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A DYNAMIC STATE VARIABLE MODEL OF MATE DESERTION IN COOPER'S HAWKS[1]

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Abstract. In a 4-yr study of the reproductive strategies of Cooper's Hawks (*Accipiter cooperii*) nesting in north-central New Mexico, >50% of the females deserted during the fledgling-dependency period and did not renest. A dynamic state variable model was developed to study the females' brood-rearing strategies. In this model a strategy consisted of combinations of staying at the nest, hunting, and deserting. The modeling assumptions were: a female's strategy during brood rearing maximizes her reproductive fitness, defined as the weighted average of the expected probability of survival of her current offspring and her expected future reproduction; and the reproductive fitness function depends 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 predictions were compared to the observations of female strategies in this population of Cooper's Hawks. To insure a valid comparison, the model parameters were estimated from sources other than the observed population. The best match between observations and predictions (84–96%) was obtained when the nestlings' survival and the female's future reproductive potential were equally weighted during the nestling stage, but weighted in favor of the female's reproductive potential during the fledgling stage.

A 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 70–85% of the desertions. The sensitivity analysis also indicated that a 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 agreement of model predictions and observed strategies supported the modeling assumptions. These results combined with the sensitivity analysis indicated that dynamic state variable modeling is an excellent tool for studying mate desertion.

Key words: Accipiter cooperii; Cooper's Hawk; dynamic state variable model; mate desertion; parental investment; sensitivity analysis.

INTRODUCTION

Background

Mate desertion is defined here as the termination of care by one parent 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, Myers 1981, Blumer 1986, Beissinger 1986, 1987b, Beissinger and Snyder 1987, Ezaki 1988, Fujioka 1989, Beissinger 1990).

Mate desertion can be viewed as a behavioral strategy with fitness trade-offs: by deserting, an individual may reduce the fitness of its current offspring but increase its chances of successfully breeding again. These trade-offs 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/or (3) the deserter's contribution to parental investment is relatively small (Trivers 1972, Maynard Smith 1977, Beissinger 1986, Beissinger and Snyder 1987, Lazarus 1990).

Previously, several approaches have been used to study mate desertion; each of these approaches has its limitations. One approach has been to model mate desertion using the game-theoretic concept of an evo-

lutionary 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 most useful when the success of an individual's mating strategy depends 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, game theory models are not designed to predict which behavioral strategy is "best" or optimal under various conditions (Houston and McNamara 1987).

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, a limitation of 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 (Ezaki 1988, 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). In a few studies the effects of desertion on a short-term measure of fitness (Beissinger and Snyder 1987, Ezaki 1988), current reproductive success, were examined. These fitness estimates were not useful in predicting the occurrence of desertion because differences in current reproductive success between deserted and nondeserted nests were not observed.

Another limitation of the empirical approach is that risks associated with reproductive strategies are difficult to incorporate into the measure of reproductive fitness. 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.

In this study we have attempted to overcome these limitations by using a dynamic state variable modeling approach (Mangel and Clark 1986, McNamara and Houston 1986, Houston et al. 1988) to study female brood-rearing strategies, including mate desertion, in a population of Cooper's Hawks (Accipiter cooperii) nesting in north-central New Mexico. This model uses a fitness function based on current and future reproduction. The fitness function incorporates the complex interactions of benefits and risks associated with a strategy, and optimal strategies are determined by maximizing an individual's fitness function, independent of the behavioral strategies chosen by conspecifics.

Observations

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. It is commonly assumed that during brood rearing male raptors are the primary hunters, and the females either stay at the nest to protect and feed the young or hunt to augment the males' food provisioning.

The population in this study consisted of 19 nests (13 with radio-telemetry data that confirmed the adult's behavior throughout brood rearing) observed from 1984 to 1988. Seven of the 13 telemetered females in this population deserted their nests during the fledgling-dependency period when the young were 6–8 wk of age. Three females at six nontelemetered nests disappeared from their nests during the same time period. All of the desertions were by females. One of the desertions occurred in 1984, four in 1986, and two in 1988. In all cases, the male continued care until the young were independent (11–12 wk of age).

Unlike other avian species where mate desertion occurs, 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 wk, and then presumably migrated. These females were never observed near the nest after they relocated and their disappearance always occurred between late September and early October, which coincides with the peak migration times for Cooper's Hawks in New Mexico (Palmer 1988; S. Hoffman, Hawk Watch International, personal communication). Nondeserting females either remained at the nest or helped the male to hunt until the young were independent. Additional details of these observations are presented in Appendix 1 and in Kennedy (1991).

Kennedy (1991) also observed variability in the female's allocation of food, particularly when the male was not meeting the energy requirements of the family. 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, we hypothesized that the female's breeding strategies, (1) staying at the nest to protect the young, (2) hunting to augment the male's food supply, and (3) deserting, were influenced by 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. We assumed that energy intake was a random process. The dynamic state variable model incorporated these hypotheses and allowed these factors to vary over time.

The model predictions were compared to the actual strategies of the female Cooper's Hawks. To assure a valid comparison, the model parameter estimates were derived from data sources independent of the data for these Cooper's Hawks. In the sensitivity analysis the parameter estimates were varied, and the effect of these variations on the comparison results were examined. This analysis provided insight into the key factors influencing model predictions and showed how robust the model was to uncertainties in the parameter estimates.

THE MODEL

Dynamic state variable 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 (Mangel and Clark 1986, Clark 1987, 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 state variable model we developed to study female mate desertion in Cooper's Hawks used discrete time intervals. The model parameters are summarized in Table 1. The observation time period was divided into five, 2- to 3-wk 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 mea-

sure of the energy reserves of the brood. The female's state variable, $X_f(t)$, represented her body condition (i.e., her wing loading), a function of the force exerted by gravity on the female's body mass, normalized by her wing area. These state variables were random because they were functions of the energy intake of the female and the nestlings, which we 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, we grouped them into seven discrete categories (Tables A2.3 and A2.4). We 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, we assumed that

$$\text{NCRIT} \le x_n \le \text{NCAP},$$
$$\text{MCRIT} \le x_f \le \text{MCAP}.$$

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. We 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. Throughout this paper actions are indexed by subscript i.

It was assumed that some prey would always be obtained 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 discrete random variables Z_{ni} and Z_{fi} represent the energy intake of the nestlings and female. The z_{nij} and z_{fij} are realizations of these random variables where the subscript j represents one of the possible energy intake values. The energy expenditures over the time period t to $t + 1$ for action i are denoted by $\alpha_n(t)$ and α_{fi}.

The state variables changed from one time period to another depending on the energy intake value (j), the action (i), and the energy expenditures [$\alpha_n(t)$, α_{fi}] according to the following formulas:

$$x_{nij}(t + 1) = x_n(t) + [z_{nij} - \alpha_n(t)]n_t$$
$$x_{fij}(t + 1) = x_f(t) + [z_{fij} - \alpha_{fi}(t)]n_t e/s, \qquad (1)$$

where n_t is the number of seconds in time period t, s is the female's wing area, and e is a metabolic conversion factor that converts energy to mass (Appendix 2).

TABLE 1. A list of the parameters in the dynamic state variable model of mate desertion in Cooper's Hawks.

Parameter	Parameter description	Units
T_i	A discrete time period during the nesting season.	wk
T	The time at which the young reach independence.	wk
t	Beginning of an arbitrary time period.	wk
$X_n(t)$	The brood's state variable, energy reserves at t.	kJ
$x_n(t)$	A realization of the random variable $X_n(t)$.	kJ
$x_{nij}(t)$	The realization of the random variable $X_n(t)$ for action i and energy intake j.	kJ
$X_f(t)$	The female's state variable, body condition index = wing loading.	N/m^2
$x_f(t)$	A realization of the random variable $X_f(t)$.	N/m^2
$x_{fij}(t)$	The realization of the random variable $X_f(t)$ for action i and energy intake j.	N/m^2
$F_n(x_n)$	Probability the brood survives to independence given state at T is x_n.	unitless
$F_f(x_f)$	Probability of the female's future reproduction given state at T is x_f.	unitless
ϕ_n	Nestlings' expected probability of survival.	unitless
ϕ_f	Female's expected reproductive potential	unitless
ϕ	The fitness function, the weighted average of ϕ_n and ϕ_f.	unitless
γ	The weighting factor in the fitness function.	unitless
$\alpha_n(t)$	Rate of energy expenditure of the brood as a function of their age.	W
α_{fi}	Rate of energy expenditure of the female using action i.	W
Z_i	Rate of total energy delivered to the nest during a 24-h period using action i.	W
z_{ij}	Realization of Z_i.	W
$Z_{ni}/E(Z_{ni})$	Rate of energy intake by the brood using action i/expected rate of energy intake.	W/W
z_{nij}	Realization of Z_{ni}.	W
$Z_{fi}/E(Z_{fi})$	Rate of energy intake by the female using action i/expected rate of energy intake.	W/W
z_{fij}	Realization of Z_{fi}.	W
n_t	Length of time period t.	s
s	Female's wing area.	m^2
e	Conversion factor.	N/kJ
λ_{ij}	Probability of delivering prey of energy value z_{ij} using action i.	unitless
NCRIT	Critical lower boundary of the brood's state variable.	kJ
MCRIT	Critical lower boundary of the female's state variable.	N/m^2
NCAP	Upper boundary of the brood's state variable.	kJ
MCAP	Upper boundary of the female's state variable.	N/m^2
$\beta i(t)$	Risks to the brood associated with the female's action.	unitless
$\mathcal{A}$	Set of actions that the female can choose, STAY, HUNT, DESERT.	unitless
$d_t(x_n, x_f)$	A decision rule—for each time period it maps the state variables to the action.	unitless
σ	A strategy—a set of decision rules, one for each time period $\{d_1, d_2, d_3, d_4\}$.	unitless
Σ	The set of all possible strategies.	unitless
DEB	Daily energy budget.	W
E_n^*	The peak rate of daily energy expenditure of a nestling.	W
$E_n(t)$	Rate of daily energy expenditure of a nestling during time period t.	W

Suppose that $\mathcal{A}$ denotes 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 $d_t(x_n, x_f) = i$. In this application a strategy, $\sigma(x_n, x_f)$, is a set of four decision rules corresponding to the first four time periods; $\sigma(x_n, x_f) = \{d_1(x_n, x_f), d_2(x_n, x_f), d_3(x_n, x_f), d_4(x_n, x_f)\}$. The strategies are functions of the state variables, but for ease of notation we use σ only. We 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 model was based on the assumption that female brood-rearing strategies maximize reproductive fitness defined as the weighted average of the probability of survival of the current brood and the probability that the female reproduces in the next breeding season. The weighting factor can be viewed as a normalized measure of the number of offspring, e.g., $N/(N + R)$ where

N is the current brood size and R is the female's future reproductive value. This interpretation of the weighting factor is equivalent to putting the fitness function in terms of potential offspring. However, it is not necessary to restrict the weighting factor in this way. It could be a more complex function of N and R and/or depend on additional parameters (such as time). We preferred to treat the weighting factor 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.

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

$$P_f[X_f(T) \mid X_f(t) = x_f, \sigma]$$
  = 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. The values P_n (NCRIT) and P_f (MCRIT) were zero regardless of the nestlings' or female's initial condition or her strategy.

Nestling and female fitness in the current season were the expectations (E) of the random variables P_n and P_f:

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

and

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

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:

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

and

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

where x_{nij} and x_{fij} were the brood and female state variables at $t + 1$ given $d_i(x_n, x_f) = i$ 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. We assumed the female had a negligible probability of death resulting from these factors relative to the nestlings. No observations of female mortality from predation and inclement weather have been recorded during the nesting season in the north-central New Mexico study area (P. L. Kennedy, *unpublished data*), which supports this assumption. At the end of the nesting period we assumed the probabilities of survival and reproduction were known. These end-state probabilities are denoted:

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

and

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

The values of these end-state probabilities range from 0.0 to 0.8 for the nestlings (Table A2.4) and 0.0 to 1.0 for the female (Table A2.3). The rationale for these values is described in Appendix 2.

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

$$\max_{\sigma \in \Sigma} \{\Phi(x_n, x_f, t, T, \sigma)\}$$

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

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

where i was the action such that $d_i(x_n, x_f) = i$, 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 (see Houston et al. [1988] for a detailed illustration of backward induction).

Fig. 1 illustrates the results of the model predictions of optimal actions. 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.

COMPARISON OF MODEL PREDICTIONS TO OBSERVED STRATEGIES

For the model and its underlying hypotheses to have credibility, the model predictions needed to be compared with observed strategies. In general, comparing model predictions to observations can provide valuable insights into the phenomena of interest. Even when the model predictions do not agree with the observations, understanding where and how the model failed can be useful. To gain insight into the females' breeding behaviors and to test the validity of the modeling approach, we compared the model predictions of optimal strategies (Fig. 1) with the observed strategies of the 13 telemetered female Cooper's Hawks nesting in north-central New Mexico. For this comparison to be valid, the parameters used for the model predictions had to be independent of the data used for the comparison. Therefore, parameter estimates were derived from the literature and a simulation. Such a comparison does not validate the model, but it does lend credibility to
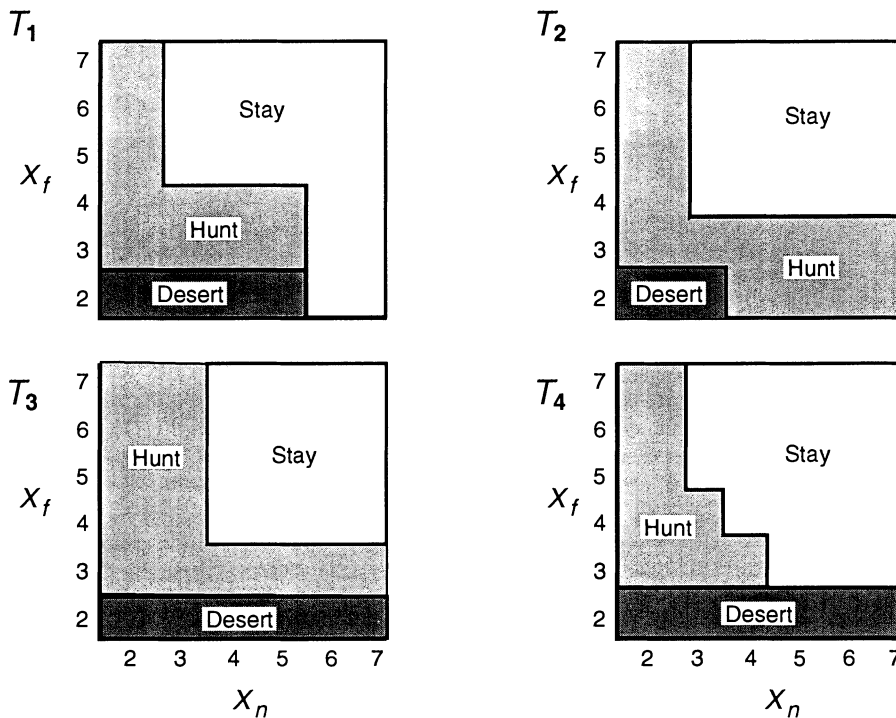
FIG. 1. An illustration of model results. The optimal actions are plotted for each time period as functions of the physical condition of the nestlings (horizontal axis) and the physical condition of the female (vertical axis). The physical conditions of the nestlings and the female increase from 2 (poor 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 A2.3 and A2.4.

TABLE 2. 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 $\gamma = \frac{1}{2}$ during all time periods.*

Female no.	Year	Time period in nesting season			
		T_1	T_2	T_3	T_4
		Action predicted/observed†			
4	1984	S	H‡	H	H
5	1984	H‡	H‡	H	H
9	1984	S	S	D	−§
10	1986	H‖/S¶	H/S	H	D
10	1988	S	D/S	D/H	D#
12	1986	S	S	S	D
13	1986	S	H/S	H	H/D
16	1986	S	H	H	D
24	1986	S	S#	H‡	H‡
26	1988	S	S‖	D/H	D
29	1988	H‖/S	H‖	H	H
30	1988	S	H	H‡	H
31	1988	S	S#	H	H

* γ defined in Table 3 footnote.
† S = stay, H = hunt, and D = desert.
‡ This action was tied with the stay action. (Ties were defined to be differences of ≤ 0.05 between the values of the fitness functions for various actions.)
§ A condition observed and imposed in the model solution is that a female who deserts does not return.
‖ This action was tied with the desert action.
¶ Bold lettering indicate situations in which the optimal action(s) differed from the female's chosen action (optimal/actual).
# This action was tied with the hunt action.

the approach when the model predictions are consistent with the observations. This type of comparison has not been done for any published mate-desertion model.

Parameter estimation

Parameter estimates are described in Appendix 2.

Observed strategies and state variables

Each female's brood-rearing strategy was determined from radiotelemetry data (see Appendix 1 for details of the behavioral monitoring) and observations at 12 different nests (Table 2) during the 1984, 1986, and 1988 nesting seasons. One female (number 10) was monitored for 2 yr, 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 (z_{fij}) and energy expenditure (α_{fi}) for a 24-h period. The energy intake estimate was based on observations of food consumption by the females at each nest. The energy expendi-

ture was based on time–energy budget models that in-corporated activity data collected on radio-tagged females and metabolism measurements of captive ac-cipiters. A detailed description of the DEB approach is in Kennedy (1991).

In general, a DEB was estimated weekly for each female during the nesting season. The DEB for a time period was based on the average of these weekly DEB estimates. The female's state variable was incremented or decremented as described in Appendix 2.

To minimize disturbance to the nest and avoid in-fluencing the females' actions, we did not measure the nestlings' hatching state. We 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 (Appendix 2). The time–energy budget approach used to develop the DEB estimates for the nestlings is de-scribed in Kennedy (1991).

Model predictions

To compare the observed strategies with the model predictions, we 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) wheth-er or not the brood's and/or the female's energy re-quirements 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 observa-tions.

Comparison of model predictions to observations

Twelve of the 13 nests had appropriate data for all four time intervals, whereas one of the nests had ob-servations in only three time intervals because of de-sertion during T_3. As a result, there were a total of 51 observations to compare with the model predictions (Table 2).

Table 2 reports the results of the comparison for γ = ½. 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) for the interpretation of γ as the normalized number of off-spring. Setting $R = N$ was a reasonable first approxi-mation for γ. 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 yr old. Therefore, we could not estimate an R for the observed females.

In Table 2, the symbols in boldface type indicate cases in which the optimal action predicted by the model was not the observed action. There were only eight such cases. In five of these cases the model pre-dicted an action 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 ob-served nest behaviors showed four patterns: Stay–Hunt–Desert, Stay–Hunt, Hunt, and Stay–Desert. The model correctly identified 8 of the 13 actual strat-egies.

Typically, the maximum value for the fitness func-tion ranged from ≈0.7 to 0.9 and was from ≈0.2 to 0.6 greater than the values for the other actions. How-ever, in a few instances the top two values of the fitness functions were quite close. In the computer imple-mentation of the model, the values of the fitness func-tion were determined by categorizing the state vari-ables 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 opti-mal. We considered as ties the cases in which the nu-merical separation of the top two actions was <0.05. These ties are identified in Table 2.

SENSITIVITY ANALYSIS

To look at the effects of different values of γ on the comparison results, two other cases were considered: $\gamma = \frac{1}{3}$ and $\gamma = \frac{2}{3}$. Using the interpretation of γ as a normalized measure of the number of offspring, $\gamma = \frac{1}{3}$ represents the situation where the female's expected number of future offspring is twice the number of cur-rent nestlings ($R = 2N$). The reverse is true for $\gamma = \frac{2}{3}$, the number of current nestlings is twice the expected number of future offspring ($N = 2R$). The results of these analyses and the $\gamma = \frac{1}{2}$ case (equally weighted) are summarized for each time period in Table 3.

In T_1 and T_2, the weighting that favored the current brood's probability of survival ($\gamma = \frac{2}{3}$) had the highest number of matches between model predictions and actual observations. In T_3 and T_4 equal weighting of current offspring survival and expected future repro-duction, $\gamma = \frac{1}{2}$, had the same or more matches than the weighting that favored brood survival, $\gamma = \frac{2}{3}$. How-ever, in T_4 the weighting that favored the probability of female future reproduction, $\gamma = \frac{1}{3}$, had the highest match (100%). These results indicated that the weight-ing 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 re-

TABLE 3. The effect of various weighting factors (γ) on the percent match between observed actions and those predicted by the model of optimal behaviors of nesting female Cooper's Hawks in north-central New Mexico.

Time period during nesting season	Weighting factor (γ)*		
	1/3	1/2	2/3
	Percent match		
T_1	69	85	100
T_2	38	77	92
T_3	69	85	85
T_4	100	92	64

* $\gamma = \frac{1}{3}$ weights the female's probability of future reproduction twice as much as the probability of survival of the current offspring; $\gamma = \frac{1}{2}$ weights them equally; $\gamma = \frac{2}{3}$ weights the current offspring survival probability twice as much as the female's probability of future reproduction.

production during T_1 and T_2 and weighted them equally in T_3 and T_4 was compared to the actual observations.

Table 4 reports the results of this comparison of the mixed-model predictions to the observed actions. For these values of γ there were only five cases where the action predicted by the model did not match the observations. In four of these cases the model predicted

TABLE 4. 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 $\gamma = \frac{2}{3}$ during T_1 and T_2 and $\gamma = \frac{1}{2}$ during T_3 and T_4.

Female no.	Year	Time period in nesting season			
		T_1	T_2	T_3	T_4
		Action predicted/observed†			
4	1984	S	H	H	H
5	1984	H‡	H§	H	H
9	1984	S	S	D	— ‖
10	1986	S	H/S¶	H	D
10	1988	S	S	**D/H**	D
12	1986	S	S	S	D
13	1986	S	**H/S**	H	**H/D**
16	1986	S	H#	H‡	D
24	1986	S	S	H‡	H‡
26	1988	S	S	**D/H**	D
29	1988	S	H	H	H
30	1988	S	H	H‡	H
31	1988	S	S	H	H

* γ defined in Table 3 footnote.
† S = stay, H = hunt, and D = desert.
‡ This action was tied with the stay action. (Ties were defined to be differences of ≤0.05 between the values of the fitness functions for various actions.)
§ This action was tied with the other two actions.
‖ A condition observed and imposed in the model solution is that a female who deserts does not return.
¶ Bold lettering indicates situations in which the optimal action differed from the female's chosen action (optimal/actual).
# This action was tied with the desert action.

TABLE 5. The categories of X_f and X_n used in the sensitivity analyses.*

State	Range of values of X_f†	Range of values of X_n/n_i‡
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	$<0.20\alpha_n(t)$

* X_f and X_n are the female's and nestlings' state variables, respectively. See Tables A2.3 and A2.4 for a comparison with the values of X_f and X_n used for parameter estimation.
† $F_f(x_f)$ associated with each category are 0.775, 0.72, 0.65, 0.57, and 0.00, respectively.
‡ $F_n(x_n)$ associated with each category are 1.00, 0.845, 0.5, and 0.00, respectively.

an action 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 observed strategies.

Using the mixed model we investigated the sensitivity of the comparison results to uncertainties in some of the parameter estimates. We were interested in discovering how robust the comparison results were to uncertainties inherent in these parameter estimates. We were also interested in determining which parameters were most important to the comparison results, thus revealing those parameters that must be carefully monitored in future experiments.

To study the sensitivity of the comparison results, we 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, we examined the effect of the number of categories for X_f and X_n on the comparison results. We did not alter the NCRIT, NCAP, MCRIT, or MCAP, but widened the categories using five states instead of the original seven states (Table 5). The $F_f(x_f)$ and $F_n(x_n)$ associated with the widened categories were the averages of the $F_f(x_f)$ and $F_n(x_n)$ associated with the original seven categories (Table 5).

We found no important differences in the comparison results from 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, we 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-
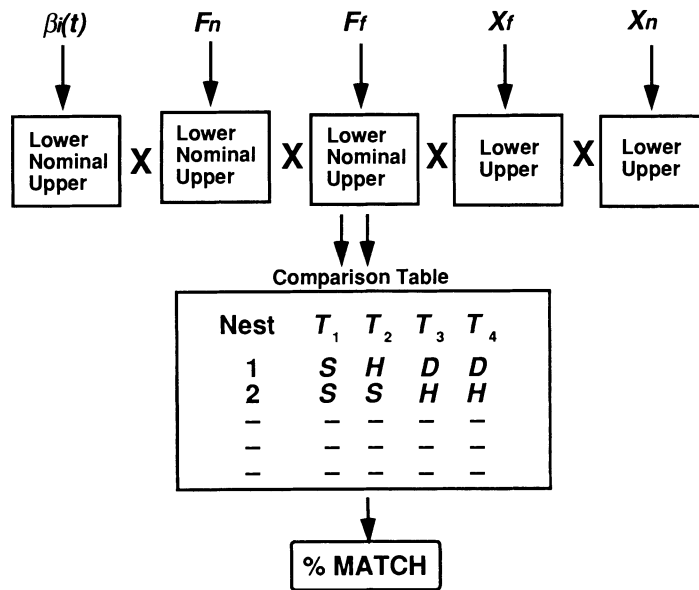
$\beta_i(t)$ Fn   Ff   Xf   Xn

FIG. 2. A schematic description of the sensitivity analysis procedures.

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 2). For X_n, we 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 2). The parameters $F_n(x_n)$ and $F_f(x_f)$ were varied 10% above and below the nominal values (the original estimates used for prediction). For $\beta_i(t)$, values that were 33% above and below the nominal values were used. These upper and lower levels represent our judgment of the possible values for the parameters and reflect the degree of uncertainty associated with the parameter estimates.

We 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, we 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, we developed a table (see Table 2 for an example) giving the percentage of agreement between the observations and model predictions. Fig. 2 is a schematic of this analysis.

We 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.

We 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. We performed a full factorial design so that we 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 (percent 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 $\beta_i(t)$ ($F = 172$) and X_f and $F_n(x_n)$ ($F = 56$), the parameters $F_n(x_n)$ ($F = 40$), X_f ($F = 16$), and possibly the parameters $\beta_i(t)$ ($F = 6$). 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.

The large interaction F value between X_f and $\beta_i(t)$ indicated that the influence on the female's optimal strategy from the $\beta_i(t)$ depended on boundary conditions of the female's state (MCRIT, MCAP) and vice versa. Similarly, the interaction between X_f and $F_n(x_n)$ indicated that the influence on the female's optimal strategy from the end-state probabilities of the nestlings, $F_n(x_n)$, depended on the boundary conditions of

the female's state (MCRIT, MCAP) and vice versa. The remaining effects had F values <2.0. This model for the ANOVA had an R^2 of 0.89. (The value of 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, percent match.)

To investigate the question of a third-order interaction, we focused on the factors X_f, $\beta_i(t)$, and $F_n(x_n)$ shown to be important in the previous ANOVA. This reduced model included 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 $F_f(x_f)$ ($F = 4$), 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 highest percent 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 lowest percent matches (average value of 84 ± 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 and $\beta_i(t)$ and $F_n(x_n)$ were low] the percentage of agreement was intermediate (average value of 90 ± 0.01%).

Varying the parameters had little 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 least pressure to desert had the lowest percentage agreement because the model did not predict desertion in 4–5 of the 7 nests where desertion occurred.

DISCUSSION

The results of this study indicated that the predictions of the dynamic state variable model were consistent with the observed breeding strategies, including desertion, used by nesting females. The agreement of model predictions and observed strategies supported, but did not prove, the modeling hypotheses that:

1) a female's strategy during brood rearing maximizes the weighted average of the expected probability of survival of her current offspring and her expected future reproductive potential, and

2) the female's strategy choices were influenced by multiple factors including 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 quantitatively support previous studies that suggest the fitness trade-offs associated with mate desertion can be based on costs and benefits associated with both current and future reproduction (Myers 1981, Ezaki 1988, Beissinger 1990). By expanding the future reproductive benefits beyond the current nesting season, we gained insights into the desertion decisions in species, such as the Cooper's Hawk, that do not immediately renest after desertion.

Although all females who were in poor physical condition did not desert, those females who did desert were in poor condition. One of the possible benefits of deserting was the potential improvement of physical condition before migration. This improved condition would increase the female's probability of surviving migration, thus increasing her probability of over-winter survival and her probability of breeding in the next season.

In addition to predicting desertion when the female's condition was poor, the model also predicted desertion when a female was in adequate condition and her brood was in poor condition with a low probability of survival. We were not able to test these predictions because these conditions were not observed in Cooper's Hawks in north-central New Mexico.

In this study, comparison of model predictions and actual strategies for various values of the weighting factor (γ) suggested that the female's strategy choice was not based solely on past investments, i.e., "Concorde fallacy" (Curio 1987). The female's current reproductive effort, which can often be equated with her past investment costs (Beissinger 1987a, Curio 1987), had a greater influence on her strategy choice 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 equal or greater influence on her choice of action than does 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 4–5 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 current nestling survival from desertion and the greatest threat to the female's future reproduction due to poor physical condition.

The second hypothesis is that the true value of the parameters were in the input space with the lowest percent 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. For example, different sources of nestling mortality may have different effects on the female's strategy (McNamara 1990). Therefore, nestling risk as a function of the female's strategy may be more accurately represented by several parameters rather than by a single parameter $\beta_i(t)$.

To determine which of the two hypotheses is correct, 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. Other estimates of the female's condition besides wing loading or mass may be necessary to accurately evaluate the change in her fat or energy reserves over time.

Although the results of this study supported the modeling hypotheses, comparisons to additional data sets are necessary before we can rule out alternative explanations for the observed strategies of the females in this population. These strategies 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 state variable 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 state variable 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 1

MATE DESERTION OBSERVATIONS

Observations of the reproductive strategies of male and female Cooper's Hawks during brood rearing were conducted during the 1984–1986 and 1988 nesting seasons within the Jemez Mountains, New Mexico and adjacent Pajarito Plateau. The study area is described in detail in Kennedy (1988). The brood-rearing period began after the eggs hatched (early to late June) and ended when the young were independent at the end of the fledgling-dependency period (mid-August to mid-September). Parental effort included food provisioning, and protecting offspring from predators and inclement weather. Observations of Cooper's Hawk parental effort were made in all 4 yr but the majority of these observations were made at nests of radio-tagged nesting adults during 1984, 1986, and 1988.

During the study, 37 nest sites were found; 19 were studied intensively during ≈670 h of observations throughout the brood-rearing period. About one-fifth of these observations were made after mate desertion occurred.

During each nesting season, mated pairs of Cooper's Hawks were observed for 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 impacts to the nest from human disturbance, we usually visited nests no more than 2–3 times/ wk. 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, we fitted 13 nesting females and 10 nesting males with transmitters during the early nestling stage of the 1984 ($N = 5$), 1986 ($N = 9$), and 1988 ($N = 9$) breeding seasons. Details of the telemetry equipment are presented in Kennedy (1991). Observations of radio-tagged birds began after the birds accepted the transmitters within a few days of tagging. Prior to desertion, the signal of a systematically chosen, radio-tagged bird was con-

tinuously monitored during 3–6 h sample periods, 1–3 times/ wk, and all observations of this bird were also recorded. We attempted to track mated pairs within 1 d whenever possible. In addition, the nest of the focal animal was usually under observation during the radio-tracking period. Details of the behavioral sampling methods are presented in Kennedy (1991).

The first time an adult could not be located near the nest site or in commonly used hunting areas during a sample period, we implemented extensive aerial and ground searches for the bird. All birds were relocated within 4–48 h after their disappearance. While the searches were in progress, an observer usually occupied a blind near the nest with telemetry equipment until the bird was relocated to determine if its mate was continuing with parental care. The relocated bird was continuously monitored for 8–16 h/d for 2–3 d to see if it returned to the nest. A bird that did not return to the nest during these intensive observation periods was assumed to have deserted. The predesertion sampling schedule was then implemented to continue the behavioral observations on all birds. Because hunting adults normally delivered prey to the nest every 2–3 h during the periods just before and after mate desertion, our observation regime was more than sufficient to detect desertion.

APPENDIX 2

PARAMETER ESTIMATION

Female's energy expenditure (α_{f_1})

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). A female that stays at the nest and does not hunt (action 1) is not very active so we equated α_{f_1} with Fischer's (1986) corrected mean value of existence metabolism (EM) for breeding female Cooper's Hawks (2.98 W). We used Fischer's mean EM value plus mean activity costs of breeding female Cooper's Hawks for α_{f_2} (4.3 W). We assumed the activity costs of a deserter (action 3) were one-half the activity costs of a hunter (action 2) (α_{f_3} = mean EM + 50% of the mean activity costs = 3.64 W) because the breeding female was hunting only for herself and did not have the transport costs of delivering prey to the nest.

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

Estimates of the brood's energy expenditures (Table A2.1) were based on the allometric equation developed by Kennedy (1991: Eq. 17) to predict peak daily nestling energy expenditure (E_n^*) as a function of adult biomass. This equation was based on literature estimates of peak daily energy expenditure for a wide variety of species with altricial young. Because of the extreme sexual size dimorphism in this species, E_n^* was estimated separately for male and female nestlings using the average masses of adult male and female Cooper's Hawks in the northern New Mexico population (Kennedy 1991). The daily energy requirement of a nestling throughout the nesting season was estimated as a percentage of the nestling's predicted peak daily requirements [$E_n(1) = 0.3E_n^*$, $E_n(2) = E_n^*$, $E_n(3) = 0.7E_n^*$, $E_n(4) = 0.5E_n^*$]. These daily energy requirements were assumed to remain constant throughout a time period. To calculate $\alpha_n(t)$, which is the brood's daily energy requirement, we summed $E_n(t)$ for each nestling in a brood. Values for this parameter are in Table A2.1.

Probability of delivering prey of energy value $z_{ij}(\lambda_{ij})$

On the basis of prey delivery rates for other nesting populations of accipiters (Snyder and Wiley 1976, Newton 1978, Kennedy and Johnson 1986, Simmons 1986), we assumed the number of daily prey deliveries would range from 1 to 5. 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_{S_i}, p_{M_i}, and p_{L_i}, respectively. Although these utilization probabilities were based on the availability of the prey size categories, we 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 Kennedy (1991) for this population of Cooper's Hawks. Each prey delivery was assigned a biomass value using the methodology described by Kennedy (1991). 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 (66 kJ), medium (263 kJ), and large (677 kJ) prey categories were the weighted averages of the energy values of all prey items assigned to each of the three categories. These energy values were based on published values (in kilojoules per gram) of avian, mammalian, and reptilian prey species corrected by assimilation efficiencies (Kennedy 1991).

TABLE A2.1. Estimates of a nestling's rate of energy expenditure [$E_n(t)$] (in watts) as a function of sex and age.*†

Age of young (Period)	Male‡	Female§
0–2 wk (T_1)	1.15	1.70
3–5 wk (T_2)	3.85	5.66
6–7 wk (T_3)	2.69	3.96
8–10 wk (T_4)	1.92	2.83

* The methodology used to develop these estimates is described in Appendix 2: Brood energy expenditure [$\alpha_n(t)$] and in Kennedy (1991).

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

‡ This is based on an average biomass of adult males of 283 g (Kennedy 1991).

§ This is based on an average biomass of adult females of 471 g (Kennedy 1991).

TABLE A2.2.　Estimates of expected rate of energy intake of the brood $[E(Z_{ni})]$ and the female $[E(Z_{fi})]$ used in each scenario.*

| | Action (*i*) | | | | | |
| | Stay (1) | | Hunt (2) | | Desert (3) | |
Scenario	$E(Z_{f1})$	$E(Z_{n1})$	$E(Z_{f2})$	$E(Z_{n2})$	$E(Z_{f3})$	$E(Z_{n3})$
1. Male hunting—family's req.† not met 　Both hunting—female's req. not met	$0.85\alpha_n$‡	$0.80\alpha_n(t)$§	$0.92\alpha_{fi}$	$\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$
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}	$0.80\alpha_n(t)$	$1.10\alpha_{fi}$	$\alpha_n(t)$	$1.25\alpha_{fi}$	$\alpha_n(t)$

* This table only includes those scenario parameters necessary for estimating $E(Z_{fi})$ and $E(Z_{ni})$.
† req. = requirements
‡ α_n = energy expenditure of the female (see Appendix 2: *Female's energy expenditure* (α_n) for details).
§ $\alpha_n(t)$ = energy expenditure of a brood (see Appendix 2: *Brood's energy expenditure* [$\alpha_n(t)$] for details).

We assumed the daily prey delivery rate, *n*, varied from 1 to 5, therefore, the daily energy delivered to the nest could vary from 66 kJ/d (one small prey) to 3385 kJ/d (five large prey) or 0.76 to 39.2 W. We divided this range of energy delivery to the nest into eight 5-W intervals, denoted by w_j = $[5(k - 1), 5k]$, $j = 1, \ldots, 8$. The random variables Z_i represented the daily energy delivered to the nest 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).

We then determined the probabilities associated with each

TABLE A2.3.　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, time $T [F_f(x_f)]$.

Female's state	Range of values of X_f*	$F_f(x_f)$†
7	62.35–59.76	0.80
6	59.75–57.17	0.75
5	57.16–51.97	0.72
4	51.96‡–46.77	0.65§
3	46.76–44.18	0.59
2	44.17–41.57	0.55
1 (no reproduction)	<41.57	0.00

* The values for X_f are body condition indices (wing loading, in newtons per square metre).
† $F_f(x_f)$ is defined in Eq. 7.
‡ This value represents the physical condition of an average female during the breeding season. See Appendix 2: *Female state variable* (X_f) *and . . .* for additional details on the other values of X_f.
§ This is the average probability of survival of female European Sparrowhawks breeding in England (Newton 1988). See Appendix 2: *Female state variable* (X_f) *and . . .* for addition details on the other values of $F_f(x_f)$.

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 (Kennedy 1991). Therefore, we 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 $s = 0, 1, \ldots, n$; $m = 0, 1, \ldots, n - s$; and $l = 0, 1, \ldots, n - s - m$, the probability of prey combination d_{sml} is

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

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 λ_{ij}, the probability that $Z_i = z_{ij}$, as follows

$$\lambda_{ij} = \sum P_i(e_{sml}), \quad (A.1)$$

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

The expected energy delivery to the nest for each action is given by

$$E(Z_i) = \sum_j \lambda_{ij} z_{ij}. \quad (A.2)$$

Scenario parameters

The expected daily energy delivered to the nest given action *i*, $E(Z_i)$ (Appendix 2: Eq. A.2), may or may not be enough energy to satisfy the total energy requirements of the female

TABLE A2.4. 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, time T.

Brood's state	Range of values of X_n/n_i†	$F_n(x_n)$* by brood size				
		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

  * $F_n(x_n)$ is defined in Eq. 6.
  † The brood's state variable is an index of energy reserves; the states were calculated as a percentage of the brood's energy requirements $[\alpha_n(t)]$.

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 assumed to be controlled by the female's allocation decisions. We developed eight scenarios that represented the range of possible conditions determining the expected energy intake of the nestlings, $E(Z_{ni})$, and the females, $E(Z_n)$, in this Cooper's Hawk population (Table A2.2). These scenarios incorporated the capabilities of the hunter(s) to meet the family's requirements (the number and size of prey deliveries) and the female's allocation decisions. 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.

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 N/m², the upper limit of $x_f(4)$ (Table A2.3). 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 Kennedy (1991).

The percent wet mass of lipids in carcasses of breeding female raptors ranges from 10 to 20% (Houston 1976, Wiemeyer et al. 1986, 1987). If a bird decreased its wing loading by 20% below the average condition, we assumed it had depleted most of its fat reserves and was in a starving condition. This is the condition we used as the lower boundary to X_f (MCRIT). Breeding female raptors generally do not gain >20% of their biomass during the breeding season (Newton et al. 1983, Hirons et al. 1984, Gonzalez 1986) so we 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 $\alpha_{fi} < z_{fij}$ (by >20%), then the female was assumed to be in a net negative or positive energy balance and mass losses or gains were expected to occur. We 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), we 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 wing area to convert to a new wing loading, and the model reevaluated her state variable based on this new wing loading.

As defined by Eq. 7, $F_f(x_f)$ is a function of the over-winter survival probability and the probability that the female 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. We 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, we incremented the probability of surviving for each state above and below $x_f(4)$ by the same percentages we 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 over-wintered, her probability of reproducing in the next breeding season was very high. Thus, we 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 A2.4. We 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 2–5 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 (sizes 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 were predicted to survive. We assumed that a brood that had its energy requirements met, $x_n(6)$ and $x_n(7)$, had a survival probability, $F_n(x_n)$, of 1.0 (Table A2.4). The survival probabilities associated with states lower than $x_n(6)$ were the midpoints of the intervals representing each state (Table A2.4).

Risks to brood, $\beta_i(t)$

The estimates of $\beta_i(t)$ were based on nestling mortality rates of a closely related species, the European Sparrowhawk (*A. nisus*) (Moss 1979). In addition, we 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,

TABLE A2.5. Predation and exposure risks $[\beta_i(t)]$ of the nestlings as a function of their age and the female's action.

Female action (i)	Time period in nesting season			
	T_1	T_2	T_3	T_4
Stay (1)	0.12	0.12	0.10	0.08
Calculation*	$A[1 - (B + C)]$	$A[1 - (B + C)]$	$0.85\beta_1(T_2)$	$0.75\beta_1(T_3)$
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	$2\beta_2(T_2)$	$2\beta_2(T_3)$	$2\beta_2(T_4)$

* 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).

the probability of nestling mortality from predation and exposure was 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. See Table A2.5 for details.