Spatial Tracking 14

A. Radio Tracking

Sean S. Walls
Biotrack, 52 Furzebrook Road, Wareham, Dorset BH20 5AX,
United Kingdom

Robert E. Kenward
Centre for Ecology and Hydrology, Winfrith Technology Center,
Dorchester
Dorset DT2 8ZD, United Kingdom

Radio-tracking has proved to be an essential tool for raptor studies. This is because it can record individual behavior systematically, not just at the nest or on a particular wintering area, but throughout the year. Radio-tracking can provide geo-specific data on foraging, roosting, and interactions with conspecifics or different species with little of the bias associated with observer location in other types of studies. Records of all tagged individuals, not merely those found at nests or dead, can be used to gain relatively unbiased estimates of breeding rates, survival and the proportionality of mortality agents. Radio-tracking often is the only way to reveal timing, routes and destinations of long-distance dispersal and migration. Such data can be crucial for assessing the impact of change in land use, checking the success of release programs, quantifying the effects of raptors on game, and investigating many other things of interest in wildlife management. Finally, radio-tracking is often the most practical method of getting data on experimental treatments and to parameterize biological models.

Most radio-tracking of raptors, which started about 40 years ago (Southern 1964), has been based on VHF (Very High Frequency) equipment. The last 20 years, however, have seen the maturing of Ultra High Frequency (UHF) technology that uses satellites, either to track tags directly or through Global Positioning Systems (GPS). Such systems can substitute for or complement VHF tracking.

VHF tags cost about $200 (U.S.), can be small (a 2.5-g tag can transmit for four months, and a 20-g tag can last 2 to 3 years) and can be located accurately (typically to within 10–100 m) by manual tracking from distances of 100 to 5000 m. UHF tags for tracking by satellite cost more than $1,000, and require additional payments for each location (typically $12–24 per day). The automated tracking saves labor costs, but there is relatively low accuracy for non-GPS units (e.g., 200–2000 m) and only about 60 transmission days for the smallest, 15-g tags. With intermittent transmission, these tags are uniquely suited for providing information on migration routes. GPS tags have the advantages of both automatic data collection and high accuracy (e.g., 10 m). Until recently, lightweight GPS tags were short-lived and had to be retrieved for downloading locations, but now a combination of solar-powered GPS units and a satellite link has created 30-g tags that supply accurate locations for longer periods, depending on the frequency of positions. That said VHF tracking remains the most successful technique for detailed tracking of small to medium-sized raptors in a local area over a long period.

Equipment, field methods and analysis techniques have been extensively reviewed (Kenward 2001, Millspaugh and Marzluff 2001, Fuller et al. 2005). Here we assume that there is a precise biological question to answer, that one or more of the references above will be consulted, and that experienced radio-trackers will be contacted for help with field techniques. We therefore concentrate on general-planning guidance.

PLANNING

The planning needed to ensure adequately tagged animals and useful data is detailed in White and Garrott (1990) and subsequent reviews. One additional planning consideration is the scope for collecting ancillary information. For example, when collecting locations to estimate home ranges and habitat use, information also can be collected on activity patterns and interactions. If tags are used to monitor whether individuals breed or die, it also is possible to test whether birds that were more active or had larger home ranges or foraged in particular areas were more likely to die or have reduced fecundity. Such a holistic approach leads to understanding of the mechanisms underlying population processes. To maximize the value from an investment in radio-tagging, it is worth considering from the outset what ancillary questions might be investigated.

Movements

The most important point to remember when collecting radio-tracking data is that the number of individuals tracked is a far more important component of sample size than is the number of locations. Simply put, it is better to get adequate samples of locations from many individuals than to get excessive detail on too few individuals. Unless standardized data-collection protocols from previous studies are available, pilot work is needed to assess how often to record locations and check whether individuals have emigrated or died.

If range areas or habitat use is required, is it for an annual or seasonal estimate or a series of snap-shots? If the former, locations should be recorded one or two times a week, at different times of day to avoid timetabling bias. If the latter, analysis of autocorrelation can help to decide how often locations can be recorded without spatio-temporal redundancy. In all cases, incremental analysis helps to decide how many locations make a practical standard range (Kenward 2001). If great detail is required from range outlines and cores, then more locations will be needed (Robertson et al. 1998). After a pilot study to establish standards, locations collected at the same rate over the same period enable robust tests for differences among individuals, populations, sites or seasons.

Studies of static interactions between individuals are based on overlap of home range cores or other territory estimators. Studies of dynamic interactions are more appropriate for finding if related individuals or individuals from a communal roost tend to aggregate. Such analyses require standardized recording of locations from different individuals in rapid succession, with careful planning so that no data are missing (Kenward 2001).

Radio-tracking has revolutionized the study of dispersal, by showing when, how and in what social or environmental contexts individuals make long distance movements beyond a study area. It is wise to check the locations of individuals often at the start of a project on dispersal to establish when they leave. This can be time-consuming, however tracking can be less frequent after pilot work has established the main dispersal periods. Subsequent reduced tracking for each individual allows more birds to be tracked in the same period, with intensive fieldwork restricted to short dispersal periods. When searching for dispersed raptors, the tracker needs to find topographical high-points and to have conviction in following faint signals, even when they are undetectable for 20 km or more after leaving a hilltop. Ground-based searches are easiest if a vehicle can be fitted with a pneumatic mast to raise an antenna 5–10 m, but the most cost-effective searching for birds lost during dispersal may involve mounting antennas onto aircraft wing-struts and conducting aerial surveys.

Survival, Forensics and Breeding

Researchers need not search often to estimate the survival and breeding rates of large, sedentary raptors whose tags will last for several years. Three checks per year, one each during winter, incubation, and rearing, are sufficient. Pre-breeders need more frequent checks to minimize losses during dispersal periods. More frequent checks also are needed to study causes of death, as carcasses can decompose quickly and be scavenged. That said infrequent checks may enable division of deaths into those (a) caused by humans (e.g., using sensitive analyses for poisons and X-rays for traces of lead in bones) (Cooper 1978), (b) associated with human artefacts (e.g., elevated wires, roads, wells, etc.), or (c) due to natural causes. Mortality sensors can speed checking, especially if all tags can be detected from topographical high points, so that only those indicating a death need to be found. When monitoring reintroductions or rehabilitated birds, checks can highlight solvable problems. In such instances, the more frequent the checks, the quicker the remedial action and the higher the likelihood of success.

In all cases, it is imperative to find all birds possible on each survey. Not doing so risks over-estimating shorter movements, as well as survival if birds are lost because their death has produced an undetectable signal. Survival data will be most robust if tags and searching are highly reliable, and if visual or other markers are used for re-sighting checks on the fate of birds with lost signals, to provide a correction for bias.

Analysis

Data analysis should be planned at the start of a study, and suitable software then used in pilot work to optimize data collection (see Planning). Software not only should display data but also should make it quick and easy to repeat analyses on many animals. The software ought to (1) provide all analyses needed, (2) handle the volume of data required (which may be large for GPS tags), and (3) input data and export results of analyses easily. It also should have adequate user-support, including integral or e-mail help. Good software is updated regularly, and it is worth keeping in touch with manufacturers to monitor developments (Larson 2001). Software defines the most efficient way in which to record data, which can help avoid too much re-processing from notebooks or palm-top computers.

Incremental analysis is essential for planning home-range studies, and autocorrelation analysis is a convenience for snapshot estimates (see Movements). These help in the efficient collection of locations from many individuals and in avoiding redundant and pseudo-replicated data from too few birds to enable robust statistical tests. Density-based home-range estimators such as ellipses and, to a lesser extent, contours, require the least locations, but their smoothing can be less suitable for species inhabiting coarse-grained (e.g., blocky or managed environments) than are linkage-based estimators such as mononuclear and cluster polygons (Kenward 2001). Once there are standard ranges from many birds, it is possible to quantify habitat association by comparing where birds were found with what is available to them. Availability should be individual-based (home range outlines or within a circle around a center of activity) rather than map-based, because map limits are set arbitrarily. Those interested in habitat analysis should investigate both compositional analysis (Aebischer et al. 1993) and distance-based analysis (Conner et al. 2003). For survival analyses, software needs to handle staggered-entry, censored exit, and the inclusion of covariates such as age, sex and habitat (see, for example, White and Garrott 1990 and references in Millspaugh and Marzluff 2001).

EQUIPMENT

Radio-tracking equipment should be specified carefully before they are manufactured because it has to operate on the correct frequency and must be designed specifically, both for the species in question and the aims of the project. Above all, careful consideration should be given to the welfare of each raptor fitted with a tag. Trapping and tagging often is seasonal. As a result most researchers want tags at the same time of year and, consequently, manufacturers become booked at such times for months in advance.

Receiving Equipment

To receive VHF signals a receiver and an antenna are needed, both of which cover the appropriate frequency band to comply with national laws regarding wildlife telemetry. Receivers also must have enough bandwidth to cover all the tags, typically at 10 kHz intervals. The next most important feature is sensitivity (i.e., the ability to pick up weak signals). In addition to sensitivity, weight, waterproofing, and ability to store and scan through pre-set frequencies all are significant practical considerations. Receivers designed specifically for wildlife research cost $500 to $2,500, which is more than similar-looking alternatives intended for other markets, but they will last for many years and are much easier to use. For example, most commercial "scanning" receivers are designed to "modulate" a signal, keeping the same volume even if the signal is changing, which conflicts with the need to use variation in volume for direction finding. When buying a receiver, both tag manufacturers and receiver manufacturers should be consulted.

The antenna that best combines directional accuracy and gain for tracking raptors on the ground is the 3-element Yagi. Flexible elements are less awkward in thick vegetation and when putting them into vehicles. Yagis attached to aircraft should have solid elements. Additional elements can improve reception and directionality, but are cumbersome to use unless attached to a mast. Vehicles need very good suppression or diesel engines to avoid interference with weak signals when on the move.

Signals to indicate behavior and a bird's presence at feeding stations or nests can be logged without mobile tracking if the tags have sensors. The same is true for physiology. It is simpler and less expensive to record from a receiver tuned to one frequency, but for sampling several tagged individuals a programmable logging system is needed. Loggers usually search (via a connected receiver) through the frequencies of several birds, and record pulse characteristics received on each frequency. Although logging can save labor in the long run, neither set-up nor data analyses are simple, and it is important not to underestimate the time required.

Tag Types and Attachment

Tags should transmit on a frequency compatible with the receiving system and about 10 kHz apart from other tags. Tag manufacturers need to know the frequency bands of receivers available to the researcher and the frequencies of any working tags to avoid. Interference in the study area should be checked before specifying frequencies. Around cities there may be many loud extraneous signals that can damage the hearing of researchers in long-term studies.

Table 1 shows the most common tag attachments for raptors. Researchers should talk with experienced trackers and tag manufacturers about the best technique for the species and project. Minimizing the impact of tags on tagged individuals will contribute to robust and, hence, publishable results, as well as to the welfare of the bird (Murray and Fuller 2000). Tags should be comfortable and entirely humane. One should check that manufacturers have sufficient knowledge of biology or species requirements to produce transmitters without sharp edges or surfaces that may interfere with thermoregulation in cold climates. Tag and harness mass near the upper limit allowable should be avoided for each attachment technique. The allowable mass depends upon the mass and wing-loading of the bird as affected by species, sex, and race. The mass that birds can carry safely determines the battery that can be used, and therefore the life (i.e., the time that it will be active) and range of the tag. A tag that pulses faster is easier to track and a stronger pulse will produce a signal that can

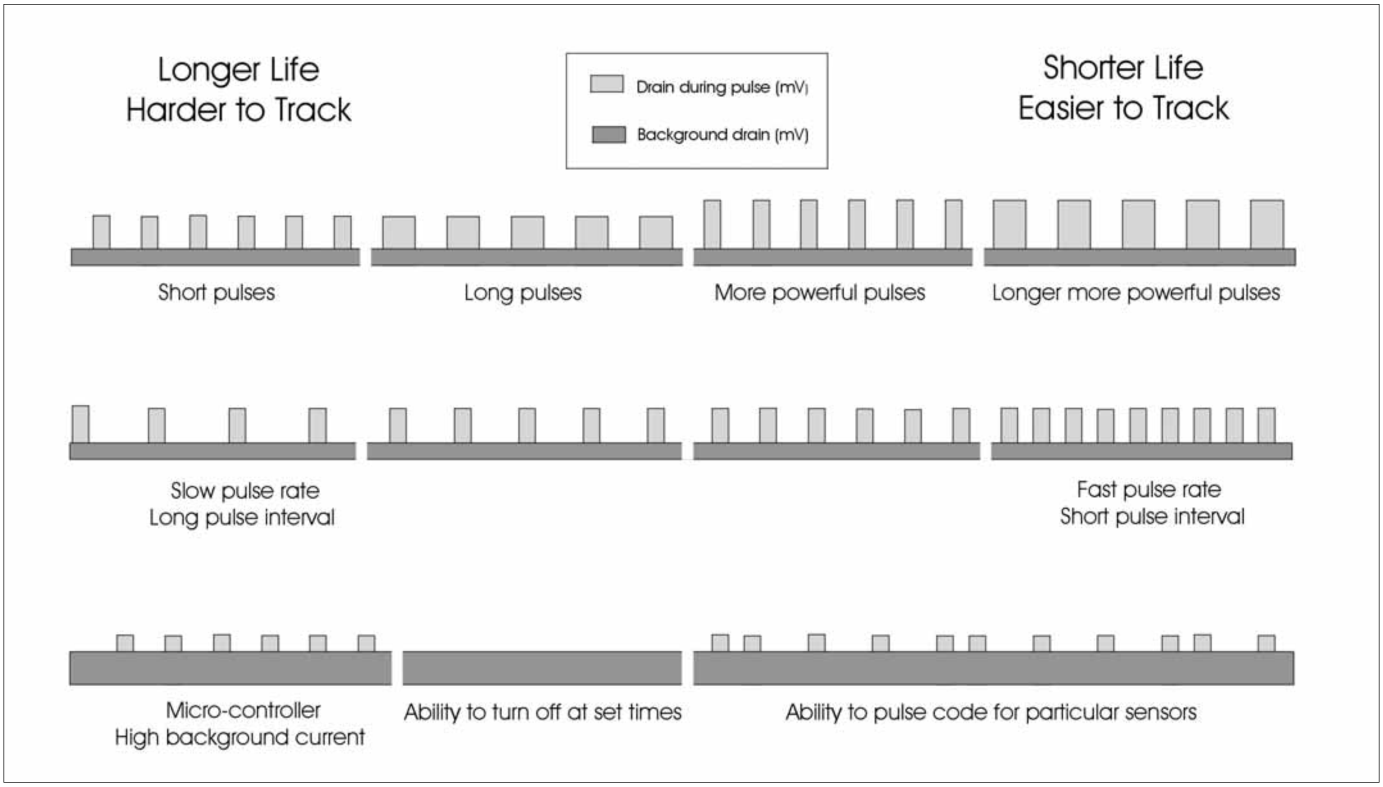

Figure 1. The effects of pulse length, pulse rate and micro-controllers on the life-time and ease of tracking of radio-tags.

Table 1. Techniques for attaching radio-tags to raptors.

Technique	Safety	Considerations
Tailmount	Probably safe if load is less than 2% body mass and attached to two or more feathers.	Feathers must be "hard penned" (i.e., fully grown), therefore one must trap fledglings when out of nest. The tracking stops when the feathers to which the tags are mounted molt.
Backpack	Harness is risky unless carefully fitted.	Can fit to all in the nest just before fledging. Can track for many years and through molts. Tagging at center of lift is best for high-tag mass.
Legmount	No published adverse affects, but might impact hunting.	Tag needs additional protection and a shorter antenna; therefore, life and range for mass of tag are reduced. Can tag all fledglings and track through molt.
Patagial	Only on large raptors with slow wing beat.	Used successfully on condors and large vultures.

be heard from a greater range. However, both requirements draw on battery capacity. To extend the life of the tag, the pulse rate and strength can be reduced to a level at which tracking is more difficult but still practical (Fig. 1). Micro-controllers also can be used to turn tags off during times when there is no need to track, such as during darkness or in winter for migrants. If such controllers are used it is important to ensure that the increased background current of a micro-controller (Fig. 1) does not offset savings from switching off the signal.

Attachment methods must minimize the possibility of entanglement and, where possible, should detach the tag when it stops transmitting. Knowledge of the species is more important than inflexible guidelines or advice from manufacturers. Where possible, potential tag effects should be tested (e.g., by comparison with independent re-sighting data from visual markers on tagged and untagged individuals). If this is not possible, one should consider testing against a low-mass alternative attachment that has little risk of impact, ideally by comparing groups of birds marked in the same season. Doing so is particularly important when using methods that are new or that have known risks. "Tests" also can be based on conservative assumptions. For example, if survival is better than that found with other methods (e.g., banding), effects of tags are probably negligible. Finally, it is worth remembering that males of size-dimorphic raptors may compare best with females if fitted with lighter tags.

LITERATURE CITED

AEBISCHER, A.E., P.A. ROBERTSON AND R.E. KENWARD. 1993. Compositional analysis of habitat use from animal radio-tracking data. *Ecology* 74:1313–1325.

CONNER, L.M., M.D. SMITH AND L.W. BURGER. 2003. A comparison of distance-based and classification-based analyses of habitat use. *Ecology* 84:526–531.

COOPER, J.C. 1978. Veterinary aspects of captive birds of prey. The Steadfast Press, Saul, United Kingdom.

FULLER, M.R, J.J. MILLSPAUGH C.E. CHURCH AND R.E. KENWARD. 2005. Wildlife radiotelemetry. Pages 377–417 in C.E. Braun [ED.], Techniques for wildlife investigations and management, 6th Ed. The Wildlife Society, Bethesda, MD U.S.A.

KENWARD, R.E. 2001. A manual for wildlife radio-tagging. Academic Press, London, United Kingdom.

LARSON, M.A. 2001. A catalog of software to analyze radiotelemetry data. Pages 398–422 in J J. Millspaugh and J.M. Marzluff [EDS.], Radio tracking and animal populations. Academic Press, San Diego, CA U.S.A.

MILLSPAUGH, J.J. AND J.M. MARZLUFF [EDS.]. 2001. Radio tracking and animal populations. Academic Press, San Diego, CA U.S.A.

MURRAY, D.L. AND M.R. FULLER. 2000. Effects of marking on the life history patterns of vertebrates. Pages 15–64 in L. Boitani and T. Fuller [EDS.], Research techniques in ethology and animal ecology. Columbia University Press, New York, NY U.S.A.

ROBERTSON, P.A., N.J. AEBISCHER, R.E. KENWARD, I.K. HANSKI AND N.P. WILLIAMS. 1998. Simulation and jack-knifing assessment of home-range indices based on underlying trajectories. *J. Appl. Ecol.* 35:928–940.

SOUTHERN, W.E. 1964. Additional observations on winter Bald Eagle populations: including remarks on biotelemetry techniques and immature plumages. *Wilson Bull.* 76:222–237.

WHITE, G.C. AND R.A. GARROTT. 1990. Analysis of wildlife radio-tracking data. Academic Press, New York, NY U.S.A.

B. Satellite Tracking

Bernd-U. Meyburg
World Working Group on Birds of Prey,
Wangenheimstrasse 32, D-14193 Berlin, Germany

Mark R. Fuller
U.S. Geological Survey, Forest Rangeland Ecosystem
Science Center, Snake River Field Station, and
Boise State University Raptor Research Center,
970 Lusk Street, Boise, ID 83706 U.S.A.

INTRODUCTION

Satellite telemetry has revolutionized the study of raptor migration and life histories and will continue to do so in the future (Table 1). This is because tracking systems used in satellite telemetry can regularly estimate and record an individual's location worldwide for several years. Satellite telemetry with birds started in the 1980s (Strikwerda et al. 1986). Since then, satellite telemetry has been based on Ultra High Frequency (UHF) technologies such as the Argos system, that includes the Collecte Localisation Satellites (CLS). More recently, transmitters and Global Positioning Systems (GPS) receivers have become small enough to use on birds. In some cases GPS satellite telemetry will soon supersede land-based VHF tracking.

The Argos System

Satellite telemetry for raptor studies has used the Argos system. Individual birds must be able to carry transmitters, called Platform Transmitter Terminals (PTTs), weighing about 5 g or more. The Argos system provides location estimates and sensor data (e.g., battery voltage, activity, temperature, pressure) from PTTs anywhere around the world. The basics of operation are described in the Argos User Manual (www.argosinc .com/system_overview.htm). Additional recent information is available in the *Proceedings of the Argos Animal Tracking Symposium, 24–26 March 2003* (CLS America 2003), which is available on CD from CLS America, 1441 McCormick Drive, Suite 1050, Largo MD 20774.

Location Estimates of Transmitters by Argos

PTTs are located using the Doppler phenomenon. Polar-orbiting satellites carry Argos receivers. As a satellite approaches the PTT, the frequency received will be higher than the nominal transmitted frequency (401.650 MHz), whereas frequencies lower than 401.650 MHz will be received at the satellite as it moves away from the PTT. At the point of inflection of the Doppler curve, that is, when the received and transmitted frequencies are equal, the position of the transmitter will be perpendicular to the satellite ground track. The system estimates two possible PTT locations, which are symmetrical on each side of the satellite ground track. Argos selects one of these as plausible, but biologists should confirm the validity of the location selected by Argos.

Location estimates based on PTT transmissions and the Argos satellite system are assigned to location classes (LC). *"Location accuracy varies with the geometri-*

Table 1. Topics and questions regarding raptors for which data from satellite telemetry have or are expected to provide information. Some references are provided, and more can be found at the U.S. Geological Survey Raptor Information System (http://ris.wr.usgs.gov/). The keywords below and others can be used to find citations to publications listed in the Raptor Information System.

Annual Movements	• Annual movements (Brodeur et al. 1996, Fuller et al. 2003, Meyburg et al. 2004b, Laing et al. 2005, Steenhof et al. 2005) • Differences among years (Alerstam et al. 2006)
Migration	• Mapping routes of migrating raptors (Meyburg et al. 1995a, 1995b; Brodeur et al. 1996, Fuller et al. 1998, Ellis et al. 2001) • Individual variation (Alerstam et al. 2006) • Ecological barriers, leading lines (sea, mountains, deserts) (Meyburg et al. 2002, 2003) • Bottlenecks; do all individuals pass a narrow area, at what time? (Fuller et al. 1998) • Navigation and orientation (Hake et al. 2001, Thorup et al. 2003a, 2003b, 2006b) • Migration period and timing (Schmutz et al. 1996, Kjellen et al. 2001, Meyburg et al. 2004b) • Age and sex differences, breeding status (Ueta et al. 2000, Ueta and Higuchi 2002, Hake et al. 2003, McGrady et al. 2003, Meyburg et al. 2005, 2006, Soutullo et al. 2006b) • Speed and altitude of migration (Hedenström 1997, Kjellen et al. 2001) • Variation throughout migration (Meyburg et al. 2006) • Daily distances, travel rates (Fuller et al. 1998, Meyburg et al. 1998, Soutullo et al. 2006a) • Daily behavior, stopovers (time of starting and stopping), hunting (Meyburg et al. 1998) • Weather conditions (Meyburg et al. 1998, Thorup et al. 2003b, 2006a) • Ecological conditions along migration routes
Winter or Austral Summer	• Geographical situations of wintering grounds (Woodbridge et al. 1995, Martell et al. 2001, Haines et al. 2003, Higuchi et al. 2005, Steenhof et al. 2005) • Discovery of unknown wintering grounds (Meyburg et al. 1998) • Ranges on wintering grounds (McGrady et al. 2002) • Fidelity to the same area in successive years (Fuller et al. 2003)
Nesting Season	• Home range size, habitat use, and territorial behavior (Meyburg et al. 2006) • Dispersal, philopatry (Rafanomezantsoa et al. 2002, Steenhof et al. 2005) • What accounts for later or earlier arrival in spring at the nest site (influence of weather during migration, later or earlier departure to wintering grounds) (Meyburg et al. 2007b) • Pair continuity over a number of years (Meyburg 2007a) • Behavior of nonbreeding adults, floaters (arrival, fidelity to nest site after failed nesting attempt, possible nomadism) (Meyburg 2007b)
Movements during Immature Stage	• Return to breeding area or remain on the "wintering grounds" (Meyburg et al. 2004a) • Ranging behavior (Meyburg et al. 2004a)
Survival, Mortality, Threats	• Human activity (Eastham et al. 2000) • Other causes (Goldstein et al. 1999, Hooper et al. 1999, Henny et al. 2000, Millsap et al. 2004, Steenhof et al. 2006) • Fate of release birds (Rose et al. 1993, Launay and Muller 2003, Dooley et al. 2004)

cal conditions of the satellite passes, the stability of the transmitter oscillator, the number of messages collected and their distribution in the pass. This means in particular that a given transmitter can have locations distributed over several classes during its lifetime. Classes for which accuracy is estimated and their related values: Class 3: better than 150 m on both axes, 250 m radius, Class 2: better than 350 m, 500 m radius, Class 1: better than 1000 m, 1500 m radius, Class 0: over 1000 m, 1500 m radius. These are estimations at one sigma." (www.cls.fr/html/argos/general/faq_en.html).

Argos location methods are based on three major assumptions: (1) transmission frequency is stable during the satellite pass, (2) the PTT is motionless during the satellite pass, and (3) the altitude of the PTT is known. The LC assigned by Argos usually underestimates the error associated with wildlife applications largely because these assumptions often are violated to some extent when the PTT is on an animal (e.g., Britten et al. 1999, Craighead and Smith 2003). Usually, the accuracy given by Argos is better for the latitude than for the longitude. The given accuracy (e.g., 1 km for LC 1) does not mean that all of the calculated locations (and attributed to LC 1) fall within 1 km, but that about one sigma (one standard deviation) of all estimates are in the nominal accuracy range.

It is important to remember that the best two LCs (LC 2 and LC 3) usually are achieved only 10% to 15% of the time from birds. This occurs for numerous reasons, not the least of which is that many wildlife PTTs do not transmit 1 W of power, upon which the Argos system was designed. Power often is programmed to 0.15 to 0.25 W to conserve energy for prolonged PTT operation. Power output in solar-powered PTTs is adjustable (e.g., from 0.1 to 0.5 W). Reduced radiated power can result in fewer location estimates, and consequently fewer data with which Argos can estimate locations most accurately.

Argos routinely provides Standard LCs (LC 3, LC 2, LC 1, see above), but also can provide Auxiliary LCs (LC 0 > 1000 m, LC A and LC B = no estimate of location accuracy, and LC Z = invalid locations). The Auxiliary LCs are especially important because often there are few Standard LCs from wildlife tracking. Furthermore, the best LC classes do not always include the most accurate location estimates. Thus, wildlife researchers, especially those tracking birds, will want as many location estimates as possible from which to select appropriate data.

Location-estimate error from a given project can vary dramatically depending on the speed of the animal and its behavior, including changes in elevation or altitude (www.cls.fr/manual/; see Appendix 2, Argos location), environmental variables (topography, vegetative cover, marine, atmospheric conditions), and data acquisition and analysis options. Users may specify to Argos values for some factors (e.g., PTT velocity, altitude) and discuss options (e.g., use of digital elevation model, multi-satellite service), and Argos will incorporate these in the estimation procedures. Users also should consult with equipment manufacturers to maximize performance (e.g., PTT power, transmission repetition rate) for the circumstances and objectives of the study. Biologists must determine if the Argos system is appropriate for their objectives, especially if they require regular location accuracy of less than 1 km.

Reduced Argos Performance

A significant difference in actual receptions of PTT transmissions exists in the European region and in Asia (Mongolia, China, Japan), and thus can reduce receptions to less than 10% of the expected data. The affected area is about the size of the satellite footprint (5,000 km in diameter) and seems to be centered in the region of southern Italy (Howey 2005). The cause is ambient broadband noise of significant amplitude around the Argos operating frequencies, which causes interference and affects all PTTs, including GPS models. It essentially limits the number of signals that are received by the satellite (Gros and Malardé 2006). We recommend that users contact CLS to discuss their specific requirements and take advantage of ways to optimize Argos system performance.

Argos Data-validation Procedures

Researchers should examine and carefully filter location estimates before selecting those for analyses. Filtering or data validation procedures usually involve establishing criteria based on animal movement capabilities and behavior (e.g., maximum speed, local versus migration movement; Hays et al. 2001) and inspecting the Argos data for time and distance relationships among location estimates. Many LC 0, LC A, and LC B class points might need to be discarded by filtering, but so might some LC 1, LC 2, and even LC 3 class points. Careful screening also might reveal that some LC 0, LC A, and LC B locations are well within the distance that an animal could have traveled during the period between location estimates, and within a direction that is logical.

Raptor researchers must remember that locations from Argos are estimates and that accuracy and precision vary with animal and environmental factors that are largely unknown. In our experience, the proportion of higher quality LCs (LC 2 and LC 3) varies among PTT-marked animals. Therefore, we recommend that each person establish criteria for the study objectives, species, and environment and then apply those criteria when selecting the location estimates to be used in analyses.

Data Transmission through the Argos System

PTTs transmit a coded identification and data from up to 32 sensors. The signals are digitally encoded on a pulse width of ~ 0.36 seconds and a pulse interval usually between 40 and 90 seconds. The transmitting schedule (i.e., the duty cycle) can be programmed for more transmissions during different periods (e.g., seasons), which can prolong the operational life of battery-powered PTTs.

Transmissions from PTTs are received on polar orbiting satellites and are relayed to processing centers in France and the United States. Records of processed data can be distributed to users in a variety of formats, including Internet access to data received about four hours previously. The cost of data acquisition from Argos varies according to the different agreements between countries and Argos. Costs are assessed as a fee for use of each active platform, for hours of use per day, automatic data distribution service (data via email), fax, telnet, data acquired from the Argos website, and monthly compact discs (CD).

GPS Location of Transmitters

The GPS provides location accuracy to within a few meters. A GPS receiver can be integrated with an Argos PTT. A GPS receiver collects transmissions from at least four satellites, enabling computing of position (in three dimensions), velocity, and time. GPS units can be programmed to collect data at pre-set intervals. Data can be logged in memory and downloaded from the unit (usually requiring recapture), or they can be coded in PTT messages and relayed to users via the Argos system. The GPS estimates are transmitted to Argos during the "on time" of a PTT duty cycle.

The GPS receiver requires considerable energy. Thus, there are radio-tag size and longevity constraints that come into play when using battery power for bird studies. Alternatively, solar-powered GPS-PTTs weigh as little as 22 g. These units include sensors and a 12-channel GPS receiver.

Selection of the PTT

A crucial consideration when choosing a unit is how the PTT size, weight, and attachment might affect the bird (Murray and Fuller 2000). The energy requirements for satellite telemetry limit the minimum mass of units to about 5 g. The mass of the transmitter increases the energy the bird must expend for locomotion. Battery mass and surface areas of solar arrays also are limiting factors for unit size.

Deciding whether to use battery- or solar-powered tags must be made early in study planning. Battery-powered PTTs offer generally reliable performance, but have the disadvantage of a rather short operating life, thus long-term studies (more than three years) normally are not possible. Using 30- to 90-g battery-powered PTTs we regularly received locations from 6 to 18 months, depending on radiated power and duty cycle. Solar-powered transmitters can provide locations for up to several years, and the regularity of data is dependent on enough light on the solar array to charge a battery or capacitor with energy for transmission of the radio signal. Solar-powered GPS-PTT tags need more energy than PTTs. Thus, the problem of recharging these tags is even more acute. One must be sure the feathers do not occlude the solar array to the extent that there is insufficient exposure to light for minimal PTT function. Bird habitat use, such as under-canopy or cave nesting, also can affect solar charging.

The decision of whether to use solar or battery-powered PTTs depends not only on the geography and expected movements of the species to be studied, but also on other factors such as budget, lifestyle of the species, aim of the study (long- versus short-term), etc. In 2007 the price of a PTT was about $3000 (U.S.), and that of a GPS-PTT was about $4000. Costs of delivering data (see above) for several years can be as much or even more than the tag price, depending on how tags are programmed and what Argos services are used.

Attachment of Transmitters

Radio tags can be mounted on tail-feathers, legs, and wings, but in most studies they are attached to the bird's back using a harness (Fuller et al. 2005). These "backpacks" have the advantage of being fixed near the center of lift which is best for high tag mass. Tags can be fitted to nestlings just before fledging and can be tracked for several years. Most researchers use Teflon® ribbon as harness material, but we found that some raptors (e.g. Asian Imperial Eagles [*Aquila heliaca*] and Lesser Spotted Eagles [*A. pomarina*], Prairie Falcons [*Falco mexicanus*]) remove tags by pulling and cutting through the Teflon® strips with their beaks (Steenhof et al. 2006). The potential complication of feathers over the solar panels on backpacks might be overcome by incorporating a feather guard (Snyder et al. 1989) or thick neoprene rubber on the bottom of the transmitter to elevate the solar array. These modifications might create additional aerodynamic drag and thus, energy needed for flight.

What Causes Termination of Transmissions?

Manufacturers can program a unit to stop transmitting, but most researchers probably would like to receive transmissions for as long as possible. Battery-powered units transmit information about battery voltage so that one can predict depletion of the battery energy. Often however, failure to receive transmissions occurs earlier than expected, raising a question as to what has happened. The causes of failure to receive data are sometimes difficult to determine.

Juvenile and immature birds often die from "natural causes," or perish from persecution. Adults also are subject to heavy persecution in many parts of the world or are killed by electrocution, collisions, etc. Nevertheless, based on observing the bird, recapturing it, or finding it dead much later, we confirmed that several solar-powered PTTs had failed while the birds were alive. In some cases we, or the manufacturer, were unable to determine a reason for the failure. Study planning should account for death of radio-marked birds and the failure of some transmitters.

Our record for long-term tracking is an adult female Greater Spotted Eagle (*A. clanga*). The bird was fitted with a PTT in July 1999 that was still transmitting data in August of 2007. An adult male Lesser Spotted Eagle was tracked as far as Israel on its way back to the breeding grounds almost 6 years after having been marked. When it arrived one month later in Germany we observed the bird with its PTT without an antenna. An Osprey also lost or removed the antenna after only a few months. It is much easier to find the reasons for tag failure in breeding adults that return to their nest site year after year. There are methods for locating PTTs that are transmitting from a dead bird or detached from the bird (Howey 2002, Bates et al. 2003, Peske and McGrady 2005). Finding the PTT can provide valuable biological information and be cost-effective because most units can be refurbished for about $300 to $500, and used again.

Tracking Options

Finally, satellite telemetry is one of many options for marking raptors. Before deciding to use telemetry we encourage persons to consider carefully (1) their objectives and (2) the possible effects of marking on the birds and their implications for the results. The literature provides many examples of studies in which satellite telemetry has provided valuable information (Table 1). Consultation with manufacturers about options can be very useful, and is especially important for programming the function of transmitters and receivers to maximize performance.

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LITERATURE CITED

Alerstam, T., M. Hake and N. Kjellén. 2006. Temporal and spatial patterns of repeated migratory journeys by Ospreys. *Anim. Behav.* 71:555–566.

Bates, K., K. Steenhof and M.R. Fuller. 2003. Recommendations for finding PTTs on the ground without VHF telemetry. Proceedings of the Argos Animal Tracking Symposium, 24–26 March 2003, Annapolis, Maryland. Available on a CD from Service Argos, Inc., Largo MD U.S.A.

Britten, M.W., P. L. Kennedy, and S. Ambrose. 1999. Performance and accuracy evaluation of small satellite transmitters. *J. Wildl. Manage.* 63:1349–1358.

Brodeur, S., R. Décarie, D.M. Bird and M.R. Fuller. 1996. Complete migration cycle of Golden Eagles breeding in northern Quebec. *Condor* 98:293–299.

CLS America. 2003. Proceedings of the Argos Animal Tracking Symposium, 24–26 March 2003, Annapolis, Maryland. CLS America, Largo, MD U.S.A.

Craighead, D. and R. Smith. 2003. The implications of PTT location accuracy on a study of Red-tailed Hawks. Proceedings of the Argos Animal Tracking Symposium, 24–26 March 2003, Annapolis, Maryland. Available on a CD from Service Argos, Inc., Largo MD U.S.A.

Dooley, J.A., P.B. Sharpe and D.K. Garcelon. 2004. Abstract: Monitoring movements and foraging of Bald Eagles (*Haliaeetus leucocephalus*) reintroduced on the northern Channel Islands, California using solar Argos/GPS PTTs and VHF telemetry. Pages 26–27 in Program and abstracts: Raptor Research Foundation-California Hawking Club annual meeting, Bakersfield, California, 10–13 November 2004. Raptor Research Foundation, Clovis, CA U.S.A.

Eastham, C.P., J.L. Quinn and N.C. Fox. 2000. Saker *Falco cherrug* and Peregrine *Falco peregrinus* falcons in Asia; determining migration routes and trapping pressure. Pages 247–258 in R.D. Chancellor and B.-U. Meyburg [Eds.], Raptors at risk. World Working Group on Birds of Prey and Owls, Berlin, Germany and Hancock House, London, United Kingdom.

Ellis, D.H., S.L. Moon and J.W. Robinson. 2001. Annual movements of a Steppe Eagle (*Aquila nipalensis*) summering in Mongolia and wintering in Tibet. *Bombay Nat. Hist. Soc.* 98:335–340.

Fuller, M.R., W.S. Seegar and L.S. Schueck. 1998. Routes and travel rates of migrating Peregrine Falcons *Falco peregrinus* and Swainson's Hawks *Buteo swainsoni* in the western hemisphere. *J. Avian Biol*. 29:433–440.

———, D. Holt and L.S. Schueck. 2003. Snowy Owl movements: variation on the migration theme. Pages 359–366 in P. Berthold, E. Gwinner, and E. Sonnenschein [Eds.], Avian migration. Springer-Verlag, Berlin, Germany.

———, J.J. Millspaugh, K.E. Church and R.E. Kenward. 2005. Wildlife radio telemetry. Pages 377–417 in C.E. Braun [Ed.], Techniques for wildlife investigations and management, 6th Ed. The Wildlife Society, Bethesda, MD U.S.A.

Goldstein, M.I., T.E. Lacher, Jr., B. Woodbridge, M.J. Bechard, S.B. Canavelli, M.E. Zaccagnini, G.P. Cobb, E.J. Scollon, R. Tribolet and M.J. Cooper. 1999. Monocrotophos induced mass mortality of Swainson's Hawks in Argentina, 1995–96. *Ecotoxicology* 8:201–214.

Gros, P. and J.-P. Malardé. 2006. Argos performance in Europe. *Tracker News* 7:8.

Haines, A.M., M.J. McGrady, M.S. Martell, B.J. Dayton, M.B. Henke and W.S. Seegar. 2003. Migration routes and wintering locations of Broad-winged Hawks tracked by satellite telemetry. *Wilson Bull.* 115:166–169.

Hake, M., N. Kjellén and T. Alerstam. 2001. Satellite tracking of Swedish Ospreys *Pandion haliaetus*: autumn migration routes and orientation. *J. Avian Biol*. 32:47–56.

———, N. Kjellén and T. Alerstam. 2003. Age-dependent migration strategy in Honey Buzzards *Pernis apivorus* tracked by satellite. *Oikos* 103:385–396.

Hays, G.C., S. Akesson, B.J. Godley, P. Luschi and P. Santidrian. 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Anim. Behav.* 61:1035–1040.

Hedenström, A. 1997. Predicted and observed migration speed in Lesser Spotted Eagle *Aquila pomarina*. *Ardea* 85:29–36.

Henny, C.J., W.S. Seegar, M.A. Yates, T.L. Maechetle, S.A. Ganusevich and M.R. Fuller. 2000. Contaminants and wintering areas of Peregrine Falcons, *Falco peregrinus*, from the Kola Peninsula, Russia. Pages 871–878 in R.D. Chancellor and B.-U. Meyburg [Eds.], Raptors at risk. World Working Group on Birds of Prey and Owls, Berlin, Germany and Hancock House, London, United Kingdom.

Higuchi, H., H. Shiu, H. Nakamura, A. Uematsu, K. Kuno, M. Saeki, M. Hotta, K. Tokita, E. Moriya, E. Morishita and M. Tamura. 2005. Migration of Honey-buzzards *Pernis apivorus* based on satellite tracking. *Ornithol. Science* 4:109–115.

Hooper, M.J., P. Mineau, M.E. Zaccagnini, G.W. Winegrad and B. Woodbridge. 1999. Monocrotophos and the Swainson's Hawk. *Pesticide Outlook* 10: 97–102.

Howey, P. 2002. Useful tips - finding a lost PTT (part 2). Microwave Telemetry, Inc., Newsletter Winter 2000:4. (http://microwave telemetry.com/newsletters.winter00_page4.pdf) (last accessed 7/6/2006).

———. 2005. Argos performance in Europe. *Tracker News* 6:8.

Kjellén, N., M. Hake and T. Alerstam. 2001. Timing and speed of migration in male, female and juvenile Ospreys *Pandion haliaetus* between Sweden and Africa as revealed by field observations, radar and satellite tracking. *J. Avian Biol.* 32:57–67.

Laing, D.K., D.M. Bird and T.E. Chubbs. 2005. First complete migration cycles for juvenile Bald Eagles (*Haliaeetus leucocephalus*) from Labrador. *J. Raptor Res.* 39:11–18.

Launay, F. and M.G. Muller. 2003. Falcon release and migration. *Falco* 22:22–23.

Martell, M.S., C.J. Henny, P.E. Nye and M.J. Solensky. 2001. Fall migration routes, timing, and wintering sites of North American Ospreys as determined by satellite telemetry. *Condor* 103:715–724.

McGrady, M.J., T.L. Maechtle, J.J. Vargas, W.S. Seegar and M.C. Porras Peña. 2002. Migration and ranging of Peregrine Falcons wintering on the Gulf of Mexico coast, Tamaulipas, Mexico. *Condor* 104:39–48.

———, M. Ueta, E.R. Potapov, I. Utekhina, V. Masterov, A. Ladyguine, V. Zykov, J. Cibor, M. Fuller and W.S. Seegar. 2003. Movements by juvenile and immature Steller's Sea Eagles *Haliaeetus pelagicus* tracked by satellite. *Ibis* 145:318–328.

Meyburg, B.-U., W. Scheller and C. Meyburg. 1995a. Migration and wintering of the Lesser Spotted Eagle *Aquila pomarina*: a study by means of satellite telemetry. *J. Ornithol.* 136:401–422.

———, J.M. Mendelson, D.H. Ellis, D.G. Smith, C. Meyburg and A.C. Kemp. 1995b. Year-round movements of a Wahlberg's Eagle *Aquila wahlbergi* tracked by satellite. *Ostrich* 66:135–140.

———, C. Meyburg and J.-C. Barbraud. 1998. Migration strategies of an adult Short-toed Eagle *Circaetus gallicus* tracked by satellite. *Alauda* 66:39–48.

———, J. Matthes and C. Meyburg. 2002. Satellite-tracked Lesser Spotted Eagle avoids crossing water at the Gulf of Suez. *Br. Birds* 95:372–376.

———, P. Paillat and C. Meyburg. 2003. Migration routes of Steppe Eagles between Asia and Africa: a study by means of satellite telemetry. *Condor* 105:219–227.

———, M. Gallardo, C. Meyburg and E. Dimitrova. 2004a. Migrations and sojourn in Africa of Egyptian Vultures (*Neophron percnopterus*) tracked by satellite. *J. Ornithol.* 145:273–280.

———, C. Meyburg, T. Belka, O. Sreibr and J. Vrana. 2004b. Migration, wintering and breeding of a Lesser Spotted Eagle (*Aquila pomarina*) from Slovakia tracked by satellite. *J. Ornithol*. 145:1–7.

———, C. Meyburg, T. Mizera, G. Maciorowski and J. Kowalski. 2005. Family break up, departure, and autumn migration in Europe of a family of Greater Spotted Eagles (*Aquila clanga*) as reported by satellite telemetry. *J. Raptor Res.* 39:462–466.

———, C. Meyburg, J. Matthes and H. Matthes. 2006. GPS satellite tracking of Lesser Spotted Eagles (*Aquila pomarina*): home range and territorial behaviour. *Vogelwelt* 127:127–144.

———, C. Meyburg and F. Franck-Neumann. 2007a. Why do female Lesser Spotted Eagles (*Aquila pomarina*) visit strange nests remote from their own? *J. Ornithol.* 148:157–166.

———, C. Meyburg, J. Matthes and H. Matthes. 2007b. Spring migration, late arrival, temporary mate change and breeding success in the Lesser Spotted Eagle *Aquila pomarina*. *Vogelwelt* 128:21–31.

Millsap, B., T. Breen, E. McConnell, T. Steffer, L. Phillips, N. Douglass and S. Taylor. 2004. Comparative fecundity and survival of Bald Eagles fledged from suburban and rural natal areas in Florida. *J. Wildl. Manage.* 68:1018–1031.

Murray, D.L. and M.R. Fuller. 2000. Effects of marking on the life history patterns of vertebrates. Pages 15–64 in L. Boitani and T. Fuller [Eds.], Research techniques in ethology and animal ecology. Columbia University Press, New York, NY U.S.A.

Peske, L. and M.J. McGrady. 2005. From the field: a system for locating satellite-received transmitters (PTTs) in the field. *Wildl. Soc. Bull.* 33:307–312.

Rafanomezantsoa, S., R.T. Watson and R. Thorstrom. 2002. Juvenile dispersal of Madagascar Fish-eagles tracked by satellite telemetry. *J. Raptor Res.* 36:309–314.

Rose, E.F., W. English and A. Hamilton. 1993. Abstract: Paired use of satellite and VHF telemetry on rehabilitated Bald Eagles. *J. Raptor Res.* 27:92.

Schmutz, J.K., C.S. Houston and G.L. Holroyd. 1996. Southward migration of Swainson's Hawks: over 10,000 km in 54 days. *Blue Jay* 54:70–76.

Snyder, N.F.R., S.R. Beissinger and M.R. Fuller. 1989. Solar radio transmitters on Snail Kites in Florida. *J. Field Ornithol.* 60:171–177.

Soutullo, A., V. Urios and M. Ferrer. 2006a. How far away in an hour? Daily movements of juvenile Golden Eagles (*Aquila chrysaetos*) tracked with satellite telemetry. *J. Ornithol.* 147:69–72.

———, V. Urios, M. Ferrer and S.G. Peñarrubia. 2006b. Post-fledging behaviour in Golden Eagles *Aquila chrysaetos*: onset of juvenile dispersal and progressive distancing from the nest. *Ibis* 148:307–312.

Steenhof, K., M.R. Fuller, M.N. Kochert and K.K. Bates. 2005. Long-range movements and breeding dispersal of Prairie Falcons from southwest Idaho. *Condor* 107:481–496.

———, K.K. Bates, M.R. Fuller, M.N. Kochert, J.O. McKinley and P.M. Lukacs. 2006. Effects of radio marking on Prairie Falcons: attachment failures provide insights about survival. *Wildl. Soc. Bull.* 34:116–126.

Strikwerda, T.E., M.R. Fuller, W.S. Seegar, P.W. Howey and H.D. Black. 1986. Bird born satellite transmitter and location program. *Johns Hopkins APL Tech. Digest* 7:203–208.

Thorup, K., T. Alerstam, M. Hake and N. Kjellén. 2003a. Can vector summation describe the orientation system of juvenile Ospreys and Honey Buzzards? An analysis of ring recoveries and satellite tracking. *Oikos* 103:350–359.

———, T. Alerstam, M. Hake and N. Kjellén. 2003b. Bird orientation: compensation for wind drift in migrating raptors is age dependent. *Proc. Royal Soc. London, B* 270:S8–S11.

———, T. Alerstam, M. Hake and N. Kjellén. 2006a. Traveling or stopping of migrating birds in relation to wind: an illustration for the Osprey. *Behav. Ecol* 17:497–502.

———, M. Fuller, T. Alerstam, M. Hake, N. Kjellén and R. Strandberg. 2006b. Do migratory flight paths of raptors follow constant geographical or geomagnetic courses? *Anim. Behav.* 72:875–880.

Ueta, M. and H. Higuchi. 2002. Difference in migration pattern between adult and immature birds using satellites. *Auk* 119:832–835.

———, F. Sato, J. Nakagawa and N. Mita. 2000. Migration routes and differences of migration schedule between adult and young Steller's Sea Eagles *Haliaeetus pelagicus*. *Ibis* 142:35–39.

Woodbridge, B., K.K. Finley and S.T. Seager. 1995. An investigation of the Swainson's Hawk in Argentina. *J. Raptor Res.* 29: 202–204.

C. Stable Isotopes and Trace Elements

KEITH A. HOBSON
Environment Canada, 11 Innovation Blvd.,
Saskatoon, Saskatchewan, S7N 3H5, Canada

INTRODUCTION

Raptors are relatively large migratory birds and as such are amenable to being equipped with both radio and satellite transmitters. Radio and satellite tracking provide the very best information on individual movements and making connections between breeding, wintering, and stopover sites (Webster et al. 2001). However, in addition to expense and limitations of battery life, like all mark-and-recapture techniques where "recapture" is a locational fix, tracking is limited by the initial marked sample, which is not necessarily representative of the population of interest. This also applies to the use of leg bands and other external markers. Such concerns can be overcome to some degree by the use of endogenous markers, which, because initial marking is not required, rely only on the recaptured population (Rubsenstein and Hobson 2004). Endogenous markers of interest include naturally occurring stable-isotope and trace-element profiles as well as genetic and other molecular markers. Here, I focus on the use of stable isotopes and trace elements to track spatial movements of raptors. Interestingly, raptors have figured prominently in the development of these techniques.

STABLE ISOTOPES

Isotopes are forms of an element that differ only in atomic mass due to a differential number of neutrons in the nucleus. Typically, they have identical chemical properties, but their mass difference confers different kinetic properties on molecules that include them. Stable-isotope abundance of any element is usually expressed as a ratio of the more rare, heavy form to that of the more common, lighter form. Stable-isotope ratios of light elements of greatest interest to ecological applications are those of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), sulfur ($^{34}S/^{32}S$), hydrogen ($^{2}H/^{1}H$) and oxygen ($^{18}O/^{16}O$). Isotopes of heavier elements such as strontium (^{87}Sr) and lead (^{210}Pb) also are particularly useful but require more involved analytical procedures. Stable-isotope ratios of the light elements are measured with isotope-ratio mass spectrometry (IRMS) and are expressed in abundance relative to international standards in delta (δ) notation, and are reported as parts-per-thousand deviation from those standards. This is an extremely well-established field in analytical chemistry and highly accurate measurements are routinely achieved in most laboratories. Fortunately, various biogeochemical processes in nature result in materials that differ in their stable-isotope abundance and these differences can be exploited to infer origins of organisms that come into equilibrium with local food webs.

The basic premise of all stable-isotope applications to animal studies is that isotopic abundance in diet is related directly to isotopic abundance in the consumer. In many cases, consumer tissues differ in their isotopic composition relative to diet by a relatively constant discrimination factor. This simple relationship brings up two important principles in applying stable isotope measurements to food webs in general and to migratory tracking in particular. First, the diet-tissue isotopic discrimination factor can be tissue-specific and these specifications may need to be established experimentally

(Hobson and Clark 1992a). Second, for metabolically active tissues, this relationship is not static but is based on equilibrium time constants related to elemental turnover rates in the tissue (Hobson and Clark 1992b). Thus, choice of tissue is of fundamental importance when deciphering isotopic information. For example, Duxbury et al. (2003) provided experimental evidence that juvenal down or juvenal plumage, but not natal down, of nestling Peregrine Falcons (*Falco peregrinus*) accurately reflects their local diet. Three key components must be considered when inferring origins of migrant birds: (1) the isotopic signature of the source and how this varies spatially, temporally, or both, (2) the isotopic discrimination associated with the tissue being used to reflect that source, and (3) the isotopic turnover rate of that tissue.

CHOICE OF TISSUE

Tissues for isotopic measurement can be metabolically active or inactive. Metabolically active tissues provide a "moving window" of past origins and the width of that window depends on the elemental turnover rate associated with that tissue. For fast-metabolic-rate tissues like liver or blood plasma, the window is in the order of a week (Hobson and Clark 1992a). Muscle and whole blood have slower turnover rates and information can be derived for a period of the order of up to six weeks. Bone collagen has an exceptionally slow turnover rate and so can provide dietary information averaged over years. The problem facing researchers who wish to use metabolically active tissues to infer origins of migratory birds is that precise metabolic turnover rates for wild, migrating birds essentially are unknown (Hobson 2005a).

Metabolically inactive tissues including keratin of feathers and talons present information on origins typical of the period of growth (assuming no endogenous reserves are used in their formation). In cases involving raptors whose molt schedules are well known, the isotopic measurement of a single feather can be a powerful tool in determining migratory connectivity. The disadvantage to using feathers is that if they are lost they can be replaced at locations other than those where they first grew. In addition, we still do not understand molt schedules of several species well enough, and it is possible, although difficult to corroborate, that failed breeders might leave the breeding grounds early and molt en route. The good news is that stable-isotope methods can be used to determine molt patterns as well as breeding origins. Wassenaar and Hobson (2001) confirmed that adult Swainson's Thrushes (*Catharus ustulatus*) molted flight feathers south of their actual breeding grounds. Talons of birds arriving in the spring may give good isotopic information on environments occupied on the wintering grounds because they grow relatively slowly (Bearhop et al. 2003, Mazerolle and Hobson 2005) and so will represent diet on the order of the previous weeks to months.

ISOTOPIC LANDSCAPES

Fortunately, several isotopic patterns known in nature can be exploited to infer origins of migratory birds and other organisms. These patterns vary according to individual isotopes, and how they behave in various biogeochemical reactions. For our purposes, these patterns can be grouped into dietary signals that are related to local biome or climatic conditions and "isoscapes," or to those related to larger-scale isotopic patterns based on underlying geology or continental patterns in precipitation.

The most studied and well known stable isotopic pattern in nature is that of stable carbon isotope signatures associated with photosynthetic pathways. This process is based on fundamentally different molecular fixation of carbon during photosynthesis that results either in a three- (C-3) or four- (C-4) carbon molecular substrate and corresponding different behavior of ^{13}C and ^{12}C in each case. Plants with a C-3 photosynthetic pathway have tissues that are more depleted, or lower in their $\delta^{13}C$ values, than those with a C-4 or CAM pathway. C-3 plants also show remarkable variation in $\delta^{13}C$ signature based on mechanisms associated with water-use efficiency (reviewed by Lajtha and Marshall 1994). The net result is that C-3 plants generally become more enriched in ^{13}C under more xeric conditions than under cooler or more mesic conditions (e.g., Marra et al. 1998). Hobson and Wassenaar (2001) demonstrated that wintering Loggerhead Shrikes (*Lanius ludovicianus*) in the southern United States and northern Mexico originated from areas with food webs ranging from pure C-3 to pure C-4 photosynthetic composition. However, because we do not have useful spatial resolution of the distribution of C-3 versus C-4 biomes throughout much of the range for most species, such information will be quite limited in inferring origins of birds such as shrikes (but see Still et al. 2003). CAM plants are relatively rare in North America but are well represented in dry areas by cacti. Wolf and Martinez del Rio (2000) and Wolf et al. (2002) have examined the dependence of White-winged Doves (*Zenaida asiatica*) and Mourning Doves (*Z. macroura*) on saguaro cactus (*Carnegiea gigantea*) and are currently using this as a marker for populations of doves originating in the American Southwest.

The stable isotopes of several elements including C, N, H, O, S, differ in marine versus terrestrial and freshwater food webs due to isotopic differences in inorganic nutrients available to primary production and, as a result, marine inputs to raptor diets can be traced isotopically. Lott and Smith (2006) were able to correct deuterium isotope (δD) values of feathers from nine different raptor species (see below) to account for links with marine food webs using δ^{34}S measurements. Certainly, dietary reconstructions based on raptor ingestion of seabirds or marine fish, or scavenging on marine-mammal carcasses should be relatively routine using the isotope approach, although there are cases where some terrestrial food webs overlap isotopically with marine food webs (e.g., terrestrial evaporative deposits can have similar δ^{34}S values as marine systems).

Stable-nitrogen isotope ratios (δ^{15}N) are extremely useful as indicators of trophic position (Kelly 2000). However, within terrestrial systems, land-use practices can influence stable-isotope abundance in food webs. Most notably, agricultural practices can alter δ^{15}N values in both upland and wetland systems. Soil nitrogen can vary isotopically within and among sites, but two processes can result in agricultural soils being more enriched in ^{15}N than temperate forest soils. These are the presence of animal-based fertilizers and the greater volatilization of isotopically lighter nitrogenous compounds such as ammonia from agricultural soils as a result of tillage and their lower acidity (Nadelhoffer and Fry 1994).

Deuterium

Without question, the single isotope that has shown the greatest potential for helping to elucidate origins of migratory birds in North America is deuterium. Its usefulness is based on the fact that stable-hydrogen isotope ratios in precipitation show a continent-wide pattern with a general gradient from enriched values in the southeast to more depleted values in the northwest (Fig. 1). This phenomenon is due to the fact that evaporation and precipitation are processes that can discriminate against or favor heavier, deuterium-containing water molecules and are, in turn, influenced by temperature, relative humidity, distance from oceans and elevation (see Bowen et al. 2005). Following the first avian applications by Chamberlain et al. (1997) and Hobson and Wassenaar (1997), several studies have confirmed the strong association between growing-season average δD values in precipitation and those in feathers of birds grown at those locations (Bowen et al. 2005). Meehan et al. (2001) conducted the first deuterium study on raptors using feathers of Cooper's Hawk (*Accipiter cooperii*) and confirmed the continent-wide pattern could be used to estimate natal origins of birds migrating through Florida. The growing-season deuterium precipitation map was recently constructed for Europe (Hobson 2003). Duxbury (2004) conducted an isotopic baseline study on feathers of Burrowing Owls (*Athene cunicularia*) and Peregrine Falcons with the intent of ultimately tracking migrants to natal or molt origin. However, the most comprehensive feather deuterium map for North American raptors was constructed by Lott and Smith (2006). These authors measured feather δD values from museum specimens of raptors originating from sites across North America and provide a convenient digital isotopic surface amenable to geographic information systems (GIS) queries.

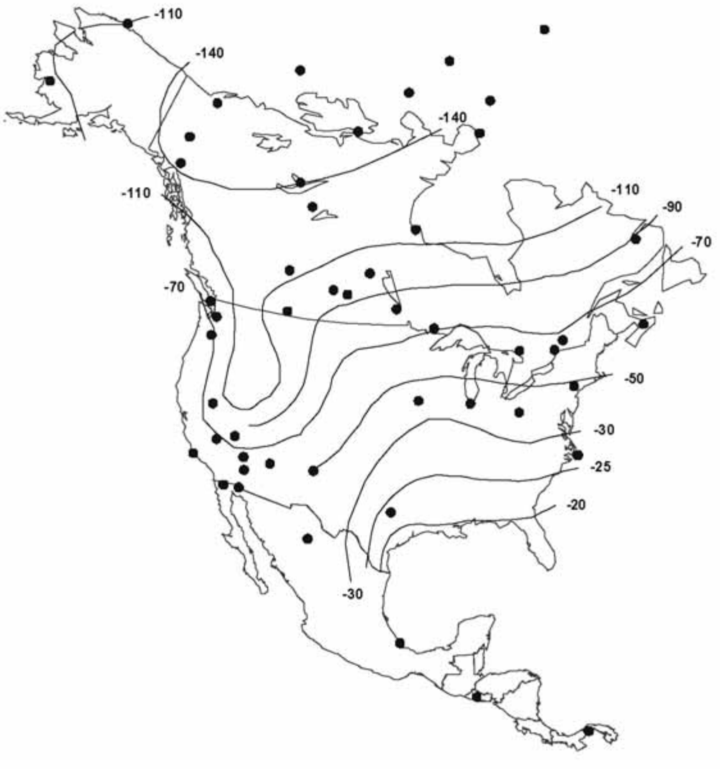

Figure 1. Pattern of growing-season average deuterium (‰) in rainfall for North America (after Hobson and Wassenaar 1997). Dots indicate long-term sampling stations. Note that feathers will be depleted relative to these contours due to isotopic discrimination.

A common question arising from the application of growing-season average precipitation contour maps for deuterium, based on the International Atomic Energy Agency (IAEA) database, is the robustness of the kriged (i.e., geographic) relationships. In any given year, how much variation in these patterns might be expected? This is not an easy question to answer because the geographical and temporal coverage in sampling sites for this database are variable. The patterns depicted by Hobson and Wassenaar (1997) and Hobson (2003) are based on about a 35-year IAEA record. However, several considerations increase our confidence in these relationships, at least qualitatively. The first is that short-term variation in precipitation signals will, to some extent, be smoothed out by the longer-term averaging of the growing season itself. Thus, in many areas, each feather measurement will, in effect, represent the average of many rainfall events and so will tend to smooth short-term fluctuations. This will not necessarily be the case in areas or times of lower precipitation or in areas that are subject to single or synoptic rainfall events. Nor will it apply to areas where groundwater or reservoirs form a significant source of hydrogen for local food webs. For a group of European sites where long-term data are available, several showed extremely small inter-year variation in average growing-season δD in precipitation, of the order of measurement error, whereas others, notably coastal sites, showed variation at least three to four times as high (Hobson 2005b). However, despite numerous potential sources of error, it is remarkable how well long-term average values of δD in precipitation are correlated with δD values of feathers grown in any given year, a relationship now demonstrated independently by several research groups. How well this relationship holds in future given climate change scenarios, of course, is unknown and will be an important area of additional research (Hobson 2005a).

Alternatives to using the long-term average contour maps include the direct measurement of isotopic patterns of interest for a particular year of interest (e.g., Hobson et al. 1999), and the creation of feather isotopic basemaps for each species or taxonomic group of interest (Duxbury 2004, Lott and Smith 2006). Meehan et al. (2003) determined that feathers grown by nestling Cooper's Hawks were more depleted in deuterium than those of attending adults grown at the same site. There are a number of possible explanations for this result including the possibility of dietary differences between age groups. Another possibility is that adult breeding raptors become relatively enriched in deuterium due to evaporative cooling throughout the extended nestling period (Meehan et al. 2003). Experiments with captive birds are needed to confirm if special consideration needs to be given to raptors when associating tissue δD values to origin.

Recently, Smith and Dufty (2005) examined feather δD values of adult and nestling Northern Goshawk (*A. gentilis*) feathers representing breeding territories across western North America. As expected, these authors found a general depletion in feather isotope δD values with latitude and distance from the coast. As with Meehan et al. (2003), these authors found that nestlings had lower δD values than adults at the same location. After controlling for location and local temperature, they also found considerable inter-individual variation in feather isotope profiles related to sex. Adult females had considerably higher δD values than males. Support was found for the hypothesis that such patterns arise from differences in evaporative cooling in those raptors that "work" during feather growth while provisioning young. These authors recommend that future studies using feathers to delineate origin should consider different isotopic basemaps for adults and juveniles.

Trace Elements

Patterns of trace elements in feathers ultimately are derived from diet, which, in turn, is influenced strongly by surficial geology, and as such are expected to provide spatial information. The use of trace elements was a comparatively early approach to using endogenous signatures in avian-migration tracking (early reviews by Means and Peterle 1982, Kelsall 1984). The method has great intuitive appeal because it is possible to measure relative abundance of numerous elements in feathers and so the chances of acquiring a unique signature for an individual or population are increased. Recent developments in analytical techniques allow the routine measurement of concentrations in feathers of numerous elements, including As, Cd, Mg, Mn, Mo, Se, Sr, Co, Fe, Zn, Li, P, Ti, V, Ag, Cr, Ba, Hg, Pb, S, Ni, and Cu. Despite the potential of this technique, the field was largely abandoned a decade ago owing to several concerns over its reliability. Some of these criticisms have since been addressed through improvement in sample-preparation and measurement techniques that made elemental measurements much more reliable, but the stigma remains.

The first attempts to use trace-element analysis to infer geographical origin were in waterfowl (e.g., Devine and Peterle 1968, Kelsall and Calaprice 1972, Kelsall et al. 1975, Hanson and Jones 1976, Kelsall and Burton 1979). These studies met with variable success but were followed by an excellent study by Parrish et al. (1983), which clearly distinguished three natal populations of Peregrine Falcons by measuring as few as five trace elements in feathers (Fig. 2; see also Barlow and Bortolotti 1988). However, several studies presented evidence of considerable intrapopulation variation in feather elemental profiles related to age (Hanson and Jones 1976) and sex (Hanson and Jones 1974, Kelsall and Burton 1979, Bortolotti and Barlow 1988). The causes of such differences are poorly understood but are likely related to hormonal and metabolic mechanisms influencing secretion of trace elements into feathers. Such variation has been problematic because it usually makes discrimination among populations difficult or may create results that are artifacts of sampling biases (Bortolotti et al. 1990).

In addition to doubts raised over intrapopulational variation in elemental profiles, a more fundamental issue that has not been addressed adequately is how such profiles change among disparate populations. For example, Bortolotti et al. (1989) found that Spruce Grouse (*Falcipennis canadensis*) from similar forest types hundreds of kilometers apart had similar feather elemental compositions, whereas those from adjacent populations occupying different forest types were quite different. Similarly, Szép et al. (2003) determined that feathers from populations of Sand Martins (*Riparia riparia*) grown at locations across Europe varied with age within colonies, and they also showed that similarity and differences in elemental profiles were not related to distance separating colonies. The value of trace-element profiles in making connections between breeding, wintering, and stopover sites, therefore, will depend on the case in question and on how spatially discrete the populations of interest are.

For highly colonial or aggregated species, it may well be possible to characterize the different colonies or breeding regions according to trace-element composition in feathers. If we are fortunate, such areas may have useful elemental fingerprints. For more dispersed species it simply may simply be impossible to describe the trace element profile patterns across the range well enough to reach unambiguous conclusions about origins. This is not to suggest that this field of research will not prove fruitful. Rather, in contrast to the use of continental deuterium precipitation maps, it will simply be difficult to make *a priori* predictions about expected trace element profiles, especially at regional scales, without detailed geological information. Trace element profiles in bird feathers may well be useful for less traditional applications. Szép et al. (2003), for example, suggested that because trace element analysis is sensitive to micro-geographical differences among individuals, this approach might be better suited to elucidating migration or wintering behavior at the level of the individual or small group. Bortolotti et al. (1990) suggested that if the effects of age and sex on trace-element profiles were well known, then population demographic information might be gleaned from elemental patterns within study populations.

Measurement techniques for establishing trace-element profiles in tissues have advanced tremendously over the last several decades. Some approaches such as Inductively Coupled Plasma (ICP) techniques require the dissolution of the sample to a liquid form prior to spectral analysis, whereas others such as the Neutron Activation Technique require that the sample be irradiated but not destroyed. Both approaches have advantages and disadvantages. The recent development of ICP-MS technology, which interfaces a mass spectrom-

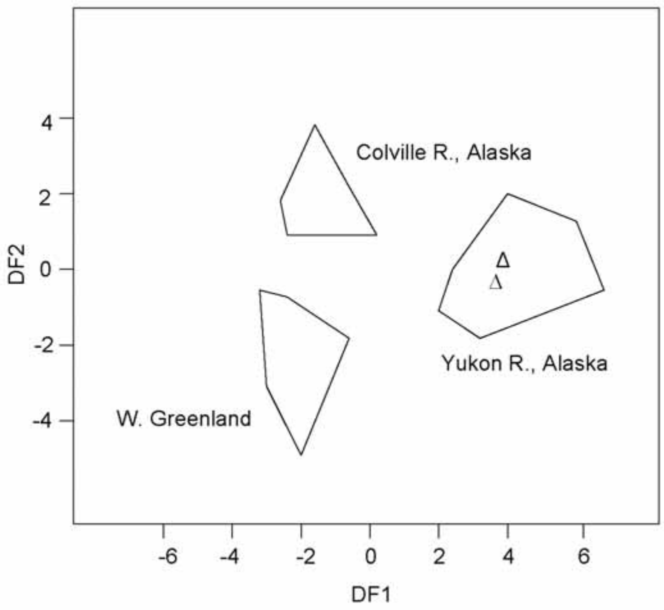

Figure 2. Trace element segregation of three populations of Peregrine Falcons (*Falco peregrinus*). Discriminant function scores based on 14 nestling feather trace-element concentrations as predictors. Polygons represent total outer boundaries of each nestling sample and Δ represents two adult birds captured at South Padre Island, Texas (after Parrish et al. 1983).

eter with an ICP machine to provide isotopic measurements of a suite of elements, certainly holds great promise for migration-tracking studies. By increasing the number of elements and species of isotopes that can be examined, it presumably allows for much greater resolution and for tracing isotope signatures hitherto impossible by more conventional MS techniques.

FUTURE DIRECTIONS

The use of stable isotopes and trace elements to track diet and geographical origins of raptors in North America and elsewhere shows significant promise and several programs are now underway that routinely collect feathers for this purpose. Clearly, an understanding of precise molt patterns for various feather tracks will be invaluable for all species of interest. Ideally, obtaining feathers that represent breeding and wintering grounds would allow analysis of two temporal and spatial samples from the same individual. Raptors can be raised in captivity and the continued investigation of isotopic and trace element behavior in experimental birds is highly encouraged.

A number of important areas require continued research (Hobson 2005a, Smith and Dufty 2005, Lott and Smith 2006). For raptors we need to know if feather growth during breeding results in increases in feather δD values and if so, how we might produce appropriate isotopic basemaps for these birds (Lott and Smith 2006). Second, we must better understand factors contributing to variance in precipitation and feather δD values and incorporate a more rigorous statistical approach to how we assign individual birds to origins. Certainly, the advent of GIS tools and Bayesian statistical techniques will be incorporated increasingly into isotopic studies involving raptors (e.g. Mazerolle et al. 2005, Wunder et al. 2005, Lott and Smith 2006). Raptor biologists and enthusiasts are uniquely positioned as a group to assist in the necessary controlled studies involving birds raised on known, isotopically homogenous diets and water sources to answer some fundamental questions related to isotope and trace element techniques. Apart from issues surrounding the evaporative cooling enrichment of raptor tissues during work, more basic information related to elemental turnover and patterns of isotopic distributions among feathers and other tissues within and between individuals are now needed.

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LITERATURE CITED

BARLOW, J.C. AND G.R. BORTOLOTTI. 1988. Adaptive divergence in morphology and behavior in some New World island birds: with special reference to *Vireo altiloquus*. Pages 1535–1549 in H. Ouellet [ED.], Acta XIX Congressus Internationalis Ornithologici, Ottawa, Ontario, 1986. National Museum of Natural Sciences, Ottawa, Ontario Canada.

BEARHOP, S., R.W. FURNESS, G.H. HILTON, S.C. VOTIER AND S. WALDRON. 2003. A forensic approach to understanding diet and habitat use from stable isotope analysis of (avian) claw material. *Functional Ecol.* 17:270–275.

BORTOLOTTI, G.R. AND J.C. BARLOW. 1988. Some sources of variation in the elemental composition of Bald Eagle feathers. *Can. J. Zool.* 63:2707–2718.

———, K.J. SZUBA, B.J. NAYLOR AND J.F. BENDELL. 1989. Mineral profiles of Spruce Grouse feathers show habitat affinities. *J. Wildl. Manage.* 48:853–866.

———, K.J. SZUBA, B.J. NAYLOR AND J.F. BENDELL. 1990. Intrapopulation variation in mineral profiles of feathers of Spruce Grouse. *Can. J. Zool.* 68:585–590.

BOWEN, G.J., L.I. WASSENAAR AND K.A. HOBSON. 2005. Application of stable hydrogen and oxygen isotopes to wildlife forensic investigations at global scales. *Oecologia* 143:337–348.

CHAMBERLAIN, C.P., J.D. BLUM, R.T. HOLMES, X. FENG, T.W. SHERRY AND G.R. GRAVES. 1997. The use of isotope tracers for identifying populations of migratory birds. *Oecologia* 109:132–141.

DEVINE, T. AND T.J. PETERLE. 1968. Possible differentiation of natal areas of North American waterfowl by neutron activation analysis. *J. Wildl. Manage.* 32:274–279.

DUXBURY, J.M. 2004. Stable isotope analysis and the investigation of the migration and dispersal of Peregrine Falcons (*Falco peregrinus*) and Burrowing Owls (*Athene cunicularia hypugaea*). Ph.D. thesis. University of Alberta, Edmonton, Alberta, Canada.

———, G.L. HOLROYD AND K. MUEHLENBACHS. 2003. Changes in hydrogen isotope ratios in sequential plumage stages: an implication for the creation of isotope base-maps for tracking migratory birds. *Isot. Environ. Health Stud.* 39:179–189.

HANSON, H.C. AND R.L. JONES. 1974. An inferred sex differential in copper metabolism in Ross' Geese (*Anser rossi*): biogeochemical and physiological considerations. *Arctic* 27:111–120.

——— AND R.L. JONES. 1976. The biogeochemistry of Blue, Snow, and Ross' geese. *Ill. Nat. Hist. Surv. Spec. Publ.* 1.

HOBSON, K.A. 2003. Making migratory connections with stable isotopes. Pages 379–391 in P. Berthold, P. Gwinner, and E. Sannenschein [EDS.], Avian migration. Springer-Verlag, Berlin, Germany.

———. 2005a. Stable isotopes and the determination of avian migratory connectivity and seasonal interactions. *Auk* 122:1037–1048.

———. 2005b. Flying fingerprints: making connections with stable isotopes and trace elements. Pages 235–248 in R. Greenberg and P.P. Marra [Eds.], Birds of two worlds: the ecology and evolution of migratory birds. Johns Hopkins University Press, Baltimore, MD U.S.A.

——— and R.W. Clark. 1992a. Assessing avian diets using stable isotopes. II: factors influencing diet-tissue fractionation. *Condor* 94:189–197.

——— and R.W. Clark. 1992b. Assessing avian diets using stable isotopes. I: turnover of carbon-13 in tissues. *Condor* 94:181–188.

——— and L.I. Wassenaar. 1997. Linking breeding and wintering grounds of neotropical migrant songbirds using stable hydrogen isotopic analysis of feathers. *Oecologia* 109:142–148.

——— and L.I. Wassenaar. 2001. A stable isotope approach to delineating population structure in migratory wildlife in North America: an example using the Loggerhead Shrike. *Ecol. Applic.* 11:1545–1553.

———, L.I. Wassenaar and O.R. Taylor. 1999. Stable isotopes (δD and δ^{13}C) are geographic indicators of natal origins of monarch butterflies in eastern North America. *Oecologia* 120:397–404.

Kelly, J.F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Can. J. Zool.* 78:1–27.

Kelsall, J.P. 1984. The use of chemical profiles from feathers to determine the origins of birds. Pages 501–515 in J. Ledger [Ed.]. Proceedings of the 5th Pan-African Ornithological Congress, Lilongwe, Malawi 1980. South African Ornithological Society, Johannesburg, South Africa.

——— and R. Burton. 1979. Some problems in identification of origins of Lesser Snow Geese by chemical profiles. *Can. J. Zool.* 57:2292–2302.

——— and J. R. Calaprice. 1972. Chemical content of waterfowl plumage as a potential diagnostic tool. *J. Wildl. Manage.* 36:1088–1097.

———, W.J. Pannekoek and R. Burton. 1975. Chemical variability in plumage of wild Lesser Snow Geese. *Can. J. Zool.* 53:1369–1375.

Lajtha, K. and J.D. Marshall. 1994. Sources of variation in the stable isotopic composition of plants. Pages 1–21 in K. Lajtha and R.H. Michener [Eds.], Stable isotopes in ecology and environmental sciences. Blackwell Scientific, Oxford, United Kingdom.

Lott, C.A. and J.P. Smith. 2006. A GIS approach to estimating the origins of migratory raptors in North America using hydrogen stable isotope ratios in feathers. *Auk* 123:822–835.

Marra, P.P., K.A. Hobson and R.T. Holmes. 1998. Linking winter and summer events in a migratory bird using stable carbon isotopes. *Science* 282:1884–1886.

Mazerolle, D. and K.A. Hobson. 2005. Estimating origins of short-distance migrant songbirds in North America: contrasting inferences from hydrogen isotope measurements of feathers, claws, and blood. *Condor* 107:280–288.

———, K.A. Hobson and L.I. Wassenaar. 2005. Combining stable isotope and band-encounter analyses to delineate migratory patterns and catchment areas of White-throated Sparrows at a migration monitoring station. *Oecologia* 144:541–549.

Means, J.W. and T.J. Peterle. 1982. X-ray microanalysis of feathers for obtaining population data. Pages 465–473 in Transactions of 14th International Congress of Game Biologists.

Meehan, T.D., C.A. Lott, Z.D. Sharp, R.B. Smith, R.N. Rosenfield, A.C. Stewart and R.K. Murphy. 2001. Using hydrogen isotope geochemistry to estimate the natal latitudes of immature Cooper's Hawks migrating through the Florida Keys. *Condor* 103:11–20.

———, R.N. Rosenfield, V.N. Atudorei, J. Bielfeldt, L. Rosenfield, A.C. Stewart, W.E. Stout and M.A. Bozek. 2003. Variation in hydrogen stable-isotope ratios between adult and nestling Cooper's Hawks. *Condor* 105:567–572.

Nadelhoffer, K J. and B. Fry. 1994. Nitrogen isotope studies in forest ecosystems. Pages 22–44 in K. Lajtha and R.H. Michener [Eds.], Stable isotopes in ecology and environmental science. Blackwell Scientific, Oxford, United Kingdom.

Parrish, J.R., D.T. Rogers, Jr. and F.P. Ward. 1983. Identification of natal locales of Peregrine Falcons (*Falco peregrinus*) by trace element analysis of feathers. *Auk* 100:560–567.

Rubenstein, D.R. and K.A. Hobson. 2004. From birds to butterflies: animal movement patterns and stable isotopes. *Trends Ecol. Evol.* 19:256–263.

Smith, A.D. and A.M. Dufty, Jr. 2005. Variation in the stable-hydrogen isotope composition of Northern Goshawk feathers: relevance to the study of migratory origins. *Condor* 107:547–558.

Still, C.J., J.A. Berry, G.J. Collatz and R.S. DeFries. 2003. The global distribution of C3 and C4 vegetation: carbon cycle implications. *Global Biogeochemical Cycles* 17:1006–1029.

Szép, T., A.P. Møller, J. Vallner, B. Kovacs and D. Norman. 2003. Use of trace elements in feathers of Sand Martins *Riparia riparia* to identify molting areas. *J. Avian Biol*. 34:307–320.

Wassenaar, L.I. and K.A. Hobson. 2001. A stable-isotope approach to delineate geographical catchment areas of avian migration monitoring stations in North America. *Environ. Sci. & Technol.* 35:1845–1850.

Webster, M.S., P.P. Marra, S.M. Haig, S. Bensch and R.T. Holmes. 2001. Links between worlds: unraveling migratory connectivity. *Trends Ecol. Evol.* 17:76–83.

Wolf, B.O. and C. Martinez del Rio. 2000. Use of saguaro fruit by White-winged Doves: isotopic evidence of a tight ecological association. *Oecologia* 124:536–543.

———, C. Martinez del Rio and J. Babson. 2002. Stable isotopes reveal that saguaro fruit provides different resources to two desert dove species. *Ecology* 83:1286–1293.

Wunder, M.B., C.L. Kester, F.L. Knopf and R.O. Rye. 2005. A test of geographic assignment using isotope tracers in feathers of known origin. *Oecologia* 144:607–617.


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