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Reproductive Strategies of Northern Goshawks and Cooper's Hawks in North-Central New Mexico

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REPRODUCTIVE STRATEGIES OF NORTHERN GOSHAWKS AND COOPER'S HAWKS IN NORTH-CENTRAL NEW MEXICO

by

Patricia L. Kennedy

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

in

Biology Ecology

Approved:

Major Professor	Committee Member
Committee Member	Committee Member
Committee Member	Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

1991

This dissertation is dedicated to

the memory of Reba Beidleman and her husband, Dick, who got me started in ecology;

my husband, George and my step-sons, Tom, Ken and Dan, for their unconditional love and support;

and to the memory of my grandfather, Elmer Kennedy, who challenged me to explore and question and whose curiosity and patience influenced and inspired me.

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ABSTRACT

Reproductive Strategies of Northern Goshawks and Cooper's Hawks in North-central New Mexico

by

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Utah State University, 1991

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I assumed that the reproductive strategies of the two Accipiter species investigated in this study, the northern Goshawk (A. gentilis) and the Cooper's hawk (A. cooperii), would be similar to the strategies of other monogamous raptors with sex role partitioning. Any differences in the species' reproductive strategies, particularly hunting strategies, were expected to be a function of their size differences. Contrary to predictions, results indicated that, in north-central New Mexico during brood rearing, both species had similar hunting strategies and utilized similar prey species. These results also indicated that the reproductive strategies of the Cooper's hawk were not adequately described by simple models of sex role partitioning.

In this population, over 50% of the female Cooper's hawks deserted during the fledgling-dependency period and made no attempt to renest. In all cases of desertion, the male provided uniparental care until the young were independent. Based on time-energy budget estimates, the deserting females were in poorer physical condition at the time of desertion than were the nondeserting females. This was attributed to the deserter preferentially feeding the nestlings when the quantity of food delivered to the nest by either parent was inadequate to meet the family's requirements.

Based on these observations, I developed a dynamic stochastic optimization model to explore the hypotheses that (1) the optimal reproductive strategy of the female Cooper's hawks is the strategy that maximizes her reproductive fitness; and (2) the major factors affecting the female's reproductive fitness and, thus, her optimal strategies are her physical condition, the physical condition of the nestlings, the risks to the nestlings associated with each strategy, and the foraging capabilities of her mate. The model defined reproductive fitness as the weighted average of the nestlings' expected survival and the female's expected reproductive potential in the next breeding season. Using independent sources for the parameters, the model validation compared the model predictions with actual observations of the behavior of radio-tagged, nesting females in this population of Cooper's hawks. The model correctly predicted 90% of the strategies exhibited by the nesting females, which supported the initial hypotheses.

(236 pages)

CHAPTER I

DIURNAL RESTING METABOLIC RATES OF ACCIPITERS

One of the major sources of error in using time budgets to estimate avian daily energy expenditure is the estimate of maintenance metabolism (Weathers et al. 1984, Goldstein 1988, Nagy 1989). Resting metabolic rate (RMR) is often calculated from an allometric equation derived from measurements on other, sometimes unrelated, species. For example, Aschoff and Pohl's (1970) allometric equations for nonpasserine birds are typically used to estimate the active phase and resting phase RMR of falconiforms (Tarboton 1978, Wakeley 1978, Koplin et al. 1980), although they do not include data from falconiforms.

Recently, Wasser (1986) has rendered the use of these equations even more dubious by demonstrating that they do not conform well to the relationship of RMR to body mass during the resting phase of falconiforms. Information on falconiform RMR during the active phase is limited. My objective here is to help fill this gap by (1) measuring active phase RMR in accipiters, a group of falconiforms for which few metabolism measurements are available, and (2) comparing my empirical results with the predictions from allometric equations in the literature.

Methods.--Metabolism was measured using sharp-shinned hawks (Accipiter striatus), two females and one male; Cooper's hawks (A. cooperii), three females and two males; northern goshawks (A. gentilis), one female and one male; and a black and white goshawk (A. melanoleucus), one female. To minimize any potential variation in metabolic rates resulting from age class differences only adults were used.

Five of the accipiters (the black and white goshawk, the two northern goshawks, and two of the Cooper's hawks [one male and one female]) were long-term captives from a private breeding and falconry facility in San Diego, California. These birds were maintained in outdoor aviaries under natural conditions of temperature and photoperiod. Their metabolism measurements were taken at the San Diego facility during September 1988.

The six additional birds (the three sharp-shinned hawks, and three of the Cooper's hawks [two females and one male]) were migrants that were trapped in bow nets or mist nets at the southern end of the Goshute Mountains in Elko County, Nevada during September 1985. The measurements were taken near the trapping site soon after the birds were captured.

To collect the metabolism measurements, I confined each bird in a metabolism chamber of 4-30 L depending upon the size of the bird. I measured the temperature within the chambers with a copper-constantan thermocouple. The chamber temperatures ranged from $19^{o}C$ - $31^{o}C$, and were well within the thermoneutral zone of most raptors (Wasser 1986).

I measured the rate of oxygen consumption ($\dot{V}O_2$ in L O_2 min^{-1}) of each bird in an open-flow system using a portable Ametek S-3A oxygen analyzer that had been calibrated with atmospheric air. I removed carbon dioxide and water from the air stream by circulating the air through Ascarite and Drierite after it exited the metabolism chamber. Air then passed through a rotameter that was calibrated with a Vol-u-meter (Brooks Instrument Division, Emerson Electric Co.) before and after $\dot{V}O_2$ was measured. For each experiment I selected a flow rate between 1.5 and 1.8 L min^{-1} (STPD) depending on the bird's size and the size of the metabolism chamber.

The $\dot{V}O_2$ of a bird was measured for 60-90 minutes. At the end of a measurement the bird was calm and its $\dot{V}O_2$ was judged to be in a steady-state. I calculated the rate of oxygen consumption with Equation 4b of Withers (1977) and the rate of metabolic heat production ($\dot{H}_{ma}$ in mW) from $\dot{V}O_2$ by assuming 19.6 kJ of heat is produced per liter of O_2 consumed. This was based on an assumed Respiratory Quotient (RQ) of 0.7. Gessaman and Nagy (1988) found that errors in converting gas exchange measurements to energy metabolism for uricotelic carnivores were minimized when an RQ of 0.72 was used as compared with higher RQ values.

The San Diego birds were not fed 12-24 hours before the experiment and consequently, were in a postabsorptive condition. The absorptive status of the Nevada birds could not be determined with certainty. I assumed these birds were postabsorptive because their crops were empty (determined by palpation). If the migrants were actively digesting and assimilating prey their metabolic rates should have been significantly higher than the captive birds' metabolic rates because of the produced heat increment of feeding.

To test this prediction, I used an analysis of covariance to examine whether or not the migrant metabolic rates were significantly different from the captive birds. Biomass was treated as a covariate in this analysis. The metabolic rates of the wild birds were not significantly different from the captive birds ($\underline{F} = 1.59$, df = 1, $\underline{P} = 0.24$) which supports my assumption that the migrants were postabsorptive when measured.

All experimental measurements were made between dawn and dusk, the active phase of these diurnal raptors. Each bird was weighed to the nearest 0.1 g immediately after each experiment.

Metabolism-body weight relationships are generally presented as allometric equations generated by standard regression techniques (Lasiewski and Dawson 1967; Zar 1969; Aschoff and Pohl 1970). I did not generate an allometric equation because my data were from only four species with a narrow range of body sizes (100-958 g). The validity of the relationship of such a narrowly defined allometric equation is questionable (Zar 1969). Differences in metabolic rates between species were evaluated using analysis of variance. Paired t-tests were used to compare the measurements with the predictions of Aschoff and Pohl (1970) and Wasser (1986) for nonpasserines and falconiforms, respectively, of equivalent body size.

Results and Discussion.--Larger accipiter species had significantly higher rates of metabolic heat production than smaller species (Table I-1, $F = 30.26$, $P < 0.01$). Sample sizes were too small for all species to test for significant differences between sexes but mean values for male sharp-shinned hawks and Cooper's hawks were smaller than the mean values for the larger-bodied female conspecifics.

From regression analysis, Aschoff and Pohl's (1970) relationship between the body mass (M in g) of nonpasserine birds and (1) their active phase RMR (H_{ma} in W) can be expressed as

$$\dot{H}_{ma} = 0.028\ M^{0.729} \qquad (1)$$

and (2) their resting phase RMR (H_{mr}) can be expressed as

$$\dot{H}_{mr} = 0.022\ M^{0.734} \qquad (2).$$

The mean active phase RMR of accipiters in my study was not significantly different than Aschoff and Pohl's

(1970) predictions (Equation 1) for nonpasserine birds of similar mass (Table I-1; $\underline{t} = -1.41$, $\underline{P} = 0.19$).

Wasser (1986) derived an allometric equation for predicting falconiform RMR during the resting phase of the daily cycle. This relationship expressed in the units of Equation 1 is

$$\dot{H}_{mr} = 0.035\ M^{0.64} \qquad (3).$$

In general, Aschoff and Pohl's equation for nonpasserines of similar mass (100-1000 g) predicts a resting phase RMR that is higher than the RMR predicted by Wasser suggesting that most falconiforms, but not accipiters, have a lower resting phase RMR than other nonpasserines.

The mean active phase RMR of accipiters was significantly higher (28.8%) than Wasser's (1986) predictions for falconiforms during the resting phase of their diurnal cycle (Table I-1; $\underline{t} = -76.9$, $\underline{P} < 0.01$). Wasser measured only two accipiters in his study of 22 species of falconiforms; consistent with my results, both of Wasser's measurements were approximately 20% higher than what was predicted by his regression equation.

Although commonly cited as examples of "sit-and-wait" predators (Pianka 1974), recent telemetry studies (Widén 1984, Fischer 1986, Chapter III) indicate accipiters are very active and do not perch for long periods of time. As a result of these high activity levels, the metabolic rates of accipiters appear to be higher than those of other falconiforms of similar size throughout the daily cycle.

Since the values of active phase RMR computed from Aschoff and Pohl's equation (Equation 1) for nonpasserines were similar to the RMRs that I measured, it is reasonable to use their equation to predict the RMR of accipiters during the active phase of the daily cycle. Furthermore, Aschoff and Pohl's equation for nonpasserines during the resting phase (Equation 2) may be more appropriate for estimating accipiter resting phase RMR than Wasser's equation for falconiforms (Equation 3).

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TABLE I-1

METABOLIC HEAT PRODUCTION OF ACCIPITERS DURING THE ACTIVE PHASE OF THE DAILY CYCLE

SPECIES	SEX	MASS (g)	$\dot{H}_{ma}$ (mW)	Aschoff & Pohl (1970)[a]	Wasser (1986)[b]
Accipiter striatus	M	101.0	0.85	0.83	0.66
	F	170.0	1.18	1.21	0.93
	F	172.7	1.10	1.22	0.94
Avg. Females		171.4	1.14		
A. cooperii	M	286.9	2.60	1.77	1.30
	M	384.0	2.43	2.19	1.56
Avg. Males		335.5	2.52		
	F	436.2	2.56	2.40	1.69
	F	427.8	3.08	2.37	1.67
	F	536.5	2.33	2.79	1.93
Avg. Females		466.8	2.66		
A. gentilis	M	751.0	4.28	3.57	2.40
	F	958.2	3.62	4.26	2.80

A. melanoleucus	F	919.0	3.02	4.14	2.73
AVERAGE DEVIATION FROM MEASUREMENTS (%)				-0.17	-28.82

a. Active phase RMR for nonpasserine birds, calculated from the relation $W = 28.6\ M^{0.729}$.

b. Resting phase RMR for falconiforms, calculated from the relation $W = 34.62\ M^{0.64}$.

CHAPTER II

THE DIET OF NORTHERN GOSHAWKS AND COOPER'S HAWKS DURING THE NESTING SEASON

Abstract: During 1984-1988 I assessed the diet of Cooper's hawks (Accipiter cooperii) and northern goshawks (A. gentilis) nesting in north-central New Mexico by direct observation of 203 prey deliveries, and analyzing 420 prey remains and 214 pellets collected at nests, perches or plucking posts. The ranking of the prey eaten by both Accipiter species, categorized by taxon, did not differ between the 3 dietary sampling methods. These results support the assumption that periodic samples of prey remains at nests characterize the species composition of the diet of breeding raptors. In interspecific comparisons, no differences were found in the ranking of the prey taxa used by the 2 Accipiter species in New Mexico. They fed predominantly on 7 common, medium-sized vertebrates in the study area: northern flickers (Colaptes auratus), Steller's jays (Cyanocitta stelleri), American robins (Turdus migratorius), chipmunks (Tamias sp.), Abert's squirrels (Sciurus aberti), red squirrels (Tamiasciurus hudsonicus) and cottontails (Sylvilagus sp.). These results are in contrast to a sympatric population of northern goshawks and Cooper's hawks in eastern Oregon where the 2 species used different prey taxa during the nesting season. These

results indicate sympatric nesting populations of northern goshawks and Cooper's hawks do not necessarily feed on different prey species during the nesting season. Because these 2 Accipiter species are generalists and feed on a large number of taxa throughout their range, I suggest that the variation in prey taxa overlap is probably indicative of substantial opportunism in foraging by these 2 Accipiter species.

Diets of Accipiter species have been examined in North America (Meng 1959, Storer 1966, Snyder and Wiley 1976, Reynolds and Meslow 1984, Kennedy and Johnson 1986, Delannoy and Cruz 1988), Europe (Opdam 1975, Goszczynski and Pilatowski 1986, Newton 1986), Africa (Brown and Brown 1979, Dewhurst 1986, Simmons 1986), and the South Pacific (Diamond 1985, Aumann 1988). The interest in diets of Accipiter species results from the body-size relationships that occur among (males are smaller than females) and within the coexisting species. Studies of the dietary overlap among the North American species indicate that sympatric species have dietary differences (Storer 1966, MacArthur 1972, Hespenheide 1975, Reynolds and Meslow 1984). These differences are primarily in prey size and prey taxon; small species take small terrestrial vertebrates and larger species capture larger terrestrial vertebrates.

As Reynolds and Meslow (1984) pointed out, data used to examine dietary overlap of the North American _Accipiter_ in earlier studies (Storer 1966, MacArthur 1972, Hespenheide 1975) are based on diet information that is pooled over a variety of geographic areas, seasons and years. The taxonomic composition of _Accipiter_ species diets is known to vary, e.g., mammals make up a variable proportion (15% in the north-central U. S. to 57% in central Utah [Reynolds 1989]) of Cooper's hawk diets, probably as a result of geographic and seasonal variations in prey composition and abundance. Therefore, it cannot be determined whether the diet differences reported by these investigators are due to seasonal and regional differences in prey availability or to different patterns of prey selection from similar prey populations.

To correct for these problems, Reynolds and Meslow (1984) did a careful study of the food habits of the three North American _Accipiter_ species in 2 small areas of Oregon where the _Accipiter_ species are known to coexist during the nesting season. They found that the Cooper's hawk and northern goshawk overlapped broadly in prey size but tended to take different taxa during the nesting season. However, their interspecific comparisons are based on a dataset in which the prey are originally identified to species or genus and then collapsed into broader taxonomic categories such as family and class. Collapsing resource states to the same identification level is shown to seriously misrepresent the rank order of dietary overlap estimates of sympatric predators (Greene and Jaksić 1983). Based on these results Greene and Jaksić (1983) recommend that overlap comparisons be based on the highest possible level of taxonomic resolution of prey categories, generally species or genus level for vertebrates.

To reduce the aforementioned potential biases in diet comparisons using lower-level taxonomic categories, prey species and genera were primarily used in this taxonomic comparison of the diets of a sympatric population of northern goshawks and Cooper's hawks nesting in north-central New Mexico. I compared these results with a similar taxonomic analysis of Reynolds and Meslow's (1984) data to examine geographic variation in the dietary overlap of prey taxa used by these 2 species during the nesting season.

Diets of raptors have been commonly determined from prey remains (Opdam 1975, Reynolds and Meslow 1984, Newton 1986), but as Reynolds and Meslow (1984) pointed out, this method is not entirely free of bias. To examine this potential bias in the prey remain data, I also tested 3 methods of dietary analysis for differential assessment of Accipiter species diets, and determined if these differences influenced conclusions about the importance of the various prey taxa.

METHODS

Study Area

The study area was within the Jemez Mountains, New Mexico and adjacent Pajarito Plateau. These mountains are characterized by steep terrain dominated by typical southwestern montane habitat types such as ponderosa pine and mixed conifer forests. The Pajarito Plateau, a table-like extension of the eastern flank of the Jemez Mountains, is cut into numerous, narrow, finger-like mesas by southeast-trending, intermittent streams. The mesas are dominated by pinyon-juniper woodland. The drainages contain riparian habitats dominated by ponderosa pine (Pinus ponderosa) or cottonwood (Populus sp.) stands and flow into the Rio Grande. Habitat along the Rio Grande is characterized by a variety of deciduous riparian communities. The study area is described in detail in Kennedy (1988).

In this area, nest sites of both Accipiter species occurred in most of the habitats in the study area (Kennedy 1988, Kennedy unpubl.). One exception was the lower elevation riparian areas that were dominated by cottonwood stands. Only Cooper's hawk nests were located in this habitat (N = 2). Although northern goshawks were not located in this upper sonoran habitat, it should not be excluded as potential nesting habitat because this species does nest in a variety of upper sonoran habitats in other parts of its range (Reynolds 1989). Data collected on the foraging patterns of radio-tagged birds indicate that both species hunt in all of the major habitats in this area (Chapter III, Kennedy unpubl.).

Diet Assessment Methods--Prey Remains and Pellets

During brood rearing (the nestling and fledgling dependency periods) of 1984-1988, I collected prey remains and pellets at 8 northern goshawk (5 in 1984, 3 in 1985, 4 in 1986, 2 in 1987, and 2 in 1988) and 22 Cooper's hawk (7 in 1984, 12 in 1985, 13 in 1986, 4 in 1987, and 10 in 1988) nest sites. Collections were not made at all nests during each year because nest discovery was an on-going process throughout the study and not all nest sites were occupied each year. Of the 22 Cooper's hawk nest sites, 9 sites were sampled during 1 year, 7 sites were sampled during 2 years, 3 sites were sampled during 3 years, 1 site was sampled during 4 years, and 2 sites were sampled during all 5 years of the study. Of the 8 northern goshawk nest sites, 3 were sampled during 1 year, 2 were sampled during 2 years, and 3 were sampled during 3 years.

Most nests were visited a minimum of 3-4 times per month during brood rearing to collect all remains and pellets found near the nest, plucking posts, and perches. A total of 420 prey remains and over 800 pellets were collected during the study; 316 prey remains and over 500 pellets were from Cooper's hawk nests and 105 prey remains and over 300 pellets were from northern goshawk nests.

I used the identification technique described by Reynolds and Meslow (1984) for reconstructing and aging the prey items from the remains. Feathers were compared with the New Mexico Department of Game and Fish feather reference collection. Mammalian and avian bone fragments were compared with the synoptic collections of the Museum of Southwestern Biology at the University of New Mexico. Herpetological remains were identified by Howard Snell and his staff at the Museum of Southwestern Biology.

Accipiter pellets do not contain readily identifiable skeletal material or remiges and rectrices as do owl pellets. Therefore prey species identification of the pellet contents was based on hair, contour and down feathers, and reptilian scales. Because the process is very time-consuming, a random subset (*N* = 214) of the more than 800 pellets collected during the 5 years was analyzed. This subset consisted of 151 Cooper's hawk pellets and 63 northern goshawk pellets.

Pellets were oven-dried at 76°C for approximately 48 hr. Each pellet was then dissected to separate the hair, feathers, and reptile scales. One pellet can contain the remains from more than 1 meal (Marti 1987). To determine the mammalian species represented in each pellet, 10 hairs were systematically selected from each pellet for identification. Dorsal guard hairs that were not excessively damaged by digestion were preferred. The selection process was designed to maximize the number of species found in a pellet. The selected hairs were cleaned in alcohol and xylene. Hairs were identified by comparing their cuticular scale and medulla patterns with taxonomic keys by Mathiak (1938), Mayer (1952), Adorjan and Kolenosky (1969), Moore et al. (1974), and Tumlison (1983). In addition, the hairs were compared to reference hairs collected from specimens of diurnal mammals in the study area. In all cases, a hair could be identified to family and in most cases to genus and species.

To restore the color in the contour and down feathers from the pellets, the feathers were washed in a warm solution of mild soap and water and rinsed in warm water. Feathers were compared with specimens from the Museum of Southwestern Biology and the U.S. National Fish and Wildlife Forensics Laboratory in Ashland, OR. The reptile scales in the pellets were identified by Howard Snell and his staff at the Museum of Southwestern Biology.

Diet Assessment Methods--Prey Deliveries

The final method of acquiring dietary data was to monitor prey deliveries to the nests. An observer occupied a blind 15-60 m away from the nest for 3-10 hr per observation period. In general, each nest was monitored at least once a week during brood rearing until the nest failed or the young were independent. During the nestling stage, prey items were identified by observing the nest with a Celestron C-90 spotting scope or binoculars. During the fledgling dependency period, the fledglings handled prey for long periods of time and perched fledglings could easily be observed with binoculars or the telescope. At the end of each observation period the remains of the prey deliveries below the nest, perches, or plucking posts were collected to validate visual identification. A total of 158.5 hr and 670.6 hr, respectively, were spent observing prey deliveries at 7 of the 8 northern goshawk nests and at 17 of the 22 Cooper's hawk nests during the 5 years.

All prey items delivered to the nest during each observation period were identified to species and, if possible, classified by age and sex. Thirty-six northern goshawk and 167 Cooper's hawk prey deliveries were identified.

Statistical Analyses

Diet Assessment Method Comparison.-- The proportion of each prey taxon in the diet of each *Accipiter* species was expressed for each method as the number of occurrences of each prey taxon divided by the total number of samples. For each species, the prey taxa were ranked in order of their proportion in the diet for each of the 3 methods (Tables II-1 and II-2). Friedman's method for randomized blocks (Sokal and Rohlf 1981) was used to test the null hypothesis that the rankings of the prey taxa did not differ significantly between the 3 methods. If the null hypothesis was not rejected, this implied that any of the 3 methods could be used to assess the relative importance of different prey taxa in this *Accipiter* population during the nesting season.

Only prey taxa that occurred more than once were used in all analyses because I assumed that infrequently occurring prey were not likely to be important and could distort results. However, if a prey species occurred once but unidentified representatives of that genus also were represented, all occurrences of that genus were pooled and the genus was used as the taxon in the analysis. For example, only 1 individual of the Cordilleran flycatcher (*Empidonax occidentalis*) was recorded as a prey remain in the Cooper's hawk diet. However, 2 unidentified *Empidonax* individuals were also recorded as prey remains (Table II-1). In all the analyses this would be incorporated as 3 unidentified *Empidonax* prey with the prey remains method.

Taxonomic Comparison of Accipiter Diets--New Mexico.--A Mann-Whitney U Test (Sokal and Rohlf 1981) was used on the same data set to test the null hypothesis that there was no significant difference in the rankings of the prey taxa used by northern goshawks and Cooper's hawks.

Taxonomic Comparison of Accipiter Diets--Eastern Oregon.--A similar analysis was conducted on the diet data presented in the Appendix in Reynolds and Meslow (1984) for a sympatric nesting population of Cooper's hawks and northern goshawks in eastern Oregon. This Appendix contains the estimated number of adult and juvenile individuals of each prey species or genera collected at Cooper's hawk and northern goshawk nests during 1974 in eastern Oregon. A total of 120 prey were identified from 18 Cooper's hawk nests and a total of 228 prey were identified from 59 northern goshawk nests. These prey were identified primarily from prey remains so this analysis was comparable to the taxonomic comparison of prey identified from prey remains collected at Cooper's hawk and northern goshawk nests in north-central New Mexico.

In this analysis of the Appendix data, I combined the number of juveniles and adults recorded for each prey taxon, calculated the proportion of each taxon in the diet of each Accipiter species, and ranked the taxa in order of their proportions in the diet. These ranked data were also compared with a Mann-Whitney U test to test the null hypothesis that there was no significant difference in the rankings of the prey taxa used by northern goshawks and Cooper's hawks in this eastern Oregon nesting population. Similar to the analyses of the New Mexico data, only prey taxa that were represented more than once were included in the analysis and species were lumped into genera where appropriate. All statistical tests were conducted with the CoStat statistical software (CoHort Software 1986) on an IBM PC. The significance level was P = 0.05 for all tests.

RESULTS

Diet Assessment Method Comparison

There was no significant difference in the rankings of the Cooper's hawk (X^2 = 1.10, df = 2, P = 0.58) (Table II-1) and northern goshawk (X^2 = 1.74, df = 2, P = 0.42) (Table II-2) prey taxa identified in New Mexico using the 3 methods.

Taxonomic Comparison of Accipiter Diets--New Mexico

Based on data collected with all 3 methods, a total of 32 avian prey taxa, 9 mammalian prey taxa, and 3 reptilian prey taxa were identified in the Cooper's hawk diet (Table II-1). A total of 21 avian prey taxa and 8 mammalian prey taxa were identified in the northern goshawk diet (Table II-2). Sixty-seven percent of the avian prey taxa and 87.5% of the mammalian prey taxa represented in the northern goshawk diet were represented in the Cooper's hawk diet.

Because there were no significant differences in the rankings of the prey taxa among the 3 methods, the taxonomic comparison of Cooper's hawk and northern goshawk diets in New Mexico was done only with the prey remains dataset. The prey remains dataset was used because it is comparable to the eastern Oregon dataset (Reynolds and Meslow 1984). The rankings of the prey taxa in the New Mexico dataset did not differ between the 2 Accipiter species ($U_s = 661$, $P = 0.28$).

The dominant prey taxa (> 5% of the prey remains) that comprised 66% of the Cooper's hawk diet were the northern flicker, Steller's jay, American robin, mourning dove, chipmunk, and cottontail. The dominant taxa that comprised 65% of the northern goshawk diet were the cottontail, northern flicker, Abert's squirrel, Steller's jay, and red squirrel. Northern goshawks used chipmunks and Cooper's hawks used tree squirrels but they were not > 5% of the prey remains. Excluding the mourning dove that was only recorded in the diet of Cooper's hawks, these 7 taxa were all observed as frequent prey deliveries (> 4% of the deliveries) and comprised 89% and 72% of the direct observations at northern goshawk and Cooper's hawk nests, respectively (Tables II-1 and II-2).

Of the 105 northern goshawk prey remains, 38 (36.2%) were assigned to an age class. Six percent of the aged mammals and 48% of the aged birds were juveniles. Forty percent of the 316 Cooper's hawk prey remains ($N = 126$) were assigned to a juvenile or adult age class. Seventy-nine percent of the aged mammals and 34.8% of the aged birds were juveniles.

Taxonomic Comparison of Accipiter Diets--Eastern Oregon

Thirty-one percent fewer prey taxa ($\underline{N}$ = 30) were identified at Cooper's hawk nests in eastern Oregon (see Appendix in Reynolds and Meslow 1984) as compared with the number of taxa recorded at New Mexico Cooper's hawk nests. Although a comparable number of mammalian taxa ($\underline{N}$ = 9) were identified, only 21 avian taxa (as compared with 32 avian taxa in New Mexico) were recorded in the Cooper's hawk diet in eastern Oregon. Also no reptiles were identified as Cooper's hawk prey in eastern Oregon. More prey taxa ($\underline{N}$ = 37; avian taxa $\underline{N}$ = 25; mammalian taxa $\underline{N}$ = 12) were identified at Oregon northern goshawk nests than were identified at New Mexico northern goshawk nests. Sixty percent of the avian prey taxa and 75% of the mammalian prey taxa represented in the Oregon Cooper's hawk diet were represented in the Oregon northern goshawk diet.

The rankings of the prey taxa in the diets of the 2 Accipiter species in Oregon were significantly different ($\underline{U}_{\underline{S}}$ = 597, $\underline{P}$ = 0.05). The dominant prey taxa ($\geq$ 5% of the diet) that comprised 65% of the diet of the Oregon Cooper's hawks, were the chipmunk (23.3%), golden-mantled ground squirrel (16.6%), Steller's jay (7.5%), dark-eyed junco (Junco hyemalis) (6.7%), American robin (5.8%), and northern flicker (5.0%). The dominant prey taxa that comprised 51.8% of the Oregon northern goshawk diet were the Steller's jay (12.7%), snowshoe hare (Lepus sp., primarily _L. americanus_) (10.8%), American robin (8.8%), golden-mantled ground squirrel (7.5%), northern flying squirrel (_Glaucomys sabrinus_) (6.6%), and Douglas' squirrel (_Tamiasciurus douglasi_) (5.7%).

Assuming all of the prey in Reynolds and Meslow's (1984) were age classed, 17.5% of the avian prey (_N_ = 10) and 3.2% of the mammalian prey (_N_ = 2) of Oregon Cooper's hawks were juveniles. Juveniles were 24.3% of the avian prey (_N_ = 25) and 0.8% of the mammalian prey (_N_ = 1) of Oregon northern goshawks.

DISCUSSION

Method Evaluation

By comparing estimates of diet composition based on prey remain collections with estimates made from direct observations, I tested an assumption in many raptor dietary studies, namely, that periodic samples of prey remains at nests accurately characterize the relative importance of prey species in the diet (see references in Sherrod 1978). The results of this comparison validates this assumption. The prey remains method can be used to estimate the composition and relative frequencies of prey eaten by northern goshawks and Cooper's hawks during brood-rearing under the minimum sampling conditions imposed in this study. These conditions include (1) searching nest stands 3-4 times a month; (2) removing all remains during each nest visit; and (3) analyzing a minimum of 100 prey remains for each raptor species.

The results of this study also suggest that the total number of taxa recorded in the diets of the 2 Accipiter species may be a function of sample size. The number of taxa in the diets decreased as sample size decreased: the diet of New Mexico Cooper's hawk contained 44 taxa ($\underline{N}$ = 316); Oregon northern goshawk, 37 taxa ($\underline{N}$ = 228); Oregon Cooper's hawk, 30 taxa ($\underline{N}$ = 120); and New Mexico northern goshawk, 29 taxa ($\underline{N}$ = 105). To minimize the effect of a potential sample size bias, future dietary comparisons of Accipiter species should use equal number of samples per species or eliminate the rare dietary items as was done in this study.

Analysis of prey remains should be augmented by pellet analysis or direct observation in an area where Cooper's hawks feed on reptiles. For example, reptiles comprised 1.3% of the prey remains but were present in 17.8% of the pellets and 3.0% of the direct observations in this study (Table II-1).

Pellet analysis and direct observations are useful methods for augmenting the results of prey remain analyses for Accipiter species. However, they are too time-consuming to be used as the sole method in determining the relative importance of prey species in diets of Accipiter species. Researchers commonly are unable to conduct continuous observations of a large number of nests throughout brood rearing. Although pellets are easy to collect in the field, pellet analysis requires many hours in the laboratory. In addition, many of the contour and down feathers cannot be identified. Forty percent of the northern goshawk pellets and 53% of the Cooper's hawk pellets contained unidentified avian species.

Although suitable for assessing species composition and the ranking of prey species in diets of Accipiter species, the prey remains method may not accurately estimate the biomass consumed by nesting birds. Collopy (1983) found that prey remains and pellets substantially underestimated the biomass of prey delivered to the nest by golden eagles. For biomass assessments, he recommended augmenting systematic collections of pellets and prey remains with periodic direct observations at nest sites.

Accipiter Diet Comparison

Reexamining Reynolds and Meslow's (1984) dietary data with higher-level taxonomic categories supports their conclusions that the two Accipiter species use different prey taxa in eastern Oregon during the nesting season. Reynolds and Meslow (1984) concluded that the prey taxa differences they observed might be a result of competition for a limited prey resource. This implies the two species are exploiting the same prey populations which are limited. Alternatively, the dietary differences they observed could be explained by differences in foraging habitat. In their eastern Oregon study area, the Cooper's hawk and northern goshawk occupy different nesting habitats; the Cooper's hawk nest sites are 50-80-year old, even-aged, second-growth stands and the northern goshawk nest sites are dense stands of mature or old-growth conifers (Reynolds et al. 1982, Moore and Henny 1983). If we assume foraging habitat is similar to nesting habitat in eastern Oregon (no data are available on the foraging habitat of these 2 species in this area), the Cooper's hawk and northern goshawk in Oregon are hunting in different habitats and thus, hunting separate prey populations. Thus, the prey taxa differences in the diets of the 2 Accipiter species might represent variation in the abundance of the common, medium-sized vertebrates in the different foraging habitats.

In contrast to the eastern Oregon population, similar prey taxa were used by the 2 Accipiter species in New Mexico during brood rearing. In New Mexico the 2 species occupied similar nesting habitat (Kennedy 1988) and radio-telemetry data indicate they hunted in many of the same habitats during the nesting season (Kennedy unpubl.). The dietary similarities between the New Mexico Accipiter species exist probably because both species hunted the same prey populations. With the exception of the mourning dove that was frequently used by the Cooper's hawk but was not taken by the northern goshawk, the dominant prey species in the diet of the 2 New Mexico *Accipiter* species were the same 7 species of medium-sized vertebrates that were abundant within the hawks' nesting and hunting habitats throughout north-central New Mexico (Findley 1987, Stahlecker et al. 1989). Preliminary data (Morrison and Kennedy 1989, Kennedy, unpubl.) indicate these species were some of the most common medium-sized, diurnal, vertebrates within the hunting habitats of these 2 *Accipiter* species during 1986 and 1988 on the study area.

I cannot explain why the mourning dove was absent in the northern goshawk diet. Its biomass is similar to other common prey of the northern goshawk (i.e., Steller's jay and American robin) and it is a common nesting species throughout north-central New Mexico (Stahlecker et al. 1989, Kennedy unpubl.). This species was preyed upon frequently by northern goshawks but was not recorded as a Cooper's hawk prey in eastern Oregon (Reynolds and Meslow 1984).

Studies of niche overlap in predators frequently evaluate prey size overlap in addition to prey taxa overlap (Jaksić et al. 1981). Prey size partitioning has been observed in other *Accipiter* populations (Storer 1966, Opdam 1975, Snyder and Wiley 1976, Reynolds and Meslow 1984). Although similar prey taxa were used by the 2 New Mexico *Accipiter* species, the tendency for Cooper's hawks to take more juvenile (thus smaller) mammals than the northern goshawk in New Mexico may result in prey size differences between the 2 species. However, as Greene and Jaksić (1983) point out, if 2 predator species are competing for prey, it doesn't matter if the predators overlap in the sizes taken within a given prey species, they are reducing each other's prey supply. If a Cooper's hawk eats a juvenile it will not become an adult and the supply of larger (adult) prey for the northern goshawk is reduced. Conversely, a prey species eaten as an adult by a northern goshawk will reduce the Cooper's hawk's supply of smaller (juvenile) prey by precluding the reproduction of a fraction of the adult prey individuals.

Alternatively, a preference for these smaller juvenile mammals by Cooper's hawks may reflect a less risky hunting strategy for this smaller _Accipiter_ species rather than a mechanism for reducing interspecific competition with the northern goshawk. The costs of prey capture and prey handling of the larger adult mammals may be too high for the smaller Cooper's hawk but not for the larger northern goshawk. However, these costs do not preclude Cooper's hawk predation on adult mammals. On several occasions I observed male and female Cooper's hawks deliver portions of animals that were larger than the hawk before the prey was dismembered. For example, a female Cooper's hawk that weighed 375 g when she was trapped, returned to the nest with the dorsal half of a cottontail which weighed 275 g (she dropped it before delivery and I weighed it in the field). This cottontail probably weighed over 400 g at the time of capture.

Competitive coexistence has been inferred in previous investigations of Accipiter communities based on the observed patterns of dietary overlap in prey taxa and prey size (Reynolds and Meslow 1984, Diamond 1985, Simmons 1986). However, prey have not been demonstrated to be limiting in any of these dietary comparisons. In the absence of information on the extent to which food is limiting, there is considerable uncertainty about how to interpret the degree of dietary overlap between coexisting Accipiter species in terms of the potential for interspecific competition. Theoretical analyses by Abrams (1986) and Holt (1987) show that resource competition may be associated with increased, decreased, or zero niche overlap between species, depending upon the population dynamics of the species and the nature of the niche dimensions considered. Other investigations have also shown that if resources are abundant, overlap may be high without fostering competition (Wiens 1977, Pianka 1981). Overlap might also decrease during resource scarcity if the different species specialize on resources that they use most efficiently, quite independently of competitive effects (Pulliam 1986).

Although the degree of interspecific competition for prey in this study cannot be evaluated, these results indicate sympatric nesting populations of northern goshawks and Cooper's hawks do not necessarily feed on different prey species during the nesting season. Because these 2 Accipiter species are generalists and feed on a large and varying number of prey species throughout their range, I suggest that the variation in prey taxa overlap noted in this study is probably indicative of substantial opportunism in foraging by these 2 Accipiter species. Prey abundance and diversity, the differential vulnerability of different prey species to Accipiter predation, and the costs and benefits of hunting various prey can account for the observed patterns in dietary overlap among Accipiter species.

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TABLE II-1. Diet of Cooper's hawks in north-central New Mexico during brood-rearing, 1984-88.

Prey Taxon	Prey Remains		Pellets		Direct Observation	
	N[a]	(%)[b]	N	(%)[b]	N	(%)[b]
BIRDS						
Unidentified Charadriformes	1	(0.3)	0	(0.0)	0	(0.0)
American kestrel (*Falco sparverius*)	3	(1.0)	0	(0.0)	2	(1.2)
Domestic fowl (*Gallus* sp.)	3	(1.0)	0	(0.0)	0	(0.0)
Mourning dove (*Zenaida macroura*)	26	(8.2)	0	(0.0)	7	(4.2)
Band-tailed pigeon (*Columba fasciata*)	2	(0.6)	0	(0.0)	0	(0.0)
Unidentified Columbidae	2	(0.6)	0	(0.0)	0	(0.0)
Northern flicker (*Colaptes auratus*)	71	(22.5)	29	(19.2)	28	(16.8)
Red-naped sapsucker (*Sphyrapicus nuchalis*)	1	(0.3)	0	(0.0)	0	(0.0)
Williamson's sapsucker (*Sphyrapicus thyroideus*)	0	(0.0)	1	(0.7)	0	(0.0)
Sphyrapicus sp.	1	(0.3)	0	(0.0)	0	(0.0)

Hairy woodpecker (*Picoides villosus*)	1 (0.3)	1 (0.7)	2 (1.2)
Cordilleran flycatcher (*Empidonax occidentalis*)	1 (0.3)	0 (0.0)	0 (0.0)
Empidonax sp.	2 (0.6)	0 (0.0)	0 (0.0)
Ash-throated flycatcher (*Myiarchus cinerascens*)	1 (0.3)	0 (0.0)	0 (0.0)
Violet-green swallow (*Tachycineta thalassina*)	1 (0.3)	0 (0.0)	0 (0.0)
Steller's jay (*Cyanocitta stelleri*)	37 (11.7)	3 (2.0)	15 (9.0)
Scrub jay (*Aphelocoma coerulescens*)	6 (1.9)	5 (3.3)	4 (2.4)
Unidentified jay^{c}	5 (1.6)	0 (0.0)	1 (0.6)
Clark's nutcracker (*Nucifraga columbiana*)	3 (1.0)	0 (0.0)	0 (0.0)
Black-billed magpie (*Pica pica*)	1 (0.3)	0 (0.0)	0 (0.0)
Pygmy nuthatch (*Sitta pygmaea*)	1 (0.3)	0 (0.0)	0 (0.0)
Western bluebird (*Sialia mexicanus*)	9 (2.9)	1 (0.7)	6 (3.6)
Mountain bluebird (*Sialia currucoides*)	2 (0.6)	0 (0.0)	1 (0.6)
Sialia sp.	2 (0.6)	0 (0.0)	0 (0.0)

American robin (*Turdus migratorius*)	33 (10.4)	10 (6.6)	18 (10.8)
European starling (*Sturnus vulgaris*)	3 (1.0)	0 (0.0)	2 (1.2)
Yellow-rumped warbler (*Dendroica coronata*)	1 (0.3)	0 (0.0)	0 (0.0)
Unidentifed Emberizidae	1 (0.3)	0 (0.0)	0 (0.0)
Rufous-sided towhee (*Pipilo erythrophthalmus*)	7 (2.2)	1 (0.7)	0 (0.0)
Dark-eyed junco (*Junco hyemalis*)	8 (2.5)	0 (0.0)	3 (1.8)
Chipping sparrow (*Spizella passerina*)	0 (0.0)	0 (0.0)	1 (0.6)
Brown-headed cowbird (*Molothrus ater*)	1 (0.3)	0 (0.0)	1 (0.6)
Western tanager (*Piranga ludoviciana*)	1 (0.3)	0 (0.0)	0 (0.0)
Pine siskin (*Carduelis pinus*)	0 (0.0)	1 (0.7)	0 (0.0)
Lesser goldfinch (*Carduelis psaltria*)	0 (0.0)	1 (0.7)	0 (0.0)
Red crossbill (*Loxia curvirostra*)	1 (0.3)	0 (0.0)	0 (0.0)
House finch (*Carpodacus mexicanus*)	1 (0.3)	1 (0.7)	4 (2.4)
Evening grosbeak (*Coccothraustes vespertinus*)	0 (0.0)	1 (0.7)	0 (0.0)
Unidentified finch (Fringillidae)	1 (0.3)	0 (0.0)	3 (1.8)

Unidentified Passeriformes	2 (0.6)	4 (2.7)	2 (1.2)
Unidentified bird[d]	11 (3.5)	80 (53.0)	0 (0.0)
MAMMALS			
Cottontail (*Sylvilagus* sp.)	18 (5.7)	11 (7.3)	7 (4.2)
Abert's squirrel (*Sciurus aberti*)	5 (1.6)	26 (17.2)	9 (5.4)
Red squirrel (*Tamiasciurus hudsonicus*)	2 (0.6)	14 (9.3)	2 (1.2)
Unidentified tree squirrel[e]	1 (0.3)	0 (0.0)	0 (0.0)
Chipmunk (*Tamias* sp.)	25 (7.9)	84 (55.6)	41 (24.6)
Golden-mantled ground squirrel (*Spermophilus lateralis*)	1 (0.3)	15 (9.9)	1 (0.6)
Rock squirrel (*Spermophilus variegatus*)	1 (0.3)	1 (0.7)	1 (0.6)
Wood-rat (*Neotoma* sp.)	3 (0.9)	0 (0.0)	1 (0.6)
Deer mouse (*Peromyscus maniculatus*)	0 (0.0)	1 (0.7)	0 (0.0)
Peromyscus sp.	0 (0.0)	1 (0.7)	0 (0.0)
Unidentified Cricetidae	1 (0.3)	2 (1.3)	0 (0.0)
Unidentified Microtine	1 (0.3)	4 (2.7)	0 (0.0)
Unidentified rodent (Rodentia)	0 (0.0)	3 (2.0)	0 (0.0)
Unidentified mammal	1 (0.3)	1 (0.7)	0 (0.0)

REPTILES			
Eastern fence lizard			
(Sceloporus undulatus)	1 (0.3)	10 (6.6)	0 (0.0)
Sceloporus sp.	0 (0.0)	3 (2.0)	0 (0.0)
Little striped whiptail			
(Cnemidophorus inornatus)	2 (0.6)	2 (1.3)	1 (0.6)
Cnemidophorus sp.	0 (0.0)	7 (4.6)	2 (1.2)
Western terrestrial garter snake			
(Thamnophis elegans)	1 (0.3)	0 (0.0)	2 (1.2)
Unidentified reptile	0 (0.0)	5 (3.3)	0 (0.0)
TOTAL	316 (99.5)	151[f] --	167 (100.2)

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[a] For the prey remains method, this represents the minimum number of individuals.

[b] The number in parentheses is frequency of occurrence.

[c] This is either a Steller's jay or a scrub jay.

[d] This includes avian species that have not been previously identified.

[e] This is either an Abert's squirrel or a red squirrel.

[f] This is the total number of pellets analyzed. It is a smaller number than the column total because more than one species can occur in one pellet.

TABLE II-2. Diet of northern goshawks in north-central New Mexico during brood-rearing, 1984-88.

	Prey Remains		Pellets		Direct Observation	
Prey Taxon	N[a]	(%)[b]	N	(%)[b]	N	(%)[b]
BIRDS						
Cooper's hawk (*Accipiter cooperii*)	2	(1.9)	0	(0.0)	0	(0.0)
American kestrel (*Falco sparverius*)	1	(1.0)	0	(0.0)	0	(0.0)
Prairie falcon (*Falco mexicanus*)	1	(1.0)	0	(0.0)	0	(0.0)
Rock dove (*Columba livia*)	2	(1.9)	0	(0.0)	0	(0.0)
Northern pygmy-owl (*Glaucidium gnoma*)	1	(1.0)	0	(0.0)	0	(0.0)
Belted kingfisher (*Ceryle alcyon*)	2	(1.9)	0	(0.0)	0	(0.0)
Northern flicker (*Colaptes auratus*)	15	(14.3)	25	(39.7)	5	(13.9)
Red-naped sapsucker (*Sphyrapicus nuchalis*)	0	(0.0)	1	(1.6)	0	(0.0)
Williamson's sapsucker (*Sphyrapicus thyroideus*)	1	(1.0)	0	(0.0)	0	(0.0)
Hairy woodpecker (*Picoides villosus*)	0	(0.0)	1	(1.6)	0	(0.0)

Steller's jay (*Cyanocitta stelleri*)	9 (8.6)	8 (12.7)	4 (11.1)
Scrub jay (*Aphelocoma coerulescens*)	1 (1.0)	0 (0.0)	0 (0.0)
Unidentified jay[c]	2 (1.9)	0 (0.0)	0 (0.0)
Common raven (*Corvus corax*)	3 (2.9)	0 (0.0)	0 (0.0)
Clark's nutcracker (*Nucifraga columbiana*)	3 (2.9)	0 (0.0)	1 (2.8)
Western bluebird (*Sialia mexicanus*)	2 (1.9)	0 (0.0)	0 (0.0)
Mountain bluebird (*Sialia currucoides*)	0 (0.0)	1 (1.6)	0 (0.0)
Hermit thrush (*Catharus guttatus*)	1 (1.0)	0 (0.0)	0 (0.0)
American robin (*Turdus migratorius*)	7 (6.7)	5 (7.9)	2 (5.6)
European starling (*Sturnus vulgaris*)	0 (0.0)	1 (1.6)	0 (0.0)
Rufous-sided towhee (*Pipilo erythrophthalmus*)	0 (0.0)	2 (3.2)	0 (0.0)
Evening grosbeak (*Coccothraustes vespertinus*)	1 (1.0)	0 (0.0)	0 (0.0)
Unidentified finch (Fringillidae)	1 (1.0)	0 (0.0)	0 (0.0)
Unidentified Passeriformes[d]	0 (0.0)	3 (4.8)	0 (0.0)
Unidentified bird[d]	0 (0.0)	25 (39.7)	0 (0.0)

MAMMALS			
Cat (*Felis* sp.)	1 (1.0)	0 (0.0)	0 (0.0)
Cottontail (*Sylvilagus* sp.)	21 (20.0)	4 (6.4)	4 (11.1)
Abert's squirrel (*Sciurus aberti*)	9 (8.6)	26 (41.3)	11 (30.6)
Red squirrel (*Tamiasciurus hudsonicus*)	3 (2.9)	11 (17.5)	2 (5.6)
Unidentified tree squirrel[e]	7 (6.7)	3 (4.8)	1 (2.8)
Chipmunk (*Tamias* sp.)	2 (1.9)	8 (12.7)	3 (8.3)
Golden-mantled ground squirrel (*Spermophilus lateralis*)	2 (1.9)	11 (17.5)	2 (5.6)
Rock Squirrel (*Spermophilus variegatus*)	0 (0.0)	3 (4.8)	1 (2.8)
Unidentified Microtine	0 (0.0)	2 (3.2)	0 (0.0)
Unidentified rodent (Rodentia)	0 (0.0)	4 (6.4)	0 (0.0)
Unidentified mammal	5 (4.8)	1 (1.6)	0 (0.0)
TOTAL	105 (100.7)	63[f] --	36 (100.2)

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[a] For the prey remains method, this represents the minimum number of individuals.

[b] The number in parentheses is frequency of occurrence.

[c] This is either a Steller's Jay or a scrub jay.

[d] This category includes avian species that were not already included in the list.

[e] This is either an Abert's squirrel or a red squirrel.

[f] This is the total number of pellets analyzed. It is a smaller number than the column total because more than one species can occur in one pellet.

CHAPTER III

NORTHERN GOSHAWKS AND COOPER'S HAWKS: ARE THEY SIT-AND-WAIT PREDATORS?

Summary. Activity and movement patterns of hunting northern goshawks (Accipiter gentilis) (n = 8) and Cooper's hawks (A. cooperi) (n = 24) were examined with radiotelemetry during brood-rearing in 1984, 1986, and 1988 in north-central New Mexico. These accipiters foraged widely by flying for 1 to 3 min to a new perch every 8 to 13 min. Activity patterns differed between the two species and by sex but the patterns were not related to body mass. Male northern goshawks flew more often ($\bar{x}$ = 3.1 flights/hr) and spent a greater percent of their day ($\bar{x}$ = 18.2%) in flight than did the male and female Cooper's hawks and the female northern goshawks. Female northern goshawks were the least active of the accipiters (mean flight rate = 2.3 flights/hr; mean percent time in flight/day = 6.1%). Flight rates of male and female Cooper's hawks were not significantly different ($\bar{x}$ = 2.8 flights/hr in both sexes), but the males spent more time each day in flight ($\bar{x}$ = 13.7%) than the females ($\bar{x}$ = 10.7%). Flight bout duration, perching rate, and perch bout duration were not significantly different between the species or sexes. Average interperch distances for the two species and the two sexes ranged from 722-964 m and average flight velocities ranged from 5.2-13.8 m/sec.

Neither of these movement parameters differed significantly by species or sex. None of the activity and movement parameters was a function of time of day or brood size. However, all accipiters spent significantly more time in flight per day when feeding nestlings ($\underline{\bar{x}}$ = 14.7%) then when feeding fledglings ($\underline{\bar{x}}$ = 9.3%). Contrary to the literature that describes accipiters as typical sit-and-wait predators, the northern goshawk and Cooper's hawk have a typical saltatory pattern of hunting. Similarities in the foraging behavior of the two species are probably related to their dietary similarities. The results of this study do not support the hypothesis that accipiters of different species coexist by utilizing different foraging modes.

Ecologists generally categorize animal foraging strategies as either "cruise" or "ambush" (Pianka 1966; Eckhardt 1979; Gendron and Staddon 1983), depending on the animal's overall search strategy. These two categories of behavior have also been called "widely ranging" and "sit-and-wait" foraging, respectively (Huey and Pianka 1981). Ambush predation is characterized by a long motionless period of scanning and then a repositioning move. Typical ambush foragers are lions (_Panthera_ sp.), rattlesnakes (_Crotalus_ sp.), and herons. Cruise predation is thought to be characterized by uninterrupted scanning and is exemplified by large fish that swim continuously, such as tuna, and by soaring hawks.

Recently, Evans and O'Brien (1988) described a search strategy that is intermediate to cruise and ambush searching which they termed "saltatory." Saltatory foraging is characterized by a stop-and-go pattern where the animal repositions itself frequently to scan from a new location. Both ambush and saltatory foragers search for prey while pausing unlike cruise foragers that search while moving. One of the primary differences between saltatory and ambush foragers is the frequency of repositioning moves (O'Brien et al. 1989, 1990). The types of saltatory search are highly variable; some species pause briefly, whereas other species pause for longer periods and then move a short distance. Saltatory search can also vary within species in response to changes in prey availability (O'Brien et al. 1989).

Among raptors, accipiters are described as typical ambush predators (Pianka 1983:274; Schoener 1971, 1984). These original descriptions were based on limited data because the foraging behavior of free-ranging accipiters is very difficult to study; most Accipiter species are forest-dwelling and hunt below the canopy. Studies by Kenward (1982) and Widén (1984) on wintering European goshawks (A. g. gentilis) in Sweden have shown the utility of radiotelemetry for determining the frequency and duration of behavioral bouts such as flying, perching and prey handling. Their data, combined with qualitative descriptions of hunting patterns of breeding European Sparrowhawks (*A. nisus*) in Great Britain (Newton 1986), and radiotelemetry data collected by Fischer (1986) on activity patterns of breeding accipiters in Utah, suggest that accipiters perch briefly, search for prey from these perches and then move elsewhere if potential prey are not encountered within a few minutes.

In this study, I used radiotelemetry to examine activity and movement patterns of sympatric populations of Cooper's hawks and northern goshawks in north-central New Mexico to determine the type of search strategy used by hunting accipiters during brood rearing. These species differ in body size (*A. gentilis* is the larger), but both exhibit pronounced sexual size dimorphism (females are larger). In flying animals, the ratio of moving metabolic rate to basal metabolism rises with size (Peters 1983). Larger animals may compensate for these higher costs by moving less. Earlier work on avian activity patterns suggest that larger birds may be less active than smaller birds (Gibb 1954; Pearson 1968). Based on this information, I predicted that the larger *Accipiter* species should have a more sedentary or ambush-like search strategy than the smaller *Accipiter* species. In addition, I predicted that the larger females would be less active than the smaller males while searching for prey.

Other factors that could influence activity levels and subsequent search strategies were investigated in this study which included, time of day, brood size and age of young. Some populations of nesting accipiters exhibit diurnal patterns of activity (Fitch et al. 1946; Fischer 1986) while other populations are active all day (Murphy et al. 1988). Temporal variation in accipiter activity is assumed to be related to the activity patterns of their principal prey species (Fischer 1986) and/or the hunger level of the adults or offspring (Widén 1984). The hunger level of the offspring is a function of their energy requirements which is a function of the brood size and their age.

Study area

The study area was within the Jemez Mountains, New Mexico and adjacent Pajarito Plateau. These mountains are characterized by steep terrain dominated by typical southwestern montane habitat types such as ponderosa pine and mixed conifer forests. The Pajarito Plateau, a table-like extension of the eastern flank of the Jemez Mountains, is cut into numerous, narrow, finger-like mesas by southeast-trending, intermittent streams. The mesas are dominated by pinyon-juniper woodland. The drainages contain riparian habitats dominated by ponderosa pine (Pinus ponderosa) or cottonwood (Populus sp.) stands and flow into the Rio Grande. Habitat along the Rio Grande is characterized by a variety of deciduous riparian communities. The study area is described in detail in Kennedy (1988).

Methods

Data collection

During the nestling stage of 1984, 1986, and 1988, I trapped adults near their nest with a dho-gaza net and a live great horned owl (Bubo virginianus), or with balchai-tri traps (Bloom 1987) baited with a variety of suitable prey such as rock doves (Columba livia), European starlings (Sturnus vulgaris), or house sparrows (Passer domesticus) (Bloom 1987).

To obtain activity and movement information on the nesting adults, I attached single-stage transmitter packages on the dorsal surface of the bird's tail (manufactured by Biotrack, Dorset, U.K.) or back (L&L Electronics, Mahomet, IL). Tail-mounted transmitters weighed 6-10 g and backpacks weighed 12-18 g.

Each transmitter was equipped with a posture-sensitive activity switch that altered the signal pulse rate when the transmitter was positioned vertically (slow pulse, as when perched) or horizontally (fast pulse, as when in flight). Transmitter frequency was 150-151 MHz. Radio receiving equipment included an AVM Instrument Co. (Dublin, CA) Model LA-12 receiver; Custom Electronics of Urbana, Inc. (Urbana, IL) LA-12 and Merlin receivers; a

Biotrack receiver; six hand-held, 3-element Yagi antennae (Custom Electronics of Urbana, Inc.); and two null peak antennae (Custom Electronics of Urbana, Inc.).

During 1984 and 1986, all transmitters were tail mounted. Due to a few problems of premature molting of the tailmounts in 1986, I used some backpacks in 1988 on female Cooper's hawks and northern goshawks. Both transmitter attachments are described in Kenward (1987:104-107, Fig. 5-1a).

The transmitter attachments annoyed the birds for the first few days after tagging, as judged from visual observations of the birds biting or pulling on the harness material and the antennae, and preening disrupted feathers. However, the birds appeared to adjust to the package and the transmitters did not appear to hinder their hunting ability or nesting success. Nests of radio-tagged hawks (northern goshawks, $n = 6$; Cooper's hawks, $n = 12$) fledged more young (northern goshawks, $\bar{x} = 2.0$ yg/successful nest; Cooper's hawks, $\bar{x} = 2.75$ yg/successful nest) than nests of untagged birds (northern goshawk, $\bar{x} = 1.66$ yg/successful nest, $n = 4$; Cooper's hawk, $\bar{x} = 2.27$ yg/successful nest, $n = 11$). In addition, prey delivery rates at Cooper's hawk nests of tagged birds ($\bar{x} = 3.51$ prey deliveries/day) were similar to prey delivery rates at nests of untagged birds ($\bar{x} = 3.86$ prey deliveries/day). Not enough data were available on prey delivery rates of untagged northern goshawks to do a similar comparison for that species (Chapter II).

Radio monitoring for data collection commenced after the birds accepted the transmitters, which was within a few days of tagging. It continued until either the batteries failed, the birds molted the rectrices with the tail mount, or the birds left the study area. Signals were monitored simultaneously by a minimum of two mobile observers on the ground, each equipped with a receiver, a Yagi antenna, and a null peak antenna. Yagi antennae were used to obtain a general location of the bird from a distance and null peak antennae were used to acquire more accurate bearings once an observer was within 0.4 km of the bird.

The bird's location was obtained using standard triangulation techniques (Kenward 1987) at a distance that minimized the disturbance to the bird (> 100 m) and reduced the measurement error associated with the bird's true bearing. Based on 50 tests in different habitats, the standard deviation of errors between observed and true bearings was 5^{o} (calculated as in Lee et al. [1985]). This measurement error was used to estimate the error of the bird's position obtained from triangulation using the program FIXX (developed by G. A. Rinker, Los Alamos National Laboratory, unpubl.). The error analysis generated by FIXX was a measurement error analysis rather than a sampling error analysis. Sampling errors are analyzed primarily with statistical techniques. Measurement errors may be analyzed by analytical means, given some assumptions about errors in the measurements. These measurement errors are estimates of the variance associated with each location had I carried out repeated mesurements of each location for each bird.

A bird's position is determined by triangulation from two points (x_a, y_a) and (x_b, y_b) with observed bearings θ_a and θ_b. I assume the observer location, θ_a and θ_b were determined with no uncertainty. The error in x_i is then

$$(\sigma x_i)^2 = ([dx_i/d\theta_a]\sigma\theta_a)^2 + ([dx_i/d\theta_b]\sigma\theta_b)^2 \qquad (1)$$

with a corresponding expression for y_i.

This approach assumes all errors are statistically independent and combine quadratically. For example, if $(\sigma x_1)^2$ and $(\sigma y_1)^2$ are the uncertainties in coordinate x_1, y_1 and $(\sigma x_2)^2$ and $(\sigma y_2)^2$ are the uncertainties in coordinate x_2, y_2, then the estimated uncertainty in the separation (distance) between these two points is

$$\sigma_d = ([\sigma x_1]^2 + [\sigma y_1]^2 + [\sigma x_2]^2 + [\sigma y_2]^2)^{1/2}. \qquad (2)$$

The behavioral sampling method used was focal animal sampling (Altman 1974). During 2-4 hr sample periods, the signal of a systematically chosen bird was continuously monitored. Perching and flight bouts were timed to the nearest second. Preening and prey-handling movements monitored. Perching and flight bouts were timed to the nearest second. Preening and prey-handling movements produced brief changes in the pulse rate of the signal similar to the pulse rate of a very short flight. I defined a flight as a period when the fast pulse lasted at least 5 sec. Briefer periods of fast pulses and pulses of any duration that were erratic were recorded as stationary activity bouts (SABs) (Fischer 1986). I established these definitions by monitoring the behavior of trained falconry birds temporarily equipped with transmitters and by spending several hours simultaneously radiotracking and visually observing birds near nests. With some training, field personnel could consistently identify flights by changes in volume and pitch of the signal combined with a signal direction change (Kenward 1987). The SABs were not included in the analyses because they were comprised of a variety of unidentifiable behaviors that I assumed did not reflect searching behavior.

To examine diurnal patterns in activities, daylight hours were divided into four, 4-hr periods: (1) 0500-0900, (2) 0900-1300, (3) 1300-1700, and (4) 1700-2100. Each sampling interval was assigned to one of these periods. Brood sizes at the time of data collection were categorized as small if they contained 1-2 young (Cooper's hawk) or one young (northern goshawk), or large if more young were present. Young were classified as either nestlings (1-5 weeks for Cooper's hawks and 1-6 weeks for northern goshawks) or fledglings (> 5 weeks for Cooper's hawks and > 6 weeks for northern goshawks). I concentrated my efforts on the nestling and fledgling-dependency periods of the breeding cycle because at this time the energy demands of the young should force adults to devote more time to hunting. Only data on adults known to be providing food to young are presented.

Statistical analyses

Frequency distributions of flight and perch durations were generated for each hawk and visually evaluated to determine if individuals within a species and sex could be pooled into a group distribution. The intra-group variation visually appeared to be smaller than the inter-group variation so the individuals within a species/sex group were pooled. These pooled distributions of the flight and perching durations were compared between species and sexes with the Kolmogorov-Smirnov test (Sokal and Rohlf 1981). Perching and flight frequencies (number/hr), mean duration of perching and flight bouts, overall percent time in flight, and mean interperch distances (m) were calculated for each 2-4 hr sample period. Only interperch distances with an estimated uncertainty (σ_d) of < 500 m were included in the analyses.

Differences between main effects (species, sex, time of day, brood size, and age of young) and all interactions were evaluated for each of the preceding six variables using a factorial ANOVA. Raw data on perching and flight duration, and interperch distances were not normally distributed, so sample means (which were normally distributed) were used as data points.

The significance level for an individual comparison was $\underline{p} = 0.1$ for all tests. When multiple comparisons were conducted the significance level for all comparisons was equal to 0.1 divided by the number of comparisons (Snedecor and Cochran 1980).

RESULTS

Activity Patterns

A total of 326.5 and 573.8 hr of activity data were collected on 8 northern goshawks and 23 Cooper's hawks, respectively. The total tracking time per bird ranged from 21.7-84.3 hr for northern goshawks ($\underline{\bar{x}} = 40.8$ hr) and 5.5-66.5 hr for Cooper's hawks ($\underline{\bar{x}} = 24.2$ hr). The number of perching and flight bouts observed for each species and sex (pooled over all individuals within each species/sex category) are presented in Figs. III-1 and III-2. The total number of sample periods for each species and sex is presented in Table III-1.

Perching duration was highly skewed toward shorter durations (Figs. III-1 and III-3a). Median perch duration was 3.5 min for male and female northern goshawks, and 1.0 min for male and female Cooper's hawks (Table III-2). Seventy-five percent of all perches had durations of 5 min or less for all accipiters (Fig. III-3a). The perch time distributions were not significantly different between male and female northern goshawks (Kolmogorov-Smirnov test, $\underline{D} = 0.023$, $\underline{p} > 0.025$) so I combined these two distributions to compare with the Cooper's hawk perching distributions. The perch time distribution for all female Cooper's hawks was not significantly different from the pooled northern goshawk ($\underline{D} = 0.045$, $\underline{p} > 0.025$) distribution. The perch time distribution for male Cooper's hawks differed from the perch time distributions of female Cooper's hawks ($\underline{D} = 0.054$, $\underline{p} < 0.025$) and northern goshawks ($\underline{D} = 0.111$, $\underline{p} < 0.025$). The male Cooper's hawk had a higher frequency of perching durations that were less than 5 min (78%) than did the other birds (70%).

Mean perching bout duration ranged between 9-13 min for the 4 species/sex classes (Fig. III-1) and mean perching rates were about 3-4 perches/hr (Table III-1) in all groups. Perching bout duration and perching rate were not significantly different between species (ANOVA, perch bout $\underline{F} = 0.02$, $\underline{p} = 0.88$; perch rate $\underline{F} = 4.05$, $\underline{p} = 0.05$), sex (perch bout $\underline{F} = 0.16$, $\underline{p} = 0.69$; perch rate $\underline{F} = 0.09$, $\underline{p} = 0.76$), or the interaction of species and sex (perch bout $\underline{F} = 0.31$, $\underline{p} = 0.58$; perch rate $\underline{F} = 0.58$, $\underline{p} = 0.45$).

were 30 sec for the northern goshawks and 15 sec for the Cooper's hawks. Seventy-five percent of all Cooper's hawk flights were 40 sec or less; 75% of all female northern goshawk flights were 20 sec or less; and 75% of all male northern goshawk flights were 80 sec or less (Fig. III-3a). Flights exceeding 2 min were frequently observed visually and consisted predominantly of fixed-wing soaring. These comprised 16.2% and 6.6% of the flights of male and female northern goshawks, respectively, and 10.2% and 10.7% of the flights of male and female Cooper's hawks, respectively.

The flight time distributions differed significantly between species ($D = 0.068$, $p < 0.025$), and the northern goshawk distributions differed significantly between the sexes ($D = 0.104$, $p < 0.025$). The flight time distribution of the male and female Cooper's hawks were not significantly different ($D = 0.031$, $p > 0.025$).

Average flight bout durations ranged from 1.1 min for the female northern goshawk to 2.3 min for the male northern goshawk (Fig. III-2). Flight bout duration was not significantly different between species ($F = 1.73$, $p = 0.19$), sex ($F = 1.18$, $p = 0.28$), or the interaction of species and sex ($F = 2.03$, $p = 0.16$). Flight rate and daily percent time in flight (Table III-1) did have a significant species and sex interaction (flight rate $F = 8.44$, $p = 0.004$; % flight time $F = 5.9$, $p = 0.016$). The male northern goshawk had the highest flight rate and spent significantly more time in flight on a daily basis than the other accipiters. Conversely, the female northern goshawk had the lowest flight rate and spent the least amount of time in flight. These two variables did not differ significantly between the sexes of Cooper's hawks.

Movement patterns

Although the trend was nonsignificant (F = 1.75, p = 0.19), the males, which had higher flight rates and spent a greater percentage of time in flight, had shorter interperch distances (northern goshawk, $\bar{X}$ = 722.1 m; Cooper's hawk, $\bar{X}$ = 802.2 m) than the females (northern goshawk, $\bar{X}$ = 918.5 m; Cooper's hawk, $\bar{X}$ = 963.8 m) (Table III-1).

Using the mean flight bout durations (Fig. III-2) and interperch distances (Table III-1) average flight velocities were calculated for the interperch movements. Average interperch velocities were: female northern goshawk-13.8 m/sec; male northern goshawk-5.2 m/sec; female Cooper's hawk-10.5 m/sec; and male Cooper's hawk-9.2 m/sec.

Daily rhythms

No significant diurnal rhythm patterns were observed in perch bout duration (F = 1.02, p = 0.39), perching rate (F = 1.04, p = 0.38), flight bout duration (F = 0.43, p = 0.73), flight rate (F = 0.69, p = 0.56), and percent time in flight ($F = 0.69$, $p = 0.56$). No significant interactions with time of day and the other main effects occurred.

Influence of brood size

Adults feeding small broods did not differ significantly from adults feeding large broods in their perch bout duration ($F = 0.20$, $p = 0.65$), perching rate ($F = 0.01$, $p = 0.91$), flight bout duration ($F = 0.29$, $p = 0.59$), flight rate ($F = 0.45$, $p = 0.50$), and percent time in flight ($F = 0.45$, $p = 0.50$) by adults feeding small or large broods. There were no significant interactions with brood size and other main effects.

Influence of offspring age

The only parameter that varied significantly between the nestling stage and the fledgling dependency stage was the percent time spent in flight ($F = 7.16$, $p = 0.008$). Significantly more time was spent in flight by birds feeding nestlings ($\bar{x} = 14.7\%$) then by birds feeding fledglings ($\bar{x} = 9.3\%$).

DISCUSSION

Although differences in the activities of the two species and two sexes were observed in this study, the activity and movement patterns had many similarities. Activity and movement patterns of all individuals were characterized by numerous perching bouts, which averaged

9-13 min (Fig. III-1), alternated with short flights, which averaged 1-2 min, (Fig. III-2) and covered distances of 700-1000 m (Table III-1).

The differences in activity and movement patterns were not related to body size. The male northern goshawk (the second largest in body size of the two species and two sexes) spent the most time in flight and had the highest flight rate. The female northern goshawk (the largest accipiter in this study) spent the least amount of time in flight and had the lowest flight rate. Both sexes of the smaller Cooper's hawk were intermediate in activity and movement patterns (Table III-1).

The activity and movement differences observed between the accipiters were probably a result of the sex role partitioning exhibited by raptors during the nesting season (Newton 1979). Although females do hunt during the latter part of the nestling stage and the fledgling-dependency stage, the male is the primary food provider throughout the nesting season. Except in cases where the male is not providing enough food to meet family requirements (Chapter IV), the female rarely delivers food at a rate equivalent to the male. This is reflected in the higher activity rates of the males as compared with females.

The absence of diurnal rhythms in activity patterns suggest the foraging birds are hunting throughout the day. Both Accipiter species in this study hunt common, diurnal medium-sized birds and mammals (Chapter II). Based on prey census data (P. L. Kennedy unpubl.), the avian prey of the hawks in this area were more active during early morning and evening periods while the diurnal mammals were more active during mid-day. Thus, prey were available throughout the day alleviating the necessity of focusing hunting activities to certain periods of the day. In addition, the hunting adults' foraging efficiency may not be high enough to meet the high energy requirements of the family (see Chapter IV) without hunting all day.

Offspring age and brood size had no significant effect on activity and movement parameters of the hunting adults, with the exception of total time in flight on a daily basis. This suggests that adult accipiters respond to the increased demands of the young (growing nestlings require more energy than do fledglings, Walsberg 1983) by spending a greater proportion of the diurnal period hunting, but do not change their hunting mode, e.g., flight bout duration, flight rate, and interperch distances.

Activity and movement data from three other populations of northern goshawks and Cooper's hawks are summarized in Table III-2. The two studies on the European goshawk were conducted during the winter. Fischer's (1986) study was conducted during the breeding season but he concentrated on the two smaller North

American Accipiter species, the sharp-shinned hawk (A. striatus), and the Cooper's hawk; he radio-tracked only one male northern goshawk. In general, the activity patterns of northern goshawks noted in the four studies were comparable; the medians were within the interquartile ranges recorded in this study (Fig. III) and most of the mean values were within the 95% confidence intervals recorded in this study (Table III-1). The exceptions were the average flight duration of the male northern goshawk in Utah (Table III-2) and the percent of time spent in flight by males of both species on a daily basis.

The average flight duration of the Utah northern goshawk and the average percent time in flight of males in the other three studies were outside the 95% confidence interval of these parameters in this study (Table III-1 and Fig. III-2). As would be expected the breeding males spent more time in flight than the wintering males because they were feeding young. It is interesting that the female northern goshawks did not spend substantially more time in flight during the nesting season than during winter (Table III-2). This is probably because they are not the primary food provider at any time during the nesting season. The difference between the mean flight durations recorded in Utah and in this study may be a result of the small sample of males observed in both studies.

The only data available for comparison of interperch distances is Kenward's (1982) on wintering European goshawks (Table III-2). His interperch distances were shorter and outside the 95% confidence intervals of the interperch distances recorded in this study (Table III-1).

The activity patterns of the Utah and New Mexico Cooper's hawks were also similar within species. The only differences were the median perch time of female Cooper's hawks (shorter in New Mexico) and the mean perch duration of males (longer in New Mexico). None of the flight parameters recorded in Utah was outside the 95% confidence intervals of the same parameters recorded in this study.

It is surprising that the data from the four studies agree so closely since the two European studies were conducted on a different northern goshawk subspecies at a different time of the year, and the prey types and habitats used by both the northern goshawks and Cooper's hawks varied among all the study areas.

To examine the type of search strategy used by the accipiters in this study, I combined means for flight bout times, perch bout times and interperch distances to portray a typical foraging bout (Fig. III-4). Based on the afore-mentioned comparison, the patterns in this figure appear to be applicable to other populations of northern goshawks and Cooper's hawks. Characteristic resource by one of the species or the interference with one species' access to the resource by another has negative effects.

In this study area the two Accipiter species did not differ significantly in their nesting habitat (Kennedy 1988) and prey taxa utilization patterns (Chapter II). Although preference analyses have not been conducted with the habitat and prey utilization data, both species use habitats and prey types that are common throughout the study area (Kennedy 1988, Chapter II). The results of this study indicate that the foraging patterns of the two species also do not differ (Fig. III-4). In the absence of evidence that prey is a limiting resource to this accipiter population, the most parsimonious explanation for these comparable foraging patterns is they are probably a result of the similar diets and hunting habitats (Kennedy 1988, Chapter II, P.L. Kennedy, unpubl. data) used by the accipiters in this study. The use of similar foraging modes to obtain similar prey that were common during the study period is probably indicative of substantial opportunism in foraging by these two Accipiter species.

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Table III-1. Mean activity rates, percent time in flight, and interperch distances of nesting northern goshawks and Cooper's hawks in north-central New Mexico during brood rearing in 1984, 1986, and 1988

	northern goshawk		Cooper's hawk	
	Male	Female	Male	Female
Sample sizes				
No. hawks	3	5	10	13[a]
No. samples	33	60	66	98
Perching rate[b]				
mean	3.17	3.12	4.15	3.6
±95% C.I.	0.66	0.60	0.49	0.4
Flight rate[b]				
mean	3.12	2.28	2.83	2.8
±95% C.I.	0.71	0.54	0.46	0.4
% Time in flight[c]				
mean	18.24	6.14	13.74	10.7
±95% C.I.	3.80	3.38	3.70	2.4
Interperch distance (m)				
mean	722.1	918.5	802.2	963.8
±95% C.I.	148.8	394.1	268.2	342.4

[a] One female that was tracked during both 1986 and 1988 was paired with a different male during both nesting periods so in the analyses she is treated as a different bird during each year.

[b] Rates are number/hr

[c] Percent of daylight hours was based on 2-week averages of daylength data collected at a meteorological station in the study area at Los Alamos National Laboratory (see Chapter IV for additional details on the meteorological station).

Table III-2. A summary of activity and movement patterns of different populations of northern goshawks and Cooper's hawks

Study	Location	Perching duration (min)		Flight duration (min)		% Time flight[a]	Inter-perch distance (m)
		$\bar{X}$	Median	$\bar{X}$	Median	$\bar{X}$	$\bar{X}$
Northern goshawk							
Kenward (1982)[b]	central Sweden/ England[c]	NA[d]	3[e]	NA	0.2-0.3[f]	NA	100-200[f]
Widén (1984)	central Sweden						
male		8.6	3	1.4	0.4	4	NA
female		10.4	3	1.6	0.4	3.5	NA
Fischer (1988)	Utah						
male		8.6	4	1.1	0.3	11.2	NA
This study	New Mexico						
male		11.2	3.5	2.3	0.5	18.2	722.1
female		12.7	3.5	1.1	0.5	6.1	918.5

Cooper's hawk							
Fischer (1988)	Utah						
male		6.2	2	1.2	0.3	14.9	NA
female		13.9	6	1.8	0.3	10.9	NA
This study	New Mexico						
male		8.7	1	1.5	0.3	13.7	802.2
female		11.8	1	1.5	0.3	10.7	963.8

---

[a] Percent of daylight hours was based on 2-week averages of daylength data collected at a meteorological station in the study area at Los Alamos National Laboratory (see Chapter IV for additional details on the meteorological station)

[b] The results are not separated by sex in this study

[c] The two studies on the European goshawk were conducted during the winter

[d] NA=data not available

[e] These are median perch durations for wild European goshawks in Sweden

[f] These are estimates calculated by Fischer (1986) and are based on recorded median flight distances for partially tamed European goshawks released in England of 100 m in woodland habitat and 200 m in open habitat, and an assumed average flight speed of 10 m/sec

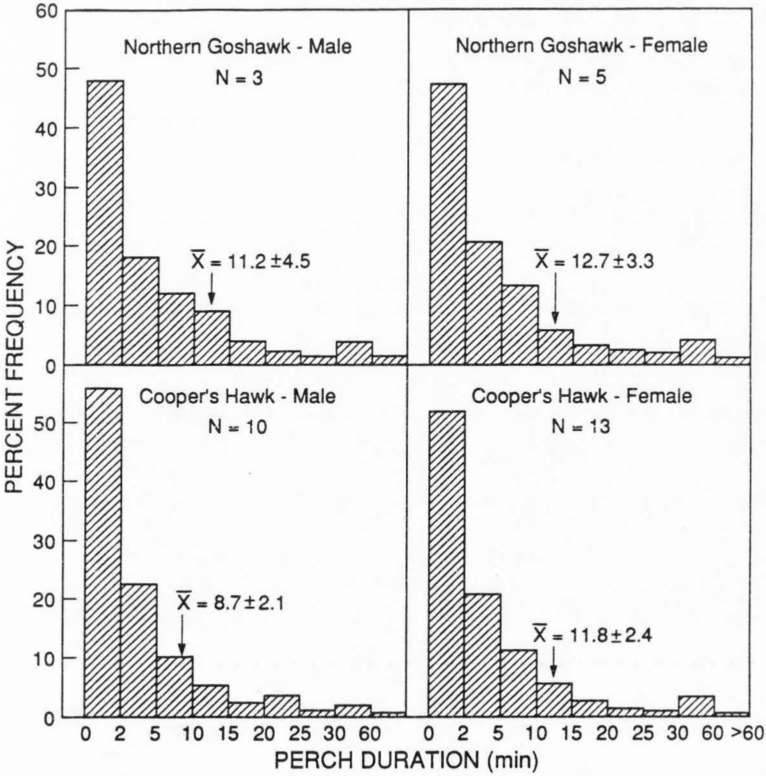

Fig. III-1. Perching duration frequencies of northern goshawks and Cooper's hawks feeding young in north-central New Mexico. Each bar represents the percent of observed perches that were within a certain duration range. For example, 20% of all perches recorded for male Cooper's hawks were > 2 min and ≤ 5 min in duration.

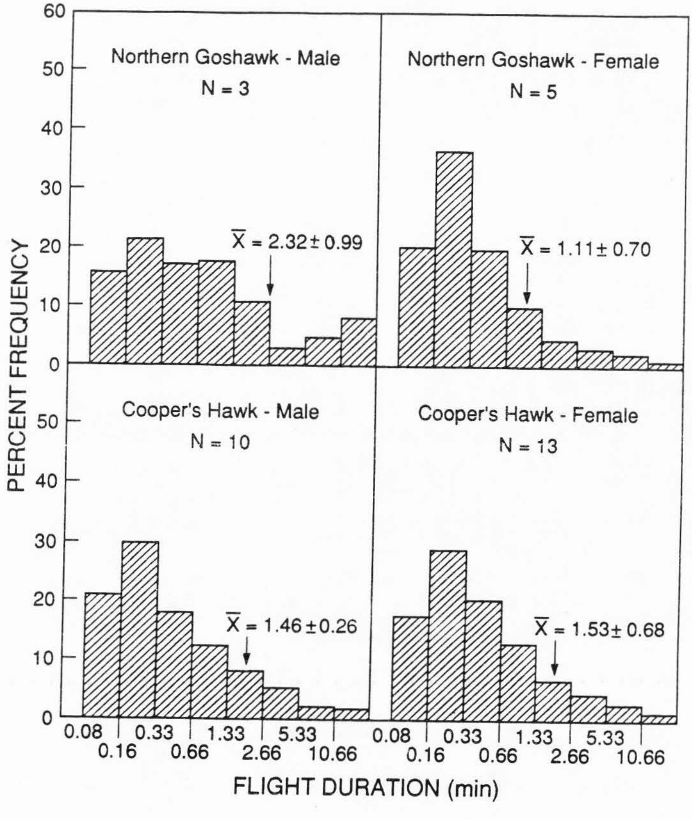

Fig. III-2. Flight time frequencies of northern goshawks and Cooper's hawks feeding young in north-central New Mexico. Each bar represents the percent of observed perches that were within a certain duration range. For example, 30% of all flights recorded for male Cooper's hawks were > 0.16 min and ≤ 0.32 min in duration. By definition (see text) there were no flights < 0.08 min.

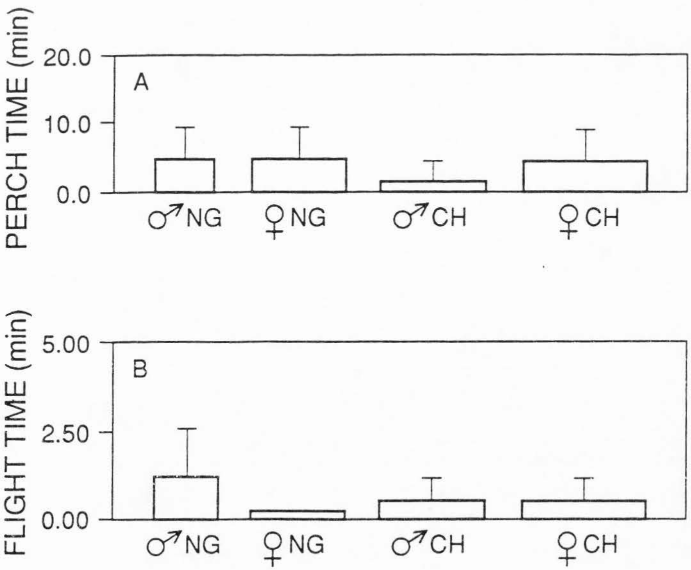

Fig. III-3. Box plots of perch times (A) and flight times (B) of northern goshawks and Cooper's hawks feeding young in north-central New Mexico. The boxes represent the middle inter-quartile range and the box width reflects the relative sample size (see Figs III-1 and III-2 for sample sizes). The bars above and below the box are 1.5 times the inter-quartile distance represented by the box. NG = northern goshawk and CH = Cooper's hawk.

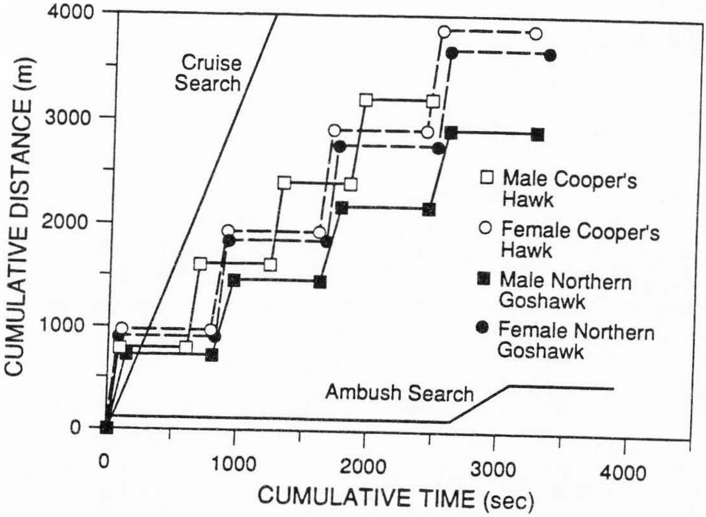

Fig. III-4. Foraging patterns of northern goshawks and Cooper's hawks feeding young. Typical cruise and ambush search patterns (based on information in O'Brien et al. 1990) are presented for comparison.

CHAPTER IV

MATE DESERTION IN THE COOPER'S HAWK

Abstract. Mate desertion by females during the breeding season was documented at 7 of 13 (58.3%) Cooper's hawk (Accipiter cooperii) nests in north-central New Mexico between 1984 and 1988. The desertions all occurred during the fledgling-dependency period when the young were six to eight weeks old. In all cases of desertion, the male provided uniparental care until the young were independent (11 to 12 weeks old). Unlike deserters in other avian species, none of the females renested after desertion. Following desertion, the females moved to areas 8 to 20 km away from the nesting area. They stayed in these areas for four to six weeks and then migrated. The nondeserting females either remained at the nest until the young were independent or hunted for the family, in conjunction with the male, until the young were independent. Brood sizes of nests with deserting females and nests with nondeserting females were not significantly different. Offspring mortality was significantly higher during the nestling stage at nests with nondeserters than at nests with deserters, and no offspring mortality was recorded at nests after desertions occurred. Daily energy budgets (DEB) were estimated for the broods and the females throughout the nestling and fledgling-dependency periods. The DEB of

nestlings was not significantly different between nests with nondeserters and nests with deserters.

These results support the parental investment prediction that desertions occur when the current offspring no longer require biparental care to reach independence. Although daily energy expenditures were not significantly different between deserters and nondeserters, the net difference between the daily energy intake and daily energy expenditure of deserters was significantly more negative than for nondeserters throughout brood rearing. These results indicate the deserters may be in poorer condition at the time of desertion than nondeserters. A female's poor physical condition at the time of desertion is attributed to her preferentially feeding the nestlings when the quantity of food delivered to the nest by either parent is inadequate to meet the family's requirements. In species with sex role partitioning during the nesting season, such as the Cooper's hawk, desertion by the parent not providing the majority of the food (the female) may actually benefit the nestlings by increasing their food supply. By deserting, she curtails her energy cost of parenting and has four to six weeks to allocate all of her energy to improving her deteriorated physical condition prior to migration. This will improve her chances of over-winter survival and of reproducing in the next breeding season. Mate desertion by the male is not predicted to occur in

Cooper's hawks because of his role as the primary food provider throughout the breeding season.

Biparental care and monogamy are prevalent in raptors and other nidiculous birds, presumably because of their external eggs and altricial chicks which require extensive attention before independence (Lack 1968, Oring 1982, Fujioka 1989). In most birds with biparental care, parental tasks are shared. However, in raptors the parents have markedly different roles during the breeding season. Commonly, males provide the family with food throughout the breeding season while females incubate, brood, feed and defend the offspring. It is commonly assumed that in raptors, the female will usually hunt to supplement the male's provisioning when the young are in the greatest need of food (late nestling stage just prior to fledging) and continue food provisioning with the male until the young are independent (Reynolds 1972; Snyder & Wiley 1976; Andersson & Norberg 1981; Mueller & Meyer 1985).

Recent studies have documented facultative uniparental desertion by both sexes (ambisexual desertion) within populations of biparental raptors (black-shouldered kite [Elanus caerulus] Mendelsohn 1981; 1989; Tengmalm's owl [Aegolius funereus] Solheim 1983; snail kite [Rostrhamus sociabilis] Beissinger 1987b; Beissinger and Snyder 1987). The deserters apparently renest immediately following desertion, resulting in a polygamous mating system. Although mating systems of most vertebrates are characterized by uniparental desertion, the deserter is usually the male who mates immediately with a new female, resulting in polygyny. Desertion by females (potential polyandrous or multi-clutch systems) is far less common in birds (Oring 1982; Fujioka 1989).

In this paper I describe a regular pattern of nest desertion by female Cooper's hawks nesting in north-central New Mexico. The Cooper's hawk is a medium-sized raptor that occupies forested habitats throughout North America and preys on a wide variety of vertebrates (Reynolds 1989; Chapter II). Mate desertion has not been previously reported in this species or in any monogamous raptor. I describe the proximate factors influencing the occurrence of desertion among female Cooper's hawks in this population. These factors include the physical condition of the female and her offspring throughout the brood rearing period (which is a function of the male's and female's foraging capabilities) and the risks to her offspring of her desertion. The fitness tradeoffs influencing the females' choice of reproductive strategies, including mate desertion, are discussed in Chapter V.

Methods

Behavioral Studies

Field studies were conducted during the brood rearing periods of the 1984-1988 nesting seasons, except 1987. The brood rearing period began after the eggs hatched (early to late June) and ended when the young were independent at the end of fledgling-dependency (July-September). Observations of Cooper's hawk parental effort were made in all five years. Parental effort included food provisioning, and protecting offspring from, predators and inclement weather. These observations were made on the behavior of radio-tagged nesting adults combined with behavioral observations collected near active nests.

The study area was within the Jemez Mountains, New Mexico and adjacent Pajarito Plateau. These mountains are characterized by steep terrain dominated by typical southwestern montane habitat types such as ponderosa pine and mixed conifer forests. The Pajarito Plateau, a table-like extension of the eastern flank of the Jemez Mountains, is cut into numerous, narrow, finger-like mesas by southeast-trending, intermittent streams. The mesas are dominated by pinyon-juniper woodland. The drainages contain riparian habitats dominated by ponderosa pine (Pinus ponderosa) or cottonwood (Populus sp.) stands and flow into the Rio Grande. Habitat along the Rio Grande is characterized by a variety of deciduous riparian communities. The study area is described in detail in Kennedy (1988).

During the five years of field studies, 37 nest sites were found; 17 were studied intensively during approximately 670 h of observations throughout the brood rearing period. About one-fifth of these observations were made after mate desertion had occurred.

Mated pairs of Cooper's hawks were observed for observation periods of 3-10 h each from concealed locations 15-60 m from nest sites. The adults are sexually dimorphic in size so the sexes of breeding birds were easily distinguishable. To minimize the chances of causing desertion, I rarely visited actual nest sites more than once a week. Nest progress was monitored from after hatching until the fledglings were no longer present and being fed by the parents in the vicinity of the nest.

To augment the observations of parental effort and accurately distinguish desertions from mortalities, I fitted 13 nesting adult females and 10 nesting adult males with transmitters during the early nestling stage of the 1984 ($\underline{N}$ = 5), 1986 ($\underline{N}$ = 9), and 1988 ($\underline{N}$ = 9) breeding seasons. Observations of radio-tagged birds began after the birds accepted the transmitters within a few days of tagging. I continued to monitor their behavior until either the batteries failed, the birds molted the rectrices carrying the transmitter, or the birds left the study area, probably for migration. Winter distributions of Cooper's hawks (Palmer 1988; Root 1988), band returns of Cooper's hawks wintering in southern New Mexico (approximately 250 km south of the study area) that were banded on the study area as nestlings (P. L. Kennedy unpubl. data), and the large numbers of Cooper's hawks recorded during the fall migration in the Sandia Mountains east of Albuquerque, NM (approximately 160 km southeast of the study area) (S. Hoffman, Hawk Watch International, pers. comm.) support my assumption that this population of Cooper's hawks is migratory. The transmitters and telemetry data collection methods are described in Chapter III.

Energetics Model

I calculated daily energy budgets for each radio-tagged female (*N* = 13) and her offspring throughout brood rearing as estimates of the parents' (particularly the male's) ability to meet the family's energy requirements and as an index of their physical condition throughout the brood rearing period. Sample days were grouped into four periods: early nestling (weeks 1 and 2 after hatching) (*N* = 13 observation days, $\bar{X}$ = 1 day/female); late nestling (weeks 3-5 after hatching) (*N* = 33, X = 2.5 days/female); early fledgling-dependency (weeks 6-7 after hatching) (*N* = 25, $\bar{X}$ = 1.9 days/female); and late fledgling-dependency (weeks 8-10 or 11) ($\underline{N} = 27$, $\bar{X} = 2.1$ days/female).

Female

I used a time-energy budget (TEB) model that Masman et al. (1986a) developed for estimating European kestrel (Falco tinnunculus) energetics throughout their annual cycle. I chose this model because it was developed for a raptor, it was applicable to the breeding season, and it showed a good correlation between the model predictions and measurements of daily energy expenditure with doubly-labeled water (DLW) ($\underline{r} = 0.83$, $\underline{P} < 0.001$) (Masman et al. 1986a). In a recent review of the accuracy of bioenergetics models, Nagy (1989) reports good agreement (within 7%) between TEB models and DLW estimates of energy expenditure for large birds living in nonstressful (thermoneutral) conditions. Cooper's hawks during the breeding season meet these conditions.

The general form of the TEB model for a female in maintenance conditions is

$$\text{Daily Energy Intake } (DEI_f) = \text{Daily Energy Expenditure } (H_{tdf}). \tag{1}$$

If $DEI_f < H_{tdf}$, then the female is in a negative energy balance and is losing energy reserves. If $DEI_f > H_{tdf}$, the female is in a positive energy balance and is gaining energy reserves. The methods used to estimate DEI_f and

H_{tdf} for each female are described below. A list of the symbols and abbreviations used in the TEB model are presented in the Appendix A.

Daily Energy Intake.--The DEI_f is calculated using a modification of a daily energy intake model developed by Masman et al. (Equation (1); 1986c). Daily energy intake can be expressed as

$$DEI_f = GDEI_f Q \tag{2}$$

where

$GDEI_f$ = gross daily energy intake in watts (W) and

Q = assimilation efficiency.

The female's gross daily energy intake can be expressed as

$$GDEI_f = GDED - GDEI_n + GDEU \tag{3}$$

where

$GDED$ = the gross daily energy delivered to the nest by both parents (W),

$GDEI_n$ = portion of the GDED that is allocated to the offspring (W), and

$GDEU$ = gross daily energy of her prey captures she consumes prior to delivery (W).

The gross energy delivered to the nest is

$$GDED = t_{\alpha}/f(\Sigma M_d l_i - \Sigma M_u l_i) \text{ (kJ day}^{-1}\text{)} \tag{4}$$

where

t_α = daylength at this date (h),

f = length of the observation period (h),

ΣM_d = total biomass of the observed prey species (g),

l_i = caloric content of each prey species (kJ g^{-1}), and

ΣM_u = total biomass of prey not eaten at the nest (g).

The data used to estimate the parameters in this model were from observations of prey deliveries to the nests during the nestling and fledgling dependency periods. The estimates of $GDEI_f$ and $GDEI_n$ assume that the frequency and size composition of prey brought during the observation periods were representative of that brought throughout the day.

All prey items delivered to the nest during an observation period (see Chapter II for procedures on the prey identification and sampling) were identified to species and, if possible, to age and sex. The sex of the parent delivering the prey and the time of delivery was also recorded. The parent that captured and delivered the prey could be identified by the activity of the radio-tagged birds prior to delivery. In addition, prey deliveries by either sex could usually be identified by food exchange vocalizations (see Palmer 1988 for a description of these vocalizations).

Each prey item delivered to the nest was assigned an average species biomass (M_d) based on the biomass of individuals trapped in the study area. For a few prey species, I used literature estimates of biomass. Table IV-1 summarizes the average biomass values of prey delivered to the nests in this study. The frequency at which these prey items were delivered to nests in the study population is presented in Table II-1.

A caloric value for each prey item (l_i) was estimated from its biomass. For avian prey, I used the caloric value of 6.84 kJ g^{-1} of wet biomass, an average of values for avian raptor prey reported by Wijnandts (1984) and Masman et al. (1986c). For mammalian prey, I used the caloric value of 6.63 kJ g^{-1} of wet biomass, an average of values for rodents reported by Gorecki (1967), Wijnandts (1984) and Masman et al. (1986c). The caloric value of reptilian prey was estimated with an allometric equation in Vitt (1978).

The daylength for each observation date (t_α) was estimated from solar radiation readings collected at the Los Alamos National Laboratory meteorological station (TA-59) in Los Alamos, NM. This station is located in the center of the study area, and the meteorological instruments are in the open at 22 m above ground level (Los Alamos National Laboratory 1987). The average daylengths for each period in the brood-rearing period are presented in Table IV-2.

The uneaten portion of the prey (ΣM_u) includes the parts of the prey lost in plucking, the portion of the prey eaten or cached by the adult prior to delivery, or the uneaten portions left at the nest as a result of satiation. The body parts of the prey not consumed at the nest during the observation period were recorded. The biomass of these uneaten portions was estimated from the average weights of prey remains for that species collected during the study or estimated from allometric equations in Calder (Table 3-4, 1984) that predict the biomass of vertebrate body parts from the total biomass. For example, on the average, a plucked and headless prey item was estimated to be 85% of the total prey biomass. I assumed the proportion of the prey not delivered to the nest and not removed during plucking was eaten by the adult prior to delivery.

GDED was converted from kJ day^{-1} to W to conform to SI unit standards.

The percentage of the prey delivered to the nest by both parents that was eaten by the female was estimated as the number of pieces she ate divided by the total number of pieces eaten by her and her offspring.

For avian, mammalian and reptilian prey I used the assimilation coefficients (Q) of 0.752, 0.704 and 0.704, respectively. The avian and mammalian coefficients are the average assimilation rates of breeding European kestrels measured during food trials (Masman et al. 1986c). No data are available on the Q for predators eating reptilian prey so I assumed it was comparable to the Q for mammalian prey. The energy assimilated from digesting each prey species is presented in Table IV-1.

DEI_f was not estimated for females after they deserted because their food consumption could not be monitored accurately.

Daily Energy Expenditure.--The H_{tdf} was calculated for each day using the energy expenditure model in Masman et al (Equation (1), 1986a):

$$H_{tdf} = H_b + (H_t - H_h) + H_a + H_s \text{ (W)} \tag{5}$$

where

H_b = basal component of energy expenditure (W),
H_t = cost of thermogenesis (W),
H_h = heat increment of feeding (W),
H_a = energetic costs of activity (W), and
H_s = energy expended in synthesis of tissue (W).

Basal Component of Energy Expenditure.--The basal component of H_{tdf} (H_b) is the rate of energy expenditure of a fasting, postabsorptive, nonmolting bird under thermoneutral conditions. I showed in Chapter I that this level is proportional to body mass, M (g), and different for the rest and activity phases of the circadian cycle. Mass of each female was measured at the time I trapped her and fitted her with a transmitter (Table IV-3). The basal component was calculated using a modification of Equation (3) in Masman et al. (1986a). It is

$$H_b = [(t_{\alpha s}-t_f)H_{ma} + \rho H_{mr}]/1000 \text{ (kJ day}^{-1}\text{)} \qquad (6)$$

where

$t_{\alpha s}$ = daylength for that date (sec day^{-1})
t_f = daily time (sec day^{-1}) spent in flight,
ρ = 86,400 - $t_{\alpha s}$ (sec day^{-1})
H_{ma} = active phase resting metabolic rate (W), and
H_{mr} = resting phase resting metabolic rate (W).

The t_f was estimated from time-activity budgets calculated for each female for each observation day. The time-activity methods and results are presented in Chapter III. The H_{ma} and H_{mr} were computed with Equations (1) and (2) in Chapter I, respectively. The H_b and other energetic estimates that were originally calculated in kJ day^{-1} were converted to W.

Costs of Thermogenesis.--H_t is the energetic cost of thermoregulation when the mean ambient daily temperature (T_m) ($^{\circ}C$) is below the lower critical temperature (T_{lc}) ($^{\circ}C$). For days when $T_m = T_{lc}$, $H_t = 0$; for days when $T_m < T_{lc}$, H_t is given by:

$$H_t = (T_{lc} - T_m)CM \quad \text{(W)} \qquad (7)$$

where C = thermal conductance ($W[g^{o}C^{-1}]$).

I calculated a T_{lc} of 20.8°C for female Cooper's hawks using the technique of Wasser (1986) and a mean body temperature of 41.3°C reported for the Cooper's hawk (Wasser 1986).

The T_m was estimated for each observation day with a modification of the mean daily temperature model of Walsberg (1978). This model does not include periods of the day when $T_m > T_{lc}$ nor periods of the day when the bird is in flight and energy expenditure is temperature-independent (Walsberg 1978). The T_m is defined as

$$T_m = [\Sigma(T_{lc}-T_a)/(n_i P_{nf})] + 1.5^{o}C \qquad (8)$$

where

T_a = an hourly ambient temperature < T_{lc} for a date (°C),

n_i = the number of temperature hours estimated for a date, and

P_{nf} = proportion of time not in flight during the day.

Early and late in the nesting season, nighttime temperatures dropped below thermoneutral. In general, hourly temperatures (T_a) were based on 15 min weighted averages recorded at the hour throughout the breeding season at the Los Alamos National Laboratory meteorological station (Los Alamos National Laboratory unpubl.). Readings for some hours were not available as a result of equipment malfunction and n_i corrects for an incomplete daily weather database. The T_m was increased by 1.5°C to adjust for the warmer temperatures occurring in the forested canopy than in the location of the meteorological station (Denmead 1984). The P_{nf} was estimated from the time-activity budget data (Chapter III). The average T_m for each period of brood-rearing is presented in Table IV-2.

Heat Increment of Feeding.--H_h has been estimated in food trials on raptors and passerines (Brody 1945; Ricklefs 1974; Kendeigh et al. 1977; Wijnandts 1984; Masman et al. 1986b). The value of H_h, which can range from 10 - 24% of gross energy intake, depends on the amount of food intake, the digestibility of the food and the ambient temperature. I assumed H_h was 10% of the DEI_f for the nondeserting and deserting females prior to the time of desertion. The H_h for females after desertion was assumed to be 10% of H_{tdf}. I also assumed that H_h replaced H_t which is supported by data on H_h and H_t measured at various temperatures for 2 raptor species (Wijnandts 1984; Masman et al. 1986b).

Activity Costs.- My daily energy expenditure model distinguishes only between the metabolic costs of flight and nonflight activities. Lumping behaviors into these two energetic cost categories is justified because the cost of flight (both passive and active) is 3-13 times greater than that of other types of behaviors (Tucker 1972; Baudinette & Schmidt-Nielsen 1974; Flint & Nagy 1984), and there is little variation among the estimates of metabolic costs of nonflight behavior, e.g., perching, preening, or nest attendance (Mugaas & King 1981). Furthermore, the costs of some nonflight activities are unknown.

The costs of nonflight activity were incorporated into the H_{ma} estimates. Costs of flight were estimated 3 ways and each was evaluated for its effect on the overall estimate of H_{tdf}. Methods 1 and 2 are empirical models of flight costs based on morphometrics and Method 3 is based on aerodynamic theory.

Method 1.--estimates daily flight costs as

$$H_{a1} = t_f e_{f1}/1000 \text{ (kJ day}^{-1}\text{)} \quad (9)$$

where

e_{f1} = avian flight costs predicted from an allometric equation developed by Masman & Klaassen (Equation 6, 1987) (W);

This is expressed as

$$e_{f1} = 17.36M^{1.013}b_w{}^{-4.236}s_w{}^{1.926} \quad (10)$$

where

M = mass of the female + transmitter mass,

b_w = wing span (cm), and

s_w = wing area (cm^2).

I analyzed morphometric data, i.e., mass, wing chord and wing span, on Cooper's hawks (Table IV-4) and the closely related northern goshawk (Table IV-5) using multiple regression to determine if wing span could be predicted from mass (M) and wing chord (c_w) (cm). Wing span was significantly correlated with wing chord ($\underline{r}^2 = 0.939$), the predictive relationship is

$$\log(b_w) = 0.562 + 0.972\log(c_w) \qquad (11)$$

In Equation (11), $\underline{S}_{Ea} = 0.04$ and $\underline{S}_{Eb} = 0.03$. Inclusion of mass into the equation did not significantly improve the fit ($\underline{r}^2 = 0.942$). Wing area (s_w) was also estimated from c_w as

$$s_w = (c_w/0.62^2)/1.93 \text{ (cm}^2\text{) (Greenwalt 1962).} \qquad (12)$$

The measured and estimated morphometric values of each female are presented in Table IV-3.

<u>Method 2.</u>--estimates daily flight costs as

$$H_{a2} = t_{fh}e_{f2} \text{ (kJ day}^{-1}\text{)} \qquad (13)$$

where

t_{fh} = daily time (h day^{-1}) spent in flight,

$e_{f2} = 3.167M^{1.464}c_w^{-1.614}$ (kJ h^{-1}) (Equation b, Castro & Myers 1988).

Method 3.--The activity and movement patterns of female Cooper's hawks is characterized by numerous perching bouts ($\overline{X}$ = 11.8 min) alternated with short flights ($\overline{X}$ = 1.5 min) that covered distances of 700-1000 m (Chapter III). The energetic costs of these types of short flights can be estimated with aerodynamic models presented in Pennycuick (1989) and in Pennycuick and DeSanto (1989). This method estimates daily flight costs as

$$H_{a3} = (t_f P_{min})/1000 \text{ (kJ day }^{-1}\text{)} \qquad (14)$$

where

P_{min} = power required to fly at the minimum power speed (V_{mp}) (W) (Pennycuick 1989).

The P_{min} was calculated for each female using the program BASIC (Pennycuick 1989). I assumed that on the average, the females flew close to V_{mp} which is the power speed that minimizes the amount of work done per unit time. I modified the program to: 1) replace the regression equation derived by Lasiewski & Dawson (1967) for estimating P_{met} with Equation (2) in Chapter I, and 2) change the conversion efficiency of the muscular system (η) from 0.23 to 0.15, based on muscular efficiencies measured in flying European kestrels (Masman and Klaassen 1987). The input parameters for BASIC were wing span (m), mass (kg), transmitter mass (kg), and air density at 2000 m (1.01 kg m^{-3}).

Energy Expended in Synthesis.--The only synthesis cost incorporated into H_{tdf} during the brood-rearing period of the nesting season is the cost of feather growth (H_s) (Masman et al. 1986a). The female Cooper's hawk molt is initiated during egg-laying and is not completed until after the young are independent (Henny et al. 1985). The synthesis cost associated with molt is

$$H_s = (M_{pl}/T_d)F \text{ (kJ day}^{-1}\text{)} \tag{15}$$

where

M_{pl} = total mass of new plumage (g dry weight),
T_d = length of the molt (days), and
F = energy content of new feathers [kJ(g dry weight) $^{-1}$].

The M_{pl} is estimated as

$$M_{pl} = 0.85(0.064M^{0.95}) \tag{16}$$

where M is the mass of the female in kg (Calder 1984). The dry weight of the plumage was calculated from the fresh mass assuming an average water content of 15% observed by Kirkwood (1981) in European kestrel plumage. The T_d is 120 days, the average molt duration for female Cooper's hawks (Henny et al. 1985; Palmer 1988). The F is

109.4 [kJ(g dry weight) $^{-1}$], the energy content of dry European kestrel plumage (Masman et al. 1986b).

Initial Physical Condition.--The female's wing loading (Pa) was calculated from her wing area (converted to m^2) and weight (mass converted to newtons) (Pennycuick 1989) at the time of trapping (Table IV-3). Wing loading is used as an index of the females' energy reserves at the beginning of brood rearing. I used wing loading instead of mass because I wanted to normalize her condition by her linear dimensions so that larger-bodied individuals could be compared with smaller-bodied individuals.

Offspring

Daily Energy Intake.--The daily energy intake of the brood (DEI_n) was estimated with the procedures described for calculating DEI_f. During the nestling stage, the gross daily energy intake ($GDEI_n$) of the brood is based on the portion of each prey item allocated to the brood by the parents, usually the female. During the fledgling dependency stage, the $GDEI_n$ is equivalent to GDED.

Daily Energy Expenditure.--I did not measure the nestlings growth rates to eliminate the disturbance to the nest and to prevent influencing the parents' behavior. I used literature values in estimating their daily energy expenditure (H_{tdn}). A number of workers have estimated the peak energy requirements of nidiculous young (see Table IV-6). These estimates are typically derived from food trial measurements of the nestling's food intake and excretory loss of energy (e.g., Dunn 1980) or by combining estimates of the nestling's resting metabolic rate with measurements of the energy invested in the growth of new tissues (e.g., Ricklefs et al. 1980).

Walsberg (1983) noted that the peak daily energy expenditure per nestling during the nestling period (E_n^*) is a function of adult biomass (M). I derived the following equation with least-squares regression of logarithmically transformed values of E_n^* and M in the literature (see Table IV-5).

$$\log(E_n^*) = 1.729 + 0.757\log(M) \text{ (W)}. \tag{17}$$

In Equation (17) $\underline{r}^2 = 0.934$, $\underline{S}_{Ea} = 0.137$ and $\underline{S}_{Eb} = 0.061$.

The H_{tdn} of each brood is estimated for each of the 4 stages of the brood-rearing period. The approach used to estimate H_{tdn} is the same approach used to estimate $E_n(t)$ in Chapter V (Section VB.2). The estimates of H_{tdn} for individual male and female nestlings at different stages of the breeding season are presented in Table VB-1.

Statistical Analyses

Statistical analyses were conducted using the SAS program on a MicroVax at Los Alamos National Laboratory.

The normality assumption of parametric models was examined and nonparametric statistics were used when this assumption was violated. Statistical tests were examined cautiously because, in many analyses, small sample sizes could lead to Type II errors. The significance level was $\underline{P} = 0.05$ for all tests. Unless otherwise stated, means ($\overline{X}$) are reported with standard deviations ($\underline{SD}$) and the sample sizes ($\underline{N}$).

Results

Who Deserted

Mate desertion occurred at 7 of 13 nests with radio-tagged adults. All of the desertions were by females. Four desertions occurred during 1986, one in 1984 and two in 1988. Two of the desertions were made by the same female (10) during two different nesting seasons (1986 and 1988) (Table IV-3). She was paired with a different mate during each of the two breeding seasons.

In a sample of intensively monitored nests ($\underline{N} = 6$; 3 in 1984 and 3 in 1985), where the adults were not radio-tagged, 3 of the 6 females (1 in 1984, 2 in 1985) disappeared during the fledgling-dependency period. I assume these were desertions but they cannot be distinguished with certainty from mortalities.

The Timing of Desertion

In all cases, mate desertion occurred when the young were 6-8 weeks of age, which is during the early and late fledgling-dependency periods. Nestling Cooper's hawks in this area typically fledge at 4 - 5 weeks depending upon the sex of the nestling (males fledge earlier).

The average brood sizes of nests with deserters and nests without deserters were not significantly different during any of the time periods (Wilcoxon Rank Sum, early nestling - $\underline{Z} = -0.075$, $\underline{P} = 0.94$; late nestling - $\underline{Z} = -1.29$, $\underline{P} = 0.20$; early fledgling-dependency - $\underline{Z} = -0.83$, $\underline{P} = 0.41$; late fledgling-dependency - $\underline{Z} = 0.83$, $\underline{P} = 0.41$) (Table IV-7). Based on the observations of the brood collected during the weekly nest site visits, the apparent causes of brood reduction were predation, weather or starvation. Brood reduction was only observed during the nestling stages (Table IV-7) and brood reduction was significantly higher at nondeserted nests than at deserted nests during the early nestling stage (Wilcoxon Rank Sum, $\underline{Z} = 1.93$, $\underline{P} = 0.05$). Brood reduction was not significantly different between deserted and nondeserted nests during the late nestling stage ($\underline{Z} = 0$, $\underline{P} = 1.0$).

Postdesertion Behavior of Deserters and Tenders

At all 7 nests where female desertion occurred, the male cared for the young alone for 3-5 weeks. Males successfully reared all young to independence.

Because of the radio transmitters, I was able to monitor the activity and movement patterns of the deserters after desertion. Following desertion, each of the 7 females moved to areas that were 8-20 km from the nesting area, stayed within these areas for 4-6 weeks, and then disappeared. The disappearance always occurred between late September and early October which coincides with the peak migration times for Cooper's hawks in New Mexico (S. Hoffman, Hawk Watch International, pers. comm.). These females were never observed near the nest after they relocated. I will refer to these relocation areas as pre-migratory areas throughout the remainder of the paper.

There was no evidence of renesting by the deserters following desertion. The observations of radio-tagged deserters indicate they hunted in these pre-migratory areas and did not engage in any sedentary renesting behaviors, such as courtship and preparation for egg-laying. Although renesting attempts could have been missed because of the behavioral sampling procedure, it is unlikely these females would attempt to renest 4-6 weeks prior to migration because of the amount of time required for incubation (4 weeks) and fledging young (4-5 weeks).

The nondeserting females either remained at the nest until the young were independent and rarely, if ever, hunted, or they hunted for the family in conjunction with the male until the young were independent (see Table V-1 for a summary of the behavioral strategies adopted by each female during brood rearing).

Evaluation of the Three Flight Cost Methods

The flight costs estimated by the three methods varied considerably. The average flight costs predicted by Methods 1, 2 and 3 for all females were 1.52 W (± 1.67), 2.0 W (± 2.19) and 2.87 W (± 3.18), respectively. On the average, Method 2 estimated flight costs that were 31.6% higher than Method 1 and 30% lower than Method 3. The estimates from Method 3 were 88.8% higher than the estimates from Method 1.

In the subsequent estimates of H_{tdf}, I only used flight costs estimated with Method 1. I ruled out Method 3 because theoretically predicted costs are consistently and significantly higher than empirical doubly-labeled water estimates of flight in free-ranging birds (Flint & Nagy 1984; Tatner & Bryant 1986; Nagy 1989).

I eliminated Method 2 because the equation includes data from laboratory as well as field studies (Castro & Myers 1988). Allometric analysis reveals a systematic difference between flight costs measured in the laboratory (using wind tunnels) and those measured in the field (using doubly labeled water or estimates of fat loss during flight) - wind tunnel studies yield flight costs that average 50% greater than field studies (Masman et al. 1986c).

The allometric equation in Method 1 is based only on field data and explains 84% of the observed variation in field estimates of flight costs. As a result, Goldstein (1988) notes that this empirically derived relationship appears at this time to hold the greatest promise for predicting the cost of flapping flight in unstudied species of birds.

Physical Condition of the Females

The wing loading of the females at the beginning of brood rearing averaged 49.95 Pa for deserters and 48.73 Pa for nondeserters (Table IV-3) and were not significantly different (Wilcoxon Rank Sum, $Z = -0.82$, $P = 0.41$). These values are similar to the average wing loading values for early nesting season females in Oregon (51.96 Pa; Table VB-3) (morphometric data from Henny et al. 1985).

The H_{tdf} and its components are summarized in Table IV-8 for all females during the four stages of brood rearing. The 95% confidence interval of the H_{tdf} pooled over all females and all age classes was 4.29 - 4.83 W.

The two other estimates of H_{tdf} for female Cooper's hawks were lower (3.74 W - central Utah nesting population [Fischer 1986]) and higher (5.19 W - eastern Oregon nesting population [Reynolds 1979]) than this confidence interval. No estimates of variation are available for these other H_{tdf} estimates.

The H_{tdf} approximated a normal distribution ($\underline{W}$ = 0.968, $\underline{P}$ = 0.33) so I examined differences in H_{tdf} as a function of desertion status, age of the young, and the interaction with a randomized block ANOVA. The H_{tdf} were not significantly different between deserters and nondeserters ($\underline{F}$ = 0.62, $\underline{P}$ = 0.44), age of the young ($\underline{F}$ = 0.83, $\underline{P}$ = 0.49) and the interaction of the two variables ($\underline{F}$ = 2.33, $\underline{P}$ = 0.09).

The flight costs, which contribute approximately 25 - 40% of the H_{tdf} depending upon the age of the young, were not significantly different between the four stages of brood rearing (Kruskall - Wallis, Method 1 χ^2 = 3.26, $\underline{P}$ = 0.35). or between deserters ($\overline{X}$ = 1.57 W) and nondeserters ($\overline{X}$ = 1.45 W) (Wilcoxon Rank Sum, Method 1 $\underline{Z}$ = -0.21, $\underline{P}$ = 0.84).

Although H_{tdf} does not vary significantly between deserters and nondeserters, there is a significant difference between the two groups of females in the net difference between their DEI_f and H_{tdf} ([DEI_f - H_{tdf}/H_{tdf}] [Wilcoxon Rank Sum, $\underline{Z}$ = -3.477, $\underline{P}$ = 0.0005] [Figure IV-1]). On the average, the deserters were in a negative energy balance throughout brood rearing prior to desertion. On the average, the nondeserting females were only in a negative energy balance during the early nestling stage and it was not as negative as the deserters at this time. The biggest difference in daily energy budgets between deserters and nondeserters occurred during the late nestling stage.

This decrease in the deserting females' condition estimated with the TEB is supported by additional biomass data I obtained on two females, one that deserted (10-1988) and one that did not desert (4-1984) (Table IV-3). Female 4 was retrapped 12 days after her initial trapping and her biomass had declined 0.4 g day^{-1} from 530 g to 525 g. Female 10 was retrapped 6 days after her initial measurements and her biomass had dropped 3.0 g day^{-1} from 470 g to 452 g. These biomass changes can partially be explained by circadian patterns of food intake (the crops were empty at the time of weighing) but it is likely that an 18-g difference in Female 10 reflects a true decline in fat reserves.

Physical Condition of the Nestlings

Contrary to the females' daily energy budgets, the net difference between H_{tdn} and DEI_n (DEI_n - H_{tdn} /H_{tdn}) was not significantly different between broods of deserters and nondeserters (Figure IV-2) (Wilcoxon Rank Sum, $\underline{Z} = -0.55$, $\underline{P} = 0.58$). The daily energy budget of broods was positive from the late nestling stage until independence and it did not decline after desertion. The negative energy balance of nondeserters' broods during the early nestling period might partially account for the significantly higher offspring mortality at these nests during this period (Table IV-7).

Discussion

To my knowledge, the Cooper's hawk is unique among raptors, with only females observed deserting their fledglings. It is unclear why female desertion was common at this study area and has not been reported in other populations or in populations of its congeners. Female desertion may have been overlooked in previous studies of raptors and other birds because (1) of the difficulties associated with monitoring adult avian behavior away from the nest; (2) the focus of many behavioral ecology studies during the nesting season terminates with fledging; and (3) full biparental care is presumed obligate in monogamous birds. By assuming obligate biparental care in monogamous birds, it is possible that desertions have been misreported as female mortalities late in the nesting season.

Mate desertion by female Cooper's hawks in this study occurred after fledging. Judging by the high success rate of single males in raising their broods unaided (zero offspring mortality (Table IV-7) and positive energy balance of fledglings (Figure IV-2) following desertion), desertion occurs when the offspring no longer require biparental care to reach independence, as predicted by parental investment theory (Maynard Smith 1977; Grafen & Sibley 1978).

Although offspring of deserters were in good physical condition at the time of desertion, this was not the case for the adult females. The initial condition of deserters was not significantly different from that of nondeserters. However, the DEB of deserters was significantly lower than the DEB of nondeserters throughout brood rearing, indicating the female's physical condition may be influencing her decision to desert (Figure IV-1).

The lower DEB of the deserters is not a result of lower H_{tdf}. The H_{tdf} was not significantly different between deserters and nondeserters and did not vary significantly with the age of the young. Therefore, the deserting female's poorer physical condition at the time of desertion is attributed to a lower DEI_f which resulted from her preferentially feeding the nestlings the food delivered to the nest when there was not enough food to meet the family's requirements.

Other investigators (Wijnandts 1984) have noted female raptors preferentially feeding young at the female's expense. Because the male feeds the female throughout courtship and incubation in many raptor species, the female enters the nestling stage in many cases with a surplus body weight (Newton et al 1983; Wijnandts 1984; Masman et al. 1986a). This surplus body weight probably represents extra fat reserves that allow her to reduce her energy intake, if necessary, during the nestling stage without threatening her survival. Thus, she can allocate the majority of the male's prey deliveries to the growing nestlings and increase their probability of survival. In addition, if the male can meet the brood's energy requirements, the female can fast rather than hunt and decrease the offspring's risk of predation or mortality due to inclement weather.

The DEB data on the early nestling stage for both the female (Figure IV-1) and the nestlings (Figure IV-2) indicate that even if the female preferentially feeds the young, there may not be enough food for all of the offspring. However, by preferentially feeding herself less than a nondeserter (Figure IV-1), a deserter may reduce the potential offspring mortality as a result of starvation (Table IV-7).

Mate desertion behavior presumably evolved because, for deserters, the benefits of deserting were greater than the costs (Trivers 1972; Boucher 1977; Maynard Smith 1977; Beissinger & Snyder 1987; Lazarus 1990). For most deserters, one of the major benefits of deserting is an increase in their current reproductive output by immediately renesting Beissinger 1987b; Beissinger &

Snyder 1987; Fujioka 1989). In raptors, which have long periods of parental care, renesting benefits from desertion would only occur in populations with prolonged breeding seasons, e.g., snail kite (Rostrhamus sociabilis) in Florida (Beissinger and Snyder 1987).

For the female Cooper's hawk which does not renest immediately following desertion, the main benefit to desertion is avoidance of the risks and further physical deterioration associated with brood care (Beissinger & Snyder 1987). Although I was not able to estimate the DEB of females after they deserted, I assumed the immediate benefit to the female from deserting is the improvement of her physical condition prior to migration. This will increase her chances of surviving the migration and the winter, and thus increase her probability of future reproduction. Henny et al. (1985) has observed an arrested molt in some nesting female accipiters. Arrested molt in female accipiters occurs during the late nestling and early fledgling dependency periods when females may be in poor condition. By deserting and improving her physical condition, the female could complete her molt prior to migration rather than after migration. The fitness tradeoffs between a female's current reproduction and her future reproduction resulting from desertion are explored in more detail in Chapter V.

Although deserting by females without immediate renesting has not been previously recorded in birds, it may be occurring in other avian species where the desertions are assumed to be followed by renesting. In several studies that have a high incidence of female desertion (Beissinger 1986, 1987a; Fujioka 1989), the observations of renesting by these females are sparse (Beissinger & Snyder 1987) or nonexistent (Fujioka 1989). It is possible that these deserters do not immediately renest.

The female may leave the nesting area for her pre-migratory areas to remove her impact on the nestlings' food supply. The significance of these pre-migratory areas is unknown but they may have been natal territories where the females learned to hunt or are areas of high prey availability during the late summer and early fall. The potential significance of these areas is supported by the observation that one female (10) occupied the same pre-migratory area after deserting in both 1986 and 1988.

Alternatively, if the deserter is a less efficient hunter because she has not been hunting for several months, or because of body size considerations (as suggested by sexual size dimorphism theory [Reynolds 1972; Andersson & Norberg 1981; Mendelsohn 1989]), deserters may be forced to leave their nesting territories and move around in search of better feeding areas.

Deserters appear to incur no substantial costs to their current reproduction by deserting. Deserters usually abandoned their mates without a reduction in the current reproductive output since the males always successfully reared all young to independence (Table IV-7). In addition, desertion by the parent who is not the primary food provider may actually benefit the young by increasing their food availability. After desertion, the offspring no longer have to share the males' prey deliveries with the female. Although the differences are not significant, the net daily energy gain by nestlings from nests with deserters does increase throughout brood rearing (Figure IV-2) indicating an increase in food availability to the fledglings following desertion.

Although the female may not be required to provision the offspring during the fledgling-dependency period, she may play a large role in training the fledglings to hunt. If this is the case, a potential cost of desertion would be less training provided to the young which could substantially reduce their probability of surviving migration. Currently there is no evidence that suggests adult raptors actually train the fledglings to hunt.

Beissinger (1986) predicted that ambisexual mate desertion might be expected to occur when (1) desertion happens relatively late in a reproductive bout; (2) the operational sex ratio, hence the opportunity to remate, is variable; (3) parental duties are shared throughout a reproductive bout such that either sex is equally capable of rearing the young alone; and (4) the costs of establishing a new nest site or territory are minimal. Ambisexual mate desertion was not recorded in this population of Cooper's hawks and if Beissinger's predictions are correct, I would not expect ambisexual mate desertion to occur in any Cooper's hawk population. Although desertion happens relatively late in the reproductive bout, the operational sex ratio is irrelevant because the environment limits the species ability to renest, and, most importantly, the parental duties are not shared throughout the reproductive bout. As the primary food provider, the male's contribution to parental investment is important throughout brood rearing. Because the female has not been hunting regularly for approximately three months, I assume she is not familiar with the hunting territories and thus, is not as likely as the male to meet the energy requirements of the young to independence. As a result, I predict the male Cooper's hawk would not desert because of the higher risk to his current reproduction due to poorer provisioning by the female.

Appendix

List of Symbols

DEB	daily energy budget
TEB	time-energy budget
DLW	doubly-labeled water

DEI_f	female's daily assimilated energy
H_{tdf}	female's daily energy expenditure
$GDEI_f$	female's gross daily energy intake
Q	assimilation efficiency
GDED	gross daily energy delivered to the nest
$GDEI_n$	nestlings' gross daily energy intake
GDEU	gross daily energy the female consumes prior to delivering her prey to the nest
$t\alpha$	daylength at a particular date
f	length of observation period
M_d	average biomass for a prey species
l_i	caloric content of prey species i
M_u	biomass of prey not eaten at the nest
H_b	basal component of H_{tdf}
H_t	cost of thermogenesis
H_h	heat increment of feeding
H_a	energetic cost of activity
H_s	energy expended in synthesis of tissue
t_f	daily time spent in flight
ρ	nocturnal portion of day
H_{ma}	active phase resting metabolic rate
H_{mr}	resting phase resting metabolic rate
T_m	mean daily temperature
T_{lc}	lower critical temperature
C	thermal conductance
M	mass
T_a	ambient temperature

n_i	number of temperature hours used to estimate T_m
P_{nf}	proportion of daily time not in flight
e_f	energetic cost of flight
b_w	wing span
s_w	wing area
c_w	wing chord
P_{min}	power required to fly at V_{mp}
V_{mp}	minimum power speed
η	muscular efficiency
P_{met}	metabolic power
M_{pl}	mass of new plumage
T_d	length of the molt
F	energy content of new feathers
DEI_n	nestlings' daily assimilated energy
H_{tdn}	nestlings' daily energy expenditure
E_n^*	peak nestling energy expenditure

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Table IV-1. Mean biomass (M_d) and caloric values (l_i) for prey species eaten by Cooper's hawks during brood rearing in north-central New Mexico[a]

Prey taxon	N	Biomass (g)	Assimilated caloric value (kJ)
BIRDS			
Northern flicker (*Colaptes auratus*)	9	139[b]	714.88[c]
Steller's jay (*Cyanocitta stelleri*)	19	108[d]	555.44
American robin (*Turdus migratorius*)	12	82[d]	421.73
Mourning dove (*Zenaida macroura*)	8	118[b]	606.87
Western bluebird (*Sialia mexicanus*)	3	24[b]	123.43
Dark-eyed junco (*Junco hyemalis*)	24	20[d]	102.86
Scrub jay (*Aphelocoma coerulescens*)	9	80[e]	411.44
Unidentified jay[f]	--	94	483.44
House finch (*Carpodacus mexicanus*)	3	22[e]	113.15
American kestrel (*Falco sparverius*)	--	111[g]	570.87
European starling (*Sturnus vulgaris*)	7	77[b]	396.01

Hairy woodpecker (*Picoides villosus*)	4	66[b]	339.44
Mountain bluebird (*Sialia currucoides*)	20	26[b]	133.74
Chipping sparrow (*Spizella passerina*)	1	10[b]	51.43
Unidentified finch (Fringillidae)	--	20	102.86
Brown-headed cowbird (*Molothrus ater*)	10	35[b]	180.01
Unidentified Passeriformes	--	20	102.86
MAMMALS			
Chipmunk (*Tamias* sp.)	644	57[h]	266.02[i]
Abert's squirrel (juvenile) (*Sciurus aberti*)	10	304[j]	1,418.77
Cottontail (*Sylvilagus* sp.)	3	217[k]	1,012.85
Golden-mantled ground squirrel (*Spermophilus lateralis*)	32	179[j]	835.39
Red squirrel (juvenile) (*Tamiasciurus hudsonicus*)	23	232[j]	541.37
Woodrat (juvenile) (*Neotoma* sp.)	15	94[l]	438.70
Rock squirrel (juvenile)			

(*Spermophilus variegatus*)	24	236[h]	1,101.41
REPTILES			
Little striped whiptail (*Cnemidophorus inornatus*)	--	17[k]	102.34[m]
Whiptail (*Cnemidophorus* sp.)	--	17[k]	102.34
Western terrestrial garter snake (*Thamnophis elegans*)	--	109[k]	634.78

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[a] The frequency of these prey items in the Cooper's hawk diet in this study area are presented in Table II-1.

[b] The average fresh biomass of adult birds collected in northern New Mexico during the summer of 1986 (P. L. Kennedy and D. W. Stahlecker unpubl. data)

[c] The assimilated caloric value of avian prey is based on 6.84 kJ g^{-1} of wet biomass and an assimilation coefficient (Q) of 0.752.

[d] The average biomass of birds trapped in the study area during fall migrations (J. Travis unpubl. data) and data from P. L. Kennedy and D. W. Stahlecker (unpubl. data)

[e] The average biomass of birds trapped in the study area during fall migrations (J. Travis unpubl. data).

[f] The average values for the Steller's jay and the Scrub jay.

[g] From Dunning (1984)

[h] The average biomass of sciurids trapped in the study area during the 1986 and 1988 nesting seasons (J. L. Morrison and P. L. Kennedy unpubl. data).

[i] The assimilated caloric value of mammalian prey is based on 6.63 kJ g^{-1} of wet biomass and a Q of 0.704.

[j] The average fresh biomass of specimens in the Museum of Southwestern Biology at the University of New Mexico that were collected in the study area.

[k] From Steenhoff (1983).

[l] The average fresh biomass of woodrats live-trapped in the study area during the 1989 nesting season (J. L. Morrison unpubl. data).

[m] The assimilated caloric value of reptilian prey is from Vitt (1978) and a Q of 0.704.

Table IV-2. Mean daily temperatures (T_m (°C))[a] and daylengths (α) used to estimate daily energy expenditures (H_{tdf}) of female Cooper's hawks during brood rearing in north-central New Mexico

		T_m (°C)			Daylength (h)	
Stage	N[b]	X	Range	SD	X	SD
Early nestling	22	22.95	16.69 - 39.01	6.15	14.15	0.13
Late nestling	49	21.29	16.08 - 37.48	3.26	13.86	0.30
Early fledgling	37	19.78	14.83 - 27.34	2.51	13.41	0.36
Late fledgling	56	18.72	0.33 - 29.03	4.07	12.71	0.56

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[a] T_m was calculated from Equation (8).

[b] The total number of days for which Tm was calculated and daylength data were available.

Table IV-3. Morphometric measurements[a] and estimates of morphometric parameters for the female Cooper's hawks trapped during the early nestling stage, 1984-1988, in north-central New Mexico

Female	Desert	Mass (g)	Wing Chord (cm)	Wing Area[b] (cm^2)	Wing Span[c] (cm)	Trans. Mass[d] (g)	Wing Loading[e] (Pa)
4-1984	No	530	26.1	918.21	86.91	10	56.62
5-1984	No	510	26.6	953.72	88.53	10	52.66
9-1984	Yes	467	25.6	883.36	85.29	10	52.06
10-1986	Yes	447	26.9	975.36	89.5	10	44.75
10-1988	Yes	470	27.0	982.62	89.82	18	47.05
12-1986	Yes	507	26.0	911.18	86.59	10	54.58
13-1986	Yes	455	26.5	946.57	86.59	7	46.98
16-1986	Yes	542	27.5	1,019.35	91.44	10	52.13
24-1986	No	445	26.3	932.33	87.56	10	46.92
26-1988	Yes	494	26.3	932.33	87.56	10	52.11
29-1988	No	391	25.2	855.97	84.00	10	44.60
30-1988	No	448	26.4	939.44	87.88	18	46.78

31-1988	No	415	26.0	911.18	86.59	10	44.74

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[a] The measured parameters were adult mass, transmitter mass and wing chord. The remaining parameters were estimated.

[b] Estimated with Equation (12).

[c] Estimated with Equation (11).

[d] Transmitter mass.

[e] This is mass (kg) (converted to weight [newtons])/ wing area (m^2).

Table IV-4. Morphometric measurements of adult Cooper's hawks used to derive an allometric equation for predicting wing span (b_w) in accipiters[a]

Population/Source	Sex	Mass (g)	Wing Chord (cm)	Wing Span (cm)
California (P. Bloom, unpublished)	F	490	25.4	82.6
	F	425	25.0	81.3
	F	425	23.9	80.5
	F	410	23.7	82.6
	F	445	25.7	83.8
	F	520	25.4	83.5
	F	495	25.7	84.3
	F	540	24.9	83.5
	F	440	24.6	83.8
	F	440	24.3	79.3
	F	480	24.3	82.0
	M	285	21.7	73.0
	M	---	20.2	68.7
	M	295	21.4	72.4
Wisconsin (R. Rosenfield, unpublished)	M	403	24.0	77.8
	M	423	24.5	79.4
	M	396	23.5	79.7
	M	366	24.1	78.7

M	376	24.3	78.7
M	309	23.0	75.3
M	385	24.0	78.1
F	561	27.8	88.9
F	574	27.4	89.5

[a] Data in this table and Table IV-5 were used to derive the following allometric equation for predicting wing span (cm) from wing chord (cm):
$\mathrm{Log}(\text{wing span}) = 0.5621 + 0.9720\ \mathrm{Log}(\text{wing chord})$, $r^2 = 0.939$, $SE_a = 0.04$, $SE_b = 0.03$.

Table IV-5. Morphometric measurements of adult northern goshawks used to derive an allometric equation for predicting wing span in accipiters[a]

Population/Source	Sex	Mass (g)	Wing Chord (cm)	Wing Span (cm)
California (P. Bloom, unpublished)	F	1,150	33.2	110.6
	F	990	35.3	115.2
	F	885	32.4	110.0
	F	965	33.5	111.8
	F	880	32.8	109.4
	F	910	33.3	110.8
	F	1,030	33.4	112.2
	F	885	32.1	112.3
	F	950	32.7	111.2
	F	955	33.2	111.5
	F	885	32.0	109.6
	F	1,000	33.2	113.0
	F	955	33.2	112.5
	F	945	33.0	109.7
	F	1,000	33.6	112.6
	F	965	33.0	111.7
	F	1,120	32.7	110.3
	F	930	33.2	110.5
	F	935	33.2	111.3
	F	950	32.7	112.0

F	1,010	33.3	112.0
F	1,075	32.7	111.8
F	1,075	33.3	112.5
F	885	32.9	113.3
F	1,075	35.1	115.5
F	845	32.8	110.3
F	1,110	33.1	112.3
F	1,050	33.7	112.5
F	920	33.6	112.3
F	880	32.9	111.8
F	1,000	33.5	112.3
F	910	32.7	110.2
F	870	32.8	110.2
M	680	31.8	106.2
M	660	31.7	107.3
M	760	30.3	103.7
M	670	30.8	105.2
M	710	30.3	103.9
M	685	30.7	106.0
M	745	30.7	106.5
M	660	29.9	103.4
M	735	30.8	104.8
M	730	30.6	104.1
M	750	32.1	107.1

California (P. Dietrich, unpublished)	F	890	35.4	108.1
	F	930	34.9	110.5
	F	950	35.6	106.7
	F	930	34.3	110.5
	F	850	34.6	108.6
	F	910	34.3	109.9
	F	910	34.3	102.9
	F	930	34.3	96.5
	F	900	34.3	106.7
	M	730	31.1	104.6
	M	730	31.8	101.6
	M	710	31.1	106.0

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[a] Data in this table and Table IV-4 were used to derive the following allometric equation for predicting wing span (cm) from wing chord (cm): Log(wing span) = 0.5621 + 0.9720 Log(wing chord), $\underline{r}^2 = 0.939$, $\underline{SE}_a = 0.04$, $\underline{SE}_b = 0.03$.

Table IV-6. Literature estimates of peak energy expenditure (E_n^*) for a nestling in a typical brood[a]

	Average Adult mass (g)	E_n^* (W)	Source
Leach's Storm-Petrel (*Oceanodroma leucorhoa*)	45	1.12[b]	Ricklefs et al. 1980
Double-crested Cormorant (*Phalacrocorax auritus*)	1,679[c]	23.02	Dunn 1980
Dunlin (*Calidris alpina*)	326	1.84	Dunn 1980
Herring Gull (*Larus argentatus*)	1,135[c]	10.31	Dunn 1980
Pigeon Guillemot (*Cepphus columba*)	484	4.97	Dunn 1980
Swainson's Hawk (*Buteo swainsoni*)	989[c]	9.70	Kirkley 1985
European Kestrel (*Falco tinnunculus*)	208	4.99	Kirkwood 1981
Long-eared Owl (*Asio otus*)	275	3.62	Wijnandts 1984

House Martin (Delichon urbica)	19	0.56	Bryant & Gardnier 1979
Red-backed Shrike (Larius collurio)	23	0.50^b	Diehl & Myrcha 1973
Starling (Sturnus vulgaris)	82^c	1.45	Dunn 1980
Savannah Sparrow (Passerculus sandwichensis)	18	0.39	Williams & Prints 1986
House Sparrow (Passer domesticus)	28^c	0.86	Blem 1975

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[a] Peak daily energy expenditure for a nestling is estimated using Equation (17).

[b] This estimate of E_n^* accounts only for growth and maintenance metabolism. Activity costs are not included, so this value is probably an underestimate of peak energy expenditure.

[c] Adult biomass was not presented in the reference. These values are average values for the species given in Dunning (1984)

Table IV-7. A comparison of brood size and offspring mortality in broods of deserting and non-deserting female Cooper's hawks in north-central New Mexico

	Deserters (N = 7)				Non-deserters (N = 6)			
	Brood Size		% Mortality		Brood Size		% Mortality	
Time Period	$\bar{X}$	(± SD)	$\bar{X}$	(± SD)	$\bar{X}$	(± SD)	$\bar{X}$	(± SD)
Early Nestling	3.29	(± 1.11)	0.00	(± 0.00)	3.17	(± 0.75)	18.06	(±21.35)[a]
Late Nestling	3.29	(± 1.11)	9.52	(±25.20)	2.50	(± 0.55)	5.56	(±13.61)
Early Fledgling	3.00	(± 1.41)	0.00	(± 0.00)	2.33	(+ 0.52)	0.00	(± 0.00)
Late Fledgling	3.00	(± 1.41)	0.00	(± 0.00)	2.33	(± 0.52)	0.00	(± 0.00)

[a] This is significant at *P* = 0.05 (*Z* = 1.93, Wilcoxon Rank Sum).

Table IV-8. Daily energy expenditures (H_{tdf}) of nesting female Cooper's hawks at different stages of brood rearing in north-central New Mexico[a]

	Energy expenditure (W) due to:									
	Basal[b]		Thermo.[c]		HIF[d]		Activity[e]		Synthesis[f]	
Stage	X	SD	X	SD	X	SD	X	SD	X	SD
Early Nestling	2.11	0.35	0.13	0.13	0.31	0.07	1.70	1.52	0.29	0.02
Late Nestling	2.22	0.21	0.03	0.08	0.49	0.34	1.68	1.48	0.27	0.02
Early Fledgling	2.25	0.17	0.12	0.14	0.42	0.12	1.09	1.06	0.27	0.02
Late Fledgling	2.21	0.29	0.18	0.21	0.47	0.16	1.48	1.86	0.27	0.03

[a] H_{tdf} is defined in Equation (5).

[b] The basal component of H_{tdf} (H_b) defined in Equation (6).

[c] Thermoregulatory costs were estimated using mean daily temperatures (T_m °C) (Table IV-2). Thermoregulatory costs were calculated using Equation (7) for any day with a T_m < 20°C which is the estimated lower critical temperature (T_{lc}) for female Cooper's hawks.

[d] For non-deserting females the heat increment of feeding (H_h) is estimated as 10% of her DEIf. For deserting females DEIf cannot be estimated so H_h is assumed to be 10% of her H_{tdf} calculated with Method 1.

[e] Flight costs are estimated with Method 1 (Equation (9)).

[f] This is estimated using Equation (15).

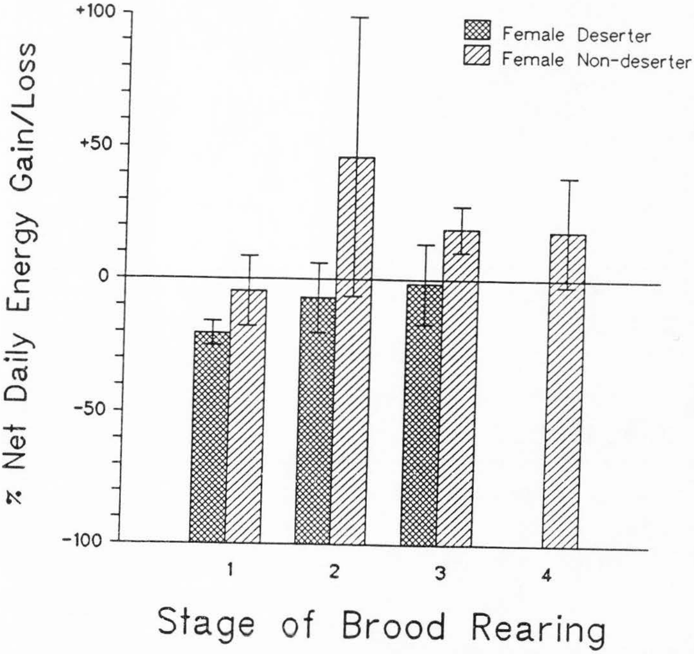

Figure IV-1. Mean net daily energy gain/loss of female non-deserters and deserters as a function of stage of brood rearing. The line at y = 0 is where Daily Energy Intake = Daily Energy Expenditure. The error bars are 95% confidence intervals. Stage 1 = early nestling, Stage 2 = late nestling, Stage 3 = early fledgling dependency, and Stage 4 = late fledgling dependency. Daily energy budgets could not be calculated for deserters following desertion because their DEI_f could not be estimated accurately.

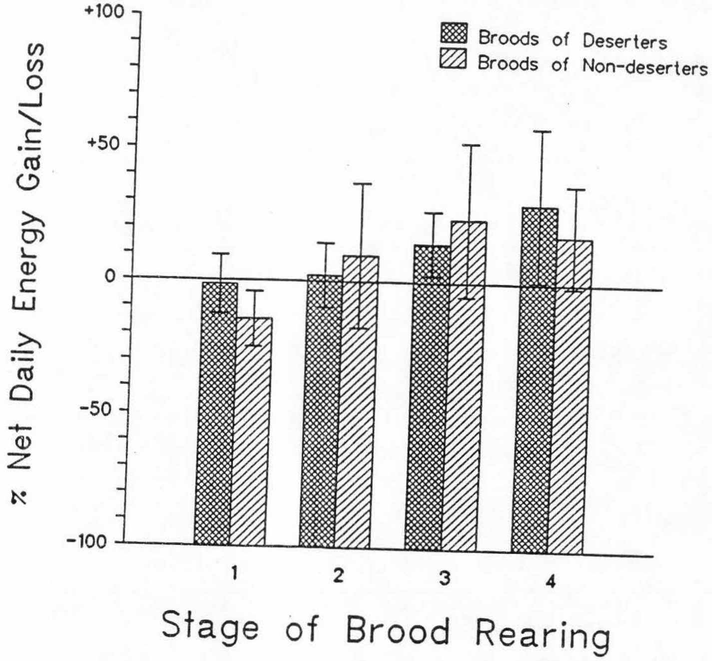

Figure IV-2. Mean net daily energy gain/loss of broods from deserters and non-deserters as a function of stage of brood rearing. The line at y = 0 is where Daily Energy Intake = Daily Energy Expenditure. The error bars are 95% confidence intervals. Stage 1 = early nestling, Stage 2 = late nestling, Stage 3 = early fledgling dependency, and Stage 4 = late fledgling dependency.

CHAPTER V

A DYNAMIC STOCHASTIC OPTIMIZATION MODEL OF MATE DESERTION IN COOPER'S HAWKS

Abstract. In a 4-year study of the reproductive strategies of Cooper's hawks (Accipiter cooperii) nesting in north-central New Mexico, more than 50% of the females deserted during the fledgling-dependency period with no attempt to renest. A dynamic stochastic optimization model based on natural selection theory was developed to study the factors that influenced the female's strategy during brood rearing. A strategy consisted of combinations of staying at the nest, hunting, and/or deserting. The model was based on the assumption that the female brood rearing behaviors had evolved to maximize reproductive fitness. In the model, the female's reproductive fitness was defined as the weighted average of the expected survival of her current offspring and her expected future reproductive potential. This fitness function depended on the physical condition of the female and nestlings, the risks to the nestlings associated with each strategy, and the male's foraging capabilities.

The model was validated by comparing the model predictions with the actual observations of female behavior in this population of Cooper's hawks. The model parameters were estimated from sources other than the data set used to validate the model. The best fit (90% correct predictions) was obtained when the nestlings' survival and the female's

long-term reproductive potential were equally weighted during the nestling stage, but weighted in favor of the female's reproductive potential during the fledgling stage. The sensitivity analysis showed that the model predictions corresponded well with the observations of staying and hunting at all parameter bounds. However, those combinations of parameter values that reflected conditions with the least pressure to desert missed 70% to 85% of the desertions. The sensitivity analysis also indicated that the key factor influencing the female's choice of strategy was the interaction between the threat to her future reproduction due to her poor physical condition and the nestlings' risk of death from predation and exposure.

The model validation results supported the hypothesis that the reproductive strategies of female Cooper's hawks during brood rearing have evolved to maximize fitness. These results combined with the sensitivity analysis indicated that dynamic stochastic optimization modeling was an excellent tool for studying mate desertion.

Introduction

Mate desertion is defined as the termination of care by one or both parents before the young are independent (Fujioka 1989). Mating systems of most vertebrates are characterized by uniparental desertion and polygyny or, less frequently, polyandry (Kleiman 1977, Ridley 1978, Blumer

1979, Baylis 1981, Wells 1981). Recent studies have documented facultative uniparental desertion by either sex (ambisexual desertion: Beissinger 1986) within populations of biparental birds and fishes (Mendelsohn 1981, 1989, Blumer 1986, Beissinger 1986, 1987b, Beissinger and Snyder 1987, Fujioka 1989).

Mate desertion can be viewed as a behavioral strategy with fitness tradeoffs: by deserting, an individual may reduce the fitness of its current offspring but increase its chances of successfully breeding again. However, these tradeoffs are part of a dynamic process that changes over time. According to parental investment theory, mate desertion should be favored by natural selection when (1) the deserter's chances of breeding again are high; (2) the current offspring no longer require biparental care to reach independence, or have a low probability of survival; and (3) the deserter's contribution to parental investment is relatively small (Trivers 1972, Maynard Smith 1977, Beissinger 1986, Beissinger and Snyder 1987, Lazarus 1990).

Mate desertion has been modeled using the game-theoretic concept of an evolutionarily stable strategy (ESS) (Maynard Smith 1977, 1982, Grafen and Sibley 1978, Schuster and Sigmund 1981, Vehrencamp and Bradbury 1984, Lazarus, 1990). Although these models illuminate the evolutionary dynamics of mate desertion, they are appropriate only if the success of an individual's mating strategy is dependent upon the success of the mating strategies used by other individuals in the population (a "game" against other individuals) (Riechert and Hammerstein 1983). As a result, the game theory models are not designed to predict which behavioral strategy is "best" or optimal under various conditions (Houston and McNamara 1987). In addition, ESS models of mate desertion tend to be static and deterministic (Houston and McNamara 1987), factors that reduce their realism.

Mate desertion has also been examined empirically by equating fitness with indirect measures of current reproductive effort of the deserter in populations in which desertion is observed (e.g., Blumer 1986, Beissinger 1987b, Fujioka 1989). These empirical studies provide insights into the environmental and behavioral conditions that are conducive to mate desertion in particular populations. However, the major drawback to these empirical approaches is that fitness is measured indirectly. The parental investment strategy that maximizes some indirect measure of reproductive effort is assumed to be equivalent to the strategy that maximizes fitness. Examples of these measures include all energy expended during the nesting cycle that is devoted to reproduction (Beissinger 1987b), nest attendance rates (Fujioka 1989), the quality of the food delivered to the nest (Mendelsohn 1989), and the ratio of caloric values of eggs to body mass (Congdon et al. 1983).

Another problem with the empirical approach is that the risks associated with reproductive strategies are rarely incorporated into the measure of reproductive effort. Beissinger (1987b) uses a subjective index to evaluate what he defines as the most risky behavior associated with reproduction in snail kites (Rostrhamus sociabilis), chasing potential predators or conspecifics. He uses these risk indices to augment observed energy expenditures as an estimate of trends in parental investment between deserters and nondeserters. Beissinger notes the limitations of this approach when he states that no method currently exists to integrate risk and other measures of reproductive effort into one unit of measurement.

The question of an appropriate "currency" for behavioral decisions receives considerable attention (Clark 1987); a recent review by McNamara and Houston (1986), recommends a dynamic Markovian (stochastic optimization) approach that incorporates a fitness function based on lifetime fitness. This approach is best applied to those cases in which the success of an individual's behavioral strategy is assumed to be independent of the success of the behavioral strategies chosen by conspecifics (a "game" against nature) (Riechert and Hammerstein 1983, Houston and McNamara 1987).

The dynamic stochastic optimization model described here was developed to examine female mate desertion in a population of Cooper's hawks (Accipiter cooperii). The Cooper's hawk is a medium-sized raptor that occupies forested habitats throughout North America and preys on a wide variety of vertebrates (Reynolds 1989). As is typical of most raptors, it has sexual role partitioning during the nesting season. The male is the primary hunter, and the female usually stays at the nest to protect and feed the young. However, the female can hunt to augment the male's food provisioning.

Over 50% of the female Cooper's hawks studied from 1984-1988 in north-central New Mexico deserted their nests (Chapter IV). The desertions all occurred during the fledgling-dependency period when the young were 6-8 weeks of age. In all desertions, the male continued care until the young were independent (11-12 weeks of age). Unlike deserters in other avian species, none of the females renested after desertion. Following desertion, the females moved to areas that were 8-20 km from the nesting area, occupied small home ranges in these areas for 4-6 weeks and then presumably migrated (Chapter IV). The nondeserting females either remained at the nest until the young were independent or helped the male to hunt until the young were independent.

I also observed variability in the female's allocation of food, particularly when the male was not meeting the energy requirements of the family (Chapter IV). Some females reduced their energy intake below their estimated energy requirements while providing enough food to meet the energy requirements of the brood. Other females shared the food equally with the nestlings which resulted in insufficient food for both the brood and the female.

Based on these observations, I hypothesized that the female's breeding strategies had evolved to maximize her reproductive fitness. These breeding strategies consisted of actions taken by the female during brood rearing. The three possible actions were (1) staying at the nest to protect the young, (2) hunting to augment the male's food supply, and (3) deserting. I also hypothesized that the major factors affecting the female's reproductive fitness and thus her optimal strategies were her physical condition, the physical condition of the nestlings, the risks to the nestlings associated with each strategy, and the foraging capabilities of her mate. The physical condition of the female and the nestlings were a function of their energy expenditures and energy intakes. I assumed that energy intake was a random process. The model incorporated these hypotheses and allowed these factors to vary over time.

The model validation compared the model predictions to the actual behaviors of a population of nesting Cooper's hawks, using parameter estimates that were independent of the observations. In the sensitivity analysis the parameter estimates were varied and the effect of these variations on model validation were examined. This analysis provided insight into the key factors influencing model validation and showed how robust the model was to uncertainties in the parameter estimates.

The Model

Dynamic stochastic optimization models have been used to model a variety of behavioral strategies, including group sizes of social predators, patch selection by foragers, offspring provisioning, oviposition site selection, and clutch size (Clark 1987, Mangel and Clark 1986, Mangel 1987, Houston et al. 1988). Details of this modeling approach are presented in Mangel and Clark (1988). Such models include the state of the animal, a set of strategies the animal may choose, dynamics describing how the state of the animal changes over time as a function of the strategy chosen, and a fitness function. The underlying assumption of this modeling approach is that the optimal strategy is the strategy that maximizes the fitness function. The fitness function incorporates the complex interactions of benefits and risks associated with a strategy, for example, foraging efficiency vs. predation risks (Mangel and Clark 1988).

The dynamic stochastic optimization model I developed to study female mate desertion in Cooper's hawks used discrete time intervals. The observation time period was divided into five, 2- to 3- week intervals. These time periods represented distinct phases in the growth and behavioral development of the current offspring, and consequently, distinct phases in parental requirements. They were deemed appropriate periods for the female to choose different actions. The first time interval (T_1) represented the early nestling period (weeks 1-2); T_2 represented the late nestling period (weeks 3-5); T_3 represented the early fledgling-dependency period (weeks 6-7); T_4 represented the late fledgling-dependency period (weeks 8-10); and T_5 (also denoted T) represented the end of the observation period, when the young reached independence. The beginning of an arbitrary interval was denoted by t.

The state of the nestlings at time t, $X_n(t)$, was a measure of the energy reserves of the brood. The female's state variable, $X_f(t)$, represented her body condition; a function of the female's weight normalized by her linear dimensions. These state variables were random because they were functions of the energy intake of the female and the nestlings, which I assumed were random processes. The actual values the random variables assumed (realizations of the random variables) were denoted by x_n and x_f. Although the state variables were continuous, I grouped them into seven discrete categories (Tables B-3 and B-4). I did not use different notation for the discrete variables, the meaning should be clear from the context.

Biological constraints dictated that the state variables have upper and lower bounds. The lower bounds for x_n (NCRIT) and x_f (MCRIT) represented the minimal physical conditions for brood and female survival. The upper bound of x_n (NCAP) represented the limits of metabolizable energy intake for birds of this size and the upper bound for x_f (MCAP) represented biomass limits of adult female Cooper's hawks. Thus, for constants NCAP, MCAP, NCRIT, AND MCRIT, I assumed that

$$\text{NCRIT} \leq X_n \leq \text{NCAP}$$

$$\text{MCRIT} \leq X_f \leq \text{MCAP} \ .$$

The state variables changed from one time period to another according to the following formulas:

$$x_{nij}(t+1) = x_n(t) - \alpha_n(t) + z_{nij}$$

$$x_{fij}(t+1) = x_f(t) - \alpha_{fi} + z_{fij} \ . \qquad (1)$$

The z_{nij} and z_{fij} represented the brood's and female's energy intake and the $\alpha_n(t)$ and α_{fi} were their energy expenditures over the time period t to t+1 for action i. The values z_{nij} and z_{fij} are realizations of the discrete random variables Z_{ni} and Z_{fi}. The subscript j denotes one of the possible values of the random variables. It was assumed that some prey would always be delivered in a time period. However, the amount and type of prey would vary, depending on the female's action and the foraging capabilities of the male or male and female if they were both hunting.

The three actions a female could choose were (1) to stay at the nest and protect the young, (2) to hunt and provide additional food for the family, and (3) to desert. I assumed that a female would chose one of these actions at the beginning of each time interval and continue this action until the beginning of the next time interval. Using dynamic programming notation, let $\mathcal{A}$ be the set of actions, then $\mathcal{A}$ = {stay (1), hunt (2), desert (3)}. A decision rule for time interval t, denoted d_t, maps the state variables to an action. That is

$d_t(x_n, x_f) = i \varepsilon \mathcal{A}$ (This reads i is in the set of actions, $\mathcal{A}$)

In this application a strategy, σ, is a set of four decision rules corresponding to the first four time periods; $\sigma = \{d_1, d_2, d_3, d_4\}$. I denote the set of all possible strategies as Σ. This set is limited by the condition that once a desertion occurs all following actions must be desertion.

The fitness function was developed by first defining the conditional probabilities:

$P_n\ [X_n(T)\ |\ X_n(t) = x_n, \sigma]$ = the probability the brood survives as a function of the brood's state at independence, X_n (T), conditioned on the brood's initial condition, x_n, and strategy, σ (2)

and

$P_f\ [X_f(T)\ |\ X_f(t) = x_f,\ \sigma]$ = the probability the female reproduces in the next breeding season as a function of her state at the end of brood rearing, $X_f\ (T)$, conditioned on her initial state, x_f, and strategy σ . (3)

The female's probability of reproducing in the next breeding season was the product of the probability of her over-winter survival and the probability of her breeding conditioned on her survival. Because these probabilities were functions of the random state variables, they too were random variables. These random functions, P_n and P_f, had as their support the intervals [NCRIT, NCAP] and [MCRIT, MCAP] respectively. The values P_n (NCRIT) and P_f (MCRIT) were zero regardless of the nestlings' or female's initial condition or her strategy.

I defined nestling and female fitness as the expectations (E) of the random variables P_n and P_f :

$$\Phi_n\ (x_n,\ t,\ T,\ \sigma) = E\{P_n[X_n(T)\ |\ X_n(t) = x_n,\ \sigma]\ \}$$

and

$$\Phi_f\ (x_f,\ t,\ T,\ \sigma) = E\{P_f[X_f(T)\ |\ X_f(t) = x_f,\ \sigma]\ \}\ .$$

(The expectation of a random variable is its mean value. For these discrete random variables the expectation or mean value is the weighted average. This weighted average is the sum of the products of the values the random variable can assume and their associated probabilities.).

The fitness expressions were written recursively by noting that surviving from t to T meant surviving from t to t + 1, then surviving from t + 1 to T. Surviving from t to t + 1 included not dying from predation and exposure and receiving adequate food. The recursive forms of these fitness expressions are:

$$\Phi_n\ (x_n,\ t,\ T,\ \sigma) = [1-\beta_i(t)]$$
$$\Sigma_j\ \lambda_{ij}\,\Phi_n\ (x_{nij},\ t+1,\ T,\ \sigma) \qquad (4)$$

and

$$\Phi_f\ (x_f,\ t,\ T,\ \sigma) = \Sigma_j\ \lambda_{ij}\ \Phi_f\ (x_{fij},\ t+1,\ T,\ \sigma), \qquad (5)$$

where x_{nij} and x_{fij} were the nestling and female state variables at t + 1 given $d_t\ (x_n, x_f) = i\ \varepsilon\ \mathcal{A}$ and energy intake j. These state variables were determined by incrementing the previous state variables as shown in Eq. 1. The parameter, $\beta_i(t)$, is the probability of nestling death from factors other than starvation, e.g., predation and exposure, resulting from the female's choice of action i. I assumed the female had a negligible probability of death resulting from these factors. At the end of the nesting period I assumed the probabilities of survival and reproduction were known. These end state probabilities are denoted :

$$F_n\ (x_n) = \Phi_n\ (x_n,\ T,\ T,\ \sigma) \qquad (6)$$

and

$$F_f\ (x_f) = \Phi_f\ (x_f,\ T,\ T,\ \sigma)\,. \qquad (7)$$

The fitness function for my model was defined to be the weighted average of the nestling and female fitness:

$$\Phi(x_n, x_f, t, T, \sigma) = \gamma\, \Phi_n (x_n, t, T, \sigma) + (1 - \gamma)\, \Phi_f (x_f, t, T, \sigma),$$

where γ is the weighting factor. This weighting factor can be viewed as a normalized measure of the number of offspring, e.g. $\gamma = N / (N + R)$ where N is the current brood size and R is the female's future reproductive value. This interpretation of γ is equivalent to putting the fitness function in terms of potential offspring. However, it is not necessary to restrict γ in this way. The parameter, γ, could also depend on factors other than the current and future brood sizes. I preferred to treat γ as a parameter that reflected the relative influence of the two components of the fitness function, nestling probability of survival and female future reproduction, on the female's optimal strategy. In this more general interpretation, γ can be viewed as a more complex function of N and R and possibly other parameters.

My goal was to determine the optimal strategies predicted by the model under various conditions and compare them to actual behaviors. The optimal strategy was the strategy that maximized the fitness function:

$$\Phi(x_n,\ x_f,\ t,\ T) = \max_{\sigma \varepsilon \Sigma} [\Phi(x_n,\ x_f,\ t,\ T, \Phi)]$$

I could solve for the optimal σ, by writing Φ recursively then using backward induction. Combining Eqs. 4 and 5, gave the recursive form for Φ:

$$\Phi(x_n,\ x_f,\ t,\ T,\ \sigma) = \gamma[1-\beta_i(t)]\ \Sigma_j\ \lambda_{ij}\ \Phi_n\ (x_{nij},\ t+1,\ T,\ \sigma) + (1-\gamma)\ \Sigma_j\ \lambda_{ij}\ \Phi_f\ (x_{fij},\ t+1,\ T,\ \sigma) \qquad (8)$$

where i was the action such that $d_t(x_n, x_f) = i$ and j ranged over all energy intake values. For each set of initial x_n and x_f, backward induction was used to determine the optimal strategies for each time period. I solved Eq. 8 for $t = T - 1$ for all decision rules (actions) $d_{T-1}\ (x_n, x_f)$. I then determined the decision rule that maximized Φ. The corresponding Φ_n and Φ_f were used in the next iteration, T - 2 to T. I continued in this way using the results from the previous iteration until $t = 1$. In this way I determined the optimal decision rules or actions for each time period and thus the optimal strategy (see Houston et al. (1988) for a detailed illustration of backward induction).

Another condition imposed on the model solution was that a female who deserted did not return. Thus, evaluation of a desertion strategy required that the probabilities associated with desertion in all later time periods be used to determine the optimal strategy.

Fig. V-1 illustrates the results of the model. The optimal actions are plotted for each time period as functions of the physical conditions of the nestling (horizontal axis) and the female (vertical axis). These plots show how the optimal actions can vary over time.

Parameter Estimation

The parameter estimates in this model were from the literature or from a simulation and not from the data used for model validation. Most of the estimates were from data on Cooper's hawks, or other raptors when information on Cooper's hawks was not available. Details of the parameter estimates summarized here are presented in Appendix B.

Female's energy expenditure (α_{fi})

The female's energy expenditures for each action were based on daily estimates of energy expenditure of female Cooper's hawks breeding in Utah (Fischer 1986). These estimates were corrected for predicted thermoregulatory costs. Since I assumed the female's action was constant throughout a time period, these daily energy expenditures represented the average energy expenditure for that action throughout the time period. The values used in the model are presented in Appendix B.

Brood energy expenditure [$\alpha_n(t)$]

Estimates of the brood's energy expenditures throughout the breeding season are presented in Table B-1. These estimates were based on the allometric equation developed in Chapter IV (Eq. 17) to predict peak nestling daily energy expenditure as a function of adult biomass. The daily energy requirements of the brood throughout the nesting season were estimated as a percentage of the brood's predicted peak daily requirements. These daily energy requirements were assumed to remain constant throughout a time period (see Appendix B for further details).

Probability of delivering prey of energy value z_j (λ_{ij})

The probability of delivering prey with energy value z_j in a 24-hr period, given action i, λ_{ij}, was a function of the hawks' foraging capabilities. These capabilities included whether or not the male was hunting alone (action 1 and 3) or with the female (action 2), the potential number of prey deliveries associated with each action, and the prey size utilization patterns of the male and female. I estimated λ_{ij} using a computer simulation of prey deliveries to the nest. The computer simulation was based on a multinomial model that included the number of foraging excursions and three possible prey types: small, medium, and large.

Scenario parameters

The amount of energy delivered to the nest given action i (Z_i), may or may not have been enough energy to satisfy the total energy requirements of the female and the brood. If the energy delivered to the nest was not adequate to meet the family's daily energy requirements, the degree to which each member of the family was in a negative energy balance was controlled by the female's allocation decisions. I developed 8 scenarios that represented the range of conditions determining the expected energy intake of the nestlings [$E(Z_{ni})$] and the females [$E(Z_{fi})$] in this Cooper's hawk population. These scenarios and the scenario-dependent estimates of $E(Z_{fi})$ and $E(Z_{ni})$ are presented in Table B-2. All estimates of $E(Z_{fi})$ and $E(Z_{ni})$ were a function of the female's (α_{fi}) and the brood's [$\alpha_n(t)$] energy requirements, respectively. These estimates also assumed equal division of food among broodmates. Additional details about the scenarios are given in Appendix B.

Brood state variable (X_n) and probability of survival [$F_n(x_n)$]

The brood's state variable (X_n) was an index of the physical condition of all the nestlings in the brood. These indices were assumed to be proportional to the level at which the brood's energy requirements were met. The values used for each state (x_n) and the associated probability distribution for brood survival at T [$F_n(x_n)$ as defined in Eq. 6] are presented in Table B-4. Detailed descriptions of X_n and $F_n(x_n)$ are presented in Appendix B.

Female state variable (X_f) and probability of future reproduction ($F_f[x_f]$)

The female's state variable (X_f) was her wing loading (Pa--mass/wing span), which was used as an index of her energy reserves in this model. I used wing loading instead of mass because I wanted to normalize the female's state variable by her linear dimensions so that large-bodied individuals could be compared with smaller-bodied individuals. The range of values for X_f is presented in Table B-3. The probability of the female reproducing in the next breeding season given her condition at T [$F_f(x_f)$ as defined in Eq. 7] is presented for each state variable category in Table B-3. The bases for these values are described in Appendix B.

Risks to the brood ($\beta_i[t]$)

The values used to estimate the brood's risks ($\beta_i[t]$) related to the female's choice of action and the calculations used to obtain these values are presented in Table B-5. These estimates were based on nestling mortality rates of a closely related species, the European sparrowhawk

(A. nisus) (Moss 1979). Details of the calculations are presented in Appendix B.

Validation of the Model: Optimal Strategy vs Observed Strategy

In order for models to have credibility they have to be validated. There are a variety of ways to validate models, and the benefits and limitations of these procedures have been discussed extensively in the ecological validation literature (see Naylor and Finger 1967, Steinhorst 1979, Leggett and Williams 1981, and Loehle 1983, for reviews). My approach to model validation was to compare the predictions of the model to the actual observations, using model parameter estimates from independent data sources. This type of rigorous model validation has not been done for any published mate-desertion model.

I compared model results (See Fig. V-1 for an example of model results) with actual observations of the strategies of female Cooper's hawks nesting in north-central New Mexico. With radiotelemetry (see Chapter III for details of the behavioral monitoring), the nesting behavior of females at 12 different nests (Table V-1) was observed during the 1984, 1986, and 1988 nesting seasons. One female (No. 10) was monitored for two years, but she was paired with a different male during each season and had different brood sizes each year.

The females' initial states were determined by morphometric measurements collected when each female was trapped at the nest during T_1. The females' energy reserves in subsequent time periods were estimated from the average daily energy budget (DEB) calculated for each female during that time period. A DEB was the net difference between energy intake and energy expenditure for a 24-hr period. The energy intake estimate was based on observations of food consumption by the females at each nest. The energy expenditure was based on time-energy budget models that incorporated activity data collected on radio-tagged females and metabolism measurements of captive accipiters. A detailed description of the DEB approach is in Chapter IV.

In general, a DEB was estimated weekly for each female during the nesting season. The DEB for a time period was the average of these weekly DEB estimates. If the average DEB for a female was negative during one time period and her energy expenditures exceeded her energy intake by more than 20%, I assumed the female was losing energy reserves. This assumption was supported by weight losses recorded in 2 females that were retrapped during T_2 and estimated to have a negative average DEB during T_1 (Chapter IV). Because a DEB estimate was not available for each day during a time period, I could not accurately estimate the amount of energy reserves a female actually lost over a 2 to 3 week period. Therefore, if my estimates indicated a female was losing energy reserves, I lowered her state variable to the next lower state for the next time period.

To minimize disturbance to the nest and avoid influencing the females' behavior, I did not measure the nestlings' hatching state. I used the average net DEB estimate during T_1 as the nestlings' initial state. The nestlings subsequent states were also estimated from the average net DEB for the preceding time period. The net DEB for nestlings was based on observations of food consumption by the broods at each nest and allometric estimates of average nestling expenditure. The time-energy budget approach used to develop the DEB estimates for the nestlings is described in Chapter IV.

To compare the actual observations with the model predictions, I determined the model predictions for those scenarios that best described the conditions of each nest. These conditions included (1) the brood size (which could vary over time as a result of nestling mortality); (2) the sex ratio of the brood; and (3) whether or not the brood's and/or the female's energy requirements were being met by the hunting hawk(s). The third condition was determined by an evaluation of the female and brood average DEB estimates for each nest during each time period. For a few nests, the model predictions for several scenarios were compared with the observations. In each case, the scenario that best reflected the conditions of the nest resulted in predictions that most closely matched the observations.

Twelve of the thirteen nests had appropriate data for all four time intervals, whereas one of the nests had observations in only three time intervals because of early desertion during T_3. As a result, there were a total of 51 observations to compare with the model predictions (Table V-1).

Table V-1 reports the results of the validation for $\gamma = 1/2$. This value of γ is equivalent to setting the current brood size (N) equal to the female's expected number of offspring in the next breeding season (R). The expected number of offspring, R, is a function of a variety of factors including the age of the female. A female Cooper's hawk cannot be aged by her plumage characteristics after she is 2 years old. Therefore, I could not estimate an R for the observed females. Setting R = N was a reasonable first approximation for γ.

In Table V-1, the boxes indicate cases in which the optimal action predicted by the model was not the actual action. There were only eight such cases. In five of these cases the model predicted an action actually chosen by the female in the next time period. The model identified six of the seven deserters and gave an 84% correct overall prediction. The observed nest strategies showed four patterns: Stay - Hunt - Desert , Stay - Hunt, Hunt, and Stay

- Desert. The model correctly identified 8 of the 13 strategies.

Typically, the maximum value for the fitness function differed greatly from the values for the other actions, e.g., varied between 0.2 to 0.6. However, in a few instances the top two values of the fitness functions were quite close. In the computer implementation of the model, the values of the fitness function were determined by categorizing the state variables and then evaluating the fitness function rather than by interpolating the fitness function. Therefore, a separation that was quite small should be viewed as a tie, indicating that either the computer implementation lacked adequate resolution or either action was optimal. I considered as ties the cases in which the numerical separation of the top two actions was less than 0.05. These ties are identified in Table V-1.

To look at the effects of different values of γ on the validation results, two other cases were considered; $\gamma = 1/3$ and $\gamma = 2/3$. Using the interpretation of γ as a normalized measure of the number of offspring, $\gamma = 1/3$ represents the situation where the female's expected number of future offspring is twice the number of current nestlings ($R = 2N$). The reverse is true for $\gamma = 2/3$, the number of current nestlings is twice the expected number of future offspring ($N = 2R$). Another way of viewing these values of γ is that for $\gamma = 1/3$, the female's probability of reproduction is weighted twice as much as the current brood's probability of survival. For $\gamma = 2/3$, the probability of survival of the current brood is weighted twice as much as the female's probability of reproduction in the next breeding season. The results of these analyses and the $\gamma = 1/2$ case (equally weighted) are summarized for each time period in Table V-2.

In T_1 and T_2, the weighting that favored the current brood's probability of survival ($\gamma = 2/3$) had the highest number of matches between model predictions and actual observations. In T_3 and T_4 equal weighting, $\gamma = 1/2$, had the same or more matches than the weighting that favored brood survival, $\gamma = 2/3$. However, in T_4 the weighting that favored the probability of female future reproduction, $\gamma = 1/3$, had the highest match (100%). These results indicated that the weighting factor may be a function of time or some factors dependent on time. Therefore a mixed model that weighted the probability of current brood survival twice as much as the probability of the female's future reproduction during T_1 and T_2 and weighted them equally in T_3 and T_4 was compared to the actual observations.

Table V-3 reports the results of this mixed model validation. For these values of γ there were only five cases where the action predicted by the model did not match the actual observations. In four of these cases the model predicted an action actually chosen by the female in the next time period. The model identified six of the seven deserters and gave a 90% correct overall prediction. The model correctly identified 9 of the 13 strategies.

Sensitivity Analyses of the Validation Results

I investigated the sensitivity of the validation results to the parameter estimates. I was interested in discovering how robust the validation results were to the uncertainties inherent in the parameter estimates. I was also interested in determining which parameters were most important to the validation results. Identifying the important parameters would give insight into the process and reveal those parameters that must be carefully monitored in future experiments.

To study validation sensitivity, I used the mixed model and fixed the scenarios for each nest. The scenario parameters were those parameters that influenced the degree to which the female and nestlings meet their energy requirements: λ_{ij}'s, $\alpha_n(t)$, α_{fi}, $E(Z_{ni})$, and $E(Z_{fi})$. The scenarios chosen were those that reflected the conditions observed at the nest: meeting requirements or not meeting requirements.

As a first step in the sensitivity analysis, I examined the effect of the number of categories for X_f and X_n on model validation. I did not alter the NCRIT, NCAP, MCRIT, or MCAP, but broadened the categories using five states instead of the original seven states (Table V-4). The

$F_f(x_f)$ and $F_n(x_n)$ associated with the broadened categories were the averages of the $F_f(x_f)$ and $F_n(x_n)$ associated with the original seven categories (Table V-4).

I developed a validation table for this categorization (using the same format as in Table V-1) and found no important differences in validation as a result of categorization changes. There were three ties where there had not been ties previously, and in one case there was no longer a tie. The percent match between the predictions and observations remained at 90%.

Because the number of state variable categories did not affect the results, I fixed the number of categories at seven and varied the remaining parameters: the risk to nestlings from the female's strategy, $\beta_i(t)$; the end-state probabilities, $F_n(x_n)$ and $F_f(x_f)$; and the boundaries of the X_f and X_n categories. In the case of X_f, MCRIT was lowered by 10% and MCAP was raised by 10%, and the same rule for forming the categories was applied (see Appendix B). For X_n, I assumed that NCRIT was already set as low as was biologically reasonable, so NCRIT and NCAP were raised by 10% and the same rule for forming the categories was applied (see Appendix B). For $\beta_i(t)$, values that were 33% above and below the nominal values (the original estimates used for validation) were used (see Appendix B for details on the bounds). Similar to X_n and X_f, $F_n(x_n)$ and $F_f(x_f)$ were varied 10% above and below the nominal values. These upper and lower limits for the various parameters represent my judgement of the bounds on the uncertainties associated with the parameter estimates. The 10% bounds for the state variables and end state probabilities reflected the same degree of uncertainty as the 33% bound on $\beta_i(t)$.

I used these bounds and the nominal values (in the case of X_f and X_n the nominal values served as a bound) as levels in a full factorial experimental design. That is, I used all combinations of these levels for the parameters as inputs to the model. There were two levels for X_f and X_n and three levels for the remaining parameters for a total of 108 different parameter combinations for each nest (scenario). For each of the 108 cases, I developed a validation table (see Table V-1 for an example) and determined the percentage of agreement between the observations and model predictions. Fig. V-2 is a schematic of this analysis.

Finally, I used an analysis of variance (ANOVA) as an exploratory technique to determine those factors that most influenced the results. Because the output variable was derived from a computer simulation that gives the same results for the same inputs, there is no real random error and significance tests are meaningless. However, the F values can be used as exploratory indicators of the relative importance of the parameters and interactions.

I used the levels associated with the uncertainty bounds to determine which parameters were influencing the results because this information would identify those parameters that must be closely monitored in future experiments. I performed a full factorial design so that I could assess not only the effects of the individual parameters, but also the interactions between the parameters.

The outcome variable was the percentage of agreement between the predicted optimal strategies and the observed strategies (% match) and ranged from 84% to 96%. The ANOVA, using a model with the five parameters and all second-order interactions, showed that the important factors were the interactions between X_f and $\beta_i(t)$ ($\underline{F} = 172$) and X_f and $F_n(x_n)$ ($\underline{F} = 56$), the parameters $F_n(x_n)$ ($\underline{F} = 40$), X_f ($\underline{F} = 16$), and possibly the parameter $\beta_i(t)$ ($\underline{F} = 6$). The remaining effects had $\underline{F}$ values less than 2.0. This model for the ANOVA had an $\underline{R}^2$ of 0.89. (The value of $\underline{R}^2$ can be viewed as a measure of whether or not the ANOVA includes the important factors for explaining the variability of the outcome variable, % match.) It is useful to remember that the different levels of X_n and X_f correspond to different levels of NCRIT and MCRIT, the body condition levels where the probabilities of survival and reproduction are zero. A lower critical value means that the brood or female is less threatened by poor body condition than in the case of a higher critical value.

Based on the previous ANOVA results, I examined a reduced model with factors X_f, $\beta_i(t)$, and $F_n(x_n)$, the three second order interactions described above, and the third order interaction. The results of this ANOVA again showed that the most important factor was the interaction between X_f and $\beta_i(t)$ (F = 156). The other possible important factors were the interaction between X_f and $F_n(x_n)$ (F = 50), and the parameters $F_n(x_n)$ (F = 36) and X_f (F = 14). The parameter $\beta_i(t)$ (F = 5), the interaction term between X_f and F_f (F = 4), and the third order interaction (F = 1) were not important relative to the other effects. The model for this ANOVA had an R^2 of 0.84 indicating that the model captured the important factors.

The important interactions suggested by the ANOVA were explained by observing that the best matches (average value of 95% ± 0.02%) were those cases where all parameters except $\beta_i(t)$ were set at nominal levels and the $\beta_i(t)$ were set at the upper bounds. In those situations, MCRIT was high, indicating that the female's future reproduction was threatened at a higher physical condition index than in the other cases. Also in those cases, the nestlings had the greatest risks as a result of desertion. The worst matches (average value of 86% ± 0.02%) occurred when MCRIT was low and $\beta_i(t)$ and $F_n(x_n)$ were high. These were the conditions with the least pressure on the female to desert; she could reach a lower index of physical condition before her future reproduction was threatened (low MCRIT), the brood's end state survival probabilities were high [$F_n(x_n)$], and the predation and exposure risks as a result of deserting were high [$\beta_i(t)$]. In those cases in which the female had the most pressure to desert (MCRIT was high), $\beta_i(t)$ was at the lower bound, and $F_n(x_n)$ was at the lower bound) the percentage of agreement was intermediate (average value of 90% ± 0.01%).

Varying the parameters did not have much effect on the percentage of agreement for the stay and hunt actions and yielded at least an 84% overall agreement between model predictions and observations. However, those cases with the lowest percentage agreement, the cases with the least pressure to desert, missed four to five of the seven deserters.

Discussion

My results indicated that the dynamic stochastic optimization model was an excellent predictor of the breeding strategies, including desertion, used by nesting females. The model validation supported my hypothesis that the breeding strategies chosen by the female Cooper's hawk were optimal strategies that maximized her expected reproductive fitness, which was a weighted average of the female's current reproductive effort and her potential reproduction in the next breeding season. The major factors influencing the female's strategy choices were her state, the state of her brood, the risks to the nestlings associated with each strategy, and the male's and female's foraging capabilities.

The results of this study indicated that the fitness tradeoffs associated with mate desertion were more complex than previously described. For example, previous studies of mate desertion have focused on species that apparently renest immediately following desertion (Trivers 1972, Maynard Smith 1977, Beissinger 1986, Fujioka 1989). As a result, the future reproductive benefits of mate desertion considered in these studies have been restricted to renesting opportunities in the current breeding season. By expanding the future reproductive benefits beyond the current nesting season as I did in this study, I gained insights into the desertion decisions in species, such as the Cooper's hawk, that do not immediately renest after desertion (Chapter IV).

In female Cooper's hawks, one of the immediate benefits of deserting was apparently the improvement of her physical condition before migration, which increased her probability of surviving migration, thus increasing her probability of overwinter survival, and thus her probability of future reproduction in the next breeding season. The female's poor physical condition at the time of desertion was attributed to her preferentially feeding the nestlings the food delivered to the nest when there was not enough food to meet the family's requirements (Chapter IV).

Although deserting by females without immediate renesting has not been previously recorded in birds, it may be occurring in avian species whose desertions are assumed to be succeeded by renesting. In several studies reporting high incidences of female desertion in other long-lived species (snail kite--Beissinger 1986, 1987b, little egrets--Fujioka, 1989), the observations of renesting by these females are uncommon (Beissinger 1986, Beissinger and Snyder 1987--one observation) or nonexistent (Fujioka 1989). It is possible that these deserters do not immediately renest and that their behavioral strategies during the nesting season are influenced by the same fitness tradeoffs examined in this study.

In addition to predicting desertion when the female's condition was poor, the model predicted desertion when the female was in adequate condition and the brood was in poor condition with a low probability of survival. However, I was not able to test these predictions because these conditions were not observed.

The fitness tradeoffs associated with mate desertion usually stress the negative effect of desertion on the survival of the current offspring (Trivers 1972, Lazarus 1990). However, in species with sex role partitioning during the nesting season, such as the Cooper's hawk, desertion by the parent not providing the majority of the food may actually benefit the current offspring by increasing their available food supply. The results of this study support parental investment predictions (Trivers 1972, Maynard Smith 1977, Beissinger and Snyder 1987) that, in most cases, desertion does not result in substantial reductions in survival of current offspring.

The model validation results also suggested that the female's decision-making was not based solely on past investments, i.e., "Concord fallacy" (Curio 1987). The female's current reproductive effort, which can be equated with her past investment costs (Curio 1987, Beissinger 1987a), had a greater influence on her decision-making than her benefits of future reproduction in the early stages of the nesting season. However, in the later stages of the nesting season, her future reproductive benefits may have had equal or greater influence on her choice of action than did her current reproductive effort.

The results of the sensitivity analysis showed that the model predictions of staying and hunting were robust to uncertainties in the parameter estimates. However, the sensitivity analysis also showed that for parameter values that represented conditions with the least pressure to desert the model missed 5 to 6 of the deserters. These results suggested two alternative hypotheses about the true values of the input parameters that are important for future experiments. The first hypothesis is that the observational data were correctly characterized by the parameter estimates that gave the highest percentage of matches: the situations with the greatest risks to both current nestling survival and the female's future reproduction due to her poor physical condition. Under this hypothesis, it is important for future studies to accurately reflect the threat to the female's future reproduction as a function of her physical condition and the threat to the nestlings' survival if she deserts. The second hypothesis is that the true value of the parameters were in the input space with the lowest % match: the cases with the least pressure on the female to desert. If this hypothesis is true, the model may have missed an additional factor(s) important for influencing desertion. In either case, the implications are that future experiments should focus on careful monitoring of the female's state variable, her probabilities of survival and reproduction as a function of those state variables, and the risks to the brood as a function of the female's strategy.

To address the question of why male Cooper's hawks do not desert, researchers can modify this model to examine the female's optimal strategies if the male deserts or dies. Her actions will clearly be a choice between hunting and deserting. The optimal strategy depends on the probability of brood survival and the female's capabilities to meet the family's energy requirements. However, a new model will have to be developed to examine the fitness tradeoffs influencing the male's breeding strategies.

Although the results of this study supported my hypothesis that the female's breeding strategies maximized her fitness, validation against additional data sets is necessary before I can rule out alternative explanations for the behavior patterns of the females in this population. These patterns could be a result of other random processes, or a female could be genetically predisposed to use a particular set of strategies, i.e., some females will always desert independent of the current conditions. A test of these alternatives will require different modeling techniques and additional data including multiple observations of the same females over several breeding seasons.

In summary, this study was a unique application of the dynamic stochastic optimization approach developed by Mangel and Clark (1986, 1988), Clark (1987), Houston and McNamara (1987), and Houston et al. (1988). These results strongly supported their conclusions that dynamic stochastic optimization models are powerful tools for studying the complexities of animal behavior from an evolutionary standpoint because they lead to quantitatively testable predictions about behavioral strategies.

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Appendix A. List of Symbols

T_i	A discrete time period during the nesting season
T	The time at which the young reach independence
t	Beginning of an arbitray time period
$X_n(t)$	The brood's state variable, energy reserves
$X_f(t)$	The female's state variable, body condition index
$F_n(x_n)$	Probability the brood survives to independence given state at T is x_n
$F_f(x_f)$	Probability of the female's future reproduction given state at T is x_f

ϕ	Female's expected reproductive potential
γ	The weighting factor in the fitness function
$\alpha_n(t)$	Energy expenditure of the brood as a function of their age
α_{fi}	Energy expenditure of the female as a function of strategy
$Z_{ni}/E(Z_{ni})$	Energy intake by the brood given action *i* / expected energy intake
$Z_{fi}/E(Z_{fi})$	Energy intake by the female given action *i* / expected energy intake
λ_{ij}	Probability of delivering prey of energy value z_j using action *i*
NCRIT	Critical lower boundary of the brood's state variable
MCRIT	Critical lower boundary of the female's state variable
NCAP	Upper boundary of the brood's state variable
MCAP	Upper boundary of the female's state variable
$\beta_i(t)$	Risks to the brood associated with the female's strategy
$\mathcal{A}$	Set of actions that the female can choose, Stay, Hunt, or Desert
$d_t(x_n, x_f)$	a decision rule - for each time period it maps the state variables to the actions
σ	a strategy - a set of decision rules, one for each time period $\{d_1, d_2, d_3, d4\}$

Σ	The set of all possible strategies
DEB	Daily energy budget
E_n^*	The peak rate of daily energy expenditure of a nestling
$E_n(t)$	Daily energy expenditure of a nestling

Appendix B. Parameter Estimation

Female's energy expenditure (α_{fi})

The female's daily energy expenditures for each action were estimated from time-energy budget estimates of daily energy expenditures of adult female Cooper's hawks nesting in Utah (Fischer 1986). Fischer does not estimate thermoregulatory costs of the breeding females and this omission can be a major source of error in time-energy budget estimates (Weathers et al. 1984, Goldstein 1988, Nagy 1989). To correct for this, I increased Fischer's estimates by 15%, which is the average thermoregulatory costs measured in breeding female European kestrels (*Falco tinnunculus*) (Masman 1986).

A female that stays at the nest and does not hunt (action 1) is not very active so I equated α_{f1} with Fischer's (1986) corrected mean value of existence metabolism (EM) for breeding female Cooper's hawks (2.98 Watts (W)). I assumed the activity costs of a deserter (action 3) were one-half the activity costs of a hunter (action 2) because the breeding female was hunting only for herself and did not have the transport costs of delivering prey to the nest. As a result, I used Fischer's mean EM value plus mean activity costs of breeding female Cooper's hawks for α_{f2} (4.3 W) and the mean EM + 50% of the mean activity costs (3.64 W) for α_{f3}.

Brood energy expenditure ($\alpha_n(t)$)

The estimates of the brood's energy expenditure throughout the breeding season (Table B-1) were based on the allometric equation described in Chapter IV (Eq. 17) to predict peak nestling daily energy expenditure as a function of adult biomass. This equation is

$$E_n^* = 53.587\ M^{0.757},$$

where E_n^* is the peak rate of daily energy expenditure of a nestling (W) and M is the average biomass (g) of an adult. Because of the extreme sexual size dimorphism in this species, E_n^* was estimated separately for male and female nestlings using the average weights of adult male and female Cooper's hawks in the northern New Mexico population (Chapter IV).

Peak nestling energy expenditure of nidicolous young occurs at the time when nestling growth and feather development are at a maximum rate (Ricklefs 1974, Walsberg 1983). On the basis of growth rate data for Cooper's hawks (Sumner 1929) and other raptors of equivalent size (Schnell 1958, Moss 1979, Kirkwood 1981, Wijnandts 1984), I estimated that in this population, E_n^* occurs during the second half of the nestling stage (T_2). Therefore, I used E_n^* for the daily energy expenditure of an individual nestling (E_n(t]) in T_2 (Table B-1). Using this growth rate information, I assumed that $E_n(1) = 0.3E_n^*$, $E_n(3) = 0.7E_n^*$, and $E_n(4) = 0.5E_n^*$ (Table B-1). To calculate $a_n(t)$ which is the brood's daily energy requirements, I summed $E_n(t)$ for each nestling in a brood.

<u>Probability of delivering prey of energy value z_j (λ_{ij})</u>

On the basis of prey delivery rates for other nesting populations of accipiters (Snyder and Wiley 1976, Newton 1978, Simmons 1986, Kennedy and Johnson 1986), I assumed the number of daily prey deliveries would range from one to five. The probability of a small, medium, or large prey being delivered to the nest was a function of the prey size utilization probabilities of the male hunting alone (actions 1 and 3) and of the female hunting in addition to the male (action 2). Size utilization probabilities of the males and females were considered separately because the larger-bodied female could potentially capture larger prey than the smaller-bodied male. The utilization probabilities were determined from the average proportion of these size categories delivered to the nest by males hunting and by males and females hunting in the New Mexico population of Cooper's hawks. The average proportion of these size categories delivered by all hunting males in this population was 0.18 for small prey, 0.45 for medium prey, and 0.37 for large prey. The average proportion of these prey sizes delivered to the nest when both males and females were hunting was 0.13 for small prey, 0.41 for medium prey, and 0.46 for large prey. These percentages were used as the utilization probabilities of small, medium, and large-sized prey and were denoted in the following calculations as p_{Si}, p_{Mi}, and p_{Li}, respectively. Although these utilization probabilities were based on the availability of the prey size categories, I did not use prey availability probabilities to estimate them because accipiters do not select prey sizes in proportion to their availability (Snyder and Wiley 1976, Kennedy and Johnson 1986).

The energy value of a small, medium and large prey was based on the prey delivery data reported in Chapter II for this population of Cooper's hawks. Each prey delivery was assigned a biomass value using the methodology described in Chapter IV. Based on these biomass values, each prey item was assigned to one of three size categories developed by Kennedy and Johnson (1986) to estimate prey size preferences of Cooper's hawks nesting in Washington. Prey not exceeding 27 g were considered to be "small." "Medium" prey were defined as those larger than 27 g but no larger than 91 g. "Large" prey exceeded 91 g.

The average energy values for small (0.76 W), medium (3.04 W), and large (7.83 W) prey categories were the weighted averages of the energy values of all prey items assigned to each of the three categories.

I assumed the daily prey delivery rate, n, varied from 1 to 5, therefore, total energy delivered to the nest in a 24-hr period could vary from 0.76 W (one small prey) to 39.15 W (five large prey). I divided this range of energy delivered to the nest into eight 5-W intervals, denoted by $w_j = [5(j-1), 5j]$, $j = 1, \ldots, 8$. The Z_i were random variables representing energy delivered over a 24-h period for action i. The z_{ij} were the possible values that this random variable could assume and were the midpoints of the intervals w_j. The parameter n is a scenario variable and indicated the capabilities of the hunter(s).

I then determined the probabilities associated with each interval w_j, and therefore, for each z_{ij}, for a given strategy i and a fixed n. The daily energy delivered to the nest depended on the combination of prey types delivered to the nest (Chapter II). Therefore, I let s, m, and l denote the number of small, medium, and large prey types delivered to the nest. Here $s = 0, 1, \ldots, n$, $m = 0, 1, \ldots, n-s$, and $l = 0, 1, \ldots, n-s-m$. The $(n+1)!$ possible prey size combinations, denoted d_{sml}, were values of a random variable that had a multinomial distribution governed by the probabilities p_{Si}, p_{Mi}, p_{Li} defined above (under the assumption that the n hunting forays (trials) were independent). That is, for s = 0, 1, ..., n; m = 0, 1, ..., n - s; and l = 0, 1, ..., n - s - m, the probability of prey combination d_{sml} is

$$P_i(d_{sml}) = \binom{n}{s}\binom{n-s}{m} p_{Si}^{s} p_{Mi}^{m} p_{Li}^{n-s-m},$$

where i denotes the action employed.

For every combination d_{sml} there was an associated variable e_{sml} representing the energy obtained from that combination of prey items. The e_{sml} were values of the random energy intake variable from n hunting forays and $P_i(e_{sml}) = P_i(d_{sml})$. Thus, under the ith strategy, one may calculate λij, the probability that $Z_i = zi_j$, as follows

$$\lambda_{ij} = \sum_{e_{sml} \varepsilon w_j} P_i(e_{sml}) , \tag{9}$$

where the summation is over all e_{sml} such that $5(j-1)\ W < e_{sml} \le 5j\ W$.

For example, the energy value for the case of all small prey for 5 hunting forays, e_{500} was 3.8 W, which was in w_1, [0,5]. The probability of this event for strategy 1 is $P_1(e_{500}) = .18^5 = 2 \times 10^{-4}$. The only e_{sml} in w_1 is for s = 5, m = 0, and n = 0. Therefore $\lambda_{11} = P_1(e_{500}) = 2 \times 10^{-4}$.

Scenario parameters

The expected energy delivered to the nest for each action was

$$E(Z_i) = \sum_j \lambda_{ij} z_j, \tag{10}$$

where the z_j are the midpoints of the energy categories and λ_{ij} is defined in Eq. 9. The expectations, $E(Z_{ni})$ and $E(Z_{fi})$, are the portions of this expected energy delivery received by the nestlings and the female, respectively.

The expected energy delivered to the nest may or may not be adequate to meet the requirements of the brood and the female. If the male hunting alone or the pair hunting together does not provide enough food to meet the family's daily energy requirements, the degree to which each member of the family is in a negative energy balance is controlled by the female's allocation decisions.

In this model I used 8 scenarios to represent the range of conditions that described the energy intake of the nestlings and the females in this Cooper's hawk population. These scenarios incorporated the capabilities of the hunter(s) to meet the family's requirements (the number of prey deliveries) and the female's allocation decisions. These scenarios and the scenario-dependent estimates of $E(Z_{fi})$, $E(Z_{ni})$ are presented in Table B-2.

All scenario estimates for $E(Z_{fj})$ and $E(Z_{nj})$ were a function of the female's and the brood's energy requirements, respectively. These estimates were based on the following assumptions: (1) when the female hunted to augment the male's provisioning, a greater percentage of the family's requirements were met; (2) when the female deserted, she was hunting for herself and was more than capable of meeting her own requirements; and (3) when the female deserted, the male was capable of meeting the energy requirements of the brood.

Female state variable (X_f) and probability of future reproduction [$F_f(x_f)$]

An average breeding female was represented by a wing loading of 51.96 Pa, the upper limit of $x_f(4)$ (Table B-3). This value was calculated from the mean mass and mean wing chord measurements for female Cooper's hawks breeding in Oregon (Henny et al. 1985). The conversion of wing chord to wing span is described in Chapter IV.

The percent wet weight of lipids in carcasses of breeding female raptors ranges from 10% - 20% (Houston 1976, Wiemeyer et al. 1980, 1986, 1987). If a bird decreased its wing loading by 20% below the average condition, I assumed it had depleted most of its fat reserves and was in a starving condition. This is the condition I used as the lower boundary to X_f (MCRIT). Breeding female raptors generally do not gain more than 20% of their biomass during the breeding season (Newton, et al. 1983, Hirons et al. 1984, Gonzalez, 1986) so I used 20% above the average condition as the upper boundary to X_f (MCAP). The other categories for X_f were logical midpoints between the average condition and MCAP and MCRIT (10% and 15% above and below the average wing loading).

If $\alpha_{fi} = z_{fij}$, then the female was assumed to be in a maintenance condition and no mass changes were predicted to occur; thus, her state variable did not change over time. However, if $\alpha_{fi} > z_{fij}$ or $\alpha_{fi} < z_{fij}$, then the female was assumed to be in a net negative or positive energy balance and mass loses or gains were expected to occur. I assumed that biomass changes reflected losses or gains of lipids and some carbohydrates (in the form of glycogen). This assumption is supported by the physiological literature (see Blem 1990, for a review), which demonstrates that during activity, such as hunting, nearly all energy is from stored lipid depots. Protein, which is not readily mobilized, is used only under extreme conditions, after both glycogen and lipid depots are nearly exhausted. Birds not involved in intensive activity, e.g., female Cooper's hawks staying at the nest or those exposed to low temperatures, obtain the majority of their energy from glycogen. However, inactive birds deprived of food use approximately 90% of their hepatic glycogen in less than 36 h. Therefore, glycogen stores generally are useful only for short-term energy demands of relatively low magnitude (Blem 1990).

On the basis of the aforementioned physiological information, I assumed that mass changes were 90% fat and 10% carbohydrate. Because carbohydrate metabolism provides 18.8 kJ/g and lipid metabolism provides 37.7 kJ/g (Blem 1990), I assumed that when the female was in a net positive or negative energy balance she gained or lost 1 g of biomass for every 35.8 kJ. Her changed biomass was then divided by her wingspan to convert to a new wing loading, and the model reevaluated her state variable based on this new wing loading.

As defined by Eq. 5, $F_f(x_f)$ is a function of her over-winter survival probability and the probability that she will breed after over-wintering given her condition at T. According to lifetime reproduction data on the European sparrowhawk in England (Newton 1988), the average probability that a breeding female will survive to the next breeding season is 0.65. I assigned this probability of over-wintering to females in average condition ($x_f(4)$). In the absence of survivorship data on female raptors as a function of their mass at the end of a breeding season, I incremented the probability of surviving for each state above and below $x_f(4)$ by the same percentages I used to increment the state variables (10%, 15%, and 20%).

In Newton's (1988) European sparrowhawk population in England, most offspring were produced by a small percentage of the females that bred annually until they died. If a breeding female overwintered her probability of reproducing in the next breeding season was very high. Thus, I assumed that if a breeding female Cooper's hawk survived the winter her probability of reproducing in the next breeding season was 1.0.

Brood State Variable (X_n) and Probability of Survival [$F_n(x_n)$]

The values used for each state (x_n) are presented in Table B-4. The rationale I used to define the upper and lower limits of each state were based on observations that raptor nestlings appear to have a limited ability to fast and continue a rapid rate of growth even when faced with sparse food supplies (Houston 1976, Kirkwood 1981). However, they can consume food quantities that exceed their requirements by variable amounts (Snyder and Snyder 1973, Newton 1978, Simmons 1986). I set the upper boundary to X_n (NCAP) at 50% above the brood's requirements which is comparable to the limits of metabolizable energy intake predicted for birds of this size (Kirkwood 1983). The quantity $x_n(6)$ was a logical midpoint between NCAP and $x_n(5)$, which represents a brood whose requirements are met. The lower limit of $x_n(5)$ represents the threshold in brood condition below which one nestling was predicted to starve. The lower limit of $x_n(4)$ represents the threshold below which broods of size 2 to 5 were predicted to be reduced by 50%, and the lower limit of $x_n(3)$ represents the threshold below which 75% of the larger broods (size 4 and 5) and 100% of the smaller broods were predicted to starve. The lower boundary to X_n (NCRIT) represents the lower limit of brood condition below which no nestlings in the larger broods (is this necessary) were predicted to survive. The survival probabilities associated with these states $[F_n(x_n)]$ were the midpoints of the intervals representing each state (Table B-4).

Risks to the brood $[\beta_i(t)]$

On the basis of detailed observations of 49 broods, Moss (1979) determined that after day 2, 21% of all nestlings died from factors other than starvation (A), and of these mortalities, 25% were from exposure to inclement weather while the female was away from the nest (B), and 17.5% were a result of predation (C). The remaining mortalities were a result of a variety of other factors.

To use this information to estimate $\beta_i(t)$ (Table B-5), I made the following assumptions: (1) the probability of nestling mortality decreased with the age of the young; (2) if the female stayed at the nest, the probability of nestling mortality from predation and exposure were zero;

(3) there was a high risk of nestling mortality if the female chose to hunt or desert while the nestlings were young (T_1); and (4) staying at the nest incurred the lowest risks, whereas deserting incurred the highest risks over all time periods. The variance associated with nestling risks were not available in the literature; so for the sensitivity analysis I assumed that the bounds on $\beta_i(t)$ were based primarily on the predation risks (C). The upper bound on $\beta_i(t)$ was arbitrarily calculated by doubling C and the lower bound was arbitrarily determined by halving C.

TABLE V-1. A comparison of the model's predicted optimal actions with the actions observed in female Cooper's hawks nesting in north-central New Mexico. In this model $\gamma = 1/2$ during all time periods.

	Time Period			
Female No./Year	T_1	T_2	T_3	T_4
4/1984	S[a]	H[b]	H	H
5/1984	H[b]	H[b]	H	H
9/1984	S	S	D	--[c]
10/1986	$\boxed{\text{H[d]/S}}$[e]	$\boxed{\text{H/S}}$	H	D
10/1988	S	$\boxed{\text{D/S}}$	$\boxed{\text{D/H}}$	D[f]
12/1986	S	S	S	D
13/1986	S	$\boxed{\text{H/S}}$	H	$\boxed{\text{H/D}}$
16/1986	S	H	H[c]	D
24/1986	S	S[f]	H[b]	H[b]
26/1988	S	S[d]	$\boxed{\text{D/H}}$	D
29/1988	$\boxed{\text{H[d]/S}}$	H[d]	H	H
30/1988	S	H	H[b]	H
31/1988	S	S[f]	H	H

---

[a] S = stay, H = hunt, and D = desert.

[b] This action was tied with the stay action. (Ties were defined to be differences of 0.05 or less between the values of the fitness functions for various actions.

[c] A condition observed and imposed in the model solution is that a female who deserts does not return.

[d] This action was tied with the desert action.

[e] The box indicates a situation in which the optimal action(s) differed from the female's chosen action (optimal/actual).

[f] This action was tied with the hunt action.

TABLE V-2. The effect of various weighting factiors (γ) on the percent match.[a]

	Weighting Factor (γ)		
Time Period	1/3[b]	1/2	2/3
T_1	69	85	100
T_2	38	77	92
T_3	69	85	85
T_4	100	92	64

---

[a] Percent match is the percentage of cases where the model predictions are the same as the action chosen by the nesting female Cooper's hawks in north-central New Mexico.

[b] $\gamma = 1/3$ weights the female's probability of future reproduction twice as much as the probability of survival of the current offspring; $\gamma = 1/2$ weights them equally; $\gamma = 2/3$ weights the current offspring survival probability twice as much as the female's probability of future reproduction.

TABLE V-3. A comparison of the model's predicted optimal actions with the actions observed in female Cooper's hawks nesting in north-central New Mexico. In this model $\gamma = 2/3$ during T_1 and T_2 and $\gamma = 1/2$ during T_3 and T_4.

	Time Period			
Female No./Year	T_1	T_2	T_3	T_4
4/1984	S[a]	H	H	H
5/1984	H[b]	H[c]	H	H
9/1984	S	S	D	--[d]
10/1986	S	$\boxed{\text{H/S}}$[e]	H	D
10/1988	S	S	$\boxed{\text{D/H}}$	D[e]
12/1986	S	S	S	D
13/1986	S	$\boxed{\text{H/S}}$	H	$\boxed{\text{H/D}}$
16/1986	S	H[f]	H[b]	D
24/1986	S	S	H[b]	H[b]
26/1988	S	S	$\boxed{\text{D/H}}$	D
29/1988	S	H	H	H
30/1988	S	H	H[b]	H
31/1988	S	S	H	H

---

[a] S = stay, H = hunt, and D = desert.

[b] This action was tied with the stay action. (Ties were defined to be differences of 0.05 or less between the values of the fitness functions for various actions)

[c] This action was tied with the other two actions.

[d] A condition observed and imposed in the model solution is that a female who deserts does not return.

[e] The box indicates a situation in which the optimal action differed from the female's chosen action (optimal/actual).

[f] This action was tied with the desert action.

TABLE V-4. The categories of X_f[a] and X_n used in the sensitivity analyses.[b]

State	Values of X_f[c]	Values of X_n[d]
5	62.35 - 57.17	$1.50\alpha_n(t) - 1.00\alpha_n(t)$
4	57.16 - 51.97	$0.99\alpha_n(t) - 0.70\alpha_n(t)$
3	51.96 - 46.77	$0.69\alpha_n(t) - 0.30\alpha_n(t)$
2	46.76 - 41.57	$0.29\alpha_n(t) - 0.20\alpha_n(t)$
1	<41.57	$<0.20\alpha_n(t)$

---

[a] X_f and X_n are the female's and nestlings' state variables, respectively.

[b] See Tables II-3 and II-4 for a comparison with the values of X_f and X_n used for parameter estimation.

[c] $F_f(x_f)$ associated with each category are 0.775, 0.72, 0.65, 0.57, and 0.00, respectively.

[d] $F_n(x_n)$ associated with each category are 1.00, 0.845, 0.5, 0.00, respectively.

TABLE B-1. Estimates of a nestling's energy expenditure $[E_n(t)]$ (W) as a function of sex and age.[a,b]

Age of Young		Male[c]	Female[d]
0 - 2 weeks	(T_1)	1.15	1.70
3 - 5 weeks	(T_2)	3.85	5.66
6 - 7 weeks	(T_3)	2.69	3.96
8 - 10 weeks	(T_4)	1.92	2.83

---

[a] The methodology used to develop these estimates is described in Appendix B and in Chapter IV.

[b] To calculate $\alpha_n(t)$, brood energy expenditure, we summed $E_n(t)$ for each nestling in a brood of a particular size during each time period.

[c] This is based on an average biomass of adult males of 283g (Chapter IV).

[d] This is based on an average biomass of adult females of 471g (Chapter IV).

TABLE B-2. Estimates of expected energy intake [E(Z_{nj}) and E(Z_{fj})] used in each scenario.[a]

	Action (i)					
	Stay (1)		Hunt (2)		Desert (3)	
Scenario	E(Z_{fj})	E(Z_{nj})	E(Z_{fj})	E(Z_{nj})	E(Z_{fj})	E(Z_{nj})
1. Male hunting - family's req.[b] not met Both hunting - female's req. not met	$0.85\alpha_{fi}$[c]	$0.80\alpha_n(t)$[d]	$0.92\alpha_{fi}$	$\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$
2. Male hunting - female's req. not met Both hunting - female's req. not met	$0.85\alpha_{fi}$	$\alpha_n(t)$	$0.92\alpha_{fi}$	$1.10\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$
3. Male hunting - family's req.not met Both hunting - family's req. met	$0.85\alpha_{fi}$	$0.80\alpha_n(t)$	$1.10\alpha_{fi}$	$1.10\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$

4. Male hunting - family's req. met Both hunting - family's req. met	α_{fi}	$\alpha_n(t)$	$1.10\alpha_{fi}$	$1.10\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$
5. Male hunting - brood's req. not met Both hunting - brood's req. not met	α_{fi}	$0.80\alpha_n(t)$	$1.10\alpha_{fi}$	$0.85\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$
6. Male hunting - family's req. not met Both hunting - family's req. not met	$0.85\alpha_{fi}$	$0.80\alpha_n(t)$	$0.92\alpha_{fi}$	$0.85\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$
7. Male hunting - female's req. not met Both hunting - family's req. met	$0.85\alpha_{fi}$	$\alpha_n(t)$	α_{fi}	$1.10\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$

8. Male hunting - brood's req. not met Both hunting - family's req. met	α_{fi}	$0.80\alpha_n(t)$	$1.10\alpha_{fi}$	$\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$

---

[a] This table only includes those scenario parameters necessary for estimating $E(Z_{fj})$ and $E(Z_{nj})$.

[b] req. = requirements

[c] α_{fi} = energy expenditure of the female (see Appendix B for details).

[d] $\alpha_n(t)$ = energy expenditure of a brood (see Appendix B for details).

TABLE B-3. The discrete categories of the female's state variable (X_f) and the associated probability distribution for future reproduction at the end of the current nesting season, T [$F_f(x_f)$].

Female's State	Values of X_f[a]	$F_f(x_f)$[b]
7	62.35 - 59.76	0.80
6	59.75 - 57.17	0.75
5	57.16 - 51.97	0.72
4	51.96[c] - 46.77	0.65[d]
3	46.76 - 44.18	0.59
2	44.17 - 41.57	0.55
1 (No Reproduction)	<41.57	0.00

---

[a] The values for X_f are body condition indices (wing loading (Pa)).

[b] $F_f(x_f)$ is defined in Eq. (7).

[c] This value represents the physical condition of an average female during the breeding season. It was based on the mean mass and mean wing chord measurements for female Cooper's hawks measured early in the nesting season in Oregon (Henny et al. 1985). See Appendix B for additional details on the other values of X_f.

[d] This is the average probability of survival of female European sparrowhawks breeding in England (Newton 1988). See Appendix B for additional details on the other values of $F_f(x_f)$.

TABLE B-4. The discrete categories of the brood's state variable (X_n) and the associated probability distribution for brood survival at the end of the current nesting season, T [$F_n(x_n)$].

		$F_n(x_n)$[a] by Brood Size				
Brood's State	Values of X_n[b]	1	2	3	4	5
7	$1.50\alpha_n(t)$ - $1.25\alpha_n(t)$	1.00	1.00	1.00	1.00	1.00
6	$1.24\alpha_n(t)$ - $1.00\alpha_n(t)$	1.00	1.00	1.00	1.00	1.00
5	$0.99\alpha_n(t)$ - $0.85\alpha_n(t)$	0.92	0.92	0.92	0.92	0.92
4	$0.84\alpha_n(t)$ - $0.70\alpha_n(t)$	0.77	0.77	0.77	0.77	0.77
3	$0.69\alpha_n(t)$ - $0.30\alpha_n(t)$	0.00	0.50	0.50	0.50	0.50
2	$0.29\alpha_n(t)$ - $0.20\alpha_n(t)$	0.00	0.00	0.00	0.25	0.25
1 (Dead)	$<0.20\alpha_n(t)$	0.00	0.00	0.00	0.00	0.00

---

[a] $F_n(x_n)$ is defined in Eq. (6).

[b] The brood's state variable is an index of energy reserves; it was calculated as a percentage of the brood's energy requirements ($\alpha_n(t)$).

TABLE B-5. Predation and exposure risks [$\beta_i(t)$] of the nestlings as a function of their age and the female's action.

	Time			
Action (i)	T_1	T_2	T_3	T_4
Stay (1)	0.12	0.12	0.10	0.08
Calculation[a]	A (1-(B+C))	A (1-(B+C))	$0.85\beta_1(T_2)$	$0.75\beta_1(T_3)$
Hunt (2)	0.42	0.21	0.17	0.12
Calculation	2A	A	$\beta_1(T_3)+(2AC)$	$\beta_1(T_4)+(AC)$
Desert (3)	0.95	0.42	0.34	0.24
Calculation	None	$2\beta_2(T_2)$	$2\beta_2(T_3)$	$2\beta_2(T_4)$

---

a. These calculations were based on nestling mortality rates of the European sparrowhawk in England (Moss, 1979). After day 2, 21% of all nestlings died from factors other than starvation (A); 25% of these mortalities resulted from exposure (B), and 17.5% of these mortalities were a result of predation (C).

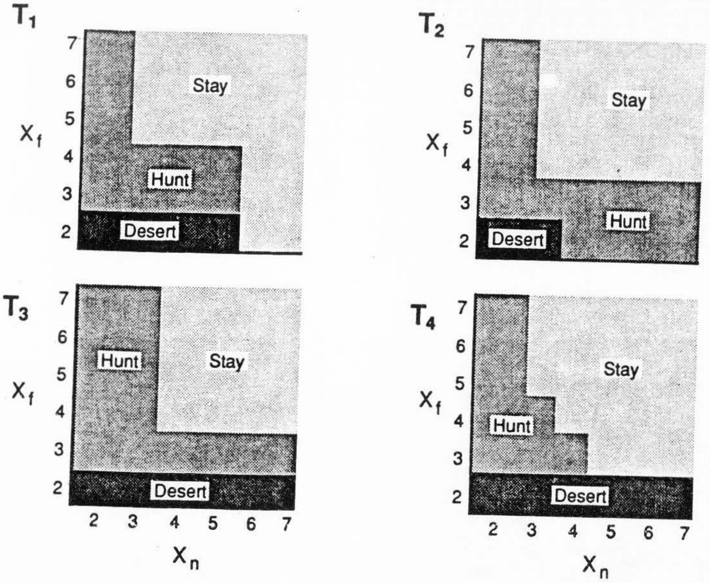

Fig. V-1. An illustration of model results. The optimal actions are plotted for each time period as functions of the physical condition of the nestlings (horizontal axis) and the physical condition of the female (vertical axis). The physical conditions of the nestlings and the female increase from 2 (poor condition) to 7 (excellent condition). T_1 is the early nestling stage; T_2 is the late nestling stage; T_3 is the early fledgling-dependency stage and T_4 is the late fledgling-dependency stage. The values associated with each state are presented in Tables B-3 and B-4.

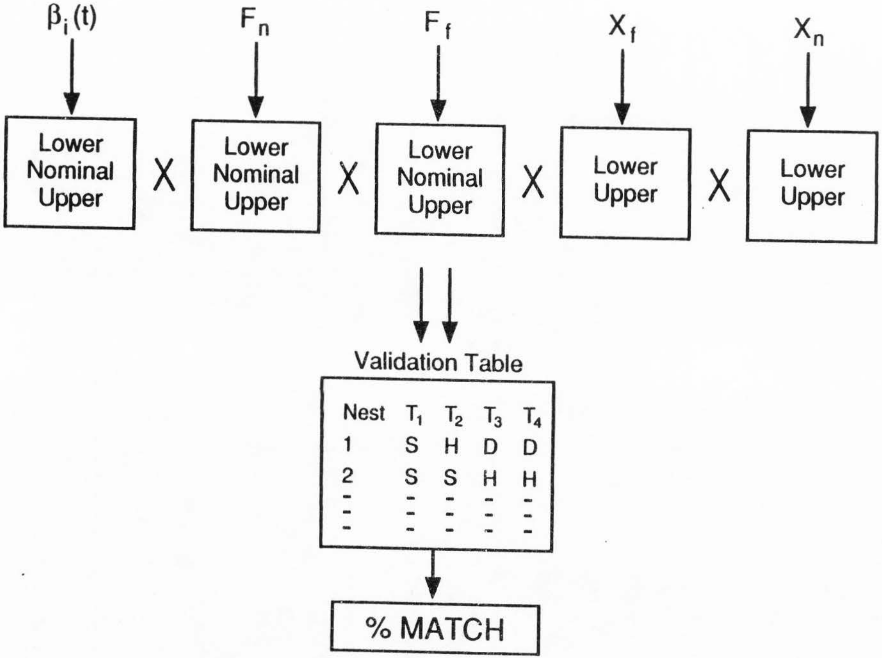

Fig. V-2. A schematic description of the sensitivity analysis procedures.

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	Washington Department of Game and Fish. $3,000
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1982	New Mexico Department of Game and Fish, Share With Wildlife Program. Nesting densities of Peregrine Falcons in north-central New Mexico. $5,000
1985-1986	U. S. Bureau of Land Management. Abundance and quality of Peregrine Falcon prey near an active molybdenum mine in northern NM. $23,000
1984-1988	New Mexico Department of Game and Fish, Share With Wildlife Program. Habitat, abundance, and foraging patterns of *Accipiter* Hawks nesting in the Jemez Mountains, NM. $38,000
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1990	U.S. Forest Service, Southwestern Region. Development of a survey protocol for locating Northern Goshawk nests. $25,000
	New Mexico Department of Game and Fish, Share with Wildlife Program. Distribution, nesting habitat, and diet of a Zone-tailed Hawk population at the northern limit of its range. $5,000

SCIENTIFIC PUBLICATIONS:

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TECHNICAL PUBLICATIONS:

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PAPERS PRESENTED AT PROFESSIONAL MEETINGS:

1976 Raptor baseline studies associated with energy development projects. Annual Meeting of the Raptor Research Foundation, Cornell University

1980 Prey size selection patterns of nesting male and female Cooper's Hawks. Annual Meeting of the American Ornithologist's Union, Colorado State University

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1987 Mate desertion in female Cooper's Hawks. Annual Meeting of the Raptor Research Foundation, Sacramento, CA

1989 Invited Seminar, The Northern Goshawk in the southwest: is it threatened? U. S. Forest Service Workshop on the Status of the Northern Goshawk in the Southwest, Northern Arizona University

1990 A dynamic stochastic optimization model of mate desertion in female Cooper's Hawks. Symposium on Applied Probability Models in Biology, Society for Industrial and Applied Mathematics, New Orleans, LA (with E. J. Kelly)

A dynamic stochastic optimization model of mate desertion in Cooper's Hawks - Model validation. Annual Meeting of the American Ornithological Society, University of California, Los Angeles (with E. J. Kelly)

Validation and sensitivity analysis for a stochastic model of hawk mate desertion. Annual Meeting of the American Statistical Association, Anaheim, CA (presented by E. J. Kelly)

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Home ranges of Northern Goshawks nesting in north-central New Mexico. Managing Wildlife in the Southwest Symposium, University of Arizona

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1982 Session Chair, General Paper Session, Annual meeting of the Raptor Research Foundation, Salt Lake City, UT

1987 Reviewer for the Proceedings of the western raptor management symposium and workshop. (1988) Pendelton, B. A., Steenhof, K., M. N. Kochert, and LeFranc, M. N., Jr., eds. Natl. Wildl. Fed. Sci. Tech. Ser. 12. Natl. Wildl. Fed., Wash. D. C.

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