The importance of radio-telemetry in arboreal squirrel research

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Radio-telemetry allows individual squirrels to be tracked through time and space, providing vital data on individual- and population-level parameters, and minimizing biases inherent in opportunistic observational studies. To emphasize the utility (if not necessity) of telemetry in squirrel research, we provide three case studies from our own research involving previously unpublished results on the North American red squirrel (*Tamiasciurus hudsonicus*) and the northern flying squirrel (*Glaucomys sabrinus*). We also provide examples of the type of research being conducted worldwide on arboreal squirrels using telemetry. We conclude by discussing advances in telemetry that help minimize the costs and risks of this important technology.

Keywords: Behaviour, mortality, radio-telemetry, reproduction, Sciuridae.

Introduction

RADIO-telemetry is the tracking of wildlife via radio signals emitted by transmitters carried by individual animals. Since the earliest published telemetry studies of arboreal squirrels in the late sixties[1,2], telemetry has been used to study common and threatened squirrel species in a variety of countries (including Belgium, Canada, Finland, Italy, Japan, Mexico, Sweden, United Kingdom and the United States). Data acquired via telemetry have proven pivotal for our understanding of animal systems, including those involving arboreal squirrels. The field continues to evolve, however, creating new research opportunities and overcoming obstacles. In this article, we provide discussion and examples that highlight the importance of radio-telemetry to squirrel research. This is not intended to be an exhaustive review of the literature concerning telemetry and arboreal squirrels; rather, we provide the background and examples of the application of telemetry, and focus on three previously unpublished examples where telemetry has revealed information that would have been otherwise unobtainable.

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What information does radio-telemetry provide?

Radio-telemetry allows individual squirrels to be tracked through time and space, providing vital data on individual-level parameters, including behaviour (together with intraspecific interactions such as mating and parental behaviour), movement patterns, dispersal, habitat use, causes of mortality, reproductive output and activity budgets (see Table 1 for examples involving arboreal squirrels). These data can be translated into population-level parameters such as survival, emigration and birth rates. Importantly, telemetry allows these data to be collected in a systematic, balanced manner, minimizing biases inherent in opportunistic observational studies.

Radio-telemetry has proven particularly valuable in field studies of arboreal squirrels. By nature, many tree squirrels are relatively cryptic and their often-rapid movement through the canopy prohibits researchers from visually tracking them effectively. Nocturnal habits of some arboreal squirrel species exaggerate these sampling issues. These characteristics of arboreal squirrels can greatly influence their detection probability, a critical issue when conducting many wildlife surveys[3]. Detection probabilities also can vary markedly depending on habitat characteristics and ambient conditions; for example, a recent study[4] showed that sugar gliders (a marsupial arboreal mammal) may be present, but were undetected during 45% of surveys. Thus, relying on observation alone can create a bias due to variable detection probabilities in different habitats. Telemetry can help minimize this bias, and also can be used to determine the detectability of animals (i.e. are telemetered animals known to be present in an area reliably detected by various types of surveys). Further, telemetry generally enables researchers to locate animals more readily, a critical issue when collecting location or behavioural data on free-ranging individuals.

Telemetry often is the only way to differentiate individuals and acquire data on their physiology and habitat use. For instance, in population food-addition research[5], live trapping alone provides only broad demographics at a population level, whereas telemetry provides additional individual-level data on survival and activity budgets of individuals supplemented with food. In addition, one can derive different data by varying how the transmitter is

Table 1. Examples of studies on arboreal squirrel using telemetry to obtain data on individual-level parameters

Parameter	Examples of arboreal squirrels
Activity budgets	*Glaucomys sabrinus* (northern flying squirrel)[24] *Tamiasciurus hudsonicus* (North American red squirrel)[30,31]
Behaviour	*Sciurus carolinensis* (Eastern grey squirrel)[7,32] *Sciurus vulgaris* (Eurasian red squirrel)[7] *T. hudsonicus*[33]
Causes of mortality	*Sciurus niger* (Eastern Fox squirrel)[34] *T. hudsonicus*[15,35]
Dispersal, movement patterns	*S. vulgaris*[36] *T. hudsonicus*[8,12,16] *T. hudsonicus grahamensis* (Mt Graham red squirrel)[22]
Habitat use, home range estimation	*Callosciurus erythraeus thaiwanensis* (Formosan squirrel)[37] *G. sabrinus*[17,38,39] *G. sabrinus fuscus* (Virginia northern flying squirrel)[23] *Pteromys volans* (Siberian flying squirrel)[40] *Sciurus aberti kaibabensis* (Kaibab squirrel)[41] *S. carolinensis*[7,42] *S. vulgaris*[7,43] *T. hudsonicus*[15,16,44]
Reproduction	*S. vulgaris*[45] *T. hudsonicus*[10,11,20,46]

attached to the animal. When implanted subcutaneously, some radio-transmitters can record daily and seasonal body-temperature cycling and activity cycles. Attached externally, transmitters can provide information on environmental temperature, complementing both habitat-use patterns and thermoregulation data. For example, transmitters can record within-nest temperatures or, by time-series temperature correlation, behaviour patterns and circadian rhythms[6]. Finally, telemetry has proven successful in providing insight into how an introduced, invasive squirrel could affect a vulnerable, native squirrel, by providing data on habitat use and home-range size where the two species coexisted[7].

To further emphasize the utility (necessity) of telemetry in squirrel research, we provide here three case studies from our own research involving previously unpublished results on the North American red squirrel (*Tamiasciurus hudsonicus*) and the northern flying squirrel (*Glaucomys sabrinus*).

Case study 1: Maternal nest locations found via telemetry

These data were collected for a study on the reproductive success and dispersal of North American red squirrels in the Athabasca Sandhills of central Alberta, Canada, during the summers of 1988–1990. The key to this work was locating, enumerating and ear-tagging juvenile squirrels prior to their emergence from the nest. This permitted assessments of litter size, reproductive condition and success of the mother[8–10], growth estimates for the young squirrels[11], and enabled tracking movement of the young through dispersal[12,13]. To locate maternal nests, adult female squirrels were monitored during May–July of each year with an intense live-trapping programme. Individuals that exhibited signs of parturition were radio-collared and periodically tracked until they were detected inside their nests (see ref. 12 for a more detailed explanation of how nestlings were accessed and subsequently radio-tracked themselves). In the process of locating the litters, this procedure also provided data on the nature and location of the nests themselves. Each located maternal nest was categorized as one of the following: drey (tree nest, composed of leaves, grass or other vegetation), underground (subterranean nest) or dead tree (nest in cavity within stump or snag).

A total of 158 maternal nests were located during the study. The most commonly used nests were dreys, but a relatively large proportion of the nests (39%) were underground (Figure 1). Drey nests of squirrels often are relatively conspicuous, particularly so in the Athabasca study site where the forests are composed almost exclusively of sparse jackpine conifers (*Pinus banksiania*). Once observers developed search images, however, dreys at this site were often detected without radio-telemetry (although because females usually had more than one nest per territory, telemetry was still useful for associating the mothers with particular nests, thereby reducing the number of trees unnecessarily climbed and searched). In contrast, underground nests would have been impossible to detect without telemetry, short of investing an inordinate and very costly amount of time in visually tracking movements and (eventual) nest entries by mother squirrels. It is clear in retrospect that using a non-telemetry approach would have met with little success: even after transmitter signals had been traced, considerable effort still was required to locate nest entry holes. The larder-hoarding behaviour of red squirrels in this area creates large, conspicuous piles of debris on the forest floor, but the underground nests rarely were located within the middens (central food caches) of the females (only two of 62 underground nests were observed within middens). The use of telemetry in this study thus not only allowed data to be gathered on the litters and reproductive success of the females (see references above), but it revealed a previously under-appreciated, important natural history aspect of *T. hudsonicus*.

Case study 2: Natal dispersal outcomes determined using telemetry

In this study, dispersal and settlement of 40 juvenile North American red squirrels were documented in two distinct habitats in the Southern Interior forests of British Columbia, Canada, during the summer and autumn of 2000 and 2001. The goal of the study was to determine whether juveniles born in harvested thinned forest dispersed differently from juveniles born in mature unharvested forests, and whether there were consequences of settling in human-altered vs unaltered forest[14–16]. To obtain these data, reproductively active female squirrels were radio-collared in order to find nests, and later, emergent juveniles. As noted in case study 1, trapping and observation alone would not have allowed us to locate many nests, because: (i) part of the study area was composed of dense, mature forest where squirrels could not visually be tracked, and (ii) some squirrels had underground nests. Once juveniles were located, at least one juvenile from each nest was radio-collared and tracked until death or territory establishment. Tracking provided data describing: (i) juvenile movement and dispersal, (ii) habitat use, activity patterns and behaviour, and (iii) mortality and other fitness surrogates (see refs 11–14 for detailed methods).

First, while some movement can be documented using continuous large-scale live-trapping, there are serious limitations to this method. In this study, juvenile movements were often rapid (occurring within a single exploratory trip completed within a few hours) or occurred off the trapping grid. Telemetry allowed us to document these exploratory movements, enabling us to show that juvenile movement patterns were more variable in the human-altered habitat[16]. In addition, telemetry allowed us to document the first large-scale, successful dispersal event ever recorded for red squirrels: a male juvenile successfully established a territory approximately 4.5 km away from his natal territory[16]. Secondly, systematically locating squirrels through radio tracking allowed us to discover habitat-use patterns that otherwise would have been missed. For instance, 45% of the radiolocations for adults and 31% of the locations for juveniles (Figure 2) would not have been observable because the squirrel was not visually or audibly detected by the tracker – locations were confirmed using triangulation. Finally, a long-standing problem with using trapping data to infer demographic parameters such as survival is the inability to differentiate death from emigration. Using telemetry, we were able to document 11 natural mortality events of collared squirrels. The majority (64%) of the killed animals were found below ground, possibly due to predation by mustelids, and would never have been discovered without telemetry. These demographic data allowed us to conclude that the likelihood of survival and successful reproduction for female squirrels was lower in human-altered habitat vs mature, unaltered forest[15]. Data such as these are vital if we are to understand and manage the impact of human activity on wildlife.

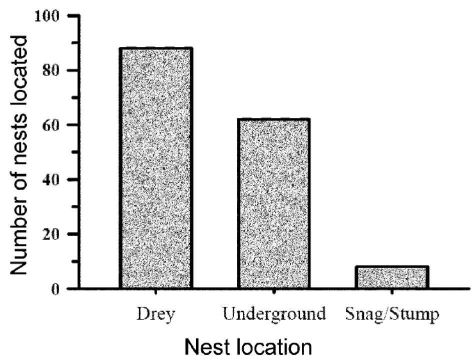

Figure 1. Maternal North American red squirrel nest locations as documented in the Athabasca Sandhills region of central Alberta, Canada, during the summers of 1988–90. A total of 158 nests were located.

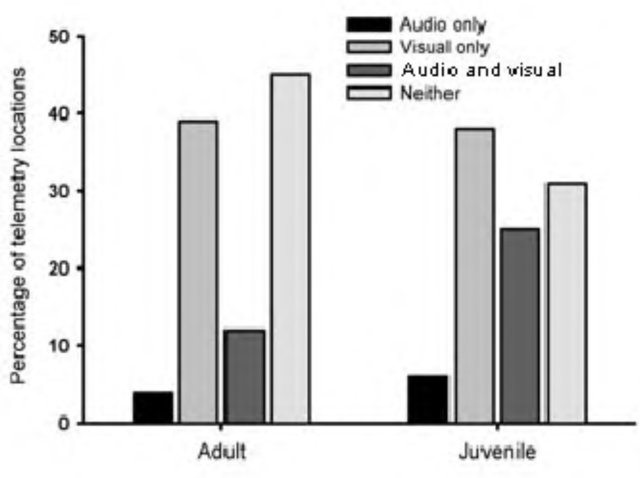

Figure 2. Percentage of radio-telemetry locations collected for adult and juvenile North American red squirrels in the Southern Interior of British Columbia, Canada, during the summers of 2000–01. A total of 1410 adult locations and 1097 juvenile locations were collected.

Case study 3: Spatial ecology documented using telemetry

In this example, the poorly known ecology of nocturnal northern flying squirrels was of interest in northwestern Canada, where industrial harvesting of the forest was accelerating. Northern flying squirrels lack audible vocalizations, use cryptic nests (often within tree cavities), are small (average weight of 140 g) and rarely seen incidentally in the field. Consequently, developing predictive habitat models for this species is difficult. Initial attempts to document the habitat use of this species employed straight-line live-capture trapping transects, whereby average capture rates were related to general habitat categories using a Geographical Information System (GIS)[17]. However, the spatial grain of available habitat inventories was inappropriate to explain variability in flying squirrel abundance: flying squirrels appeared to perceive habitat structure below the grain of available habitat data, and as a result, average capture rates within broad habitat categories insufficiently described habitat use[17]. A smaller-grained resolution was required, where fine-scale movement could be documented at night: these data were obtainable only through radio-telemetry.

Radio-collars facilitated the unbiased collection of both movement and nest-use data. Telemetry revealed aspects of flying squirrel ecology that otherwise would have been completely missed or the frequency of which would have been estimated incorrectly. Over three summers (2004–2006) in the foothills of Alberta, Canada, small-sized radio-transmitters (4 g) were collar-attached onto flying squirrels. Using radio-telemetry, 223 nests were located, the majority of which (75%) were in witches' brooms (dense clusters of abnormal tree branch growth, caused by parasitic plants and fungi) and tree cavities (Figure 3). Witches' brooms are more conspicuous than tree cavities, but the hollows that flying squirrels create for nests within the centre of the 'brooms' are not easily detected. To determine which brooms contained flying squirrel nests without telemetry would have required an immeasurable amount of time climbing all trees with witches' brooms, of which only a minor proportion actually contained nests. Similar problems hold for the detection of cavity nests (Figure 3). Even with the aid of telemetry, observers were often completely unaware that cavities were present, and considerable effort was required to locate and identify nests even after the radio-signal allowed the nest tree to be isolated.

Detailed nocturnal movements recorded for flying squirrels in this site (using telemetry and handheld GPS devices) also allowed the investigators to determine whether different life requisites for the animals were being met within different habitat patches. Such information is important, particularly in the face of increasing habitat fragmentation. For instance, older forest may be required for nesting, whereas foraging might be more optimal in young habitat patches. Telemetry enabled the field observers to also identify individual trees within which animals were foraging, travelling or resting, even without having to directly sight individual squirrels. These data revealed activity time budgets that were then related to fine-scale habitat structure, allowing a spatial comparison of live-capture trapping sites, foraging areas and nesting sites. It was determined that nests and foraging areas were in relatively close proximity to one another, but animals were travelling greater distances than normal to access the live traps (presumably because of bait; Figure 4). Ergo, telemetry in this study revealed two key spatial parameters that otherwise would have been entirely unknown: (i) the average spatial scale at which flying squirrels perceive habitat (nest to foraging area distance) was approximately 150–170 m in radius (Figure 4), and (ii) the use of baited live traps promoted above-average animal movements and as such, caused a distinct spatial sampling bias.

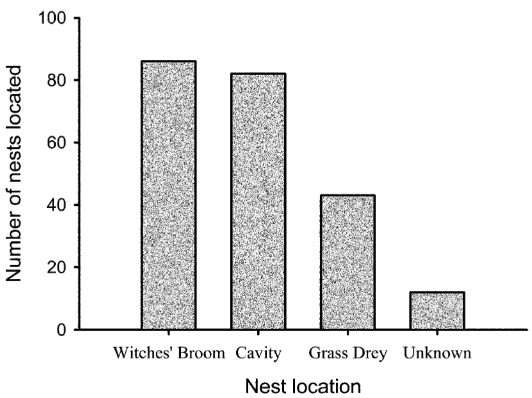

Figure 3. Nest locations of northern flying squirrels as documented near Hinton, Alberta, Canada, during the summers of 2004–06. A total of 223 nests were located. Unknown nests were those nests that could not be isolated to a specific cavity or witches' brooms even with telemetry.

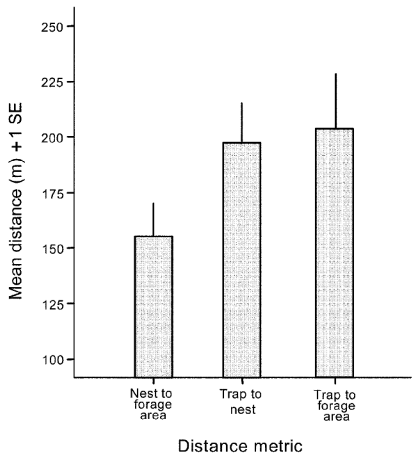

Figure 4. Mean (+SE) distances between nest, forage and capture locations as determined from nocturnal activity budgets of 34 northern flying squirrels. Data were acquired using radio-telemetry in the summers of 2004–05 near Hinton.

Risks of telemetry

The risk to the individual squirrel carrying a transmitter can be parcelled into acute capture and handling risk, and chronic risk of carrying the transmitter. Most studies of arboreal squirrels employ external transmitters. Individual squirrels are live-trapped (a risk invariably incurred in mark–recapture studies) and usually collared (the most common method of attaching transmitters in arboreal squirrel research), with the transmitter tailored snugly around the neck. The risks individuals face while carrying transmitters include increased mortality due to reduced vigilance and impedance while moving. These risks are minimized by engineering attachment methods that do not impede movement (tailoring the fit properly is critical) and by using the lightest transmitters logistically feasible (less than 4% of body mass ideally). As detailed collaring methods are rarely published (but see ref. 18), consultation with experienced researchers (e.g. see the authors cited in Table 1) is crucial when starting a telemetry programme.

Several studies have addressed telemetry risks by comparing the survival or behaviour of collared and uncollared animals. For example, Kenward[19] noted that transmitters weighing up to 7% of body weight did not affect emigration rates or mean body weight changes in grey squirrels (*Sciurus carolinensis*). Lair[20] found that radio-tagged females had gestation periods similar to that documented in a previous study of uncollared females and all collared females were able to raise the young to weaning. In another study of North American red squirrels, juveniles with transmitters attached onto the backs of the animals with cyanoacrylate glue did not suffer any adverse physical affects[21].

Other researchers have found that deaths due to trapping can exceed the number of deaths due to telemetry. During a three-year study of North American red squirrels, Haughland[14] found that human error and physiological stress to squirrels during live trapping accounted for more mortalities than collaring (six deaths in 1434 trap events vs four of 120 collared squirrels, the latter including events during collaring or as a consequence of being collared). Similarly, Wheatley found that there were more mortalities associated with live-trapping flying squirrels (from nocturnal predators, primarily pine marten (*Martes americana*), predating squirrels in traps: five predation events in 339 individual captures) than with collaring (three of 65 collared squirrels). In summary, if a transmitter is engineered and attached appropriately, the risk to the individual carrying it can be minimized so that the value of the data obtained using telemetry outweighs the risk to individual squirrels. As a case in point, the need for reliable data for conservation and management has outweighed the risks inherent in radio-tagging for at least two threatened species: the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*)[18,22] and the vulnerable Virginia northern flying squirrel (*Glaucomys sabrinus fuscus*)[23].

Advances in telemetry

Telemetry is advancing on four fronts: size, longevity, capacity and attachment methods. For example, the first radio-telemetry work on northern flying squirrels used transmitters that weighed 6 g, had a battery life of 2–3 weeks and a range[24] of 200 m. Today, squirrel transmitters weigh 4 g, have a working life of approximately 6 months and can transmit a signal over 1 km away, depending on terrain (e.g. Holohil PD-2C transmitters). Advances in global positioning system technology have allowed the construction of transmitters weighing 25 g that log position in space every few seconds and can operate[25] for 16 h. Further work needs to be carried out to investigate the potential of these transmitters for research on the larger arboreal squirrels, such as the Indian giant squirrel (*Ratufa indica*). At smaller scales, Naef-Daenzer *et al.*[26] reported a modified radio-transmitter which they had constructed, that has begun field-testing; with a weight of 0.2 g, a longevity of 100 days and a potential range of 1 km, this transmitter may have great potential for research on smaller sciurids.

Conclusion

The financial cost of using telemetry can be relatively high, but these costs often are worth incurring because of the unique data provided by telemetry. Even for a common, territorial, vocal, diurnal squirrel species such as the North American red squirrel, telemetry has revealed a wealth of knowledge that could not have been discovered without radio-telemetry. While many species of arboreal squirrels remain unstudied, the ecological role of these animals is becoming appreciated, as predators (e.g. song-bird eggs[27]), agents of dispersal (e.g. fungi[28]) and prey (e.g. owls[29]). Advances in telemetry are poised to greatly enhance future studies of arboreal squirrels and increase our knowledge of these sciurids as key components of forested ecosystems.

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