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Tools and Technology

Coupling Tracking Technologies to Maximize Efficiency in Avian Research

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ABSTRACT Direct marking and tracking of wildlife using telemetry is widespread and critical to understanding many aspects of wildlife ecology. For most species, researchers must select between multiple tracking technologies that represent trade-offs among data requirements, mass, and cost. Options tend to be more limited for smaller, volant species. We developed and tested a unique combination of a store-on-board Global Positioning System logger with an independent very-high-frequency (VHF) tag (hereafter, hybrid tag) fitted on the greater sage-grouse (*Centrocercus urophasianus*) with a modified harness design in northeastern Wyoming, USA, 2017–2018. We compared hybrid tags with other tracking technologies commonly used in avian research, namely VHF and Argos satellite relay tags. Given our research objectives, that required both frequent location data and field-based observational data, we found the hybrid tags were the most cost-effective option and capable of collecting more location data compared with Argos tags because of power savings associated with data transmission. Cost savings allowed us to avoid sacrificing sample size while still obtaining high-resolution location data in addition to field-based observational data such as the presence of chicks. We believe our hybrid tags and harness design would be beneficial to research on other avian species of comparable size to the greater sage-grouse and those that are relatively localized year-round, including many other Galliformes. © 2020 The Wildlife Society.

KEY WORDS animal tracking technologies, *Centrocercus*, global positioning system, sage-grouse, satellite relay tags, store-on-board GPS logger, telemetry, ultra-high-frequency, very-high-frequency.

Wildlife ecology has a long history of using biotelemetry to track and study animals. Very-high-frequency (VHF) tags were first designed and tested for animal studies in 1959 (LeMunyan et al. 1959) and have been critical tools to understanding many aspects of species ecology. More recently, biotelemetry technologies using internal GPS (Global Positioning System) to collect high-resolution location data have become widely available. Technological advancements have reduced effects on telemetered animals, increased data availability and reliability, and decreased costs. Reductions in the mass and size of transmitters and improved attachment methods, have opened up opportunities for researching small animals and, particularly, those that fly. With a variety of telemetry systems now available, selecting the most appropriate system for a study requires careful considerations of tradeoffs associated with different technologies and study objectives (Hebblewhite and Haydon 2010, Thomas et al. 2011, Taylor et al. 2017).

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Sage-grouse (*Centrocercus* spp.) are one of the most extensively researched species in North America and the first birds were fitted with VHF radiotransmitters in 1965 (Eng and Shladweiler 1972). Since then, researchers have tested various telemetry devices and configurations as well as attachment methods on sage-grouse. Consequently, this species provides valuable information on implementation of new and old tracking technologies and attachment methods that are applicable to many less-studied avian species.

When attaching a telemetry device (hereafter, tag) to an animal, careful consideration of the ratio of mass of the tag to the body mass of the study species is necessary (Aldridge and Brigham 1988, Samuel and Fuller 1994, Fair et al. 2010). Tag options are more limited for small, volant species (Barron et al. 2010). Research on volant species fitted with tags has shown that the additional mass of the tag can affect flight patterns and increase energetic costs (Barron et al. 2010, Vandenabeele et al. 2012). Although there is not a consensus on a specific tag-to-body mass ratio that is appropriate for all volant species (e.g., 3% or 5%), there is a general consensus that detrimental effects are reduced with proportionally lighter tags (Fair et al. 2010, Vandenabeele et al. 2012). The earliest VHF tags fitted on sage-grouse weighed 70 grams, and had a battery life of less than a month (Kenward 2001, Connelly et al. 2003). By the late 1970s, mass of VHF tags commonly used on sage-grouse was reduced to 25 g (~2% of the mass of an adult female) and battery life was extended to ≥6 months (Connelly et al. 2003).

Researchers require secure attachment of tags that does not harm the animal or affect the animal in ways that may cause systematic bias in the data (Barron et al. 2010). Over the past 50 years, sage-grouse researchers have experimented with a variety of attachment methods including neck-mounted poncho and necklace tags, backpack tags secured around the wings, and rump-mounted tags secured around the legs (Connelly et al. 2003, Bedrosian and Craighead 2010). Tags secured around the neck of the sage-grouse (hereafter, VHF necklace) have become the most commonly used tag and currently weigh between 17 and 22 g with a lifespan of approximately 2 years (Frye et al. 2014, Dinkins et al. 2016, Walker et al. 2016).

More recently, satellite relay (Argos; www.argos-system.org), GPS solar-powered Platform Transmitter Terminal (PTT) tags fitted to sage-grouse using a rump-mount harness system has become a more common used tool (Bedrosian and Craighead 2010, Dzialak et al. 2011, Hansen et al. 2014, Smith et al. 2016). Argos PTT tags weigh between 22 and 30 g (Dzialak et al. 2011, Hansen et al. 2014, Smith et al. 2016, Pratt et al. 2017) with approximately 10 additional grams in harness and attachment materials (Pratt et al. 2017). These light-weight Argos PTT tags gather and transmit GPS data via Argos satellites and are powered by batteries that recharge by solar panels (Thomas et al. 2011). The solar panel is positioned on top of the Argos unit, so these tags are fitted on the back of the grouse as a rump-mount to allow for direct sunlight to charge the battery. Unlike a backpack-style harness, the rump-mount method places the tag dorsally on the rump of the bird and the harness material is secured around the legs rather than the wings (Bedrosian et al. 2007, Smith et al. 2016).

The purchase cost of Argos PTT tags are approximately 20 times greater than VHF tags and costs of Argos systems increase with the download frequency because of satellite data download fees (Hebblewhite and Haydon 2010, Thomas et al. 2011, Hansen et al. 2014). Argos PTT tags collect a large amount of location data at frequent intervals and, in general, do not require a researcher to visit study sites to track the animals (Hebblewhite and Haydon 2010, Kays et al. 2015). However, research budget restraints and high cost of Argos PTT tags often limits the number of study animals that can be marked, which may influence statistical power and capacity of the marked population to represent the larger population of interest (Hebblewhite and Haydon 2010). The comparatively low-cost VHF units allows for larger numbers of marked birds given the same budget, and are well-suited for gathering data that require field-based observations such as nest success or brood size (Hebblewhite and Haydon 2010, Kirol et al. 2015*a*). Yet, location data obtained from VHF tags are labor-intensive, infrequent, and prone to human error and may also be constrained by limits on access due to weather, road conditions, or land ownership (Withey et al. 2001, Hebblewhite and Haydon 2010, Gerber et al. 2018). Sage-grouse studies using VHF tags usually track and collect locations for individual birds once or twice per week (Fedy et al. 2012, Walker et al. 2016). Conversely, sage-grouse studies using Argos PTT tags have collected >9–15 locations/day (Dzialak et al. 2011, Smith et al. 2016, Pratt et al. 2017, Foster et al. 2019).

In practice, the most appropriate tracking technology for a given study is highly dependent on the study objectives, which dictate factors such as required sample size, sampling rate, and precision of locations needed. Yet, many studies have the goal of population-level inference over large landscapes, and require precise and frequent location data to quantify space use and movement patterns, but may also need observational data to assess population fitness rates (e.g., nest success). In these cases, tradeoffs between GPS satellite tags and VHF tags are substantial. A hybrid technology that eliminates some of these tradeoffs would be beneficial to many studies that require both frequent location data and field-based observational data. We assessed the functionality of a new approach to tracking sage-grouse that provides frequent and accurate GPS locations, at a cost that does not severely limit sample size, and allows for field-based observational data. Specifically, we required tags that would 1) allow for a sample of ≥40 individuals, 2) cost <US$100,000 (≤US$2,500/unit), 3) have a life span of ≥2 years, 4) provide accurate GPS location data across seasons, 5) provide frequent GPS locations throughout a 24-hour period, 6) weigh <3% of body mass (Fair et al. 2010), and 7) allow real-time tracking in the field to gather observational data. In addition to these considerations, we wanted to ensure we could recover tags if they stopped transmitting for any reason (e.g., malfunction, power loss, damage due to depredation).

We developed and tested a unique combination of a store-on-board GPS logger with an independent VHF tag (hereafter, hybrid tag) to meet our research requirements. We detail a hybrid tag we developed and assessed its capacity to meet project goals and outcomes. Specifically, we present 1) the utility of the combined GPS logger and VHF tag, 2) a cost comparison among Argos PTT tags, VHF necklace tags, and hybrid tags, 3) realized benefits of the VHF add-on with an independent battery, and 4) our modified harness system to reduce effects of attaching rump-mounted tags to greater sage-grouse (*Centrocercus urophasianus*).

STUDY AREA

Our study was in the Powder River Basin, primarily in Johnson County with the northern portion extending into Sheridan County, Wyoming, USA. The area was characterized by rugged terrain bisected by deep drainages with prominent hogback ridges, knolls, and escarpments. The majority of the study area was shrub-steppe habitat dominated by Wyoming big sagebrush (*Artemisia tridentata wyomingensis*).

The climate in the study area was semiarid. Monthly average temperatures ranged from 21.6° C in the summer to −5.8° C in the winter. Annual precipitation averaged 33 cm to 43 cm and average annual snowfall ranged from 84 cm to 170 cm. More details on study area characteristics are available in Fedy et al. (2015).

METHODS

Field Methods

We captured female sage-grouse in 2017–2018 using spotlight and hoop-net methods (Giesen et al. 1982) and a mobile CODA net launcher (Sutphin et al. 2018). We fitted females with rump-mounted 13-g solar LRD (long range download) GPS-UHF (ultra-high frequency) tags (Harrier-L; Ecotone Telemetry Lech Iliszko, Sopot, Poland) combined with independent 10-g VHF tags (RI-2B; Holohil Systems Ltd, ON, Canada). Only females that weighed >1,000 g were fitted with hybrid tags. We deployed tags with approval from the University of Waterloo (Animals for Research Act and the Canadian Council on Animal Care guidelines, AUPP# 16-06).

We monitored tagged female sage-grouse weekly from April through August and bimonthly throughout the winter (Sep–Mar). We tracked females using the VHF signal with a R-1000 hand-held receivers and 3-element Yagi antennas (Communication Specialists, Orange, CA, USA) and downloaded the GPS data from GPS loggers using mobile UHF base stations and unidirectional antennas (Ecotone Telemetry Lech Iliszko). Radio activity intervals can be programed to 1, 5, or 10 minutes. We programed our GPS loggers to attempt to communicate (i.e., radio activity interval) every minute. The manufacturer of the GPS loggers (Harrier-L) suggested managing the power at a voltage >3.7. The GPS loggers were originally programed to collect GPS locations every 4 hours (6 locations/24-hr period) and maintained high voltage. The transmitters maintained high voltage when set to collect a location every 4 hours; therefore, we transmitted new settings to the loggers instructing that they record GPS locations every 30 minutes (48 locations/24-hr period), in late-summer 2008. The GPS loggers require line-of-sight for communication and download. The rough terrain in our study area dictated that we commonly had to be within ≤300 m of the female to establish line-of-site communication with the GPS logger. On occasion, if there was rock outcrops or thick vegetation obstructing line-of-site communication, we needed to get much closer than 300 m to download stored data. We used VHF tracking to isolate tagged females to a particular draw or sagebrush patch. After isolating the bird, we pointed the UHF antenna in the direction of the VHF signal and attempted to download the GPS data. If we failed to establish communication with GPS logger, we continued to track the bird and attempted to download again from a different position. We used tablet computers to power the base station, which also allowed us to visually confirm communication with GPS loggers, view location data, and adjust logger settings in the field, when needed. The base stations can be powered by any power source that has a USB port, such as cell phone boosters. The tablets allowed for real-time monitoring because we could view the GPS logger data using Google Earth (Google LLC, Mountain View, CA, USA) software while tracking. After we downloaded the GPS data from the logger, we maintained a distance of ≥50 m from the tagged sage-grouse unless we needed to visually confirm reproductive state or survival. In those cases, we downloaded the GPS data before we attempted to observe the bird. During the nesting period (mid-Apr–Jun) we used VHF tracking to approach within ≥20 m of the female to verify nesting. Once we confirmed a female was on a nest by getting a visual with binoculars, we monitored her and downloaded data weekly from ≥50 m until she was no longer on the nest. If the GPS data showed that a female was on a nest for the entire incubation period (26–28 days), we verified nest survival (i.e., nests with ≥1 hatched egg) by examining eggshells and other diagnostic signs (Wallestad and Pyrah 1974). Following a successful nesting effort, we attempted to get a visual of the female every second week to confirmed chick presence by visually locating chicks with binoculars or observing brooding behavior by the female (e.g., distraction displays, feigning injury, and clucking). We confirmed brood fate at approximately 35 days posthatch by VHF ground-tracking at night and conducting spotlight counts (Dahlgren et al. 2010). We confirmed brood survival at 35 days posthatch because the majority of chick mortality has already occurred by this age; consequently, chicks alive at 35 days are more likely to survive to breeding age (Gregg et al. 2007). We considered a brood to have survived if we observed ≥1 chick during spotlight counts (Kirol et al. 2015*a*).

We located nests that were initiated early or failed quickly, and not found during VHF ground-tracking, by using the GPS data downloaded from the female's tag to identify clusters of points suggesting a nest attempt. We then surveyed these areas to verify a nesting attempt. If we were tracking a female and suspected that she may have died, we would download and view the GPS data to determine whether the logger was stationary for an extended period of time. When GPS data suggested that the tagged sage-grouse was not moving, we would track the bird to conclusively assess fate and document any diagnostic evidence at mortality locations.

Technology and Equipment

Hybrid tags were fitted on sage-grouse with custom-made harnesses. Our harness design allowed for expansion to accommodate growth and reduced abrasion along the inside of the legs (Fig. 1). We made the harnesses from 0.64-cm tubular Teflon (Chemours, Wilmington, DE, USA) ribbon with 0.64-cm elastic inserted within the ribbon to provide for expansion. We cut the Teflon ribbon to 70 cm and cut the elastic insert to 6.5 cm. We placed marks on the ribbon at the center and at 5.0 cm on either side of the center. We used fine wire to pull the cut pieces of elastic into the ribbon. We stitched the elastic in place at one of the 5.0-cm marks with strong thread. We then used the wire to pull the elastic tight and bunch up the ribbon until the other end of

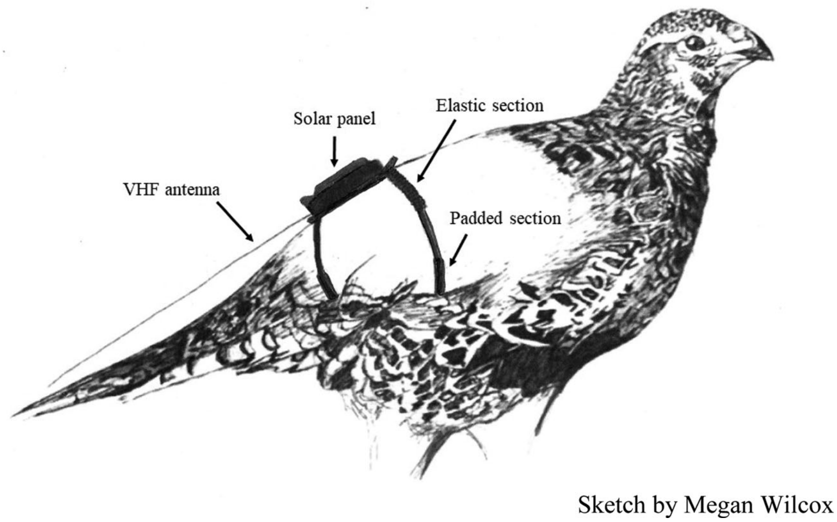

Figure 1. The tag (hybrid tag) positioned dorsally at the rump (rump-mounted) of a female sage-grouse northeastern Wyoming, USA, 2017–2018. The harness is secured snugly around the legs between the abdomen and the thigh (the harness in curved in the sketch to show how it forms around the grouse's body).

the elastic reached the second 5.0-cm mark. We stitched the elastic in place at the second mark and removed the wire (Fig. 2). This allowed the center of the harness to flex with the elastic insert.

After retrieving rump-mounted tags from sage-grouse during earlier research, in some instances, we would find abrasions and scabbing under the legs that we suspected were caused by the tubular Teflon material folding onto itself and bunching under the legs. To provide padding and some rigidity to the tubular webbing and prevent the ribbon from folding over, we cut strips of 4-mm-wide pieces of 3-mm neoprene (L Foam Neoprene Fabric; Rockywoods Fabrics, Loveland, CO, USA) to a length of 10 cm. We used needle and thread to pull the pieces of neoprene through the tubular webbing. When the neoprene strip was approximately 4 cm from the elastic stitch mark, on each side of the harness, we pulled the needle through the outside of the webbing and stitched the neoprene in place. This secured the 10-cm neoprene segment within the portion of the harness that runs between thigh and abdomen (Figs. 1 and 2). Once the harness was adjusted to the bird, we secured it with approximately 0.64-cm- (one-quarter-inch) diameter copper tubing cut into 0.64-cm-wide rings. We crimped the copper rings on the harness near the back loops of the tag to hold the harness in place (Figs. 2 and 3).

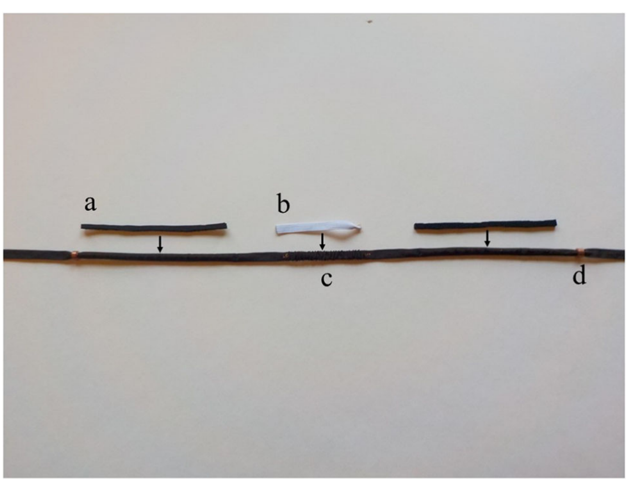

Figure 2. Components of the harness used to fit the rump-mounted tag (hybrid tag) on a sage-grouse. The pieces of 4-mm-wide 3-mm neoprene were cut to a length of 10 cm (a), inserted into the tubular Teflon ribbon, and stitched in place 4 cm from the elastic stitch marks. The 6.5-cm length of elastic (b) was inserted within the ribbon and stitched at 5-cm marks on each side of the center of the harness. The center of the harness, with the elastic insert, was bunched up between the 5-cm stitch marks to allow the center of the harness to flex with the elastic. The harness was secured on the sage-grouse by crimping approximately 0.64-cm-diameter (1/4 inch), 0.64-cm-wide rings made from copper tubing.

We attached the VHF underneath the GPS logger, rather than on the side, to keep the center of gravity over the middle of the sage-grouse laterally to reduce any potential impact on flight (Caccamise and Hedin 1985, Bedrosian and Craighead 2010). The dimensions of the VHF tag (L 40 × W 23 × H 5 mm) allowed the VHF to easily fit underneath the base of the GPS logger (L 60 × W 26 × H 14 mm; Fig. 4). When building the hybrid tags, we first centered the VHF unit and glued it to the base of the logger. We then cut a piece of 5-mm neoprene to the dimensions of the GPS logger base and cut out the outline of the VHF within the piece of neoprene. We then glued this piece of neoprene to the base of the GPS logger with the VHF nested within the neoprene (Fig. 4). We then glued a piece of 3-mm neoprene padding cut to 70 mm long and 40 mm wide onto the underneath side of the hybrid tag and completely covered the VHF tag. We cut this piece of neoprene to protrude 10 mm beyond the front and 7 mm on each side of the tag to act as a feather shield to prevent feathers from shading the solar panel. We made 2 holes in the front of this piece of neoprene to allow the harness to thread through the neoprene and front logger loops (Figs. 3 and 4).

Figure 3. Hybrid tag fitted on a female sage-grouse in northeastern Wyoming, USA, 2017–2018.

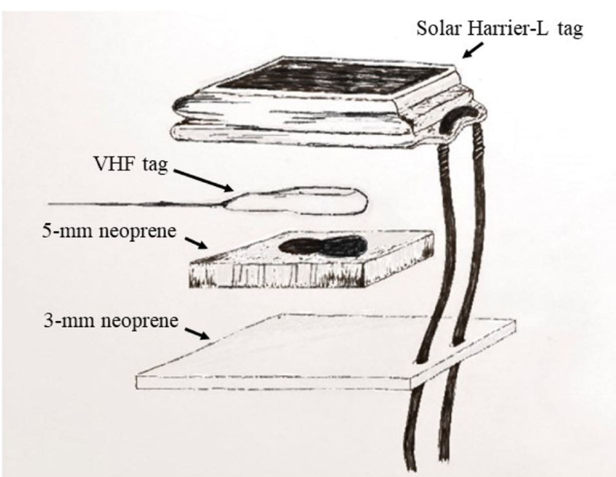

Figure 4. The components of the hybrid tag fitted on sage-grouse. The very-high-frequency (VHF) tag (RI-2B; Holohil Systems Ltd, ON, Canada) was centered and glued to the base of the Global Positioning System (GPS) logger (solar Harrier-L [long range download] GPS–UHF [ultra-high frequency]; Ecotone Telemetry Lech Iliszko, Sopot, Poland). The piece of 5-mm neoprene, with a cut out of the VHF outline, is glued to the base of the logger with the VHF nested within the neoprene. A piece of 3-mm neoprene is then glued to the bottom and the harness ribbon is threaded through the holes in the neoprene.

Based on concerns outlined in Bridge et al. (2011), we attempted to minimize aerodynamic drag by keeping the profile above the back of the hybrid tag as low as possible and positioning the VHF antenna parallel to the tail (Fig. 1). Unlike Argos PTT tags, the GPS loggers did not have an antenna protruding out of the back of the unit.

Cost Comparison

Estimating the net cost per datum of different tracking technologies has been shown to be a valid way to compare costs of different tracking technologies (Thomas et al. 2011). We compared costs per datum based upon the objectives of our study that required both location data and reproductive state information. Through the collective experience of the authors of this paper, we have used all of the tracking technologies being compared in this cost comparison while researching sage-grouse (Kirol et al. 2015*b*, Shyvers et al. 2019) We used realized costs from previous research and our current research project to provide a cost comparison per datum between VHF necklace tags (Fedy et al. 2015, Kirol et al. 2015*b*), Argos PTT tags (Hansen et al. 2014, Smith et al. 2016, Shyvers et al. 2019), and the hybrid tags used in this study. We standardized cost comparison across technologies based on marking and tracking 30 female sage-grouse for 4 months over a summer (May–Aug). To provide a conservative cost comparison of Argos technology, we assumed that sage-grouse fitted with Argos tags would require no tracking or monitoring in the field (i.e., no field visits) and satellite transmissions would occur on 5-day intervals. When using Argos technology, some field monitoring of the tagged sage-grouse might be necessary; however, some researchers have relied primarily on interpreting location and movement data to identify nesting attempts and reproductive state information (e.g., brooding or non-brooding female sage-grouse) with few field visits (e.g., Webb et al. 2012). For VHF necklace tags, we assumed a twice per week ground-tracking would be needed. This is a common monitoring interval in VHF sage-grouse studies occurring during the reproductive season because some nest attempts—nests that are initiated early and fail quickly—can be missed when grouse are monitored less frequently (Walker et al. 2016). The cost comparison included all expenses related to each technology and, based upon our current and previous research, assumed that 2 research technicians would be required to track 30 sage-grouse fitted with hybrid tags once per week and 3 research technicians would be required to track 30 sage-grouse fitted with VHF necklace tags twice per week (Table 1). For instance, costs of 3 telemetry flights used to locate missing grouse that were fitted with VHF necklace and hybrid tags were included in the cost comparison.

We explored cost comparisons for 2 GPS logger sampling frequencies. First, given the inherent disparities in the frequency of location collection of the GPS units, we compared the cost per datum based on standard collection frequencies associated with each technology. We based the estimated costs on 35 locations (i.e., 5/day) for the Argos PTT

Table 1. Cost estimates (USD) are for 30 female sage-grouse tagged with different technologies. Estimates are based on 4 months (May–Aug) of data collection. Cost estimates for very-high-frequency (VHF) necklaces (A4060; Advanced Telemetry Systems, Isanti, MN, USA) and tracking come from our previous research using these tags on sage-grouse (Fedy et al. 2015, Kirol et al. 2015*b*). Cost estimates for our hybrid tag (rump-mounted Global Positioning System [Solar GPS–UHF (ultra-high-frequency) tag, Harrier-L; Ecotone Telemetry Lech Iliszko, Sopot, Poland] fitted with a VHF [RI-2B; Holohil Systems Ltd, Ontario, Canada] add-on) come from our current study. All costs associated with field tracking and monitoring have been combined to provide a liberal estimate of costs. We derived cost estimates for the rump-mounted Argos tags (satellite up-link Argos, GPS Solar Platform Transmitter Terminal [PTT–100, Microwave Telemetry Inc., Columbia, MD, USA]) from previous sage-grouse research (Hansen et al. 2014, Shyvers et al. 2019). The estimates for the Argos tags assume that all data would come from remote data downloads and no field tracking would be necessary.

Tag type	Tags	Satellite download fee	Tracking equipment[a]	Tracking personnel[b]	Field transportation[c]	Telemetry flights[d]	Total
VHF necklace	$6,000	NA	$4,000	$29,520	$16,600	$4,500	$60,620
Argos PTT	$118,500	$6,872	NA	NA	NA	NA	$125,372
Hybrid tag	$48,000	NA	$6,500	$20,880	$14,400	$4,500	$94,280

[a] Tracking equipment for VHF tags included 3 receivers, 4 folding Yagi antennas, 3 personal GPS units, and $600 for miscellaneous and researcher safety equipment. Tracking equipment for the GPS logger–VHF included all the equipment listed above in addition to 2 UHF base stations, 2 unidirectional antennas, and 2 field tablets.

[b] For VHF necklace tags, requiring ground-tracking twice per week, we assumed that 3 researchers would be required to track 30 tagged sage-grouse. VHF necklace tag costs included hiring 3 research technicians and technician housing for 4 months. For Hybrid tags, that require ground-tracking only once per week, costs are for 2 researchers to track 30 tagged sage-grouse. Hybrid tag costs included hiring 2 research technicians and technician housing for 4 months.

[c] Field transportation costs for VHF necklace tags, included 1 truck rental and 3 ATV rentals and fuel for 4 months of biweekly ground-tracking. Field transportation costs for Hybrid tags, included 1 truck rental and 2 ATV rentals and fuel for 4 months of weekly ground-tracking.

[d] On the basis of our current and previous research, we assumed that 3 telemetry flights would be required to locate missing grouse over a 4-month tracking season. Costs are for VHF tracking from a fixed-wing aircraft for 6 hours/flight.

and hybrid tags and 2 locations/week for VHF necklaces. An Argos PTT tag sampling frequency of 5 points/day is a standard sampling frequency in the summer for sage-grouse studies using solar Argos PTT tags that occurred at a similar latitude (e.g., similar solar energy potential; Pratt et al. 2017). For the second comparison, we used the highest collection frequency we found in the sage-grouse literature of 15 points/day for Argos PTT solar tags (Dzialak et al. 2011) and compared this frequency with the highest collection frequency used in our research of 48 points/day. We only needed to ground-track our hybrid tagged sage-grouse once per week in this study, so we used this monitoring frequency in our cost comparison. It is important to note, weekly ground-tracking is not necessary if the study intent is only to collect GPS locations because, according to the manufacture, the GPS loggers (Harrier-L) can store 30,000 GPS locations on board. In fact, projects using the same equipment on other species (e.g., northern goshawk [*Accipiter gentilis*]) are designed around encountering birds twice per year to download data (Blakey et al. 2020).

RESULTS

Hybrid tags were fitted on 38 and 39 female sage-grouse in 2017 and 2018, respectively. The average body mass of the adult female (including first-year adults) sage-grouse was $1{,}428 \pm 165$ g. The GPS logger–VHF units (including the harness), weighed 29 g, which was approximately 2.0% of the body mass of all tagged females. The hybrid tag had a profile above the back of the bird of 21 mm. For comparison, the Argos PTT tags fitted on sage-grouse have a profile of approximately 20 mm, which includes 5 mm of padding. We did not find evidence of scabbing or tissue on the harness of any of the hybrid tags we retrieved after mortality events.

Throughout the year, the GPS loggers maintained high voltage (mean voltage $= 4.04 \pm 0.10$) when set to collect 6 GPS points/24-hour period. The voltage dropped very minimally (average voltage $= 4.02 \pm 0.11$) when set to collect 48 locations/24-hour period, even through the winter when annual solar radiation is lowest. When ground-tracking sage-grouse, the average distance to download GPS data from the loggers was 148.29 ± 14.04 m (range = 8.57–718.57 m).

As of October 2018, the independent VHF allowed us to recover 32 missing tags that had power loss or damage due to a predation event, unknown mortality, or, possibly, slipped tags. The majority of these were found undamaged but with the solar panel facing the ground or obstructed by vegetation. Grouse remains or evidence of depredation were present at the locations where the majority ($n = 25$) of these tags were retrieved. We did not find evidence of mortality at locations for 7 retrieved tags; therefore, it is possible these were slipped tags.

Cost Comparison

The overall costs for tags and data collection for a sample of 30 sage-grouse was highest for Argos PTT tags (US$125,372), followed by the hybrid tags (US$94,280), and VHF necklaces (US$60,620; Table 1). For the first comparison, with Argos PTT and hybrid tags standardized at 5 locations/day, the costs per datum for VHF necklaces (US$63.15) was 8 times greater than Argos PTT tags (US$7.46) and 11 times greater than hybrid tags (US$5.61). Costs per datum diverged more when hybrid tags were collecting 336 locations/week (every 30 min) versus Argos PTT tags collecting 105 locations/week (15/day) and VHF necklaces with 2 locations/week. At this collection frequency, cost per datum of Argos PTT tags (US$2.48) was 4 times more than hybrid tags (US$0.60) and costs per datum of VHF necklaces (US$63.15) was 105 times the cost of hybrid tags and 25 times the cost of Argos PTT tags.

DISCUSSION

The extensive testing and history of biotelemetry use on sage-grouse provides valuable information applicable to other, less studied, species. We tested a unique combination of a solar GPS logger coupled with an independent VHF tag to maximize our return on investment. For our research, this return resulted in frequent and reliable location data and a robust sample of tagged individuals to better inform population-level inference and demography. Coupling a GPS logger with a VHF tag proved to be beneficial in several ways, some of which were not anticipated. The hybrid tag was ideal for weekly tracking in the field to collect demographic data while simultaneously collecting high-resolution temporal and spatial data. The VHF tag, with an independent battery, proved critical in retrieving tags after a mortality. Further, our cost comparison demonstrated that the hybrid tag was the most cost-effective option given our research objectives.

Technological advances have reduced the mass and size of tags, resulting in more opportunities to collect location data from smaller species and species that fly (Bridge et al. 2011). However, combining 2 technologies into one unit, while maintaining independent power sources, is often not feasible because of the mass of the combined units exceeds tag mass-to-body mass ratio recommendations. Researchers have added independent VHF to Argos PTT tags, primarily to aid in tag recovery (Bedrosian and Craighead 2010, Hansen et al. 2014). Hansen et al. (2014) experimented with 2 types of VHF add-ons with a combined unit mass of 35–40 g, which is ≥5 g heavier than our hybrid tags and >3% body mass of an average adult female sage-grouse (Connelly et al. 2003). However, tag mass limitations were less restrictive for their research because the tags were fitted on male sage-grouse with average mass >1,000 g more than females (Beck and Braun 1978). The low mass of the GPS logger (Harrier-L) we used permitted the addition of a VHF tag with a battery life expectancy of 2 years and a pulse rate adequate for efficient tracking while staying below the commonly recommended tag to bird ratio of ≤3% (Bridge et al. 2011).

As with Argos PTT tags fitted on sage-grouse, the GPS loggers we used are dependent on the solar panel receiving enough light to maintain battery power. As a result of mortalities and obstructed solar panels, Hansen et al. (2014) lost 7 Argos PTT tags (~US$28,000) during the first year of their sage-grouse study. Some of their Argos PTT tags were retrieved by extensively searching the last GPS location that was transmitted to the satellite; however, these 7 tags were not found at the last transmitted location. The VHF add-on allowed us to retrieve 32 hybrid tags the first 2 years of our study. Without the independent VHF, we would have lost approximately US$51,000 in transmitter costs in addition to the location data stored on these loggers. Unlike Argos PTT tags, we generally did not have a GPS location to focus our searching efforts because we were manually downloading data in the field, not receiving location data remotely (e.g., remote download from satellite relay). Therefore, if the GPS logger shut off because of a lack of power, we did not have a recent location to focus our searching efforts. We did not anticipate this many tags would have power loss due to obstructed solar panels; however, similar to Hansen et al. (2014), it was common after a predation event for us to find the tag upside down with the solar panel facing the ground. Also, depending on the amount of damage inflicted on the tag, most can be refurbished for a fraction of the cost of purchasing new tags.

Power-management is an important consideration when choosing a tracking technology. The amount of sun exposure a solar tag receives changes seasonally with shorter days and low light conditions in temperate and polar winters and can also be affected by a species' behavior. For example, when tagged sage-grouse were on nests, which were underneath vegetation, the solar panels received less light and voltage dropped (≤0.2 V). Wintering sage-grouse will snow-burrow during severe winter weather, which has the potential to reduce voltage over the short-term (Back et al. 1987). Researchers using Argos PTT tags on sage-grouse have set the tags to collect from 3 to 9 locations/day (Dzialak et al. 2011, Hansen et al. 2014, Smith et al. 2016, Pratt et al. 2017, Foster et al. 2019). Dzialak et al. (2011) increased their Argos PTT tags to collect 15 locations/day from 15 May to 15 July when the solar panels were receiving sufficient sunlight. Compared with satellite systems, our GPS loggers use much less power for data transmission because these data are transmitted over a much shorter distance (Bridge et al. 2011). With a sampling frequency of 6 locations/day, our GPS loggers maintained high voltage year-round. We saw a small decrease in average voltage (voltage ~0.02) when the hybrid tags were collecting 48 locations/day. When compared with Argos PTT tags, the GPS loggers–VHF tags were able to collect 3 times the amount of location data while maintaining adequate battery power. Based on our experience, we suspect we could increase the locational frequency while maintaining power above manufacturer recommended minimum voltage.

Both the Argos PTT tags and the Harrier-L GPS loggers provide options that allow for ground-tracking using a UHF or VHF signal with additional equipment. However, the ground-tracking option is powered by the same battery; therefore, is also dependent on the solar panel receiving adequate sunlight to maintain power. Further, the ground-tracking option requires additional power from the battery that reduces the power available for gathering GPS locations and transmitting locations to a satellite or a base station.

Prior to the development of GPS tracking systems, relocation data were often impossible to collect in large enough quantities or at fine enough resolutions to answer many research questions for free-ranging wildlife (Hebblewhite and Haydon 2010, Thomas et al. 2011, Kays et al. 2015). Satellite relay GPS technology (e.g., Argos) provides highly precise spatial and temporal location data to a degree never before possible with VHF tracking (Hebblewhite and Haydon 2010, Kays et al. 2015). However, Hebblewhite and Haydon (2010) caution that there are also disadvantages of choosing GPS tracking technology over traditional VHF when researching animal ecology. Primary disadvantages, they discuss, include increased costs per tag leading to small sample sizes and poor population-level inference (Hebblewhite and Haydon 2010). Solely relying on obtaining data remotely from a computer can result in missed information and divorces ecologist from a field-based understanding of animal ecology (Hebblewhite and Haydon 2010). By coupling these 2 technologies, we believe we alleviated these tradeoffs.

Researcher presence in the field remains a necessary component of studies that require observational data. Yet, researcher presence does have a greater effect on study species, compared with data from tagged individuals that is only collected remotely (Fair et al. 2010). We took several steps to minimize adverse effects on sage-grouse in our study. For example, with the hybrid tags, we only needed to get in close proximity of tagged sage-grouse to confirm reproductive state or gather data such as the presence of chicks. Otherwise, we were able to download data from a distance that was unlikely to disturb the tagged grouse and their flock mates.

We maintained reasonable sample sizes because of the cost savings associated with using a ground-based GPS logger (data retrieved by mobile base station instead of satellite; Thomas et al. 2011) instead of a satellite relay unit. The upfront costs of our hybrid tags were less than half the costs of Argos PTT tags. These cost savings allowed us to tag twice as many individuals ($n \sim 40$) as we would have using Argos PTT tags. When considering the net cost per datum of these different tracking technologies, we found that VHF necklaces were the most expensive choice, followed by Argos PTT tags and hybrid tags. When we assessed common GPS location collection frequencies associated with these different technologies used in sage-grouse research, we found that costs per datum for our hybrid tags was 25% less than Argos PTT tags. The cost per datum diverged more when we compared our highest GPS acquisition frequency (48 points/day) with the highest Argos PTT tag frequency we found in the literature (15 points/day). We wanted to provide a conservative comparison between Argos PTT tags and our hybrid tags; therefore, we assumed that no field visits would be required when using Argos PTT tags and reproductive state would be determined based on location and movement data alone (Webb et al. 2012). However, if researchers using Argos PTT tags wanted to collect demographic data (e.g., brood survival) consistent with the data we collected using hybrid tags, a similar amount of field effort would likely be required. This, of course, would further increase the costs associated with Argos PTT tags and result in an even greater discrepancy between cost per datum.

The number of hybrid marked sage-grouse that went missing due to our inability to locate the VHF signal was relatively few during our study. However, we acknowledge the potential for large unexpected movements that would have resulted in an increase in the number of missing hybrid tags, which could affect cost comparisons for other research studies. Further, we recognize that VHF battery life, especially given the small size of VHF units used (i.e., ≤10 g), as it relates to study duration and objectives is an important issue when considering cost comparisons.

Cost per datum is a valuable way to compare different tracking technologies when high-frequency location data are required to meet research objectives (Thomas et al. 2011). However, if frequent location data are not necessary to meet the objectives of a study than cost per datum is not a valid comparison metric. For example, drawing from the sage-grouse literature, if the intent of the study is to assess how female survival rates are affected by anthropogenic features over a large landscape then a robust sample of VHF-tagged individuals is preferable to a much smaller sample fit with Argos PTT tags or hybrid tag (Dinkins et al. 2014). In this case, having an adequate sample of individuals to model survival outcomes is much more important to the objectives of the study than having frequent location data from fewer individuals. If one just looks at initial costs of the tracking technologies compared in this paper, 240 VHF necklaces could be purchased for the same price as 30 hybrid tags.

To achieve our research objectives, we regularly tracked hybrid-tagged sage-grouse in the field to verify reproductive state and gather demographic data (Kirol et al. 2015*a*, Smith et al. 2018). For instance, by ground-tracking sage-grouse weekly we were able to confirm the fate of sage-grouse nests (nest survival), confirm whether a female was brooding chicks or whether she was no longer with chicks (brood survival and reproductive state), and gather information on depredation events (causes of mortality). These data were not only important to our research objectives, but also helped us to better understand fitness outcomes associated with habitat selection, which are often overlooked in ecological research (Kays et al. 2015).

The hybrid tag we designed would be most beneficial for species of which tag mass is a limiting factor (i.e., smaller, volant species) and species that do not undergo long-distance migrations. The hybrid tag would be less effective on a long-distance migratory species because of the effort and costs associated with using a VHF to track birds over large areas (Cochran 1987, Bridge et al. 2011). For long-distance migrants, either satellite-relay GPS (e.g., Argos) or a cellular-relay GPS (GPS data is transmitted through cellar networks) tags would likely be a more appropriate choice because GPS location data could be acquired while the bird was migrating and location data would not be lost if the bird died at an unknown location during migration or did not return to the area of original capture (Bridge et al. 2011). However, researchers studying migratory raptors with high site fidelity are using Harrier-L GPS loggers to collect location data when the species returns to a breeding territory by setting up stationary base stations in these territories (Blakey et al. 2020).

Sage-grouse typically move short distances within seasonal habitats (Fedy et al. 2012). In our study region, the longest movements recorded (~12 km) occurred when sage-grouse moved to wintering areas (Fedy et al. 2012). Consequently, our tag design would be best applied to research on largely resident or short-distance migratory populations and species. Many Galliformes are either nonmigratory or only make short-distance movements. Therefore, we believe the hybrid tag would be beneficial for research on many Galliformes, especially when observation data are needed in conjunction with high-resolution location data. A few examples include the lesser and greater prairie-chicken (*Tympanuchus pallidicinctus, T. cupido*) and sharp-tailed grouse (*T. phasianellus*), in North America; black grouse (*Tetrao tetrix*), capercaillie (*Tetrao urogallus*), and red grouse (*Lagopus lagopus*) in Europe; and Reeves's pheasants (*Syrmaticus reevesii*) in Asia, all of which are relatively localized year-round (Johnsgard 1983, Giesen and Connelly 1993, Hagen and Giesen 2005, Xu et al. 2009, Johnson et al. 2011).

Many new tracking technologies have become available to wildlife researchers over the past few decades, and each has strengths and weaknesses (Bridge et al. 2011, Thomas et al. 2011, Kays et al. 2015). In designing our hybrid tag and harness system, we hoped to reduce effects on sage-grouse, increase the amount and reliability of collected location data, maintain our ability to track birds in real-time from the ground, and decrease costs and increase sample size compared with satellite GPS transmitters. Our hybrid tags proved to be the most cost-effective option to meet the objectives of our study. Cost savings compared with satellite systems allowed us avoid sacrificing sample size while still gathering high-resolution location data. Hebblewhite and Haydon (2010) argue that emerging GPS-tracking technologies should not replace field biology but be used in conjunction to effectively research animal behavior and ecology. Our hybrid tags accomplish this by coupling traditional VHF tracking methods and field-based observational data with newer GPS tracking that provides accurate and more frequent location data.

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