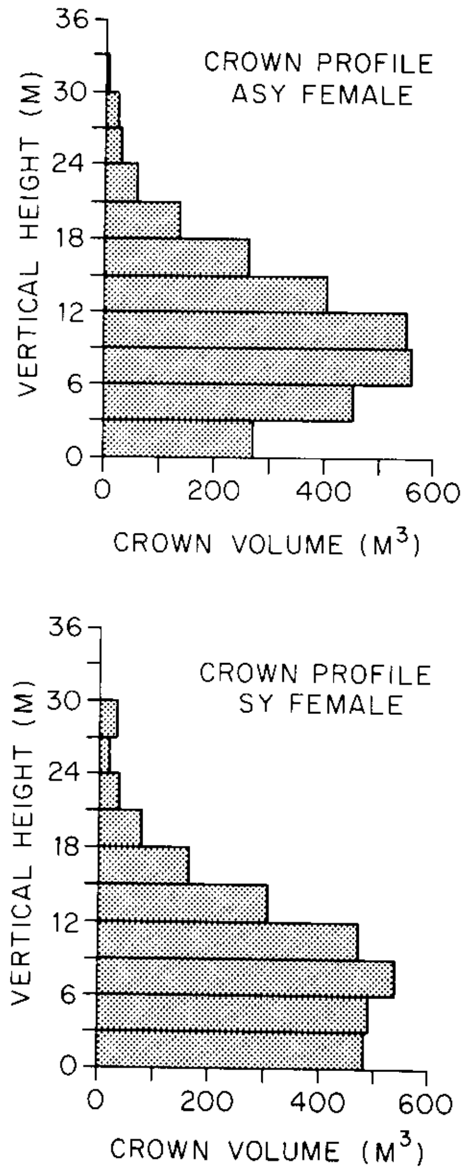

Figure 1. Crown profiles at nest sites of SY and ASY female Cooper's Hawks.

wise fashion. The discriminant function developed from this procedure then provides a means of classifying the original observations by using *a posteriori* probabilities of group membership. Nest sites of SY females were correctly classified for seven of eight observations, suggesting that structural differences existed in nest sites used by each age group (Table 4).

Age-specific separation of nest site habitat can be graphically represented by using canonical analysis of the habitat variables. Canonical analysis generates new variables which are linear combinations of the original variables, each weighted according to their power to discriminate the groups (Morrison 1967). The position of individual observa-

TABLE 3. Structural characteristics at nest sites of SY and ASY female Cooper's Hawks.

Variables	SY females $\bar{x} \pm SD$		ASY females $\bar{x} \pm SD$	
Tree size class (cm DBH)				
2.5- 8.9	90.4	95.8	79.4	63.3
8.9-16.5	49.4	25.5	40.4	22.2
16.5-31.7	21.4	10.4	26.7	12.0
31.7-41.9	4.7	2.7	6.3	4.7
> 42	1.7	1.9	2.4	3.7
Stems/0.08 ha	158.6	112.0	155.3	78.9
Basal area M²	2.6	0.8	3.2	1.4
Mean DBH cm	13.7	5.0	14.2	5.3

TABLE 4. Classification results from the discriminant analysis of nest site variables of SY and ASY females.

Group	N	SY females	ASY females
SY females	8	7 87.5%	1 12.5%
ASY females	25	4 16.0%	21 84.0%
Unknown age	6	2 33.3%	4 66.7%

tions can be plotted along the canonical functions to get a graphical interpretation of the nature and extent of group separation. Variables and their associated standardized coefficients, selected by stepwise discriminant analysis were used to specify the canonical functions. Habitat separation of nest sites between age groups is graphically displayed in Figure 2. Some nest sites were used by both ASY and SY females which increased

TABLE 5. Nest tree characteristics for SY and ASY female Cooper's Hawks.

Variables	SY females $\bar{x} \pm SD$		ASY females $\bar{x} \pm SD$	
DBH[1] (cm)	36.3	13.7	40.9	16.2
Nest height[2] (m)	10.7	3.4	12.4	2.8
Nest-crown relationship[3] (m)	3.4	3.4	1.7	5.5
Canopy coverage[4] (%)	96.2	3.4	94.7	5.7
Frequency of mistletoe use as nest structure[5]	50.0%		70.0%	

[1]$Z = 0.65$, $P > 0.50$; [2]$Z = 1.28$, $P > 0.20$; [3]$Z = 0.80$, $P > 0.40$; [4]$Z = 1.00$, $P > 0.32$; [5]$Z = 5.50$, $P < 0.01$.

overlap along the canonical axis.

Age and Nest Tree Characteristics

SY females appear to place nests lower in height than ASY females, but higher in the crown of the nest tree (nest-crown relationship, Table 5). Sites for both age classes have similar nest canopy coverage. None of these variables were significantly different between age groups (Wilcoxon rank sum test). Comparison of nest tree characteristics and crown profiles (Fig. 1) reveals a trend for each age group to build nests in strata with high crown volumes. The frequency of mistletoe use as a nest structure was significantly lower for SY females ($P < 0.01$). Mistletoe growth provides a nest building

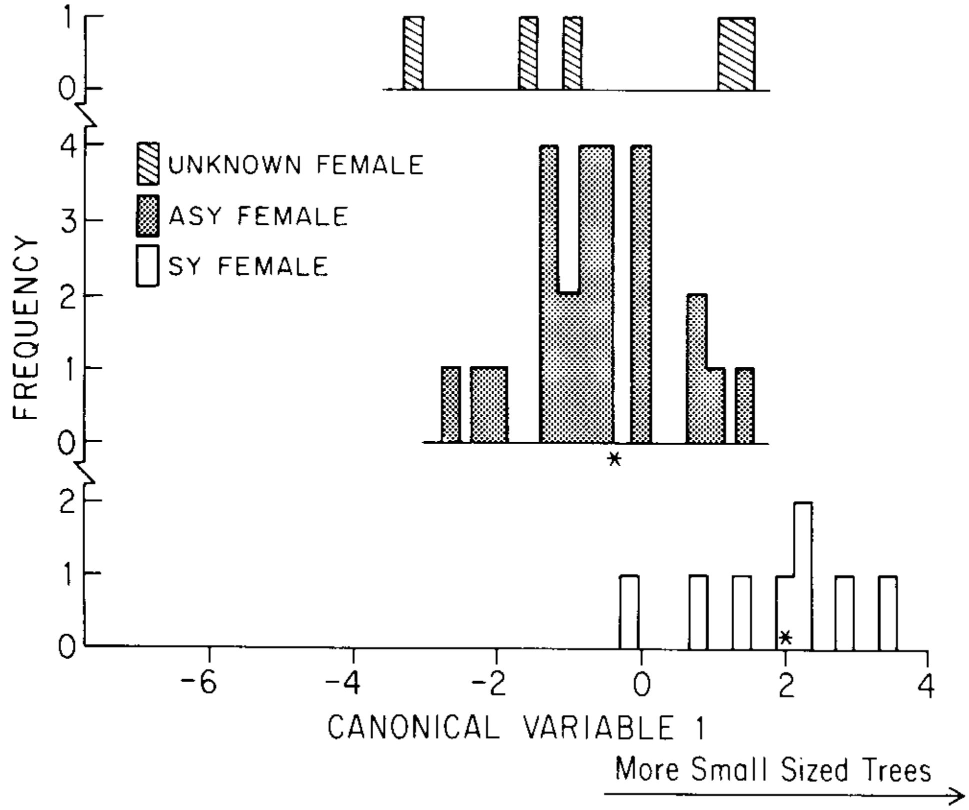

Figure 2. Distribution of observations at nest sites of SY and ASY females along the canonical axes. *Represents group means.

structure that effectively conceals nests from researchers, and possibly predators, searching from the ground. But, the percentage of nests on mistletoe that were successful (96 percent) was not significantly higher ($P > 0.28$) than for nests not on mistletoe (86 percent).

Discussion

The lower productivity of SY females may result from (1) behavioral and physiological differences associated with age, (2) habitat differences (including prey availability) where they nest, or (3) a combination of the above.

Smaller clutch sizes associated with juvenal plumaged females has been demonstrated in several species of birds including raptors (Hickey and Anderson 1969, Perrins and Moss 1974, Harvey *et al.* 1979, Newton *et al.* 1981). Charnov and Krebs (1974) predicted optimal clutch sizes to be smaller than the most productive clutch size due to the relationship between adult survival and clutch size. Energy expenditure by parents increases with brood size causing weight loss and lowered survivorship in adults (Klomp 1970, Cody 1971). This factor would be more important to longer-lived birds such as raptors which may breed several times in a lifetime. If younger birds are less experienced in foraging ability and therefore less efficient at feeding themselves and their young, then smaller clutch sizes would reduce food stress and increase survival allowing individuals to breed in subsequent years.

Given the smaller clutch size for SY females in our study, we showed an equal percentage of the eggs yielding fledged young for each age group. Our study, however, was confounded by the removal of an egg from each clutch for pesticide analysis. Removal of an egg, assuming it would hatch, lowered brood size and probably increased survival of the remaining siblings. However, once eggs are laid and incubation has begun, the males take the major responsibility of capturing prey for the female and the young up to about two weeks post hatch.

Vegetative structure differences at nest sites are suggested between age groups. The "quality" of the nest site and its effect on productivity is difficult to determine. Nest sites provide concealment and inaccessibility from predators and shelter for young from adverse weather. Nest sites probably vary in the ability to provide these factors and raptors may respond to these differences. This response may be altered by experience and younger, less-experienced, individuals may select lower quality nest sites. Nest failure during our study occurred at nests of SY and ASY females but all occurred at sites which were used by a SY female at some time during the study. A nest site occupied by an ASY female was unsuccessful in 1976; it was occupied the following year by a SY female and failed again. The same site was used the following year by another SY female and all the young were preyed on by a Great Horned Owl (*Bubo virginianus*). The site was used by three different males during those three years. The vegetative structure at this nest site may have been inadequate for concealment from predators. Possibly the concealment factor or the presence of Great Horned Owls in the vicinity precluded the use of the site by most adult females.

Success or failure of a season's reproductive effort may be important in the learning process of selecting a good nest site. However, the territory surrounding the nest site is also important. Newton (1979; Table 42) found that female European Sparrowhawks nesting in "good," "intermediate," and "poor" habitats (based on food availability) returned the following year to nest sites in good habitat more often than to nest sites in poor habitat. Also, within a given habitat category, females returned to the same territory significantly more often after a successful nest attempt than after a failure. Unfortunately, we made no assessment of food availability during the study, but 10 (59 percent) of 17 nest sites were reused the following year by an adult female. At least 3 of the sites (18 percent) were used by the same female. No sites were reused by adult females after unsuccessful nest attempts, and no SY females returned to nest sites used the previous year whether successful or not.

In this study, the proportion of SY female Cooper Hawks in the breeding population was the highest reported for the species. Newton (1976) found the greatest number of SY European Sparrowhawks breeding in the most productive habitats, which he attributed to high population turnover from shooting or the occurrence of favorable conditions necessary to induce yearlings to breed. Middleton (1979) found that breeding first-year American Goldfinches (*Carduelis tristis*) in Ontario using optimal habitat had a greater chance of nesting success than in lower quality habitats. However, studies of other passerine species indicate that young birds are often displaced into suboptimal habitat by older members of the population (Brown 1969, Krebs 1972). Henny *et al.* (1973) found that adult Red-shouldered Hawks used flood plain areas for nesting in central Maryland but non-breeding SY's were restricted to upland areas away from prime nesting habitat.

If SY females nest in suboptimal territories, then some differential mate selection by females may be operating and differences in male quality may be inferred. Banding data indicate that this population is migratory (Henny, unpublished banding data), therefore, nesting territories are established each spring. Mate selection may be occurring on the basis of territory quality or characteristics of the male such as age, breeding experience, or quality of nuptial feeding. Territory quality was most important in female choice of Red-winged Blackbird (*Agelaius phoeniceus*) mates, and male genetic quality was next in importance (Searcy 1979). Burley and Moran (1979) indicated that feral Pigeons (*Columbia livia*) showed a preference for mating with individuals with greater breeding experience and age, but individuals older than seven years were not selected as mates. Newton (1979) found that choice of mates in European Sparrowhawks was selective by age, young birds pairing and older birds pairing. The greater probability of nesting success with more experienced individuals in a breeding pair confers selective advantage to older birds in this type of pairing. Eye color darkens with age in both male and female Cooper's Hawks (Snyder and Snyder 1974). Age-related changes in eye color may convey information about the age of the individual which influences mate selection. If preferential pairing of Cooper's Hawks occurs based on these criteria, then SY females could be displaced into suboptimal habitats and forced to breed with less experienced males. Under these circumstances, the smaller clutch size of SY females may be advantageous.

In summary, we have demonstrated differences in clutch size and suggested differences in nest site habitat (more habitat data is needed) for SY and ASY female Cooper's Hawks. The role of age (behavioral and physiological) vs. habitat is an intriguing subject for future ecological research.

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