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Review of GPS Collar Deployments and Performance on Nonhuman Primates

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Abstract

Over the past twenty years, GPS collars have emerged as powerful tools for the study of nonhuman primate (hereafter, "primate") movement ecology. As the size and cost of GPS collars have decreased and performance has improved, it is timely to review the use and success of GPS collar deployments on primates to date. Here we compile data on deployments and performance of GPS collars by brand and examine how these relate to characteristics of the primate species and field contexts in which they were deployed. The compiled results of 179 GPS collar deployments across 17 species by 16 research teams show these technologies can provide advantages, particularly in adding to the quality, quantity, and temporal span of data collection. However, aspects of this technology still require substantial improvement in order to make deployment on many primate species pragmatic economically. In particular, current limitations regarding battery lifespan relative to collar weight, the efficacy of remote drop-off mechanisms, and the ability to remotely retrieve data need to be addressed before the technology is likely to be widely adopted. Moreover, despite the increasing utility of GPS collars in the field, they remain substantially more expensive than VHF collars and tracking via handheld GPS units, and cost considerations of GPS collars may limit sample sizes and thereby the strength of inferences. Still, the overall high quality and quantity of data obtained, combined with the reduced need for on-the-ground tracking by field personnel, may help defray the high equipment cost. We argue that primatologists armed with the information in this review have much to gain from the recent, substantial improvements in GPS collar technology.

Keywords: ranging, wildlife tracking, satellite, spatial ecology, primate behavior

Introduction

Over the last twenty years, Global Positioning System (GPS) telemetry collars have significantly improved the availability and accuracy of animal location data, consequently improving our understanding of animal behavior and ecology (Cagnacci et al. 2010; Kays et al. 2015). These devices can now often acquire GPS data and establish location of collar position with high precision even in challenging field conditions (Moriarty and Epps 2015). In addition, GPS collars have become more affordable, lighter, and smaller, making them potentially valuable tools for researchers who work with small-bodied, semi-terrestrial, arboreal, cryptic, or nocturnal species (Blackie 2010; Recio et al. 2011; Forin-Wiart et al. 2015; Stark et al. 2017). For primatologists, these factors have made it possible to extend the use of GPS technology beyond large (6.5-25+kg), terrestrial species living in open savanna such as baboons (Markham and Altmann 2008; Markham et al. 2013, 2015) to much smaller (2.5-6.5kg), arboreal, or semi-arboreal species such as long-tailed macaques, vervet monkeys, and ring-tailed lemurs (Parga 2011; Dore et al. 2015; Klegarth et al. 2017a,b).

Radio tags have been used to facilitate the tracking of animal movements since the 1960s (Lord et al. 1962). The use of this technology in primatology grew in popularity in the 1980s and 1990s (e.g. Bearder and Martin 1980; Campbell and Sussman 1994; Fedigan et al. 1988), but data from this time period are sparse because of the intensive manual labor required to find animals and record locations using very high frequency (VHF) devices (Kays et al. 2015). While VHF devices continue to be deployed by primatologists due to their cost effectiveness, small size, and low weight (e.g. Gursky 2000), GPS telemetry has become an increasingly common technique to locate and follow primates. Scholars first used GPS collar technology in the 1970s (e.g.

Craighead et al. 1972), and primatologists specifically began using the technology with larger-bodied primates in the 2000s (baboons: Henzi et al. 2011; Markham and Altmann 2008; Segal 2008; chimpanzees: Humle et al. 2010; Japanese macaques: Sprague et al. 2004; Takenoshita et al. 2005; and snub-nosed monkeys: Ren et al. 2008). GPS technology has provided researchers with advanced research capabilities. With GPS collars, it is now possible to obtain spatiotemporal data automatically and in a prescheduled manner, facilitating investigations in areas and at times where obtaining animal location data was previously challenging or impossible. That is, GPS collars can facilitate the systematic collection of location data that are less constrained by topography and surrounding vegetation, which can limit the ability of observers to follow animals and record positions directly, providing more reliable data (García-Toro et al. 2019). Devices are now also able to collect data on variables such as temperature and elevation, and data analysis programs can calculate distance between GPS coordinates, which can provide information about speed, periods of activity vs. inactivity as well as elucidate nocturnal activity in diurnal species (e.g. Isbell et al. 2017). Additionally, with GPS collars, animals are free to move without the influence of observer presence, which can affect their ranging behavior (although the collars themselves may also influence ranging behavior; see Discussion). GPS technology also allows for the collection of high-resolution data at very short individuals, tracking animals in areas not possible on foot, the ability to track unhabituated animals, the simultaneous collection of high-resolution data from multiple individuals, and the ability to obtain data on individual animals' decision-making processes (e.g. Kays et al. 2015; Strandburg-Peshkin et al. 2015).

Because many species of primates are arboreal, GPS units deployed on the body of the animal (as opposed to being carried by an observer on the ground) can improve satellite reception and collect more accurate positional fixes. Fix acquisition and location accuracy is dependent on many factors such as canopy cover, terrain, time of day, weather conditions, and vertical movement patterns of the study species. Positional dilution of precision (PDOP) values assess fix accuracy; values range from 1.0 to 99.9, with lower numbers indicating wider satellite spacing and thus improved location accuracy. GPS collars also record horizontal dilution of precision (HDOP), which also ranges from 1.0 to 99.9, with lower numbers indicating lower error due to satellite height (Moen et al. 1996; Pebsworth et al. 2012a). Researchers often choose to remove fixes with high PDOP values to improve fix accuracy; more accurate GPS collars can thus lead to significantly more data. Recent advances in GPS collar technology also include activity sensors, such as accelerometers. Activity sensors are quite common in human activity studies (Huang et al. 2018) but have only recently been incorporated in wildlife GPS collars (McClintock and Michelot 2018; Pebsworth et al. 2012a). With advances in activity sensor techniques and the development of methods for activity data analysis, our ability to investigate certain types of behavior (e.g. ranging, habitat use, activity patterns) remotely will continue to increase and thus lead to significantly more usable data, improving our capability to test more precise hypotheses.

There are always risks associated with methods that allow GPS collars to be attached to primate study subjects. Important factors to consider include harm to animals as a result of darting or trapping (de Ruiter 1992), skin lesions or infections from collar wear (Müller and Schildger 1994; Anderson 2017; Klegarth et al. In press), collar impacts on behavior (e.g. activity patterns, ranging, foraging, infants' nursing) (Coughlin and van Heezik 2015), or the possibility of rejection from the troop (this is more likely to occur when the animal is removed from the group for a period of time, see de Ruiter 1992 and Juarez et al. 2011). Collars also pose an energetic cost to the animal, which may not be inconsequential. Fortunately, most VHF and GPS telemetry studies on primates report normative behavior and healthy animals post-collaring (e.g. Gursky 1998; Blakie 2010; Juarez et al. 2011; Pebsworth et al. 2012a; Matthews et al. 2013; Kenyon et al. 2015; Evans et al. 2016; Klegarth et al. 2017a,b; Hansen et al. *in prep*). However, there may be a lack of reporting of negative and deleterious effects.

Many investigations of primate behavior now feature the use of GPS technology (e.g. Ren et al. 2008; Humle et al. 2011; Parga 2011; Klegarth et al. 2017a,b; Koch et al. 2016; Springer et al. 2016; Springer et al. 2017), yet the focus of these studies is rarely on the functionality of the devices themselves (but see Sprague et al. 2004; Pebsworth et al. 2012a; Kenyon et al. 2015; Isbell et al. 2019). This leaves primatologists without reliable guidance related to choosing the appropriate device, overall device performance, and the benefits and drawbacks of different devices with regard to data collection, collar and data retrieval, collar refurbishment, and animal welfare. GPS collar field tests on primates only began in the past decade and a half (Sprague et al. 2004) and have only recently expanded as the size and cost of GPS collar units have decreased. In addition to the fact that many publications only touch on GPS collar performance issues, the results of failed field tests largely go unpublished.

In this paper, we review GPS collar deployments and unit performance in studies of primates. While GPS collar performance will always be dependent on site- and species-specific variables, our compiled dataset will serve as a reference point for primatologists interested in utilizing GPS collars in their research programs. The dataset includes strepsirrhines, both Old and New World monkeys, as well as gibbons and chimpanzees (*Pan troglodytes*). Deployments occurred in research colonies as well as on free-ranging animals across a diverse range of habitats including open savannah, Mediterranean scrub, fragmented forested landscapes, rainforests, and heavily urban areas. We outline the range of primate taxa on which GPS collars have been deployed, provide an overview of GPS collar manufacturers and collar capabilities, and summarize crucial performance statistics to compare models as best as possible across this diverse dataset. While most relevant to researchers considering GPS collars for use on primates, GPS manufacturers and individuals interested in collaring non-primate taxa living in similar ecological conditions will also benefit from this comprehensive review.

Methods

Specific details regarding individual collar deployments can be found within the publications referenced and authors cited in Table 1. In addition to published data, we also reviewed conference proceedings from 2000-2017 and solicited unpublished information on GPS collar deployments by reaching out to individual authors via email. We collected data for this review within three primary categories: 1) primate study subject characteristics, 2) collar, programming, and deployment specifications, and 3) GPS collar performance. Subject characteristics included species, age class, sex class, and weight (kg) for each GPS-collared individual. Collar, programming, and deployment specifications included collar manufacturer, collar model, locational fix schedule, collar weight (g), drop-off type (if any), deployment length (we define deployment length as the time the device was on the animal, which may or may not coincide with battery life), and the total number of attempted fixes. GPS collar performance data included the total number of acquired fixes, the total number of 3D (high quality) fixes, the average time to fix (TTF), the mean number of satellites connected per fix, the average horizontal dilution of precision (HDOP), drop-off functionality, and battery life. From these data we calculated the mean ratio of collar:animal weight by species in addition to an overall fix success rate (FSR) and a 3D FSR.

Table 1. Summary of GPS collar deployments on NHPs

Species	Brand	Model	Collar:Animal Weight (%) ± Stdev*	Study	Habitat Type** *Type/Season* .	*Canopy*
Lemur catta	Telemetry Solutions	Quantum 4000 Medium	3.08	Parga 2011	Semi-tropical Mixed Forest Year-round	Open to Moderate
Propithecus verreauxi	e-Obs Digital Telemetry	Collar 1A	2.38±0.25	Koch et al. 2016, Springer et al. 2016, Springer & Kappeler 2017	Dry Deciduous Forest Year-round	Moderate to heavy
Ateles belzebuth	Telemetry Solutions	Quantum 4000 Medium	1.50±0.05	Di Fiore and Link 2013	Tropical Rainforest, Year-round	Heavy
Ateles geoffroyi	e-Obs Digital Telemetry	Collar 1C	2	Campbell pers. comm.;	Lowland Tropical Forest Dry season	Moderate to heavy
Ateles hybridus	Telemetry Solutions	Quantum 4000 Medium	2.10±0.29	Di Fiore and Link 2013	Tropical Rainforest Year-round	Heavy
Lagothrix lagotricha	Telemetry Solutions	Quantum 4000 Medium	1.93±0.23	Di Fiore and Link 2013	Tropical Rainforest Year-round	Heavy

Chlorocebus sabaeus	Tellus	Ultra-light	5.0	Dore et al. 2015	Mixed	Open to heavy
Macaca fascicularis	Telemetry Solutions	Quantum 4000 Medium	1.81±0.23 1.57±0.25	Klegarth et al. 2017; Stark (*pers. comm.*); Tan (*pers. comm.*)	Tropical rainforest with Riparian Areas Dry and Wet Season	Open to heavy
Macaca fascicularis	Tellus	Micro	1.57±0.25	Hansen et al. in prep	Tropical Semi-arid Mixed Habitats Dry and Wet Season	Open to Moderate
Macaca fuscata	Televilt	Porsec 120	3.08	Sprague 2004	Mixed rural, including broadleaf forest	Open to Moderate
Macaca mulatta	Tellus	Ultra-light	3.33	Anderson et al. 2017	Subtropical Swamp and Forest Dec-Feb	Moderate
Macaca sylvanus	Telemetry Solutions	Quantum 4000 Medium	1.50±0.01	Klegarth et al. 2017	Subtropical Mediterranean Dry and Wet Season	Open-light scrub coverage with extensive cliffs and rocky outcroppings
Nasalis larvatus	e-Obs Digital Telemetry	Collar 1C-Light	1.08±0.24	Stark et al. 2017	Riparian Forest,	Moderate

Nasalis larvatus	Lotek	WildCell SD	1.81±0.69	Stark et al. 2017	Plantation Year-round Riparian Forest, Plantation Year-round	Moderate
Papio cyncocephalus	Advanced Telemetry Systems	G2110B	1.90±0.44	Markham et al. 2013	Semi-arid Savannah and Woodlands Apr-Aug Wet and Dry seasons	Open to Moderate
Papio ursinus	Advanced Telemetry Systems	G2110B	2.28	Pebsworth, Morgan et al. 2012; Pebsworth, MacIntosh et al. 2012	Afro-Montane Forest, Fynbos, Mixed Forest, Agriculture Year-round	Open to Moderate
Rhinopithecus roxellana	Lotek	7000SLU	2.62±0.44	Qi et al. 2014	Semi-humid Temperate Cold Mixed Forest Year-round	Moderate
Nomascus gabriellae	Lotek	WildCell	3.54	Kenyon et al. 2015	Lowland Mixed Forest Wet season	Heavy

Pan troglodytes	Telonics	TWG-4500; TWG4580	-	Humle et al. 2011	Mixed Forest, Mixed Savannah Year-round	Open to Moderate

* Depending on age class of animal, see summary of age classes in text. **Canopy cover is characterized as none, open, moderate, and heavy.

Table 1 also includes information on habitat type as reported by each contributing author on their study site. Researchers were queried on habitat type, the season(s) during deployment, as well as the degree of canopy cover. This information is meant to contextualize the environmental conditions surrounding each deployment. Given the vast range of species and habitats and the somewhat subjective nature of this reporting, habitat data are provided primarily as a resource for researchers exploring the use of GPS collars on primates in the future.

Ethical Note

All studies were carried out under each author's respective Institutional Animal Care and Use Committee approved protocols (provided in the Acknowledgements).

Data Accessibility

We have an included a supplemental file with all of our data.

Results

Subject Characteristics

The dataset comprises information on 179 individual GPS collar deployments by 16 research groups on 17 primate species between 2004 and 2018 (Figure 1). Study subjects included two species of strepsirrhines, five species of New World Monkeys, eight species of Old World Monkeys, one species of gibbon, and one great ape (Table 1). Of these, the vast majority (93.3%) of devices were deployed on adult animals. Only seven species included GPS collar deployments on subadults (6.7%) owing in part to limitations in the collar:animal weight ratios, trade-offs between collar weight and battery life, and the need to ensure the animal does not outgrow the device in the case of drop-off failure. Dispersal patterns and research questions also limit appropriate age groups. Mean collar:animal weight ratios fell well-within the standard recommendation ≤5% of total body weight (Sikes 2016), ranging from a low of 1.08% to a high of 5.0% by species.

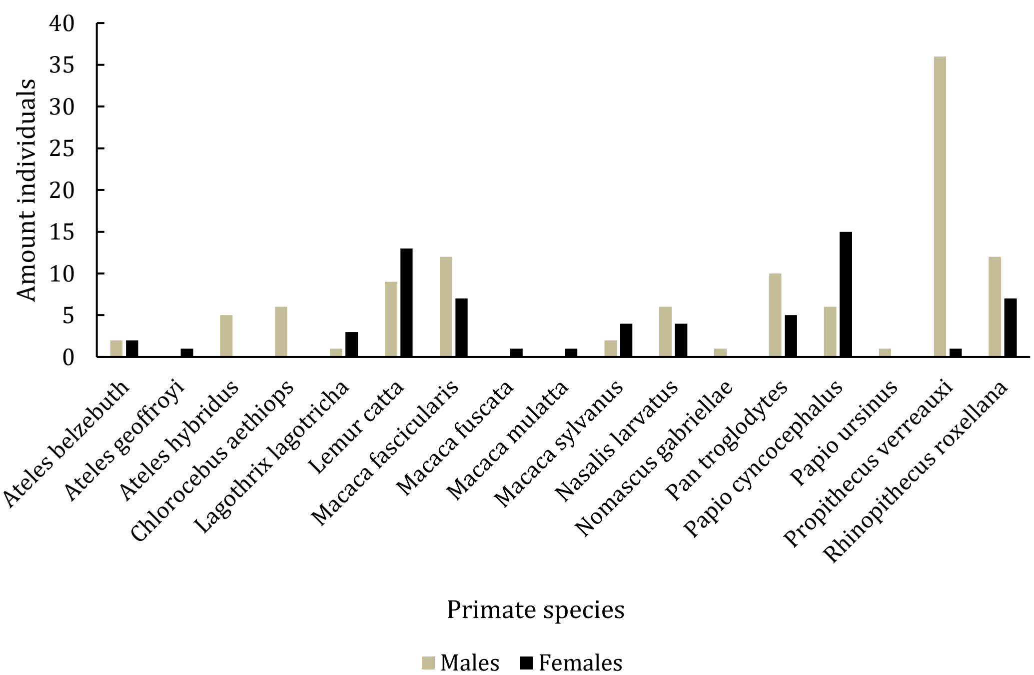

Figure 1: Number of GPS collar deployments by species and age group

In terms of sex, there were almost equal numbers of studies that collared more females than males (N=8) and more males than females (N=9). One species (*Ateles belzebuth*), had an equal number of males and females collared. Across the entire dataset, GPS collars were more commonly deployed on males, with an overall male:female ratio of 1.0:0.6 (Figure 2). Research questions, dispersal patterns, GPS collar availability, and funding all affected the choice of sex groups. Older studies (>5y) skew towards males strongly for smaller-bodied species such as vervets and long-tailed macaques and for some GPS collar brands owing to size limitations and sexual dimorphism where males are larger than females (Fooden 2006; Turner et al. 1997). An exception to GPS collar deployments favoring males in smaller bodied primates occurred with ring-tailed lemurs, where the ratio favored females (Parga 2011; Parga unpublished data) and little sexual dimorphism exists within the species (Kappeler 1991). Newer studies (<5y) have had greater GPS collar availability, as brands and models are expanding, and scholars have had greater opportunities to choose a device based on their specific research questions (e.g. a newer long-tailed macaque study; Hansen et al., *in prep*).

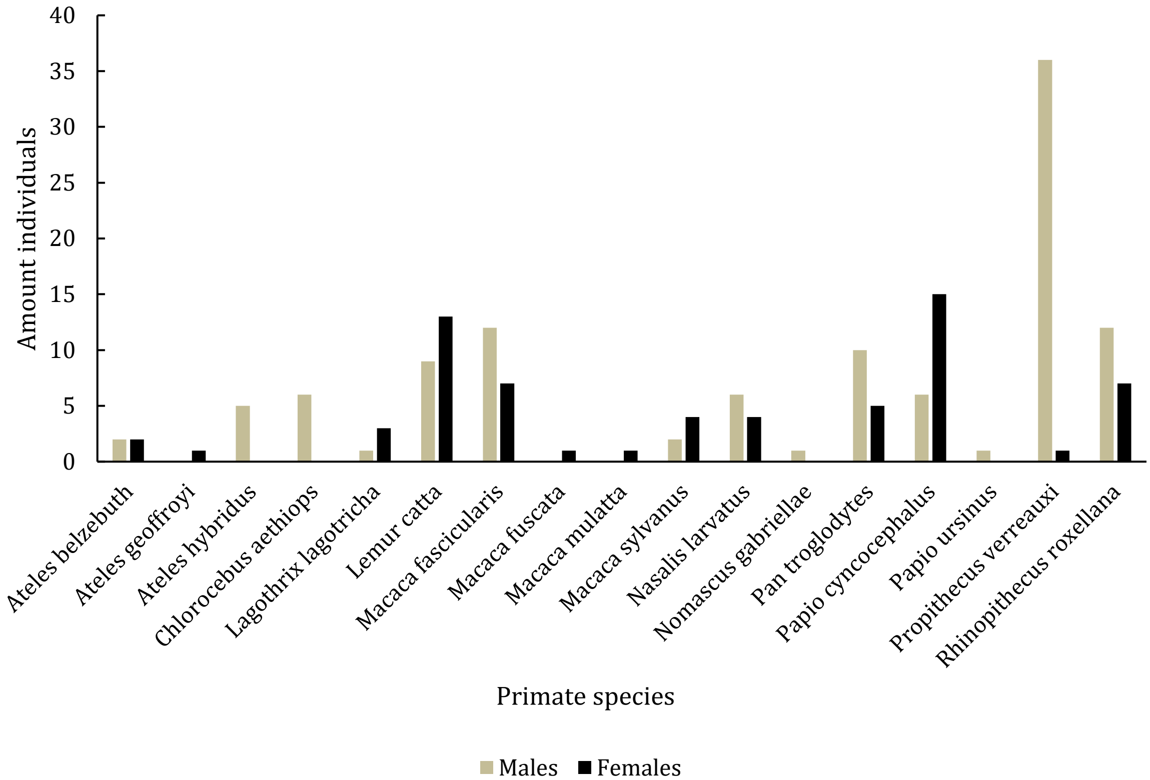

Figure 2: Number of GPS collar deployments by species and sex, mean sex ratio (M:F) 1.5:0.6

Collar, Programming, and Deployment

The two collar brands most frequently deployed on primates were e-Obs Digital Telemetry (N = 42) and Telemetry Solutions (N = 54). Telemetry Solutions were used by four independent research groups and e-Obs Digital Telemetry by three. Three independent research groups deployed Tellus collars (N=13). Advanced Telemetry Systems (N = 22), and Lotek (N = 26), collars were each deployed by two independent research groups. One research group deployed Telonics devices (N = 21). Several research groups only deployed a single unit (Televilt, Tellus Ultralight, e-Obs Digital Telemetry, Advanced Telemetry Systems, and Lotek). This is not an exhaustive review, and so there are collar manufacturers not included in the review.

All devices were placed on the necks of the animals (i.e. Figures 3 and 4), with the exception of Dore et al. (2015) (*Chlorocebus sabaeus*) and the Singapore's National Parks Board (*personal communication*) (*Macaca fascicularis*) where the devices were placed around the animals' waist like a belt (see Figure 5). This placement is suitable in situations where collars are too bulky to be worn comfortably around the neck; however, this style of deployment biases towards the use of male primates as subjects because of pregnancy concerns and thus may not be appropriate for certain research questions.

Figure 3: Savannah baboon (*Papio cyncocephalus*) with Advanced Telemetry Systems G2110B GPS collar attached around neck (credit Catherine Markham)

Figure 4: Ring-tailed lemur (*Lemur catta*) with Telemetry Solutions Quantum 4000 Medium GPS collar attached around neck (credit Joyce Parga)

Figure 5: Green monkey (*Chlorocebus sabaeus*) with Tellus Ultralight GPS collar attached around waist (credit Kerry Dore)

In addition to collar placement, GPS collars varied by: weight, presence/absence of drop-off mechanisms, fix rate, amount of time deployed, and overall collar and drop-off unit performance. Collar weight ranged from 77-1100g, and drop-off units ranged in weight from 2-150g (Figure 6). The majority of collars were programmed to take locational fixes at regular intervals either over a 24-hour period or split between daytime and nighttime scheduling. The most commonly programmed fix intervals were every 10-15 minutes (N = 40), 30 minutes (N = 51), 45 minutes (N = 12), 60 minutes (N = 37), and 120-180 minutes (N = 63). Some collars had two different fix schedules, alternating between a day and a night schedule. We counted these collars in both of their fix schedule intervals. A total of 25 deployments split their collar programming between daytime and nighttime fix acquisition schedules, 102 deployments took points over a continuous interval (e.g. every *x* minutes until battery death), and another 52 collars collected points only during the daytime period when primates were expected to be most active. Some exceptions to more standard fix acquisition programming included a collar programmed to record locations at five hour intervals (Kenyon et al. 2015), and collars programmed to take locational fixes and standard intervals several days a month and single daily points in between the high-fix days (Di Fiore and Link 2013).

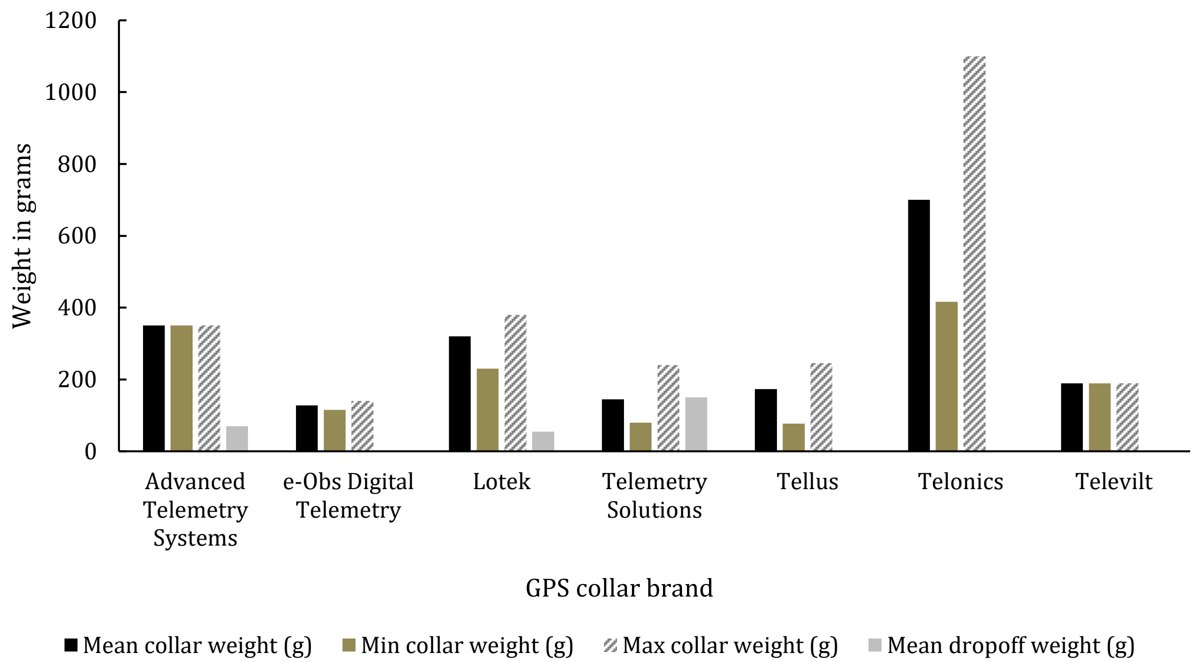

Figure 6: GPS collar weights by brand including drop-off units where applicable, and drop-off weights by brand.

Regarding length of collar deployments, some lasted less than a single day, with a total of 8 GPS collars deployed for a week or less (Parga 2011; Klegarth et al. 2017a,b). The variables that contributed to short collar deployments include collar malfunction, fix schedule, and environmental conditions (factors that are not mutually exclusive; see Discussion). Some short deployments were intentionally short; thus, these data are a simple measure of how long the devices were on the animals (i.e., a mix of successes and failures). The longest deployment of a functional GPS collar was 89 weeks long (with a fix schedule of every two hours; Qi et al. 2014). Average deployment length across all studies (excluding collars that failed to drop-off and remained on animals beyond their battery life) was 26 weeks with a median deployment length of 20 weeks. The deployment length of 23 collars was undetermined either due to the loss of the unit due to early removal (N = 5), disappearance of the animal (N = 7), or loss of unit functionality that prevented the collar from dropping off (N = 11). In the case of units that failed to drop-off and where recapture was either not possible or deemed a greater risk to animal safety than leaving the collar on, animals have been collared for up to six years with no overt signs of distress or injury (Klegarth et al. 2017a,b, In press).

Participants in this study retrieved collar data in a variety of ways, with some research groups using more than one technique. Data were retrieved by direct USB download (after physically recovering the device; 8 research groups), remote UHF download (requiring the collar be within a certain distance of an antennae; 8 research groups), GSM transmission (i.e. text messages sent via the local phone network; 4 research groups), and Iridium (satellite) transmission (1 research group). Utilizing technology that does not require recovering the physical device (i.e. the latter three options) is ideal, as it ensures that the user obtains the data if the collar unintentionally falls off and is not able to be found, the drop-off fails, or the animal is unable to be re-trapped. With regard to animal welfare, the use of biodegradable weak links (see Discussion) can ensure that the device is not left on the animal indefinitely.

GPS Collar Performance

Of the two primary data quality metrics measured, 1) HDOP and 2) 3D FSR, only four collar brands provided data on both metrics; Lotek, Telemetry Solutions, Advanced Telemetry Systems (one out of 22 units), and Tellus. Neither Televilt, nor e-Obs Digital Telemetry, nor Telonics units calculated or provided HDOP with GPS data from the collars. Among the collar brands that did provide HDOP values, Tellus and Advanced Telemetry Systems collars provided fix locations with mean HDOPs of 1.1 or 1.8 for Tellus, depending on the collar model, and 1.5 for

Advanced Telemetry Solutions. Telemetry Solutions provided fixes with a mean HDOP of 2.0. Lotek collar HDOPs had a mean value of 4.1 between both models, though the Wildcell SD model performed better than the 7000SLU units. In terms of the 3D FSR relative to the total number of acquired fixes, collars made by e-Obs had a mean a mean 3D FSR of 100%. Tellus 3D FSRs were 97.1% and Telemetry Solutions collars were 89.5%. Lotek and Advanced Telemetry Systems 3D FSRs were 86.3% and 85.9% respectively.

The other major performance metrics measured were 1) TTF (which impacts collar battery life, as the collar shuts down between fixes in most collars to save battery) and 2) overall battery life of units relative to the expected battery life at deployment based on programming. E-Obs Digital Telemetry devices obtained fixes in 22 seconds on average followed by Tellus Micro (47 seconds), which was followed closely by Advanced Telemetry Systems (50 seconds), Tellus Ultra Light and Lotek (54 seconds), and with Telemetry Solutions (77 seconds). These data were not available for Telonics devices. Of the four most commonly deployed brands (e-Obs Digital Telemetry, Telemetry Solutions, Advanced Telemetry Systems, and Telonics), Telonics and Advanced Telemetry Systems experienced the longest battery life. Early battery death was somewhat common for Lotek (12.5%), e-Obs Digital Telemetry (29.5%), and Tellus (30.0% for Ultra Light and 33.33% for Micro) devices, which reduced the amount of data acquired from those deployments. Fix schedule, TTF, and battery size, severely affected battery life and should be taken into consideration in the study design. While we are dealing with a relatively small sample size, Telemetry Solutions and Tellus Micro were the only brands with malfunctions reported that interfered with the ability to perform at least some data collection (11.3% and 33.3% of deployments, respectively). It should also be noted that the data reported here does not take into account environmental conditions, which significantly affect collar performance (see Discussion).

Drop-off Unit Performance

Of the 179 GPS collar deployments we evaluated, 91 units were equipped with remote, electronic drop-off units, some of which were purchased from separate manufacturers. Four e-Obs Digital Telemetry collars were equipped with drop-off from separate manufacturers; their drop-off functionality was not assessed in this review. Of the 91 units, 16 were lost before the scheduled drop-off time (e.g., the animals were killed or disappeared, the battery died, or the collar was somehow removed from the animal) and thus their drop-off functionality could not be assessed. In our dataset, Advanced Telemetry Systems, Televilt (N=1), and Tellus Ultralight units had drop- off performance success over 90% (Table 2). With Lotek WildCell SD, Telemetry Solutions, and Tellus Micro, approximately half worked. Lotek 7000SLU drop-off functions all failed to perform. Advanced Telemetry Systems and Telemetry Solutions deployments all included 10+ attempted drop-offs and 100 day+ mean ‘live’ deployments for collars equipped with electronic drop-off units. One unit (Lotek WildCell) was equipped with physical weak spots on the GPS collars to function as the sole drop-off mechanism. Several studies reported that drop-off function did work, though not as expected, with up to several months delay in dropping off.

Table 2. Mean deployment length, and battery performance for GPS collars used in NHP studies*

Brand	Model	N =	Collar Deployment Length (days)	FSR	Battery Life Performance (%)**** *> Expected*	*Maintained*	*< Expected*	Drop-off Performance (%)***** *Worked*	*Fail*
Advanced Telemetry Systems	G2110B	22	324±35	86±11.8	95.5	-	4.5	100	-
e-Obs Digital Telemetry	Collar 1A, 1C, 1D	42	172.5±41.5	93.2±7.5	41.4	29.1.0	29.5	NA******	
Lotek	Wildcell SD	7	431±36	82.8±16.8	58.4	16.6	25	50	50
Lotek	7000SLU	19	275±145	91.0±19.6	10.5	84.2	5.2	-	100
*Telemetry Solutions***	Quantum 4000	54	140±122	87.8±8.7	41.7	58.3	-	66.7	33.3
Televilt	Porsec 120	1	9	20.0	-	100.0	-	100	-
Tellus	Ultralight	7	67±16	96.1±2	-	91.7	8.3	100	–
*Tellus****	Micro	6	81±21***	65.9±4.24	-	-	100	50	- 50
Telonics	TGW-4580; 4583; 4500	21	143±77	13.2±2.1	100	-	-	NA	

*Not all data was available for all collars. FSR is the overall fix success rate based on the total number of programmed. **Five collars malfunctioned. ***Two collars malfunctioned*. ****Several studies were not able to recover collars and thus the battery life performance of these units is unknown and accounts for the discrepancy in the reported percent battery life performance not summing to 100% for all collars listed. Sample sizes are indicated for full collar deployments only, where collar remained through the set study period, and exclude those collars that were removed early by either the NHP or the research team. *******

Several collars were removed by either the NHP or the researchers rather than activating the drop-off unit; sample sizes are reported only for collars with drop-off units that researchers attempted to use. ****** e-Obs Digital Telemetry does not manufacture drop-off units.

Discussion

GPS collar performance has significantly improved since the technology was first used to facilitate our understanding of primate behavior and ecology a decade and a half ago (Sprague et al. 2004). Here we have presented the first review of this technology across a diverse array of primate species (17 primate species, and 7 GPS collar manufacturers). While our results are significant and important, it is essential that researchers recognize that site- and species-specific variables will interact in complex ways to affect collar performance at their field sites. The interactions between collar manufacturer, environmental conditions, satellite availability, species behavior and habitat preferences, and fix schedule in particular will interact differently for every user. For example, a collar may perform exceptionally well for TTF and have a long battery life in open field conditions, but in high canopy cover areas the same collar performance should not be expected. We therefore see this paper as a helpful starting point, but not an exhaustive statistical review, of GPS collar performance.

While our review highlights many positive aspects of GPS collar technology for primatology, we also want to caution against using GPS collars as a substitute for standard primatological data collection techniques. Often, the high cost of GPS collars has a negative impact on sample sizes, which may reduce the strength of inference at population levels (Hebblewhite and Haydon 2010). There are clear limitations in the types of data that can be collected with GPS collars; they should therefore be combined with direct field observations of movement and habitat use patterns to enable adequate interpretation of data. For example, using one or a few devices to assess the movements of an entire troop will miss nuanced sex- or age-specific movements or behaviors only detectable through direct observations of group dynamics. In many cases, questionnaires, interviews, or ethnographic data collected from people sharing space with primates can also provide extremely important information that would be lost by relying too much on tracking technology. For example, in St. Kitts, while GIS and GPS data has been highly informative with regard to green monkeys' current behaviors and range, only through conversations with local people were primatologists able to learn the extent to which the closure of the sugar industry in 2005 affected these behaviors and movements (Dore et al., in press).

This dataset, and primate GPS collar deployments broadly, are still biased towards heavier collar units (5 of 7 brands had mean collar weights of 175+g) which can have longer battery life depending on fix schedule and TTF among other variables. Telonics collars were the largest deployed at 1100g. The larger size of units available in the early 2000s limited early primate GPS collar work to larger species like baboons, and these units still provide the longest battery life. This factor continues to make the cost-benefit calculus (e.g. risk to the animals' well-being relative to the amount and quality of data collected) for using the technology more accessible and acceptable for use on larger species.

However, as technology advances, a wider range of collars are becoming commercially available that may be suitable for collaring smaller primates. The Tellus Micro (77g) and Telemetry Solutions Quantum 4000 (80g) units are the smallest GPS collar units to have been deployed on primates to date (i.e. on vervet monkeys, long-tailed macaques, and ring-tailed lemurs). It is important to note that for some collar brands, electronic drop-off units added between 2g (Tellus Micro) and 150 g (Telemetry Solutions) in weight overall, which can present additional limitations for deployment on smaller primates. Researchers are currently developing a new protocol for great apes, GPS ankle bracelets, getting inspiration from human criminal justice systems (*personal communication*, Shauhin Edward Alavi). These may prove to be useful for small bodied primates as well. Some newly available GPS collars are available at a mere 120-140 g, including Iridium remote data download capability.

GPS collars weighing only 77 g including drop-off, as the Tellus Micro in this study, are too small to carry Iridium remote data download, yet a Global System for Mobile Communications (GSM) signal is possible. Iridium remote data communication relays GPS locational fix data to researchers without the need to directly track and download data via an ultra-high frequency (UHF) signal and/or recover store-on-board GPS units, similar to GSM-cell signal systems and ARGOS. In many remote areas, GSM download is not a possibility because of lack of cell-service or network type (i.e. some devices may work on 2G but not 4G); using smaller GPS collars without Iridium in these areas leaves remote download impossible. Information cell-service availability according to area is available online. Here UHF download combined with VHF signal is the only way to track animals and download data.

GPS collars manufactured by e-Obs Digital Telemetry and Telemetry Solutions were the most commonly deployed units on primates. Both collar brands provided large amounts of high-quality data. In our dataset, Telemetry Solutions and Tellus Micro collars were the only units where malfunctions (apart from early battery death) impacted data acquisition or drop-off functionality. Two Tellus Micro collars were tested prior to deployment without any problems, yet after deployment they immediately switched off, and only the UHF connection remained. For some Telemetry Systems device users, remote download stopped working before GPS, in some instances months before the end of battery life. These differences in performance may be related to several factors including chance, study species' tolerance of collar units, length of collar deployment, and the habitats in which collar units were deployed. Though mean collar:animal weight ratios were similar (1.95% Telemetry Solutions vs. 1.9% e-Obs Digital Telemetry), it is possible the larger ratio on the somewhat smaller species and the overall bulk (rather than weight) of the units led to those study subjects manipulating collars more frequently, which could lead to loosened internal connections between the electronic components. Another factor that may have resulted in this performance disparity is the overall mean deployment lengths to which each collar brand was subjected. Given that most of the Telemetry Solutions collars were deployed in high humidity tropical rainforests for three to six months, it is possible the drop-off unit mechanisms (which require a pin to fire and separate the collar) may have been negatively impacted by long-term exposure to high humidity.

Reducing TTF and thereby enhancing FSR and collar performance can be done through high frequency fix scheduling. This is highly efficient because GPS units remain connected to satellites (known as a 'hot' start) and these high frequency schedules predispose fix acquisition to be more rapid and require less battery power (Moriarty and Epps 2015; McGregor et al. 2016). TTF across brands was comparable with the exception of the older Televilt Porsec 120, which did not calculate this metric, and Telemetry Solutions collars, which had a considerably longer mean TTF of 77 seconds (under variable habitat conditions; Table 1).

In terms of battery life performance more broadly, Advanced Telemetry Systems and Telonics collars performed best in this study, with almost all units maintaining or exceeding their anticipated battery life expectations relative to their programmed fix schedules (Table 2). Collars manufactured by e-Obs Digital Telemetry, Lotek, and Tellus Micro experienced lower than expected battery life for either GPS units and/or the VHF or UHF signals on collars. Early loss of VHF or UHF signals impacts both the researchers' ability to relocate animals for data download and collar retrieval as well as prohibiting the ability of researchers to trigger electronic drop-off units. To enhance battery life some researchers in this review programmed GPS collars to only collect data during daytime for diurnal species. However, this produces several problems for data analysis, with some methods requiring continuous data collection at the set intervals, such as Hidden Markov Models for assessing circadian rhythm (Huang et al. 2018). Not collecting positions at night may reduce the chances of defining sleeping sites (but see Pebsworth et al. 2012a,b). Fix schedule should mirror the research question.

As many GPS collars now have the ability to connect to satellites and GSM networks and transmit locational data in real time, study animals may not need to be re-trapped in order for GPS units to be removed via remotely-triggered electronic drop-off (through satellite or GSM networks). Upon signal transmission, either pre-programmed or triggered in real-time by the researcher (typically via UHF receiver transmission), collar drop-off should engage and release for subsequent retrieval of the GPS unit within the timeframe of the extra battery unit signaling GPS position for retrieval. Unfortunately, electronic drop-offs remain among the most problematic performance aspect of GPS collars (Table 2). We suggest the greatest room for improvement in GPS telemetry technology exists here, and we urge manufacturers to enhance drop-off performance, and researchers to always use biodegradable weak links in addition to remotely triggered drop-off mechanisms. Telonics offers stand-alone, remote, timed drop-off units for sale but at a large expense ($500 USD). Telemetry Solutions (N=54), and Advanced Telemetry Systems (N=22) had the largest sample sizes and reported a high drop-off success rate (>66%). However, the Advanced Telemetry Systems drop-off unit is 65g, making it prohibitively heavy to add to most GPS collars for deployment on primates. Tellus Ultralight collars had 100% success rate on drop-offs, but a very low number of drop-off attempts (N = 3).

Some special considerations have emerged as a result of our own work and in the process of conducting this review that must be taken into account with regard to deploying any type of collar (but particularly the somewhat heavier GPS collars) on primates. First, as the greatest room for improvement across GPS collars lies in drop-off functionality, we argue that *it is essential that all GPS collars be fitted with biodegradable weak links prior to placing them on the animals*. Some individuals in this review have used cotton spacers with success; a recent paper shows that degradable washers can also be used as a time-release mechanism for telemetry collars (Thalmann 2017). Some individuals in this review field tested drop-offs first with success and then they failed in the field; weak links will assure that collars will eventually come off the animals regardless of drop-off failure or success. This fail-safe mechanism will also aid in high-risk situations (such as working with highly endangered species or species that require free-darting to capture) where the risk of recapture may be too high.

Second, investigators should ideally collect ranging data on the individuals under consideration for telemetry prior to collar deployment. This may require the use of handheld GPS units. These data can ensure that data obtained on range size or other metrics are not a byproduct of the animal wearing a telemetry device, and enable the researcher to become acquainted with the environment and the behavior of the animals (Hebblewhite and Haydon 2010).

Based on the particular individual, species, or environment under investigation, risks of trapping, trap habituation, and free-darting (tranquilizing an animal not already sequestered in a trap) may be of particular importance as well. In addition, primatologists must negotiate the risks and impacts of sedation against how long the collar can be functionally deployed and how much data can be derived from that deployment. In some scenarios, habituating animals to traps may be unethical, as it leaves the animals vulnerable to human predation. Questions also remain with regard to the frequency of injury and subject loss, and scholars must be sure to report these incidents so that the risks are fully understood. For example, while not part of our dataset, Isbell et al. (2019) found greater mortality (via leopard predation) in collared female vervet monkeys compared to uncollared females, which may have been a result of wearing the devices. We recommend visiting and updating the IPS safe capture protocols with any injuries or deaths that may be a result of wearing GPS collars (IPS, 2019). In situations where animals are lost or injuries occur, the potential for public backlash is very real (and has been a significant problem for at least one of us). Due to the relatively novel use of this technology, systematic studies on these variables have not yet been published. We encourage the explicit consideration and investigation of these factors in future primate telemetry work (Hopkins and Milton 2016; Klegarth et al. In press; Isbell et al. 2019). In at least one instance, collared monkeys became more recognizable within the local community and were targeted by individuals disgruntled with having to share the environment with monkeys. Yet some of us have experienced public support for and interest in collared individuals; in one study, tourists and local rangers spent much time paying attention to collared individuals and asking questions. This was used to inform them of the ecology of the collared primates (Hansen et al. *in prep*).

While these collars open up new methodological and analytical possibilities for assessing primate ranging patterns and habitat use, they also present a diverse array of technical, structural, and ethical concerns with doing so, and these concerns and issues should be at the forefront of the design and implementation of projects using them. In evaluating the effectiveness of the collars themselves, it is important to keep in mind the basic categories of harm that the deployment of externally-borne telemetry units can introduce in primates: potential harms associated with capture, collar attachment, and with the recovery and release options. We want to stress that the physical and social impact of the device on the animal once it is attached and returned to the social group should be monitored as comprehensively as possible (Klegarth et al. In press; Pebsworth et al. 2012a).

Conclusion

Primatologists utilizing satellite telemetry have demonstrated that GPS collars can acquire large amounts of accurate location data across a diversity of habitats, including challenging locales such as those with heavy canopy cover (Table 1, Klegarth et al. 2017a,b). Our compiled dataset shows that GPS collars have now been successfully deployed on at least 179 individual primates at sites spread across five continents. While the habitats represented in this dataset varied, collars from multiple brands were shown to perform well in even the most challenging habitats including areas with obstructive cliff faces (Klegarth et al. 2017a,b; Pebsworth et al. 2012a) and heavy rainforest canopies (Klegarth et al. 2017a,b; Di Fiore and Link 2013; Stark et al. 2017). In addition to drawing attention to the value of GPS telemetry for primatology, our review highlights a number of problematic aspects of this technology as well as important considerations that are not often addressed in scientific publications. Ultimately, we argue that primatologists armed with this information have much to gain from the recent, substantial improvements in tracking technology.

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