

Electronic tracking tag programming is critical to data collection for behavioral time-series analysis

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Abstract. Electronic tracking tags are major tools of ecological research and management, but programming sophisticated tags can be challenging. We discovered that a common programming scheme can negatively affect the quality of tracks collected by Argos tags. Here we describe the problem and how it occurred. We then simulated a series of tracks with different data collection schemes to investigate how spatial precision and temporal frequency affect the overall quality of tracking data. Tracks were simulated using a two-state composite correlated random walk (CCRW). Tracks were simulated with two spatial scales, using parameters estimated from northern elephant seal (large scale) and California sea lion (small scale) tracking data. Onto each simulated track, observations of varying precision, frequency, and censoring were imposed. We then fit the CCRW in a state-space model (SSM) to the simulated observations in order to assess how data quality and frequency affected recovery of known behavioral state and location. We show that when movement scales are small, regular observations were critical to recover behavior and location. In addition, tracks with frequent regular locations (increasing N) overcame low spatial accuracy (e.g., Argos) to detect small-scale movement patterns, suggesting frequently collected Argos locations may be as good as infrequently collected GPS in some circumstances. From these results and our experience tracking animals generally, we produce a set of guidelines for those manufacturing, programming, and deploying electronic tracking tags to maximize the utility of the data they produce.

Key words: animal tracking; Argos; geolocation; GPS; state-space model; wildlife telemetry.

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INTRODUCTION

Remote animal tracking is a common tool for the study and management of marine and terrestrial animals (Turchin 1998, Wikelski et al. 2007, Nathan et al. 2008). Thousands of animals are released each year with electronic monitoring equipment that records location, but may also report depth, salinity, internal and external temperature, light, heart rate, and acceleration. Large tagging ventures have produced great

ecological insight and deep reservoirs of data (Block et al. 2010, Boehme et al. 2010).

Methods for analyzing tracking data have been developing quickly (Turchin 1998, Moorcroft and Lewis 2006, Schick et al. 2008). Selecting a particular model or analytical approach remains challenging and the choice can greatly affect the quality and type of inferences drawn. One of the major philosophical shifts to occur in recent years has been to formally treat tracks as time-series data. Time-series methods such as state-space

and hidden Markov models make it possible to test a range of hypotheses about the small scale behavioral time-series and dynamics. This includes objectively discriminating time budgets, testing state-dependant association patterns with transient environmental features, and the estimation of parameters affecting or controlling behavior (Patterson et al. 2008, Schick et al. 2008).

Though tracking data are time-series representing a series of locations occupied by an individual through time, many methods used often ignore time and focus on spatial relationships. Locations from an entire track are sometimes treated as though they were temporally independent, even to the point where data are subsampled to lessen autocorrelation (Otis and White 1999). In effect, all locations are treated as though they were collected at once. Under this assumption, kernel densities or similar methods can be used to estimate home ranges of individuals or utilization distributions of populations (Worton 1989). These are very useful analyses, but because they ignore time, they are blunt tools for analyzing the dynamic aspects of an animal's behavior.

Given how much there was to learn from early tracking studies, when satellite transmitters were the size of small backpacks and producing functional tags was a major accomplishment, basic analytical approaches were sufficient. Complex analyses were not necessary to document that albatross circumnavigated the Southern Ocean every few weeks (Jouventin and Weimerskirch 1990) or that elephant seals crossed most of the Pacific twice a year, diving deeper than most whales along the way (Stewart and DeLong 1995).

Since these exciting early reports, tags have become less expensive and better, and those deploying them proficient at their craft. These developments recently culminated in large deployments of tags across many species, such as the Tagging of Pacific Predators (TOPP) and Marine Mammals Exploring the Oceans Pole to Pole (MEOP) programs (Biuw et al. 2007, Block et al. 2010). On the broadest scales, tracks collected in these ventures have revealed patterns similar to earlier tagging efforts. However, with many more individuals and many species contemporaneously tagged, these large programs have produced a much better understanding of com-

munity associations, dynamic ranges, and biodiversity patterns (Block et al. 2010, Costa et al. 2010). The newer tags deployed in these ventures produced many more locations per day and each location has much higher spatial precision than first generation instruments. The combination of increased spatial precision and temporal resolution allow observations of fine scale movement patterns that were not possible with early tags. With carefully constructed time-series models, it is possible to ask of such high quality data what the animals were doing, why they were doing it, and what internal and external cues were motivating them through time (Patterson et al. 2008, Schick et al. 2008, Breed et al. 2009).

As tags have become increasingly sophisticated, programming them to take advantage of the myriad data streams has become challenging. The most advanced tags offer multiple data channels, including location, depth, temperature, light and more recently oxygen, fluorometry, pH, accelerometry, salinity, heart rate, and stomach temperature, among others. This produces a quandary for those deploying tags. On which data streams should one expend battery power and/or memory and how much should be allocated to each? Battery power and memory remain major limiting factors in all electronic telemetry technologies. Efforts to conserve battery power and offer new data streams have led some manufacturers to default their units so that they collect locations during only a fraction of the day. However, as we demonstrate, this can result in significant signal loss and otherwise observable and potentially important behaviors become undetectable, even with the small spatial error offered by GPS units.

We recently encountered such programming issues while attempting to analyze a wide range of tracking data collected by a number of different tracking programs. These data problems could have been avoided if tags had been programmed slightly differently. In our case, the programming unintentionally compromised the quality of at least 166 tracks (63 California sea lions, 64 Antarctic fur seals, 16 Galapagos sea lions, 6 South American sea lions, and 17 albatrosses), making it impossible to resolve, model, or otherwise observe the small-scale movement patterns made by these animals.

The problem is associated with an attempt to

reduce power consumption and extend tag life by limiting Argos transmissions attempts to a fixed limit per day (in this case 500), which resulted in termination of data collection for the day after as little as 6 hr. This resulted in loss of tracking information for 10–18 hr in the second half of each day. A slight modification to the program could have similarly reduced power and produced a continuous track through the day.

In this case the data loss was unintentional, but deliberate duty cycling is still a common practice and will have similar effects. Additionally, this is one of a suite of potential programming schemes that could affect data quality. More subtle problems could go unnoticed but still affect inferences drawn. In a perfect world, with infinite battery power, memory, and satellite bandwidth, all tracks would have high spatial precision and high temporal resolution. With state-space models (SSMs), it is possible to make up for low spatial precision of individual locations with high temporal resolution. Deciding whether to deploy Argos or GPS tags and how to program them in order to balance spatial and temporal resolution with memory and battery life given available statistical tools and an animal's expected behavior is the focus of this paper.

EFFECTS OF PROGRAMMING ON DATA QUALITY

Case study: Argos daily uplink limit

The effect of capping Argos transmissions to 500 per day can be realized in a simple back-envelope calculation. The Argos satellite service requires Argos tags to attempt to connect to a network of polar orbiting satellites on a particular schedule. This schedule is known as the repetition period, and ranges between 40 and 200 s (Service Argos 2009). The repetition period is negotiated with Argos and in this case it was set at 43 s, a fairly typical rate for animal borne Argos transmitters. If not otherwise programmed, Argos tags set to repeat at this rate will attempt about 2000 uplinks each day. However, diving animals spend variable amounts of time underwater and a wet-dry sensor is used to prevent underwater transmissions that would waste battery power. In addition, power can be saved by programming

tags to transmit only during certain periods of the day, shut down completely, or transmit less frequently at the “slow rate” (once every 86 s in this case). The latter two (transmission at the slow rate and shutdown) typically occur in stages when tags enter “haulout” mode: slow rate for a set period after an animal leaves the water followed by shut down until the tags are immersed in sea water. Certain tags are defaulted to cap transmission attempts at 500 per day, and sometimes as low as 250 per day. When this cap is reached, transmissions stop and do not resume until midnight. A simple calculation reveals that animals remaining at the surface will transmit 84 times an hr and 500 transmissions will be reached after 5 hr 54 min. Two hundred-fifty transmissions will be reached after 2 hr 57 min. In most cases transmissions resume at 00:00 GMT (not local time), and depending on where animals are, this may result in biologically inappropriate duty cycling.

The number of transmissions attempted per day is affected by diving behavior. For example, phocid seals dive nearly continuously. Northern elephant seals in our database, for example, spend an average of only 2–3 hr/d on the surface. In that situation, they will never reach 500 attempts transmitting at the 43 s rate. In a sense, this behavior self-governs the regularity and number of transmissions, often producing excellent time series while using minimal battery power. Otariid seals, however, do not dive as long and typically spend many hours resting at the surface. During long rests at the surface, tags are wetted regularly preventing them from entering haulout mode and transmission attempts continue more or less constantly at the fast 43 s rate.

Dive data from Antarctic fur seals indicate they average around 19 hr/d at the surface during austral summer; and daily and individual variation was small. Time spent at the surface was directly related to day length as they foraged nocturnally on vertically migrating species (particularly krill), while spending long daylight hours resting at the surface. In this species, 500 transmissions were often reached after just 6 or 7 hr and transmission rarely continued for more than 10 hr each day. California sea lion dive records indicate they averaged 12–14 hr a day on the surface and were somewhat less affected by

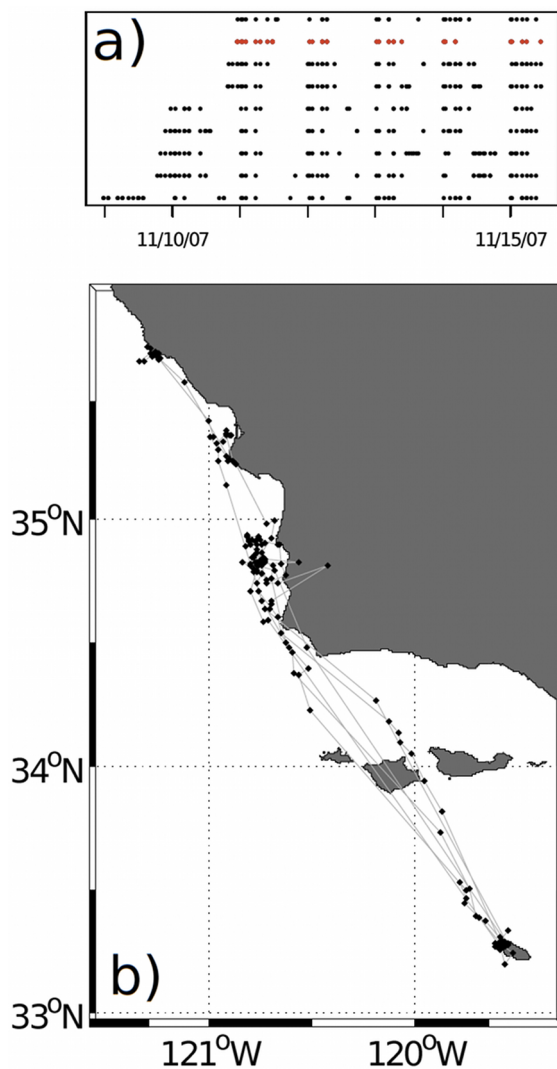


Fig. 1. Temporal resolution of 9 Argos tags deployed concurrently on California sea lions (a). Red points are a portion of the track plotted in panel (b). All tracks were inadvertently censored by limiting Argos transmission attempts to 500/d, preventing them from collecting locations from between 10–14 hr/d. In (a), x-axis ticks indicate midnight GMT.

the transmission limit. The shorter time on the surface was likely due to the shorter days at temperate latitudes for these nocturnal divers. Still, California sea lions typically reached the 500 transmission threshold after 10–16 hr (Fig. 1), which resulted in an unintentional 8–14 hr period each day when tags did not transmit. The 8–14 hr gaps in tracking were still problematic for most

individuals, and made it difficult or impossible to identify behavioral transitions between transit and resident type behaviors from tracking data using a two-state switching SSM of Jonsen et al. (2005).

The problem strongly affects time-series methods. These gaps will not obviously affect analyses that do not explicitly include time such as kernel density methods, gridding, mapping, speed filters, and spatial correlation methods such as resource selection functions. However, any analyses could potentially be biased if animals are more likely to use certain habitats or behaviors during particular times of day (Worton 1989, Manly 2002); which is in fact the for case sea lions and fur seals.

EFFECT OF OBSERVATION FREQUENCY AND CENSORING OF RELOCATION DATA

Tracking simulations

As noted we were unable to confidently estimate behavioral state or location by fitting a switching SSM to tracks with the problem described above (Jonsen et al. 2005, Breed et al. 2009). To investigate the issue, we prepared two simulated tracks that differed in the scale of movement. Tracks were simulated using a composite correlated random walk (CCRW); the CCRW was the process model from the switching SSM described and used in Jonsen et al. (2005) and Breed et al. (2009). Parameters used in these simulations were estimated by fitting the switching SSM to empirical data as described in Breed et al. (2009). The first set of parameters was estimated from a locally ranging CA sea lion tracked with a high quality GPS tag using a 60 min time step and the second estimated from an Argos tracked northern elephant seal that ranged across the North Pacific using a 480 minute time step. Because this is a simulation from a simple model, simulated tracks resemble movement patterns of animals generally, but lose many features characteristic of a particular species such as trips. However, the respective movement scales, controlled by the parameter Σ , are similar to those made by elephant seals and sea lions from which parameters were estimated.

Both simulations were 600 moves long, but different time steps (8 hr for the elephant seal-like and 1 hr for the sea lion-like simulations) made

the elephant seal-like simulation 200 days long and the sea lion-like simulation 25 days. As these are simulations, they could just as easily represent terrestrial animal movements such as elk or butterflies; the temporal and spatial scales are relative and the issues pertinent to all tracking data.

Onto simulated tracks, we further imposed a range of realistic observation frequencies and spatial observation errors. There were 4 basic observations schemes: uncensored GPS, uncensored Argos, censored GPS, and censored Argos. Spatial error was added to GPS using rates published in Costa et al. (2010) and to Argos using rates from Vincent et al. (2002). Onto these 4 basic categories, we added 4 temporal frequencies spanning the range typically produced by properly functioning Argos and GPS units in the field. Observations were made at irregular intervals, which were produced by linearly interpolating between simulated locations at times drawn from a positive Gaussian distribution whose variance was set so tracks would average 5 locations/d, 10/d, 24/d, and 45/d. Because Argos satellites are polar orbiting 5 and 10 locations/d are typical near the tropics and in temperate latitudes, 24 can be achieved in high temperate and polar regions, and 45 are possible near the poles. Under ideal conditions, GPS tags can collect hundreds of locations per day anywhere, but this must be balanced with power consumption and/or satellite bandwidth (however, see the Discussion regarding the intricacies of programming particular location collection frequencies in either tag technology).

We then censored simulated observations to mimic the programming scheme described in the case study by using only the first 10 hr of observations and masking the rest. In total we simulated 32 different combinations of behavior, tag type, observation frequency, and censoring. From these simulated observations, we attempted to recover the known locations and behavioral states by fitting a switching SSM; the CCRW process model being the same as that used to generate simulated data. Our aim was to assess the effect of temporal and spatial resolution, as well as regular censoring of data on a well established method. Testing other methods is beyond our scope, but we expect our results will give a strong indication of how most time-series

analyses will fare as data become increasingly degraded.

Effect of data quality on behavioral inference

While not unexpected, our results illustrate how and why duty cycling and censoring can be problematic. They also provide some insight into which circumstances Argos data might perform as well as GPS. In general, the more locations collected, the higher the ability to resolve fine scale behaviors. High temporal resolution (24–45/d) allowed recovery of true locations and hidden behavioral state from Argos quality data equivalent to lower temporal resolution GPS quality data (5–10/d), even when behavioral and spatial scales were small (Figs. 2, 4, Table 1). This is due to the Law of Large numbers, the same effect that increases statistical power, lowers p-values, and increases the ability to detect small differences as N increases in ordinary frequentist statistics.

Scale of movement relative to spatial and temporal resolution of data was also extremely important. In the large scale (elephant seal-like) simulation, essentially all temporal and spatial observation schemes tested provided sufficient information to recover behavioral state accurately (91–93% correctly identified in all simulations), even when censored 14 hr a day (Figs. 3, 5). Note that the absolute confidence in position has not improved much (Figs. 4, 5), but since the scale of the process is 8 times larger, the signal to noise ratio improves by a factor of 8. Consequently the relevant biological signal is easily detectable. This implies that for those interested in large scale habitat usage patterns, GPS offers little advantage over Argos. In the small scale (sea lion-like) simulation, both the spatial and temporal resolution of data greatly affected our ability to accurately recover location and behavioral state, and even the best data (uncensored GPS at 45 locations/d) failed to recover very short bouts of transiting behavior. Censoring made reliable recovery of behavioral state impossible for bouts shorter than censored periods even when locations were GPS quality and were otherwise collected frequently (Figs. 2, 4).

Haulout modes and periods of extended shutdown

In amphibious marine species such as seals, penguins, and turtles, tags can be programmed

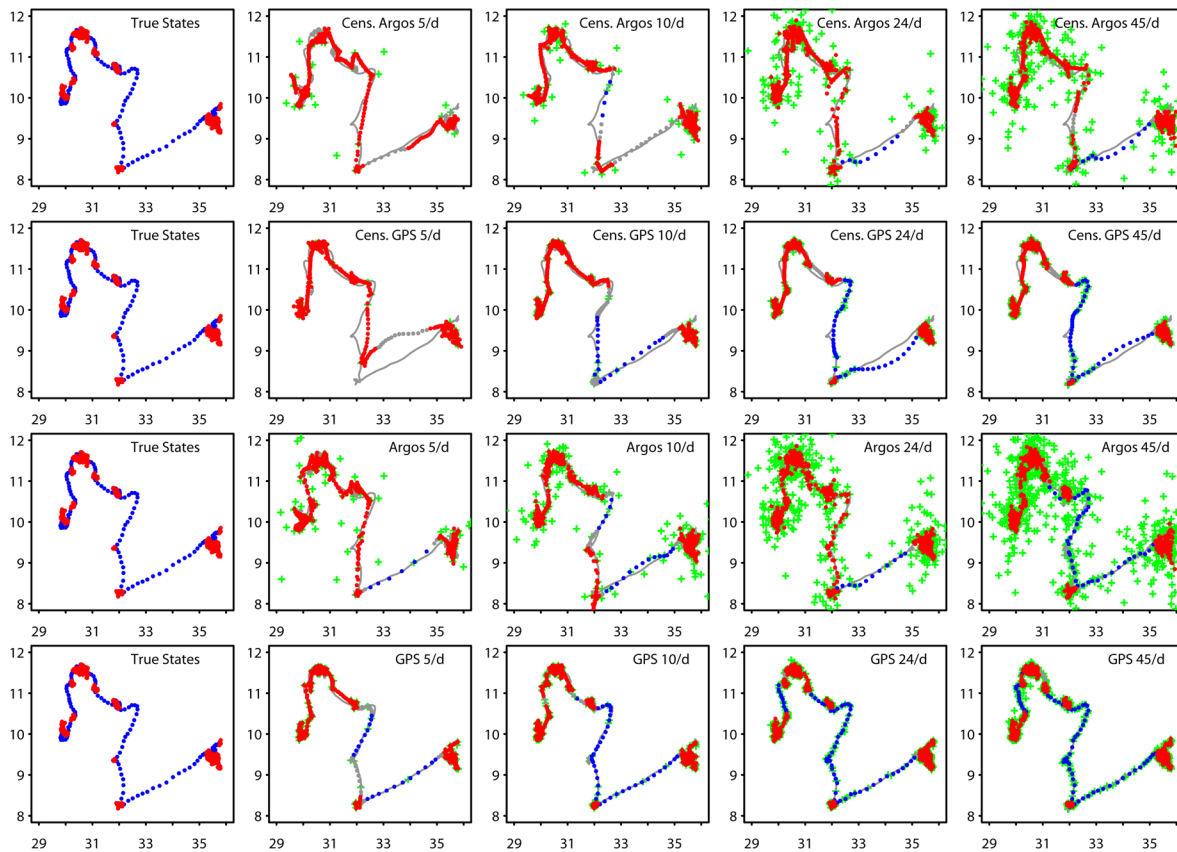


Fig. 2. Maps of SSM model fits to small scale (sea lion-like) simulated movement with rapid behavioral state switches to varying data qualities. X- and y-axis scales are arbitrary units but approximately equal to degrees of latitude and longitude. Green “+” are simulated observations, grey line the simulated track (shown with known state in the left column of panels). Location estimates are shown with color indicating inferred behavioral state. Blue is “transit”, red “resident”, and grey unclassified.

to enter ‘haulout mode’ when animals leave the water. This usually means decreasing the frequency of location observation attempts for a set period followed by shutdown until the tag is rewetted. For amphibious species, the importance of haulout mode and wet-dry switch settings is second only to deciding the pattern and frequency of location observation attempts. Unfortunately, some tags offer little flexibility in these settings. A common option is to shut down for the duration of haulout. However, this data gap is fundamentally no different from those occurring at sea, and similarly interrupts the time-series. Unless tagged animals are resighted visually or by means of VHF tags while hauled out, in a very real way, it is impossible to know where they are. This is especially true if animals

are not returning to a particular location (such as when lactating females return to a pup). Even where haulout observations are made independent of tags, integrating those observations with electronically collected location data can be problematic and tedious.

Shutdown during haulout can also complicate matters if data are already duty cycled or reach daily transmission limits. For example, if an animal hauls out after their daily complement of Argos transmissions has been spent, no locations will be collected for the entire haulout, and if wet/dry information are not recorded such as might be available on a time-depth recorder, it is possible to completely miss that a haulout occurred as locations will not be collected again until the animal reenters the water.

Table 1. Mean distances of SSM location estimates from known simulated locations \pm s.d. and % behavioral state correctly identified for each of the observation schemes imposed on the sea lion-like simulated track, ranked from best to worst. Note that censored schemes sometimes produce small mean distances from true results but have higher s.d. because error increases during censored periods and decreases during observed periods. We caution that error ranges are relative. The parameters used to simulate tracks were fit from real data, but the CCRW model used is a simplification of the much more complex system driving an animal's behavior and consequently the fits to simulations should not be compared directly to real observations. Instead the relative differences between observation schemes should be compared, as the pattern will hold in real observations.

Simulation	km from true \pm sd	% correct state
GPS 45d	2.3 \pm 1.14	82.85
GPS 24d	3.81 \pm 2.35	81.93
GPS 10d	9.02 \pm 4.65	79.01
Argos 45d	9.77 \pm 4.09	78.83
GPS cen 45d	10.6 \pm 8.42	78.28
Argos 24d	13.32 \pm 5.39	74.64
GPS cen 24d	14.23 \pm 11.99	77.74
GPS 5d	15.35 \pm 7.34	78.10
Argos 10d	19.23 \pm 5.98	76.82
GPS cen 10d	21.50 \pm 11.57	74.82
Argos cen 45d	21.85 \pm 10.69	74.64
Argos cen 24d	25.9 \pm 12.78	74.45
GPS cen 5d	30.35 \pm 15.41	71.72
Argos cen 10d	30.81 \pm 12.15	74.82
Argos 5d	31.18 \pm 11.56	73.72
Argos cen 5d	53.46 \pm 20.88	72.26

DISCUSSION

Systematic gaps in tracking data produced by deliberate or accidental duty cycles will lessen the utility of data and may not be useful for understanding behaviors that occur on scales smaller than the duty cycle. Our simulations demonstrate that frequent, regular locations are at least as important as precise location observations. This is somewhat counterintuitive and most discussions of tracking data quality focus on spatial accuracy (Bradshaw et al. 2007, Hays et al. 2007, Kuhn et al. 2009, Costa et al. 2010). However, an analysis by Lonergan et al. (2008) also suggests temporal frequency and regularity are key to extracting biological signal. That analysis indicated that any benefit of GPS

accuracy disappears when locations are collected less frequently than once every 12 hr.

In a recent analysis, Kuhn et al. (2009) also showed that the spatial accuracy of GPS data made it far superior to Argos, even after fitting with an SSM to mitigate observation error. However, Fig. 2 of Kuhn et al. shows that the Argos locations used in that analysis were unevenly distributed and might have suffered the same programming problem we describe here. Had the Argos positions been continuous, the conclusions might have been more equivocal, similar to our conclusions and those of Patterson et al. (2010).

To conserve battery life, duty cycles are often programmed and are probably acceptable when addressing broad scale ranging patterns. Such patterns, however, have been extensively described and are well understood in many tagged species (e.g., LeBoeuf et al. 2000, James et al. 2005, Shaffer et al. 2006). Tag technologies now allow observation of much smaller behavioral processes that can be used to explain why animals use particular habitats, rather than just the fact that they use them. This is where much of the important work in movement ecology remains to be done (Nathan et al. 2008). However, overlooking the importance of tag programming at deployment can drastically diminish the utility of tracking data for testing behavioral and ecological hypotheses at these small scales.

Relating transmission rate and number of locations collected

In our methods, we chose 5, 10, 24, and 45 locations per day in order to span the range typically collected by Argos tags and many GPS tags. However, it is not possible to simply set a tag to collect locations at these rates; there is a step between programming a transmission rate and the number of locations ultimately realized that is somewhat beyond the user's control. The number of locations collected is a function of satellite overpass rate, animal behavior, tag programming, and the quality of the electronics. The rates of 5, 10, 24, and 45 locations/d that we used in our simulations were chosen because they are realistic rates that can be achieved given these variables.

In general the Argos system offers less control over when locations will actually be collected

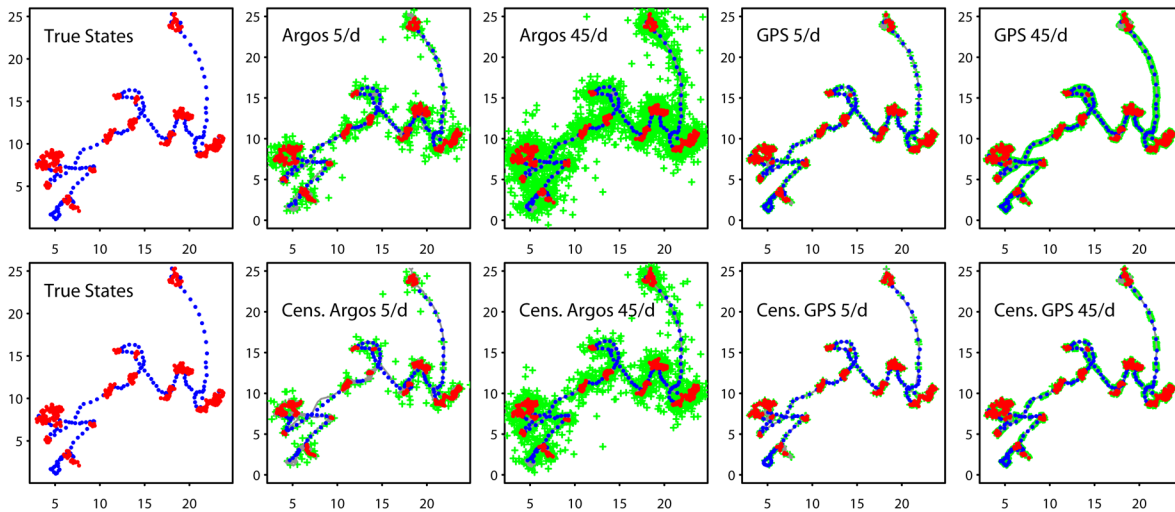


Fig. 3. Maps of model fits to large-scale (elephant seal-like) simulated movement. X- and y-axis scales are arbitrary units but approximately equal to degrees of latitude and longitude. Green “+” are simulated observations, grey line the simulated track (shown with known state in the left column of panels). See Fig. 2 for explanation of color. Because results were good in all cases, only the extreme simulated observation schemes are shown.

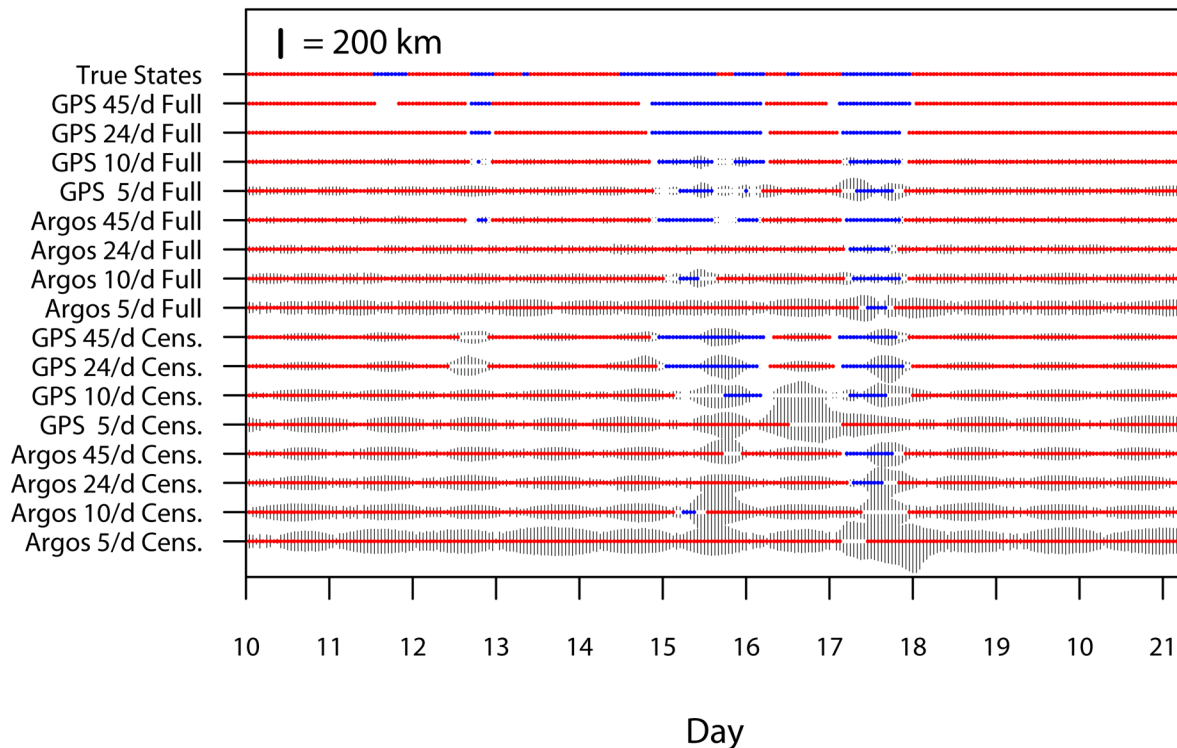


Fig. 4. Location estimate error (bars) and behavioral state estimates (colors: blue = “transiting,” red = “resident”, white = uncertain) fit to various data qualities for an 11-day segment of the small-scale track shown in Fig. 2. True states shown in top row. Error bars indicate the 95% credible limit of y-dimension (x and y errors were approximately symmetrical) at each time step. When scale of movement is small relative to observation error and frequency, error rates increased with lower spatial precision (Argos vs GPS), lower temporal frequency, and censoring.

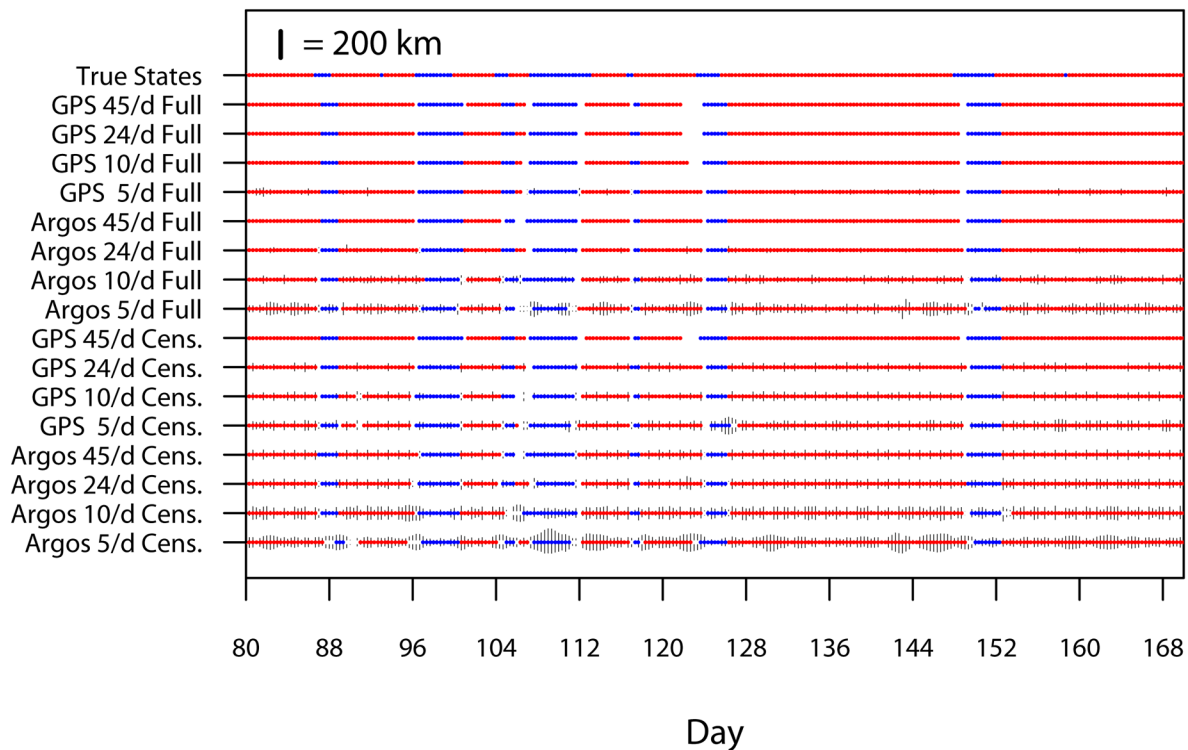


Fig. 5. Location estimate error (bars) and behavioral state estimates (colors: blue = “transiting,” red = “resident”, white = unclassified) fit to various data qualities for a 90-day segment of the large-scale track shown in Fig. 3. True states shown in top row. Error bars indicate the 95% credible limit of y-dimension (x and y errors were approximately symmetrical) at each time step. Error rates were less sensitive to data quality when movement scale is large relative to precision and frequency of observation method.

than GPS tags, and much is left to luck and circumstance of latitude and animal behavior. Argos satellites are polar orbiting, so satellite coverage is best over the poles and worst at the equator. The orbital cycle can add considerable gaps that are beyond the control of the user, particularly at low latitudes. Gaps in coverage have decreased as more satellites have been launched, but gaps of a few hours still occur at low latitude (some short gaps due to satellite coverage are visible in Fig. 1a). Conversely, GPS satellite coverage is more or less ubiquitous. Argos relocations also differ from GPS in that they use only a single satellite to calculate position by the doppler shift of the uplink frequency during a satellite overpass. This algorithm requires 3–5 consecutive satellite uplinks, which means animals must be at the surface for 2–3 minutes per location. These factors play together to make the relationship

between programming intent, battery use, and actual locations collected complex for Argos tags. Forty-five locations per day are possible, but only at very high latitudes with cooperative animals that surface frequently.

By contrast, GPS tags receive time stamps from 3 or more satellites simultaneously. To calculate locations, these time stamps are compared. Each will differ slightly due to the time it takes the signal to travel from each satellite to the tag, and from these differences a location can be triangulated. This system performs well in terrestrial applications, and is just now being perfected in marine applications. The ubiquitous satellite coverage allows GPS tags to collect regular locations, and users can program tags to collect locations at set intervals (e.g., once every 15 minutes, though animal behavior can still add irregularity). A significant drawback to the GPS system is that locations are calculated by the tag

rather than the satellite system, and each GPS location collected requires a fair amount of data. Processing these data on board requires considerable battery power, although these data can be stored and processed later. This is still problematic, because tags must be physically recovered to collect the track or data from which locations are calculated must be sent via limited satellite bandwidth. At this time, bandwidth is generally available to send only a few GPS locations a day via satellite. Thus, collecting high resolution GPS tracks is limited to situations where tags can be recovered and logged data downloaded from recovered tags. In some circumstances, modifications can be made for collected GPS data to be sent via higher bandwidth networks such as mobile phone towers (McConnell et al. 2004), but in general tags need to be physically recovered.

Tag programming as technologies evolve

Several changes are on the horizon, particularly for Argos satellite system. Collecte Localisation Satellites (CLS), who manage the Argos system, is upgrading its satellites to the new Argos-3 standard, which is capable of two-way communication with tags and floats. The two-way information will allow the Argos system to inform tags when a location has successfully been collected. More importantly, tags will be able to passively listen for satellites overhead and only transmit when they detect a satellite. This should allow much more rapid location observations as a fixed repetition rate will be unnecessary, decreasing the time animals need to remain on the surface for successful location acquisition. This will also improve battery life and transmission efficiency. At present, two Argos satellites are Argos-3 equipped, but most remain the Argos-2 standard. PTTs that can take advantage of the Argos-3 standard are experimental and being deployed only on floats. As more Argos-3 capable satellites are launched animal borne tags will be manufactured that utilize the better technology.

PROGRAMMING RECOMMENDATIONS

Many tag manufacturers have been carefully considering all of the issues discussed here. Some are serious engineering challenges. Others are simple, but could introduce serious problems if

overlooked. Tags from all major manufactures will perform as advertised if programmed properly. As such, we have prepared the following general recommendations for both users and manufacturers of electronic tracking tags.

1. Both number and regularity of locations should be maximized together. More locations are never bad, but the utility of locations for understanding biology and behavior is maximized when they are collected regularly.

2. Duty cycles on whole days should be avoided. Programming tags to transmit or collect GPS or Argos locations every other hour should conserve the same amount of power as transmitting every other day, but should produce a superior track. In most cases short period duty cycles have the positive side-effect of decreasing wear on electronic components and batteries, allowing them to last longer. However, users should consult with manufacturers as technology changes.

In some circumstances, duty cycling on whole days might save on Argos fees. However, under the current fee structure for animal tracking, this is generally not the case until the duty cycle reaches 3 days off for each day of transmission. Even in that circumstance the fee savings are marginal.

3. Lengthy data gaps, even for haulout, should be minimized. If possible, haulout mode should not shut down; if power savings are desired at haulout, consider increasing the time between GPS location or Argos satellite uplink attempts.

As a caveat to this recommendation, it should be noted that haulout mode shutdown might be reasonable for some GPS units, provided the temporal end points of a haulout are also recorded via a wet-dry sensor. GPS data are usually (but not always) precise enough that one or two locations can accurately represent a haulout location.

4. Limiting maximum Argos transmissions per day or maximum GPS location attempts per day should also be avoided. If possible, power use should be controlled by programming regular windows for transmission through the day. Tag users should be wary, however, that attempts to limit transmissions may unexpectedly bias data.

It should be noted that capping transmissions or location attempts per day may be the only way to ensure batteries last a certain duration,

particularly when deploying on species whose behavior is poorly understood. Like duty cycling, however, hourly caps could be implemented in lieu of daily caps, which should ensure that location attempts take place throughout the day.

5. Users should expect intuitive, easy-to-understand programming interfaces and thorough documentation from tag manufacturers. It should be clear when certain settings override others. Unnecessarily complex and/or poorly documented interfaces leave users bewildered as to which settings are important and which are irrelevant.

6. Complete flexibility in Argos uplink or GPS location attempt schedules should be allowed. A repeating daily schedule is appropriate in most instances, but a continuous schedule would allow for maximizing satellite exposure and accommodate expected changes in behavior through the year.

Flexibility is particularly important for synchronizing observation or Argos uplink attempts with the expected behavior of an animal, which may or may not be predictable, but also with expected satellite coverage, which is highly predictable. Synchronizing uplink attempts with satellite coverage would minimize battery usage by limiting uplink attempts to those periods when satellites are overhead.

Complete flexibility is somewhat at odds with the previous recommendation of simple programming interfaces. In lieu of complete flexibility (which many users may find difficult), tag manufacturers should be willing to work with users to achieve any desired programming scheme with minimal increased cost. In addition, tag manufacturers could offer two versions of tag programming software. One version would be easy and intuitive, but offer less programming flexibility, and another might offer total flexibility but require users be more savvy.

7. Consider the scale of movement expected from species being tagged and behaviors that will affect regularity and location quality. Some gaps are unavoidable, but tag programming should be carefully tailored to each species and refined after each deployment to maximize track continuity.

8. Audit data after every deployment to assess performance. Visual inspection of mapped tracks is usually inadequate. Communicate perfor-

mance with the manufacturer.

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