EFFECTS OF RADIOTRANSMITTERS ON NORTHERN GOSHAWKS: DO TAILMOUNTS LOWER SURVIVAL OF BREEDING MALES?

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Abstract: We used the Cormack-Jolly-Seber model to estimate the effects of radiotransmitters on survival of breeding northern goshawks (*Accipiter gentilis*). We separately compared apparent annual survival of leg-banded goshawks with (1) tailmount- and (2) backpack-style radiotransmitters (hereafter tailmounts and backpacks) to apparent annual survival of breeding adults with legbands only. The best model without radiotransmitter effects, evaluated with Akaike's Information Criterion (AIC_c), suggested no gender- or year-specific effects on survival. We then added radiotransmitter attachment type (tailmount or backpack) and mass of radiotransmitter as covariates to the base model to estimate the effect of radiotransmitters. Tailmounts on males significantly reduced apparent annual survival from 0.75 (SE = 0.02, 95% CI: 0.71 to 0.78) without radiotransmitters to 0.29 (SE = 0.15, 95% CI: 0.09 to 0.63) with radiotransmitters. Backpacks had no significant effect on survival of adults (0.79, SE = 0.17, 95% CI: 0.33 to 0.97). The strikingly lower survival of goshawks with tailmounts was surprising because tailmounts weighed less (10 g, 1.5% body mass) than backpacks (16–23 g, max = 3.4% body mass) and likely were carried for shorter periods. Due to the small number of goshawks with tailmounts (*n* = 14) in this study, our results possibly were due to chance. We therefore recommend additional study of the effects of tailmounts on survival of breeding male northern goshawks.

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Radiotelemetry is a valuable tool for studying the behavior (Boag 1972, Hooge 1991), habitat use (Bright-Smith and Mannan 1994, Linkhart et al. 1998), and demography (Lebreton et al. 1992, Forsman et al. 1996) of animals. Apart from the presumably short-term effects of trapping, handling, and attaching radiotransmitters (White and Garrott 1990), researchers often assume that little bias is associated with estimating these parameters with radiotelemetry, especially if radiotransmitters are small relative to the animal's mass. Some studies, however, show that radiotransmitters can affect courtship and breeding behavior (Ramakka 1972), vocalization rates (Sayre et al. 1981), rates of high-energy activity (Hooge 1991), foraging rates (Massey et al. 1988), reproductive rates (Paton et al. 1991, Foster et al. 1992), and survival (Johnson and Berner 1980, Small and Rusch 1985, Marks and Marks 1987). While a few studies simultaneously compared the effects of different types, attachments, and masses of radiotransmitters (Aldridge and Brigham 1988, Gessaman and Nagy 1988, Hooge 1991), other studies determined the effects of a single type of radiotransmitter by comparing the performance of animals equipped with radiotransmitters to animals equipped with only legbands. However, estimating the effects of 1 type of radiotransmitter against nonradiomarked individuals may lead to unsupported preference for a radiotransmitter type. For example, compared to owls that were leg-banded only, backpacks lowered reproduction and survival of spotted owls (*Strix occidentalis*; Paton et al. 1991, Foster et al. 1992). Without fully investigating the effects of alternative means of attachment (e.g., tailmounts) on birds, Paton et al. (1991) and Foster et al. (1992) recommended against using backpacks, and at least 2 demographic studies (Forsman et al. 1996, Franklin et al. 1996) excluded capture–recapture data from spotted owls that had backpacks while accepting data from owls that had tailmounts. A limitation of many studies of the effects of radiotransmitters on bird survival is that recapture probabilities (the probability that a bird alive in year *t* is recaptured or resighted in year *t*) were not modeled. The consequence of this is that survival estimates will be biased or imprecise (Lebreton et al. 1992).

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We separately compared the apparent annual survival of banded adult goshawks with tailmounts and harness-mounted backpacks to apparent annual survival estimates from capture–recapture studies of breeding goshawks marked only with colored leg bands. Tailmounts were used to determine habitat use of breeding male goshawks on the Kaibab Plateau, Arizona in 1991–1992 (Bright-Smith and Mannan 1994). Backpacks were used to estimate the behavior of breeding males and females during the nestling and post-fledging dependency periods and winter on the Kaibab Plateau in 1992–1994 (Reynolds et al. 1994).

STUDY AREA

Our study area included all of the Kaibab Plateau in northern Arizona, USA, more than 2,182 m elevation above sea level (approx 173,200 ha). With the exception of several narrow (<1-km wide) natural meadows, 6 burned areas, and numerous areas of relatively small timber harvests (10–16 ha), the study area contained nearly continuous forests of ponderosa pine (*Pinus ponderosa*) and mixed-conifer. The Kaibab Plateau is an isolated, oval-shaped (95 × 55 km), limestone plateau rising from a shrub-steppe plain. The plateau is bounded by escarpments of the Grand Canyon on the south side, steep slopes on the east, and gentle slopes to the shrub-steppe plain on the north and west sides. The southern one-third of our study area included the Grand Canyon National Park–North Rim, and the northern two-thirds included the Kaibab National Forest. Forests on the Kaibab Plateau were isolated from similar forests by varying distances of shrub-steppe. The nearest forest to the north was 97 km, to the east 250 km, to the west 80 km, and to the south 89 km, with the exception of a small area of forest on the south rim of the Grand Canyon at 18 km.

METHODS

We conducted capture–recapture studies of breeding adult goshawks in our study area between 1991 and 2000. We trapped breeding adult male and female goshawks with dho-gaza traps (Bloom 1987, Reynolds et al. 1994) and occasionally with Swedish goshawk traps (Kenward et al. 1983, Reynolds et al. 1994). All trapped goshawks were banded on 1 leg with a U.S. Fish and Wildlife Service band, and on the other leg with a colored band etched with an alphanumeric code readable from within 80 m with 40–60X telescopes (Reynolds et al. 1994).

We attached 2-stage tailmounts (model TW-2; Biotrack, Ltd., Wareham, Dorset, United Kingdom) to 5 breeding males in 1991 and 9 different breeding males in 1992 to assess their use of forest habitats (Bright-Smith and Mannan 1994). Tailmounts weighed 10 g and had position-sensitive activity switches. We attached tailmounts to the proximal end of the 2 central tail feathers (see Kenward 1978) of goshawks several days to 2 weeks after their eggs hatched. In 1991, between early June and early August, we radiotracked each of the 5 males during 1 4-hr period per day during which the hawks were located every half-hour. In 1992, also from early June to early August, we relocated each of the 9 males twice a day during daylight hours (Bright-Smith and Mannan 1994). We obtained relocations by triangulation and direct observation. Triangulations were obtained from within 50–200 m of a goshawk by 2 observers, both equipped with 2-way radios and hand-held antennas. Direct observations consisted of visual sightings of the males during the radiotracking periods (Bright-Smith and Mannan 1994).

Males in our study were not chosen randomly from available territorial males. Rather, we selected males from the 1991 and 1992 populations of territories that contained nests with eggs and were in relatively flat terrain. Radiotracking of male goshawks with tailmounts ceased in early August because the focus of the study was habitat use during the nesting period. Because goshawks molt their tail feathers each spring, tailmounts probably were carried no longer than 10–12 months.

During 1992–1994, 18 breeding adult male and female goshawks were fitted with backpacks in a study of behavior during the nestling, post-fledgling dependency, and post-fledgling dispersal periods. Three of the 18 goshawks lost their radiotransmitters within 72 days of attachment (exact day of loss unknown) and were removed from the sample but were retained in the banded-only sample of goshawks. Thus, 15 goshawks (4 males and 2 females in 1992, 2 males and 4 females in 1993, 1 male and 2 females in 1994) comprised the sample of goshawks with backpacks. Each goshawk was equipped with a 16-g (3 males, 4 females) or a 23-g backpack (2 males, 6 females), 2-stage radiotransmitter (Models SOPB 2380 MVS and LPB 2800 LD; Wildlife Materials, Inc., Carbondale, Illinois, USA) attached with Teflon ribbon harnesses (Reynolds et al. 1994).

We relocated adults with backpacks by approaching the goshawk on foot with a hand-held antenna about once per week through September;

thereafter, we located goshawks 2–3 times during winter from fixed-wing aircraft (Reynolds et al. 1994). Male and female goshawks that received backpacks were opportunistically chosen from the population of pairs (exclusive of males who had tailmounts) that laid eggs or attempted to lay eggs in a given year. However, our choice of goshawks that received backpacks was biased toward individuals in better condition—we rejected 2 females scheduled for backpacks because of low body mass and breast muscle condition at capture. Backpack harnesses were designed to fall off within 12–15 months after attachment. Because 2 of the goshawks with backpacks were resighted only (not recaptured) in subsequent years, we were unable to determine whether they still carried their backpacks.

Each year we used a standardized protocol, consisting of 3 sequential steps and requiring a minimum total effort of 10 person-days in each goshawk territory (less if a nest was found), to search for banded and unbanded goshawks on the study area. First, we checked all known nest structures in each territory for goshawks within 10-days of egg laying (1 person-day). Second, we conducted a systematic search for nesting goshawks in a 500-m radius area centered on the last nest used in each territory (3–4 person-days). Third, we attempted to detect goshawks by broadcasting their vocalizations from transects (configured as in Joy et al. 1994) in a 1,600-m radius area also centered on the last nest used in each territory (completed between 10 days post-egg-hatch and 7 weeks post-fledging; 6–7 person-days). The annual recapture/resighting period for estimating survival was from April through August each year (1991–2000), but most goshawks were recaptured/resighted in June and July. We did not use radiotelemetry to aid the recapture/resighting of any goshawk during any part of the calendar year of a recapture/resighting period. We based survival estimates entirely on the recapture/resighting of goshawks at their nests during the recapture/resighting period.

A total of 294 breeding goshawks (138 males, 156 females) received colored leg bands between 1991 and 2000, and all were included in capture–recapture estimates of survival. Goshawks that received legbands were handled approximately 30 min less than hawks that received radiotransmitters, and—with rare exceptions—we trapped all goshawks no more than once per year (individuals were recaptured more often in 1991–1994; thereafter, resighting of bands predominated). Estimates of apparent annual survival (φ) and recapture/resighting probabilities (p) were obtained with the Cormack-Jolly-Seber model of program MARK (White and Burnham 1999). For each year of our radiotelemetry studies, 3 individual covariates identified individuals that carried tailmounts (coded "2"), backpacks ("3"), or neither type of radiotransmitter ("0"; Appendix A). Because some goshawks likely carried backpacks >1 year, our analyses probably underestimated the effects of the backpacks. We also included an additional covariate for each year: the proportional value of the bird's mass comprised by the radiotransmitter's mass. We followed procedures recommended by Burnham and Anderson (1998) for model selection using AIC_c. We estimated an expected number of goshawks to return in the year after attachment of each type of radiotransmitter by multiplying the estimated annual apparent survival of the banded-only goshawks by the estimated probability of recapture/resighting for each year and the number of goshawks that received each type of radiotransmitter at the beginning of that year. We used chi-square analysis to evaluate possible deviations from the expected recaptures/resightings.

RESULTS

Thirteen of the 14 males with tailmounts fledged young in the year they carried radiotransmitters. The single male that did not fledge young lost his nestlings 2–3 weeks after his eggs hatched. No mortalities of the 14 males with tailmounts were noted during or after the habitat-use study period (early Jun–early Aug).

Of the 15 goshawks with backpacks, 12 fledged young in the year they carried radiotransmitters. Of the 3 (2 males, 1 female) that did not fledge young, 2 either failed to lay or lost their eggs in early incubation, and the third lost its nestlings 4–5 weeks after hatching.

We recaptured only 2 of 14 males with tailmounts in the year after radiotransmitter attachment, and each had shed their radiotransmitters. However, 2 (1 male, 1 female) of the 4 goshawks with backpacks that we recaptured the following year had retained their radiotransmitters, and a third (female)—first recaptured 4 years after receiving its backpack—also had retained its radiotransmitter (radiotransmitters were removed on recapture). Thus, 20% of backpacks were known to be carried >1 year. Because backpacks probably were carried longer than tailmounts, we expected backpacks to have greater effects on survival than tailmounts, even though

Table 1. Partial list of models, ranked using Akaike's Information Criteria corrected for sample size (AIC_c), of goshawk apparent survival and recapture/resighting parameters considered for estimating the impacts of radiotransmitters on survival on the Kaibab Plateau, Arizona, USA. Model names follow Lebreton et al. (1992): φ = apparent annual survival rate, p = recapture/resighting probability, t = time, and g = gender. Three individual covariates were included in the analysis: tailmount and backpack radiotransmitters, and the radiotransmitter's percent of the bird's body mass (Trans %).

Model	AIC_c	ΔAIC_c	w_i[a]	Model likelihood	K[b]	Deviance
$\{\varphi(.+\text{Tailmount})\ p(g+t)\}$	1,102.97	0.00	0.611	1.000	12	1,078.36
$\{\varphi(.+\text{Tailmount + Backpack})\ p(g+t)\}$	1,105.02	2.05	0.219	0.359	13	1,078.31
$\{\varphi(.)\ p(g+t)\}$	1,106.95	3.97	0.084	0.137	11	1,084.43
$\{\varphi(.+\text{Trans \%})\ p(g+t)\}$	1,108.21	5.23	0.045	0.073	12	1,083.59
$\{\varphi(.+\text{Backpack})\ p(g+t)\}$	1,108.91	5.94	0.031	0.051	12	1,084.29
$\{\varphi(.)\ p(t)\}$	1,112.22	9.24	0.006	0.010	10	1,091.78
$\{\varphi(g)\ p(t)\}$	1,113.01	10.03	0.004	0.007	11	1,090.49
$\{\varphi(g^*t)\ p(g^*t)\}$	1,143.45	40.48	0.000	0.000	35	1,068.25
$\{\varphi(.)\ p(.)\}$	1,225.18	122.20	0.000	0.000	2	1,221.15

[a] Akaike weight.
[b] Number of parameters.

multi-year effects were not modeled in the survival analyses. None of the goshawks with tailmounts—but 2 of the 15 goshawks (both females) with backpacks—were recovered dead (the first, 10 months after attachment; the second, 5 years after attachment). We observed no loss of legbands through the double banding of goshawks.

We evaluated goodness-of-fit of the mark–recapture data with program RELEASE (Burnham et al. 1987). The sum of Tests 2 and 3 for both genders was 36.54 with 44 degrees of freedom. Because the ratio of χ^2 to degrees of freedom was <1 for the combined groups, we concluded that a quasi-likelihood correction was not needed (Burnham and Anderson 1998).

Our initial analyses ignored the individual covariates concerning radiotransmitters to obtain a parsimonious model of apparent survival and recapture parameters. The minimum AIC_c model $\{\varphi(.)\ p(g+t)\}$ included no time or gender effects on apparent survival, but did include time-specific (year) and additive gender effects on the probability of recapture/resighting. We then added individual covariates to this basic model to obtain a series of models to estimate the effects of radiotransmitters on apparent survival (Table 1).

The addition of the tailmount individual covariate to model $\{\varphi(.)\ p(g+t)\}$ resulted in a new minimum AIC_c model (Table 1). This new model estimated apparent annual survival without a radiotransmitter to be 0.75 (SE = 0.02, 95% CI: 0.71 to 0.78), but only 0.29 (SE = 0.15, 95% CI: 0.09 to 0.63) with tailmounts. The backpack radiotransmitter covariate did not improve the AIC_c model-selection criterion over model $\{\varphi(.)\ p(g+t)\}$. With the backpack model, survival without a radiotransmitter was estimated to be 0.74 (SE = 0.02, 95% CI: 0.70 to 0.78) and 0.81 (SE = 0.18, 95% CI: 0.31 to 0.98) with a backpack.

The estimate of survival without a radiotransmitter was less than for the previous model because the tailmount effect was included in the estimate of survival without a backpack. Therefore, we also ran the model that included both a tail-mount and backpack effect to obtain an unbiased estimate of survival without any radiotransmitter. This model does not rank as the best AIC_c model because the backpack effect is negligible, and thus superfluous in the model. However, the estimators of survival from this model should have less bias than the model that only includes tailmounts because the backpacks are removed from the estimates of survival without radiotransmitters. The estimates from this more general model are: no radiotransmitter 0.75 (SE = 0.02, 95% CI: 0.71 to 0.78), with a backpack 0.79 (SE = 0.17, 95% CI: 0.34 to 0.97), and with a tailmount 0.29 (SE = 0.15, 95% CI: 0.09 to 0.63). These estimates of survival suggest that backpacks improve survival, but the effect clearly is not significant and likely a result of the nonrandom selection of goshawks for backpacks.

The number of males that were recaptured/resighted the year subsequent to receiving tailmounts was not different from expected (2 observed, 2.3 expected) in 1992, but was lower than expected in 1993 (0 observed, 3.3 expected; Table 2). Thus, the effect of tailmounts on survival in our model was the result of significantly less then expected recaptures/resightings in only 1 (1993) of the 2 years. We found no differences in numbers of observed and expected recaptures/resightings of goshawks in any year subsequent to backpack attachment (Table 2).

Table 2. Number of goshawks (by sex) on the Kaibab Plateau, Arizona, USA, that received tailmount and backpack radiotransmitters by year, the expected number of recaptures/resightings in the subsequent year ($\varphi \times p \times$ no. with radiotransmitter type), the observed number of recaptures/resightings, and χ^2 values.

		Goshawks with radiotransmitters				
Sex	Yr	Tail-mount	Back-pack	No. expected	No. observed	χ^2
Male	1991	5		2.31	2	0.04
	1992	9		3.28	0	3.28
Male	1992		4	1.46	2	0.20
	1993		2	0.17	0	0.17
	1994		1	0.18	0	0.18
Female	1992		2	0.94	1	0.00
	1993		4	0.54	0	0.54
	1994		2	0.54	0	0.54

The third covariate we evaluated was radiotransmitter mass proportional to individual goshawk mass. This variable was not a good explanation of the radiotransmitter effect, with a ΔAIC_c value of 5.23 relative to the base model (Table 1). The range of values in the covariate (1–3.4%) was small. Investigating the impact of radiotransmitter mass on a goshawk's survival requires a wider range of radiotransmitter masses.

DISCUSSION

In open capture–recapture models, program MARK estimates apparent survival because mortality typically cannot be distinguished from dispersal or emigration. Elsewhere (Reynolds et al., unpublished data), we demonstrated that both male and female goshawks on our study area have strong lifetime fidelity to their breeding territories (94–96% of hawks stayed on their original territory). In the few cases of individuals dispersing to another territory (breeding dispersal), the dispersed goshawks moved no further than 5 territories (maximum dispersal distance = 18.8 km). Short dispersal distances, combined with intensive, annual searching for goshawks in the known 121 of a 145 possible territories (based on territory spacing and study area size), suggested that dispersed adult goshawks had a high probability of being detected—provided they had not abandoned a territory to become permanent nonbreeders or had not permanently emigrated from our study area. We believe that any downward bias in survival estimates caused by emigration was low because emigration from the Kaibab Plateau likely was constrained by the plateau's isolation from other forests and the abrupt change from forests to shrub-steppe at the study area boundary. Nonreturning goshawks, therefore, probably had not survived the winter.

A radiotransmitter's proportional mass, the season, type of attachment, and the time period the radiotransmitter is attached can affect a bird's weight gain, reproduction, activity budget, survival, flight agility and efficiency, and energetics (Aldridge and Brigham 1988, Pennycuick and Fuller 1987). Not unexpectedly, the effects of radiotransmitters appear to be greater for animals requiring high flight maneuverability while foraging (e.g., fly catching). Backpacks attached with harnesses (vs. adhesive) reduced flight speed of homing pigeons (*Columba livia*; Gessaman and Nagy 1988), flight frequency and distance in acorn woodpeckers (*Melanerpes formicivorus*; Hooge 1991), and lowered flight maneuverability in bats (Aldridge and Brigham 1988). Aldridge and Brigham (1988) showed that the turning radius (i.e., maneuverability) of a flying animal is inversely proportional to wing loading (mass/wing area). Therefore, an increase in mass due to radiotransmitters should result in a proportionate decrease in maneuverability.

Breeding goshawks make multiple daily trips to deliver relatively large prey (up to 1,500 g; Reynolds and Meslow 1984) to their nests. Thus, loads and the aerodynamic drag created by carrying prey greatly exceed those of the radiotransmitters used in our study. Furthermore, we were surprised that a 10-g increase in load due to tailmounts could exceed the effects of 10–23 g backpacks. The different effects, however, could be associated with the means of attachment and locations of the radiotransmitters. We attached backpacks directly to the goshawks' bodies and close to their centers of gravity, whereas we attached tailmounts to the 2 central tail feathers some distance behind the goshawks' centers of gravity. Attaching radiotransmitters to 2 tail feathers might restrict the feathers' independent movement during turns and stops, and attaching radiotransmitters behind the goshawks' centers of gravity could lower their flight stability depending on radiotransmitter mass and distance aft of the center of gravity (see McCormick 1995 for effects of changing center of gravity in aircraft).

While either type of attachment could affect a hawk's flight maneuverability and efficiency, the relatively small mass of the tailmounts suggests that the effects might be subtle. However, all tailmounts were placed on breeding males, the principal foragers for a goshawk family during the 5-month-long breeding season (Squires and Reynolds 1997). Given the male's high level of foraging activity, the high flight maneuverability required for capturing birds and mammals, and the long breeding season, even a subtle lowering of flight maneuverability and efficiency could result in sufficient energy expenditures to exhaust breeding males. Exhaustion could decrease the male's probability of surviving the following winter, especially in a year of declining prey abundance (e.g., 1993–1994; S. R. Salafsky and R. T. Reynolds, Rocky Mountain Research Station, unpublished data).

Only 2 studies have compared return and recovery rates of goshawks with tailmounts. Kenward (1978) found no differences in weight gain or recapture rates among juvenile European goshawks (*Accipiter gentilis gentilis*) with leg bands versus juveniles with tailmounts. In another study, Kenward et al. (1999) reported that adult goshawks receiving tailmounts during winter suffered disproportionately high mortality during the first month following attachment (mostly due to shooting). Thereafter, recoveries (i.e., mortalities) of hawks that were banded-only exceeded recoveries of hawks with tailmounts (Kenward et al. 1999). Our study of tailmounts, however, differed in that it involved only nesting adult males.

MANAGEMENT IMPLICATIONS

We identified a statistically significant lowering of annual survival of breeding male goshawks carrying tailmounts and a statistically neutral effect of backpacks on the survival of breeding males and females. Due to the small number of goshawks that received tailmounts in our study, however, we are uncertain whether the effects on apparent survival were real or resulted from random factors affecting the recapture or resighting of these difficult-to-study hawks. Hence, despite our compelling finding, we cannot discourage using tailmounts on goshawks. Nonetheless, our results suggest that additional studies of the effects of tailmounts on survival of breeding male goshawks are needed. Because survival estimates are based on estimates of recapture probabilities, we recommend that studies of radiotransmitter effects on survival incorporate a capture–recapture design.

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Appendix A. Capture–recapture histories of goshawks that received tailmount radiotransmitters (coded as 2) and backpack radiotransmitters (coded as 3) on the Kaibab Plateau, Arizona, USA, 1991–2000. Codes in bold print represent years in which goshawks were known to have carried their radiotransmitters, "1" indicates years in which breeding goshawks were recaptured/resighted and radiotransmitters were either not attached or had been shed in the year after attachment, "0" indicates years when goshawks were not recaptured/resighted, and "*" identifies goshawks who had retained their radiotransmitters on recapture. Estimates of annual recapture probabilities are from model {φ(.+Tailmount) $p(g + t)$}.

		Year									
Hawk	Sex	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
E3A	M	**2**	1	0	0	1	1	0	0	0	0
C0	M	**2**	0	0	0	0	0	0	0	0	0
G0	M	**2**	0	0	0	0	0	0	0	0	0
R0	M	1	**2**	0	0	0	0	0	0	0	0
C5	M	**2**	1	1	0	0	0	0	0	0	0
G1	M	1	**2**	0	0	0	0	0	0	0	0
K0	M	1	**2**	0	0	0	0	0	0	0	0
L4	M	**2**	0	0	0	0	0	0	0	0	0
VA	M	1	**2**	0	0	0	0	0	0	0	0
R2	M		**2**	0	0	0	0	0	0	0	0
S1	M		**2**	0	0	0	0	0	0	0	0
R3	M		**2**	0	0	0	0	0	0	0	0
T3	M		**2**	0	0	0	0	0	0	0	0
E2	M		**2**	0	0	0	0	0	1	0	0
DC	F	1	**3**	0	0	0	1	0	0	0	0
AZ	F	1	0	**3**	0	0	1	0	0	0	0
S2	M		**3**	0	0	0	0	0	0	0	0

(continued on next page)

Appendix A. continued.

		Year									
Hawk	Sex	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000
U1	M		**3**	0	0	0	0	0	0	0	0
K3	M		**3**	1	0	0	0	0	0	0	0
A1	M		**3**	1*	1	0	0	0	0	0	0
R4	F		1	1	**3**	0	0	0	0	0	0
G5	F		1	**3**	0	0	0	0	0	0	0
X5	F		**3**	1*	0	0	0	0	0	0	0
X3	M			**3**	0	0	0	0	0	0	0
D4	M			**3**	0	0	0	0	0	0	0
Y4	F			1	**3**	0	0	0	0	0	0
CW	F			**3**	0	0	0	0	0	0	0
EV	F			**3**	**0**	**0**	**0**	**0**	1*	1	1
EB	M				**3**	0	0	0	0	0	0
p_{male}[a]			0.62	0.49	0.11	0.24	0.30	0.44	0.84	0.82	0.93
p_{female}			0.74	0.63	0.18	0.36	0.44	0.58	0.90	0.89	0.96

[a] Probability of recapture.