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# Effects of Radiomarking on Prairie Falcons: Attachment Failures Provide Insights About Survival

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## Abstract

*From 1999–2002, we attached satellite-received platform transmitter terminals (PTTs) to 40 adult female prairie falcons (*Falco mexicanus*) on their nesting grounds in the Snake River Birds of Prey National Conservation Area (NCA) in southwest Idaho. We used 3 variations of a backpack harness design that had been used previously on raptors. Each radiomarked falcon also received a color leg band with a unique alphanumeric code. We monitored survival of birds using radiotelemetry and searched for marked birds on their nesting grounds during breeding seasons after marking. Because 6 falcons removed their harnesses during the first year, we were able to compare survival rates of birds that shed PTTs with those that retained them. We describe a harness design that failed prematurely as well as designs that proved successful for long-term PTT attachment. We resighted 21 marked individuals on nesting areas 1–5 years after they were radiomarked and documented 13 mortalities of satellite-tracked falcons. We used a Cormack-Jolly-Seber model to estimate apparent survival probability based on band resighting and telemetry data. Platform transmitter terminals had no short-term effects on falcons or their nesting success during the nesting season they were marked, but birds that shed their transmitters increased their probability of survival. Estimated annual survival for birds that shed their transmitters was 87% compared to 49% for birds wearing transmitters. We discuss possible reasons for differences in apparent survival rates and offer recommendations for future marking of falcons.* (WILDLIFE SOCIETY BULLETIN 34(1):116–126; 2006)

## Key words

*attachment techniques, backpack,* Falco mexicanus, *harness, prairie falcon, radiotelemetry, radiotransmitters, reproduction, satellite telemetry, survival.*

Radiotelemetry is valuable for understanding the behavior and ecology of birds. Researchers have used several methods to attach transmitters to birds, frequently modifying common attachment techniques to accommodate transmitter size and shape, bird behavior, and study objectives (Kenward 2001, Fuller et al. 2005). Early radiotelemetry studies of raptors were short-term, but with improved technology, backpack radio tags can now be used to monitor raptors for several years (Kenward et al. 2001). Satellite telemetry can be especially useful for estimating survival because birds can be monitored as they move over large spatial areas (Strikwerda et al. 1986). A principal consideration, however, is how the transmitter and attachment technique might affect the bird and its survival probabilities (Murray and Fuller 2000). Researchers face challenges in finding a marker attachment design that will remain on a bird for the duration of the study with minimal effects on the bird and the behavior being studied.

Radiomarking can affect birds in many ways (Murray and Fuller 2000, Withey et al. 2001). Radiomarked birds expend more energy than unmarked birds because transmitter packages add mass and aerodynamic drag (Pennycuick and Fuller 1987, Obrecht et al. 1988). Radiotransmitters also can affect a bird's maneuverability (Pennycuick et al. 1989, Putaala et al. 1997), thus potentially adversely influencing an individual's ability to procure prey, its stamina during migration, and its ability to compete for a territory and mate. The harness alone can affect flight behavior (Hooge 1991), and increase energy requirements during flight (Gessaman et al. 1991*b*) by distorting the natural conformation of the body feathers, thus distorting airflow and increasing interference drag during flight (V. Tucker et al., Duke University, unpublished data).

Investigators have used backpack harnesses to attach very high frequency (VHF) transmitters to prairie falcons (*Falco mexicanus*) and saker falcons (*F. cherrug*) and satellite-received platform transmitter terminals (PTTs) to peregrine falcons (*F. peregrinus*) with no apparent adverse effects (Dunstan et al. 1978, Vekasy et al. 1996, Fuller et al. 1998, Britten et al. 1999, Kenward et al. 2001, McGrady et al. 2002). Recaptured peregrine falcons showed no adverse physical effects of PTTs (McGrady et al. 2002), and the proportion of PTT-tagged peregrine falcons that returned to Alaska breeding areas was similar to annual survival rates estimated for color-banded peregrine falcons (Britten et al. 1999). However, several studies have shown that various types of radiotransmitters and their attachments can alter a bird's behavior, reproductive rate, and survival (Withey et al. 2001, Reynolds et al. 2004 and references cited therein). For example, backpack harnesses had adverse effects on spotted owl (*Strix occidentalis*) survival and reproductive rates (Paton et al. 1991, Foster et al. 1992).

Marker loss is an important consideration in studies of

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movements and survival. Reynolds et al. (2004) noted that 3 of 18 northern goshawks (*Accipiter gentilis*) lost backpack transmitters within 72 days of attachment, and premature harness failure also occurred in a study of bald eagles (*Haliaeetus leucocephalus*; Buehler et al. 1995). We suspect that other studies have experienced harness failures that they did not report or were unable to document. Researchers studying prairie falcons in southwest Idaho (Vekasy et al. 1996) experienced several premature harness failures when they used cotton thread to sew Teflon ribbon harnesses (J. O. McKinley, personal observation). They subsequently modified the harness by using dental floss, instead of cotton thread, and metal crimps on the Teflon ribbon at all 4 corners of the transmitter; VHF transmitters with the modified harnesses remained attached to prairie falcons for the entire nesting season and sometimes for several years (J. O. McKinley, personal observation).

As part of a study to understand the movements and ecology of prairie falcons (Steenhof et al. 2005), we radiomarked adult females in the Snake River Birds of Prey National Conservation Area (NCA), Idaho, from 1999 through 2002. Each spring we attached PTTs to falcons using variations of a backpack harness design (Snyder et al. 1989, Kenward 2001) that has been used on several species of raptors. The objectives of this paper are to describe and evaluate the designs we used to attach PTTs, to discuss when and how harness failures occurred, and to document effects of transmitter packages on female prairie falcons. As part of this analysis, we present information on when and where falcon mortalities occurred, and we estimate apparent annual survival and factors influencing it.

## Equipment and Methods

We trapped adult prairie falcons in April and May at randomly selected nesting territories (Steenhof et al. 2005) within the NCA (42°50′N, 115°50′W) using dho gaza nets with a great horned owl (*Bubo virginianus*) as a lure (Bloom et al. 1992). We captured and handled all birds according to Animal Care Protocol guidelines approved by Boise State University (IACUC Number 692-98-020). We placed hoods on all birds captured and held them in a can or an "aba" (Maechtle 1998) to minimize stress. We weighed and measured all birds captured, and we applied a United States Geological Survey (USGS) aluminum band to the left leg and a black anodized band with white alphanumeric symbols (Acraft Sign and Name Plate Company, Edmonton, Alberta, Canada) to the right leg of all previously unbanded falcons. We measured wing chord to the nearest mm with a ruler according to instructions in Pyle (1997), and we measured tail length in mm by inserting a ruler between the central rectrices to the point of their insertion. We measured length of exposed culmen in mm with calipers according to Bortolotti's (1984) diagrams, and we measured footpad length in mm with calipers from the distal end of the pad on the hind toe (hallux) to the distal end of the pad on the middle (third) toe, with the toes maximally extended. We classified birds with wing chords >320 mm as females (United States Fish and Wildlife Service and Canadian Wildlife Service 1977), and we classified adult falcons as "first year birds" (11–13 months old) if the legs or cere were pale yellow with a hint of blue or if the breast showed streaks rather than spots (Steenhof 1998).

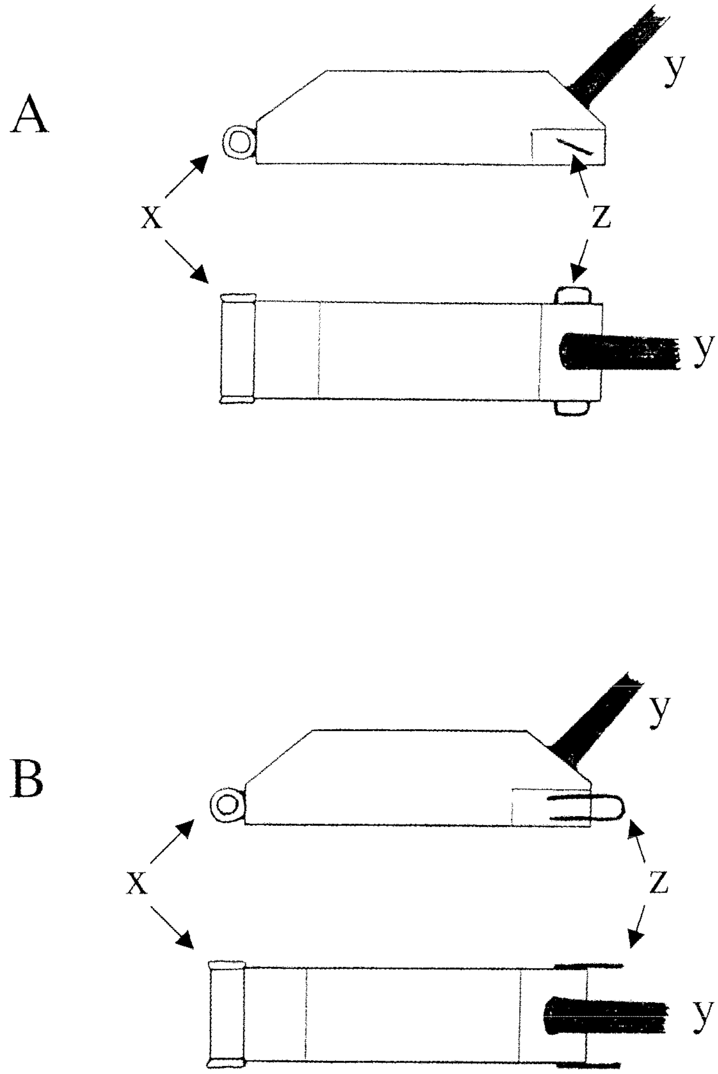


***Figure 1.*** Top and side views of Microwave PTT-100 units used on prairie falcons, showing anterior attachment tubes (x) and antennae (y): (A) 1999 model with posterior wire loops (z) extending perpendicular to the PTT axis; (B) 2000–2002 model with wire loops (z) extending posterior from the PTT.

Each year we attached PTTs to 10 adult female prairie falcons. We radiomarked females only if they weighed at least 835 g and only if there was evidence that the trapped bird was a resident of the randomly selected target territory. Two of the 40 females we radiomarked had been trapped and banded as adults in November 1998 in southwest Idaho. Based on plumage characteristics and soft tissue color, at least 9 of the females probably were first year birds when we radiomarked them.

The PTT-100 units were manufactured by Microwave Telemetry, Inc. (Columbia, Maryland), weighed approximately 33.6 ± 0.9 g (range: 32.1–35.5 g; $n = 40$), and contained sensors for battery voltage, motion, and temperature. The PTTs we attached weighed 3.4–4.1% (mean = 3.8 ± 0.2%) of the bird's mass. Each year we used PTTs with the same general shape and dimensions (70 mm × 15 mm × 15 mm). All PTTs had an attachment tube on the anterior end (Fig. 1) in place of the standard single wire attachment loop. In 1999 we used PTTs with wire loops extending perpendicular to the axis of the PTT at the posterior

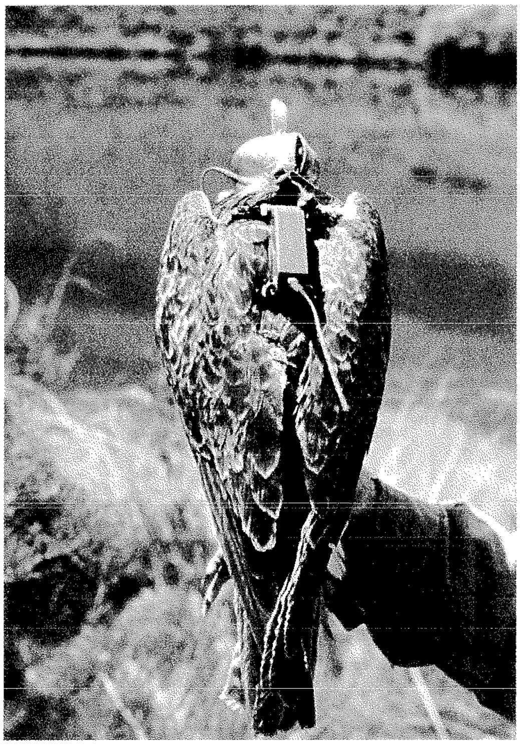

***Figure 2.*** Radiomarked prairie falcon prior to release in 1999, showing the position of the PTT resting on the dorsum and the antennae extending over the back.

end (Fig. 1A). After 1999 we used PTTs with wire loops extending posterior from the PTT (Fig. 1B).

We attached PTTs as backpacks using harnesses with neck and body loops (Kenward 2001). We fitted all harnesses individually to each falcon using procedures described by Snyder et al. (1989) and Kenward (2001). Each PTT rested on the dorsal surface along the midline of the back between the falcon's wings, with the antenna angled at approximately 45 degrees from the PTT posterior (Fig. 2). The basic harness consisted of 6-mm wide tubular Teflon ribbon (Bally Ribbon Mills, Bally, Pennsylvania), waxed dental floss as thread, Superglue (cyanoacrylate glue), and 3.5-mm long sections of 4-mm diameter copper tubing. We filed the ends of the copper tubing to smooth the cut edges and form rings. All but 4 harnesses had a leather piece (approximately 17 mm × 17 mm × 2 mm) with a 6-mm diagonal slit in each corner (Fig. 3). In 2002 we experimented with not using the leather piece (e.g., Snyder et al. 1989) on 4 birds to reduce mass, but found that fitting the harness without it was more difficult.

We used 3 combinations of materials and designs for attachment during the study. In all designs we used copper rings to secure the PTT in position by binding segments of Teflon ribbon because this technique (J. O. McKinley, personal observation) had been successful in an earlier study (Vekasy et al. 1996) of prairie falcons in our study area. We used small alligator clips to temporarily hold the PTT and harness while adjusting the fit. When the fit was complete, we used pliers to crimp the copper rings around the Teflon ribbon, and we trimmed all excess ribbon.

In 1999 we placed 2 equal lengths of Teflon ribbon through 2 slits on the left and right sides of the leather piece but did not

***Figure 3.*** Ventral view of a radiomarked prairie falcon, showing the leather breast piece, through which the Teflon ribbon was passed and stitched. This photo illustrates the modified design, used after 1999, which is similar to the "X Attachment" described by Buehler et al. (1995). In this prerelease photo, the Teflon ribbon has not yet been placed under the body feathers.

cross the ribbon. This formed an hourglass configuration with the leather piece in the center. The leather piece held the Teflon ribbon lengths at the junction of the neck and body loops about midway along the apex of the sternal keel (Fig. 3; Snyder et al. 1989). We sewed each of the ribbon lengths to the leather using 2 stitches of waxed dental floss and covered each knot with a drop of Superglue. We passed the upper end of each ribbon through a copper ring and then passed one end of each ribbon through the anterior PTT tube, in opposite directions to form the neck loop. We slid the copper rings around the overlapping segments of ribbon, against each end of the anterior PTT tube (Fig. 4). We then passed the other ends of ribbon through the wire loops on the posterior end of the PTT and folded each end back on itself and

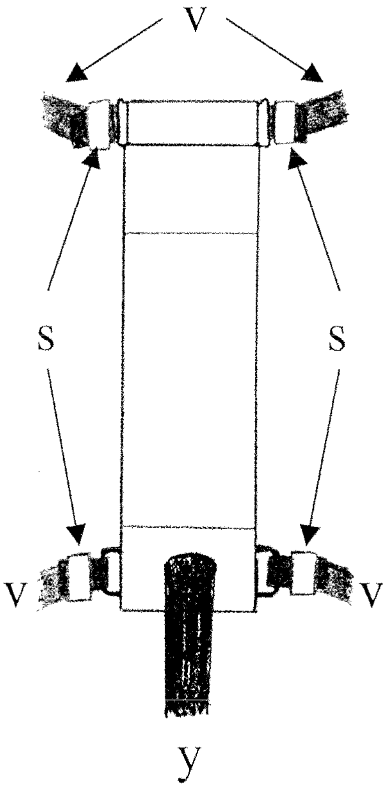


***Figure 4.*** Top view of the PTT used on prairie falcons in 1999 showing the position of crimped copper rings (s) on Teflon ribbon (v) in relation to the PTT and antenna (y).

through the copper ring (Figs. 4, 5A) to form the body loop. Harnesses used in 1999 weighed approximately 3.5 g.

Because some prairie falcons removed their PTTs during the first year, we used 2 alternative attachment designs after 1999. Both alternative designs had a single length of Teflon ribbon that crossed on the breast, usually through a leather piece to which it was stitched (Fig. 3). We continued to crimp copper rings at the PTT anterior tube, but we modified the process for securing the neck loop at the tube. We sewed the overlapping segments of ribbon together with 1 stitch on the left or right side of the tube and crimped a copper ring over the stitch. We then stitched the same 2 segments of ribbon so that the position of this stitch, after final fitting, was inside the anterior tube. We crimped a second copper ring on the opposite side of the anterior tube to hold the PTT in position.

The 2 alternative attachment designs used after 1999 had different types of plastic tube between the posterior wire loops of the PTT (Fig. 5B,C). We attached epoxied tube harnesses to 10 individuals from 2000–2001. The "epoxy" design had a 14-mm section of 5-mm-diameter hard styrene plastic tubing fit tightly between the wire loops on the posterior end of the PTT (Fig. 5B). We pushed a section of shrink tubing through the plastic tube and extended it approximately 6 mm from each end of the plastic tube. We inserted the Teflon ribbon length through the shrink tubing until its center was inside the plastic tube. We secured the ribbon in the posterior tube by sewing the ribbon with waxed dental floss through 2 holes (0.25-mm diameter) drilled perpendicularly through the center of the plastic tube and shrink tubing. Before going to the field, we used 30-min epoxy to secure the hard plastic tube to the PTT posterior, coating over the stitches and stitch holes. Epoxy harnesses weighed approximately 4 g.

We attached flexible tube harnesses to 20 individuals from 2000–2002. The "flex" design had a 13-mm-long section of 5-mm-diameter, clear, flexible plastic tubing (aquarium tubing) with 1 or 2 4-mm-long sections of 4-mm diameter copper tubing

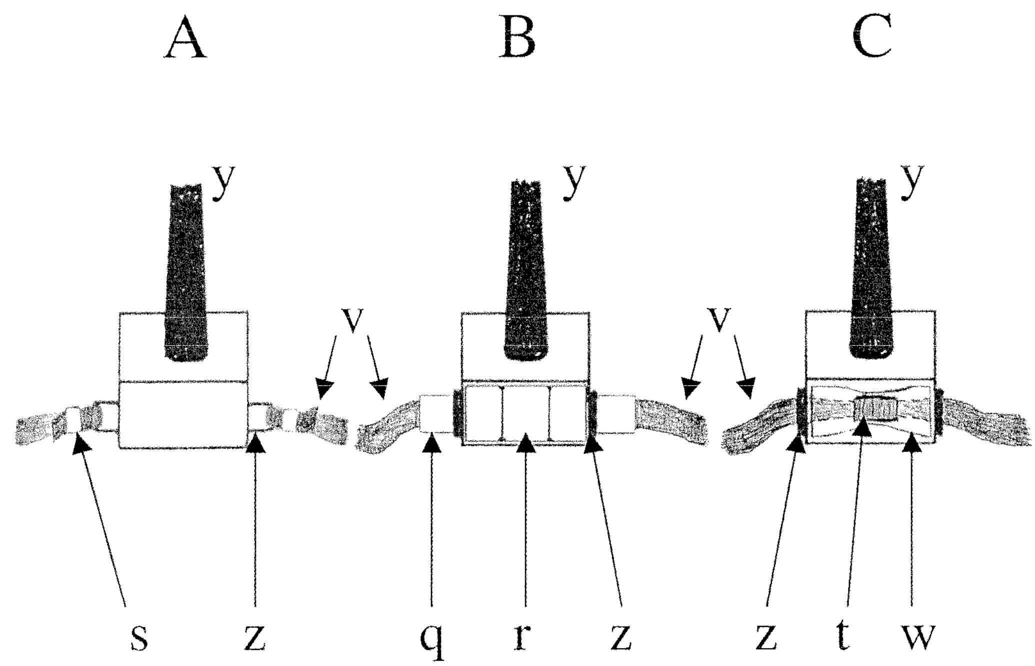


***Figure 5.*** Posterior views of 3 attachment designs used on prairie falcons: (A) 1999 design, (B) epoxy design used from 2000–2001, and (C) flex design used from 2000–2002. Note the modified orientation of wire loops in the epoxy and flex designs, which have different types of posterior attachment tubes. Components include crimped copper rings (s), antennae (y), posterior wire loops (z), Teflon ribbon (v), shrink tube (q), hard plastic styrene tube (r), crimped copper tube (t), and flexible plastic aquarium tube (w).

centered inside (Fig. 5C). We threaded the Teflon ribbon through the plastic and copper tubing and secured the ribbon at its midpoint by crimping the tubing flat with pliers. We then ran the ribbon ends through the posterior wire loops, centering the tube between the loops. Flex harnesses weighed approximately 4.5 g.

To determine if the transmitter package or handling adversely affected the bird's initial flight or behavior, we observed each radiomarked falcon for at least 1 hr after release or until it disappeared from view. We revisited nesting territories with radiomarked birds every 1–2 weeks during the nesting season to determine whether birds had lost their PTTs.

We used the ARGOS-TIROS satellite system (ARGOS 1996) to obtain estimates of PTT locations, temperature, and motion. Individual PTTs transmitted useful data for periods that ranged from less than 2 months to 21 months. We determined that a PTT was no longer attached to a live bird when ARGOS data showed minimal or no activity changes and temperature values that fluctuated with ambient temperatures. In each of these events, we tried to confirm mortality or determine if the transmitter had been removed from a falcon by searching for the PTT on the ground. We used ARGOS data to identify the general locations of these PTTs and to predict transmission periods, and we used ARGOS RMD receivers, manufactured by SERPE-IESM (Guidel, France), and a Radio Shack Pro-70 Scanner (Tandy Corporation, Fort Worth, Texas) to find and retrieve PTTs and any associated carcasses (Bates et al. 2003). Searches for PTTs occurred 2 weeks to 4 months after the PTTs stopped moving. Using these techniques, we recovered 6 shed PTTs and 13 from birds that died. In addition, in 2003 we retrapped a female on her nesting territory and recovered the PTT harness that she had partially removed.

During the 2000–2004 nesting seasons, we tried to find females that we had radiomarked in previous years, using a combination of visual observations and radiotelemetry. We searched for marked birds in their previous territories and, if necessary, in adjacent territories. Unless the bird was known to have died or moved to a different territory, we observed her previously occupied territory (or territories) for at least 5 hr on at least 2 visits or until we found unbanded falcons occupying the territory. Searches began in early March and continued through the breeding season. We used telemetry location estimates to determine general locations of females wearing functional PTTs. We also searched for marked birds throughout the canyon during surveys of abundance and productivity in 2002 and 2003 (USGS, unpublished data), and we conducted intensive searches of areas where other scientists and technicians had reported incidental sightings of marked prairie falcons in the canyon. We used Leica APO Televid (Leica Camera AG, Solms, Germany) and Kowa TSN-820 spotting scopes (Kowa Optimed, Torrance, California) with 20–60 zooms to spot antennas and to read bands. We tried to determine nesting success of all females that had been radiomarked in prior years, whether or not they were still wearing a PTT. We aged nestlings using a photographic aging key (Moritsch 1983) and considered nesting attempts successful if $\geq$1 young reached 30 days of age. To compare nest success rates, we used StatXact 3.1 software (Cytel Software Corporation 1989) to calculate likelihood ratio statistics ($G$-tests) and one-sided asymptotic $P$-values.

To estimate apparent survival and to evaluate factors that influence it, we divided each year into 3 intervals: 1 March–30 June; 1 July–15 October; and 16 October–28 February. We used a Cormack-Jolly-Seber (CJS) model to estimate apparent survival and resighting probability (Lebreton et al. 1992). Estimation was performed in Program MARK (White and Burnham 1999). We evaluated band resightings and telemetry data as separate groups in the initial model, fixing resighting probability to 1.0 for birds with working transmitters. Estimated survival estimates from resightings (0.77 $\pm$ 0.07) and telemetry data (0.80 $\pm$ 0.04) were similar, so we estimated a common survival parameter for both groups. We considered models with the following covariates: nesting stratum, year marked, age of the bird when radiomarked (first year or older), distance to wintering area, and whether the bird had shed its transmitter. We also included a measure of the transmitter burden on the bird: the ratio of bird size (the principal component score for wing chord, tail length, foot pad, and culmen) to transmitter mass. Covariates were included in the CJS model in a general linear models framework using a logit link (Lebreton et al. 1992). We used information-theoretic methods to evaluate hypotheses and rank alternative models using the small-sample adjusted Akaike's Information Criterion ($AIC_c$, Akaike 1973, Burnham and Anderson 2002).

## Results

### *Short-Term Effects of Radiomarking*

The banding, measuring, and PTT-harness attachment process (time from capture to release) took an average of 1 hr 50 min per bird (range = 1 hr 5 min–3 hr 35 min). Attachment times were similar for all 3 harness designs. All radiomarked birds flew well upon release. Most preened extensively during the first hr after release; most pulled at their leg bands as much as or more than they tugged at their backpack harness. At least 8 returned to incubate or brood young within 1 hr of release. One returned to her nest in less than 23 min.

Capture and marking had no apparent effect on the falcons' nesting success during the year of radiomarking. Thirty of the 40 female prairie falcons that we trapped and radiomarked produced young in the year that we trapped them. We confirmed failures at only 6 territories where females had been trapped and radiomarked in the same year, and we could not determine nesting success of 4 radiomarked females. Both the maximum possible success rate (83%) and the minimum possible success rate (75%) for radiomarked falcons compare favorably with the long-term average nesting success rate for prairie falcons in the NCA (63%), (Steenhof et al. 1999), suggesting no immediate adverse effects of transmitters or the trapping process.

### *Harness Failures*

Falcons removed 6 of 10 harnesses applied in 1999 within 6 months of marking. Four of these falcons removed their harnesses within 8 weeks and before leaving their Snake River Canyon nesting areas. Two others removed them in October on their non-nesting grounds. The location at which the harness attachment failed varied among the 6 harnesses. Five of the 6 harnesses failed near one, or both, of the PTT posterior wire loops. In 3 of these harness failures the ribbon was severed between the copper crimp and a posterior wire loop. The fourth harness was severed on the

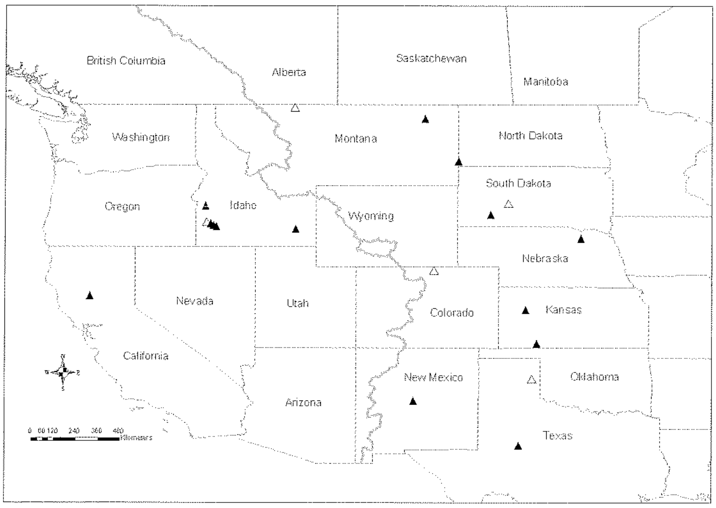


*Figure 6.* Locations of confirmed (solid triangles) or suspected (open triangles) deaths of 19 radiomarked female prairie falcons, 2000–2003. Gray line represents the Continental Divide.

distal side of the posterior crimp. In the fifth failure, the harness ribbon was pulled through the crimp at a posterior wire loop. The sixth harness failed at the leather breast piece, and the falcon was able to remove the harness over the wings. We confirmed only 1 other harness failure during our study. A female fitted with a flex-style harness in 2002 partially removed her harness while on her nesting area, between 9 April and 20 May 2003.

### Nesting Seasons Following Radiomarking

Of 40 females radiomarked, 19 either died or were never resighted in a subsequent nesting season. Three of these 19 returned to the nesting grounds but died before nesting. Of 21 that survived through a nesting season after radiomarking, 12 were reobserved on their nesting areas for a single year after radiomarking, and 9 were resighted during 2 or more nesting seasons following radiomarking. Four of the 9 that survived at least 2 nesting seasons had shed their transmitters in 1999. Five surviving females that carried PTTs after 2 years included 2 marked in 1999, 1 marked in 2000, 1 marked in 2001, and 1 marked in 2002. Survivors that carried PTTs from 1999 had spent winters in Montana and Texas. All survivors with transmitters from 2000–2002 wintered in southwest Idaho (Steenhof et al. 2005). During 2004 nesting surveys, we found only 3 falcons that had worn PTTs. One of these birds had been marked in the final year of trapping (2002) and had migrated only 140 km from her nesting area; the other 2 had been marked in 1999 and had shed their PTTs in that year.

Four of 5 females that shed their transmitters (80%) nested successfully in the year following radiomarking, compared to only 9 of 17 females (53%) that still wore PTTs ($G_1 = 1.26$, $P = 0.13$). Of birds that carried PTTs, 5 of 8 that wintered in Idaho nested successfully, compared to only 3 of 8 that over-wintered east of the Continental Divide (Steenhof et al. 2005). We had information about nesting chronology in consecutive years for 7 of these individuals: falcons that returned from distant wintering areas wearing transmitters hatched their young 13 days later than in the year they were marked ($n = 2$), but hatching dates for falcons that wintered in Idaho were similar to or earlier than in their year of marking ($n = 5$).

### Mortality Determined via Radiotelemetry

We confirmed deaths of 13 prairie falcons wearing functioning transmitters, and we suspected deaths of 5 others based on data received from ARGOS and the fact that these birds were never resighted on the breeding grounds. Another falcon was known to have died >1 year after its last telemetry reception; a citizen found and reported the carcass and transmitter. Mortalities occurred in 9 states (Fig. 6) and in all months except May, September, and October. No mortalities occurred in Canada, even though 12 of 31 marked falcons summered in Alberta and Saskatchewan (Steenhof et al. 2005). In most cases we found carcasses too late to ascertain cause of death, but we suspect electrocution in at least 1 case and shooting in at least 1 other. Conflicts with other raptors may have caused the death of ≥1 falcon in the Snake River Canyon. Nine of 18 mortalities that we could assign to season occurred on the wintering grounds, and 7 of 9 winter deaths occurred in the Great Plains. In addition, we suspect that 1 falcon may have died during a March snowstorm in Colorado, while enroute from Kansas toward Idaho. One winter mortality occurred in California, and 1 occurred in southwest Idaho. Three individuals died in the Snake River Canyon soon after arriving on the breeding grounds in March or April. One of these birds had just completed a migration from Texas, and the other 2 had wintered in southwest Idaho. Raptor predation was the suspected cause of death of 1 of these birds. One prairie falcon disappeared in the NCA at the end of the nesting season, and 4 falcons died east of the NCA during summer.

### Survival

Apparent survival differed depending on whether a bird shed its transmitter. The best CJS model based on $AIC_c$ incorporated the effect of shedding the transmitter on apparent survival (Table 1). The sum of the Akaike weights for models including the transmitter effect was 0.95, suggesting transmitter effect is an important model component. Birds that shed their transmitters increased their probability of survival substantially. The $\beta$ parameter estimate for the increase in survival was 1.69 (95% C.I. = 0.17–3.17) on the logit scale. Estimated annual survival for birds that shed their transmitters was 87% (95% C.I. = 76–97%) compared to 49% (95% C.I. = 40–61%) for birds wearing transmitters. Age of the bird, season, nesting stratum, and transmitter burden did not contribute significantly to the model. Increased transmitter burden as measured by a ratio of the size of the bird to the transmitter mass showed a trend toward reducing apparent survival, but the estimate was imprecise ($\hat{\beta} = 5.32$, 95% CI = −3.84–14.47). Neither season nor year marked had a strong influence on apparent survival. Distance to wintering area did not contribute significantly to a model that evaluated apparent survival of a subset of 27 birds that survived into the first winter with a functioning transmitter (Table 2).

## Discussion

### Harness Failures

Harness failures have been reported from a limited number of raptor studies, and few have documented how the failures occurred. One backpack harness failure occurred during a study of bald eagles when the transmitter's glass tubing cut the Teflon ribbon, and 2 others failed when the ribbon stitching unraveled

***Table 1.*** Model selection results for the prairie falcon survival analysis including telemetry data and re-sighting data for 40 females radiomarked from 1999–2002.

| Model[a] | $AIC_c$ | $\Delta AIC_c$ | $w_i$[b] | $K$[c] | Deviance |
|---|---|---|---|---|---|
| {phi(shed) *p*(radio=1, resight)} | 247.923 | 0.000 | 0.296 | 3 | 241.746 |
| {phi(season+shed) *p*(radio=1, resight)} | 248.587 | 0.664 | 0.212 | 5 | 238.139 |
| {phi(shed+size ratio) *p*(radio=1, resight)} | 248.661 | 0.738 | 0.204 | 4 | 240.364 |
| {phi(shed+age) *p*(radio=1, resight)} | 249.892 | 1.970 | 0.110 | 4 | 241.596 |
| {phi(group+shed) *p*(radio=1, resight)} | 249.925 | 2.003 | 0.109 | 4 | 241.629 |
| {phi(shed+strata) *p*(radio=1, resight)} | 253.411 | 5.488 | 0.019 | 6 | 240.779 |
| {phi(group) *p*(radio=1, resight)} | 253.935 | 6.012 | 0.015 | 3 | 247.758 |
| {phi(.) *p*(radio=1, resight)} | 253.982 | 6.059 | 0.014 | 2 | 249.894 |
| {phi(size ratio) *p*(radio=1, resight)} | 255.580 | 7.657 | 0.006 | 3 | 249.404 |
| {phi(age) *p*(radio=1, resight)} | 255.605 | 7.683 | 0.006 | 3 | 249.429 |
| {phi(group+age) *p*(radio=1, resight)} | 255.713 | 7.790 | 0.006 | 4 | 247.416 |
| {S(year marked) *p*(radio=1, resight)} | 256.583 | 8.660 | 0.004 | 5 | 243.951 |
| {phi(strata) *p*(radio=1, resight)} | 259.300 | 11.377 | 0.001 | 5 | 248.852 |
| {phi(group+strata) *p*(radio=1, resight)} | 259.420 | 11.498 | 0.001 | 6 | 246.789 |

[a] Season = 1 March – 30 June, 1 July- 15 October, and 16 October-28 February; Shed = whether or not the individual had shed its PTT; Age = first year or older; Strata = area of the NCA where the bird nested (west, west-central, east, or east-central); Size ratio = principal components of wing chord, tail length, foot pad and culmen divided by transmitter mass.

[b] $w_i$ is the Akaike weight.

[c] $K$ is the number of estimable parameters in the model.

(Buehler et al. 1995). Female prairie falcons in our study apparently severed the Teflon ribbon of the harness we used in 1999 by using the posterior wire loop and the adjacent crimp as a fulcrum, and the edge of the crimp as a "knife." Platt (1980) reported that prairie falcons caused extensive wear to Herculite leg markers by biting and pulling action. Our modified flex and epoxy designs prevented birds from using the wire loop as a fulcrum for twisting and turning and apparently resulted in increased harness retention.

Previous researchers in the NCA (Dunstan et al. 1978, Vekasy et al. 1996) did not report a high incidence of harness failure when they used backpack harnesses on prairie falcons, except as noted above. The VHF transmitters they used were smaller and lighter than the PTTs we used, and they did not have metal attachment loops. Teflon ribbon was embedded in the outer protective epoxy covering of VHF transmitters used in the 1970s (Dunstan 1972), and it was threaded through a posterior tube within the transmitter package used in the 1990s (J. O. McKinley, personal observation). The perpendicular orientation of wire loops in our original harness design likely provided greater leverage for pulling and twisting actions that caused the crimp to cut the Teflon ribbon. In addition, we suspect the larger size of the transmitter that we used, in volume and mass (34-g PTT versus 12–18-g VHF transmitters) may have increased the falcons' persistence and motivation to remove the harness (Hooge 1991).

### *Effects of Radiomarking*

We found no evidence for short-term effects of PTTs on nesting female prairie falcons. Our findings support Vekasy et al.'s (1996) observation that backpack harnesses had no adverse effect on nesting success of prairie falcons during the year of marking. Vekasy et al. (1996) reported that radiomarked prairie falcons had similar nest attendance and prey delivery rates as unmarked falcons in the nesting season that they were marked. Although radiomarking affects the energy required to provision nestlings, those effects might only have negative consequences during certain ecological circumstances (Pennycuick et al. 1989, Hamel et al. 2004) or be detected only with certain study methods (Pennycuick et al. 1990). Effects of PTTs on female prairie falcons during the nesting season may have been mitigated by the fact that their mates shared in providing food for young.

Prairie falcons that shed their transmitters clearly increased their probability of survival. Estimated annual survival of falcons wearing PTTs (49%) was lower than previous estimates of adult prairie falcon survival rates (65–81%), based on banded birds that were not radiomarked (Enderson 1969, Denton 1975, Runde 1987). Estimated annual survival for prairie falcons that shed their transmitters in our study (87%) was similar to Runde's (1987) estimated survival rate of 81% for banded breeding adult prairie falcons in Wyoming, Colorado, and Alberta. Open capture–recapture models estimate apparent survival because mortality cannot be distinguished from dispersal and emigration (Martin et al. 1995). Year-round tracking by satellite reduced bias due to emigration. Biases in estimated survival due to dispersal after radio failure probably were minimal in this study, because Steenhof et

***Table 2.*** Model selection results for the prairie falcon survival analysis in relation to distance to wintering areas based on 27 radiomarked falcons that survived into the first winter with a functioning transmitter.

| Model | $AIC_c$ | $\Delta AIC_c$ | $w_i$[a] | $K$[b] | Deviance |
|---|---|---|---|---|---|
| {phi(categorical distance) p( radio=1, resight)} | 136.639 | 0.000 | 0.413 | 3 | 130.406 |
| {phi(.) p( radio=1, resight)} | 137.032 | 0.393 | 0.340 | 2 | 132.916 |
| {phi(exact distance) p( radio=1, resight)} | 137.667 | 1.029 | 0.247 | 3 | 131.434 |

[a] $w_i$ is the Akaike weight.

[b] $K$ is the number of estimable parameters in the model.

al. (2005) confirmed long-distance (>10 km) breeding dispersal in only 1 of 24 female prairie falcons.

The PTTs probably affected falcons more during migration and winter than during the nesting season because PTTs would have created greater energetic demands on falcons during migration (Pennycuick and Fuller 1987, Gessaman and Nagy 1988) and winter (Gessaman et al. 1991*a*). During our study, satellite-tracked prairie falcons traveled up to 4,600 km between nesting, post-breeding, and wintering areas each year (Steenhof et al. 2005). Winter may be an important time for prairie falcons as 9 of 18 mortalities occurred during that season. Platform transmitter terminals may affect falcons that winter in the southern Great Plains more than those that winter in Idaho. Seven of 9 winter mortalities occurred in the southern Great Plains, even though more than half of the radiomarked prairie falcons wintered elsewhere. Falcons that wintered east of the Continental Divide arrived on nesting areas 2–3 weeks later than those that wintered in southwest Idaho (Steenhof et al. 2005). Late arrivals may represent an effect of radiomarking: falcons that returned from distant wintering areas wearing transmitters tended to nest later than in the year they were marked, whereas falcons returning from Idaho wintering areas nested at the same time or earlier than in their year of marking. Falcons that wintered in the Great Plains also tended to have lower nesting success rates than falcons that wintered in Idaho in years after radiomarking (Steenhof et al. 2005). Later nest initiation and lower productivity of mallards (*Anas platyrhynchos*) wearing backpack radio harnesses were associated with lower feeding rates than unmarked mallards (Pietz et al. 1993).

Our findings add to the relatively small amount of literature about effects of radiomarking on birds (Murray and Fuller 2000, Withey et al. 2001), and they raise questions about why other studies have not reported adverse effects of radiomarking on raptors. We suspect that many species of raptors studied thus far (e.g., buteos, eagles, ospreys [*Pandion haliaetus*]) have flight dynamics that would make them less susceptible than falcons to radiomarking effects. We also suspect that many researchers did not have the opportunity to evaluate effects. Either sample sizes were too small to include a control group or subjects were not tracked for long enough periods to observe effects.

Relative mass of the transmitter package is one factor that may influence survival. Increased transmitter burden as measured by a ratio of the size of the prairie falcon to transmitter mass showed a trend toward reducing apparent survival in our study. The PTTs we attached weighed 32.1–35.5 g, and harnesses weighed 3.5–4.5 g. The total PTT/harness load was less than the 5% recommended for larger birds by Cochran (1980) and authorized by our Animal Care and Use Permit, but it was greater than the 3% recommended by the Bird Banding Laboratory. These guidelines are arbitrary because they were not based on experimental data. More appropriate guidelines would consider wing morphology and flight characteristics of individual species (Caccamise and Hedin 1985, Pennycuick et al. 1994). Our results, along with those of Hooge (1991), Ward and Flint (1995), and Phillips et al. (2003), reveal negative effects for some species radiomarked with more than 3% of their body mass.

Peregrine falcons are similar to prairie falcons in mass, wing morphology, and flight characteristics; (Cade 1987), and Britten et al. (1999) used the same size PTTs on female peregrine falcons with no apparent effects on survival. We suspect that differences in response may be associated with ≥3 factors. First, the neoprene harness used by Britten et al. (1999) on peregrine falcons might have been less intrusive than the Teflon harnesses that we used. Second, the disposition of individual species also may influence how birds respond to markers. Prairie falcons are known for their aggressiveness and high-strung temperament (Cade 1987). Their behavior toward markers may have amplified any adverse effects of markers. We suspect that prairie falcons would have torn through neoprene harness material. Finally, the peregrine falcons marked by Britten (1998) wintered mainly in low elevation coastal areas at more southerly latitudes than the prairie falcons in our study (Steenhof et al. 2005). Adverse effects of PTTs may increase during periods with colder temperatures and shorter day-lengths because of increased energetic demands and the potential for increased heat loss from the portion of the bird's dorsum that contacts the transmitter. Captive radiomarked bald eagles had higher resting metabolic rates than untagged eagles when air temperatures were ≤0° C (Gessaman et al. 1991*a*).

Understanding that radiomarking has a subtle, adverse effect on falcons has implications for interpreting research results about prairie falcons and similar-sized raptors. The ability to generalize data from marked individuals to unmarked animals and populations can be seriously compromised (Murray and Fuller 2000). Our findings suggest that any estimates of survival based on PTT-tagged falcons may be biased downward and should be viewed with caution. Radiomarking probably does not affect where birds go during long-range migrations, but it might affect the timing of those movements. The PTTs probably affected the breeding chronology of some prairie falcons in our study, but we have no evidence that they biased the general nature of long-range movements (Steenhof et al. 2005).

## Recommendations

We recommend that before radiomarking raptors, biologists should consult the literature and colleagues, practice attaching packages to captive birds, and, when possible, conduct a pilot study to test for potential short-term effects on free-flying birds. Our experiences demonstrate that successful attachment methods for radiomarking birds must consider specific bird species characteristics, transmitter package dimensions and mass, attachment materials, and fitting the attachment to each individual. Researchers always should consider alternative attachment techniques. Some methods provide better retention rates and fewer adverse effects than backpack harnesses (Hooge 1991, Phillips et al. 2003), although this is not always the case (Reynolds et al. 2004).

To minimize harness failure and loss of PTTs, we recommend using PTTs with tubes instead of wire loops. Many models of VHF transmitters and PTTs are now offered with tubes front and back, or on the sides. Modified harness designs similar to our epoxy or flex designs with tubes between rear-facing loops on the posterior end also will be effective. Using crimps saves time compared to stitching, but we suggest that researchers avoid using crimps or use them only when they will not promote "cutting" of harness material.

To minimize effects of radiomarking, we recommend using the lightest, most streamlined transmitter packages that will meet the study's requirements for duration and power of transmission. Streamlining packages and minimizing the frontal area can reduce drag and decrease energetic costs (Obrecht et al. 1988). The PTTs we used likely created more drag than lower-profile VHF designs that have been used on prairie falcons.

We recommend additional studies to evaluate how transmitter mass, drag, attachment style, and fit affect flight behavior, energetics, and ultimately survival. Kenward (2001) describes some general procedures to test for effects of radiomarking. Comparing treatment and control birds in captivity can provide insights about physiological effects (Small et al. 2004), and comparing radiomarked and unmarked birds in the wild can provide information about effects on behavior, provisioning, and reproduction (Hamel et al. 2004). Reviews by Murray and Fuller (2000), Withey et al. (2001), and Kenward (2001) contain many examples of how radiomarking effects have been studied.

Finally, techniques for studying animals should not "prejudice" either the welfare of the study subjects or the scientific quality of the results (Kenward et al. 2001). When marking birds, researchers should assess the relative costs and benefits of obtaining important data and minimizing adverse effects on study subjects. Despite the critical need for survival and demographic parameters, certain techniques to obtain complete information can in themselves affect the parameters of interest. Researchers must carefully consider the effects of radiomarking birds, and falcons in particular, to ensure that any benefits gained from the study will outweigh costs to individual animals.

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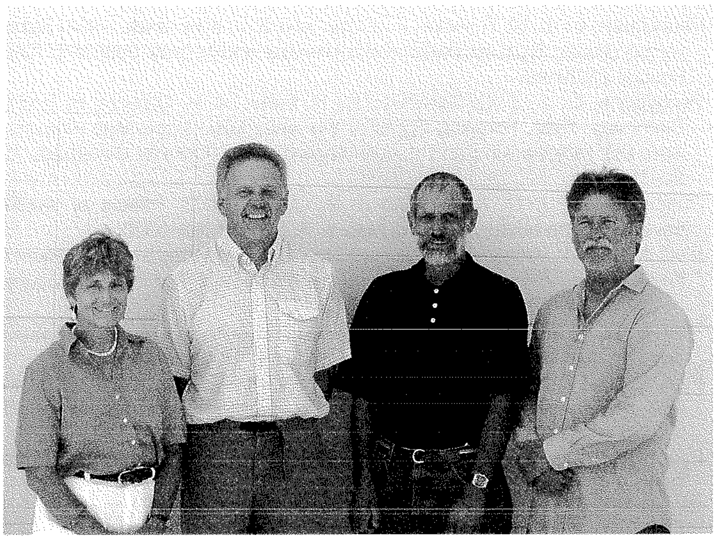

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