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Space Use and Annual Survival of Hybridized Mouflon Sheep in Hawaii and Comparing Estimates of Population Size through Instantaneous Sampling and Photographic Capture-Recapture

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Space Use and Annual Survival of Hybridized Mouflon Sheep in Hawaii and

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and Photographic Capture-Recapture

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ABSTRACT

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Significant efforts in conservation are devoted to the management and study of ungulates, due to their significant roles in ecosystems as well as their potential economic value. This is especially true for species considered exotic, such as mouflon sheep (*Ovis musimon*) in Hawaii. Effective management of an exotic species requires an understanding of ecological metrics such as space use, survival, and population size. We provided these metrics for a population of mouflon that have hybridized with feral sheep (*Ovis aries*) on the island of Hawaii. In Chapter 1, we quantified space use and annual survival of sheep in an area where sheep are managed for hunting opportunity. We determined that sheep have relatively small home-ranges and high rates of annual survival (>90%). In Chapter 2, we provided the first estimate of population size for the same study area while simultaneously testing the viability of a novel method of estimating population size, currently known as Instantaneous Sampling. Using photographic capture recapture as a comparison method, we compared estimates derived from both techniques and provided support for Instantaneous Sampling as an alternative method for estimating population size.

Keywords: Mouflon sheep, Hawaii, space use, survival, Instantaneous Sampling, remote camera, photographic capture-recapture

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CHAPTER 1

Space Use and Survival of Hybridized Mouflon Sheep in Hawaii

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ABSTRACT

Mouflon sheep (*Ovis musimon*) were introduced to the Hawaiian Islands in the 1960's, and have since crossbred with feral sheep (*Ovis aries*). These mouflon-feral hybrids have proliferated throughout the island of Hawaii, including areas identified as critical habitat for endemic species. State agencies have historically implemented management goals focusing primarily on eradication and exclusion, with less resources devoted to understanding basic ecology such as space use and survival which can inform policy. Our objective was to estimate space use and survival for a population of mouflon-feral hybrid sheep on the island of Hawaii. We captured sheep during September 2016 and October 2017 in the Pu'u Wa'awa'a and Pu'u Anahulu management areas on the island of Hawaii and fit a sample of adults with VHF or GPS collars. We monitored 63 adult sheep for two years and estimated space use (i.e., seasonal home-range and core-area size) and annual survival. Sheep had larger home-ranges during the wet season and when located within Pu'u Anahulu. Sex did not influence the size of home-range or core-areas. Annual survival was 0.920 (SE = 0.044) and 0.930 (SE = 0.039) during 2017 and 2018, respectively.

INTRODUCTION

Exotic ungulates on islands are a source of significant controversy due to their potential impacts on native species, vegetation, and soil characteristics (Hannon & Bradshaw, 2013; Lohr et al., 2014; Long et al., 2017). These impacts can include altered vegetation due to herbivory, which can lead to cascading effects on other species. For example, several species of endemic reptiles reliant on understory vegetation were negatively impacted by herbivory by spotted deer (*Axis axis*) in the Andaman Islands (Mohanty et al., 2016). Bird abundance and diversity was also negatively influenced by unmanaged populations of Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) due to change in understory habitat from herbivory (Chollet et al., 2013; Chollet et al., 2015). Herbivory attributed to sheep and goats also reduced biomass and composition of both exotic and endemic plant communities (Cassinello et al., 2004; Vavra et al., 2007). Management of exotic ungulates, however, is complicated due to opposing views amongst stakeholders on how to manage these species.

The economic contribution of ungulates through money spent on hunting and ecotourism is well established globally (Gordon et al., 2004). For instance, the CAMPFIRE association in Zimbabwe generated over US$20 million in a 12-year period with the vast majority of funds coming from hunting (Frost & Bond, 2008). The harvest of red deer (*Cervus elaphus*) in Scotland generates more than £5 million every year and over 700 jobs (Reynolds & Staines, 1997). In the U.S., funds generated by the Pittman-Robertson act alone contributed more than $1.1 billion in funding for conservation programs in 2018 (https://www.fws.gov/southeast/news/). These funds support management under the multiple-use paradigm throughout the U.S.

Wildlife in the Hawaiian Islands are managed for both consumptive and non-consumptive purposes. Hunting has historically played a large role in the economy and culture of Hawaii, including the hunting of introduced ungulates (Duffy, 2010). However, increasing concerns for the preservation of endemic biodiversity have divided stakeholders over hunting policy (Lohr et al., 2014). Current management goals are distributed between diametric sentiments: the preservation and recovery of natural Hawaiian ecosystems and the provision of recreational hunting. Regardless of sentiment, the proper dissemination of policy must be informed by scientific evidence (Cooke et al., 2017; Sutherland et al., 2004), which holds true for exotic ungulates.

Mouflon sheep (*Ovis musimon*) were introduced to Hawaii in the 1960's, and have since hybridized with pre-established herds of feral sheep (*Ovis aries*). Once established, these mouflon-feral hybrids (hereafter, sheep) experienced a dramatic population increase due to abundant resources and limited predation (Scowcroft & Giffin, 1983). Introduced sheep have since caused concern for native species (Scowcroft & Sakai, 1983). For instance, sheep are known to graze, browse, and strip the bark of endemic plants that have not evolved alongside large herbivores (Scowcroft & Giffin, 1983; Scowcroft & Sakai, 1983). Sheep have also been theorized to be the primary source of habitat damage negatively influencing the palila (*Loxioides bailleui*), an endemic species of Hawaiian honeycreeper (Banko et al., 2013; Hess & Banko, 2011). The mamane tree (*Sophora chrysophylla*), an important source of forage and shelter for palila, is also vulnerable to browsing (Banko et al., 2013; Hess & Banko, 2011). Due to the negative impacts of herbivory from sheep, court-ordered eradications were conducted to control sheep populations on the island of Hawaii, including the slopes of Mauna Kea (Banko et al.,

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2014; Duffy, 2010). In other areas, populations of sheep still thrive, as they are maintained by managers and private landowners for hunting.

With stakeholders divided over how sheep should be managed, an improved understanding of the basic ecology of these exotic ungulates could help inform policy. Regardless of management goals, information on space use and survival are critical to evidence-based management. Our objective was to provide wildlife managers with information on annual survival and seasonal space use by 1) quantifying seasonal home-range and core-area sizes and 2) estimating annual survival rates. We also identified factors impacting survival and space use to further explain how sheep interact with their ecosystem. We hypothesized that an abundance of resources available to sheep would result in relatively smaller home-ranges (compared to sheep in other areas) for both sexes as sheep would not need to travel far to acquire resources necessary for growth and reproduction. Additionally, we hypothesized that minimal sources of predation and sufficient forage resources would result in high adult survival. Our aim was to provide ecological data useful in the decision-making process for all possible management goals.

METHODS

Study Area

The study area encompassed the southern extent of the Pu'u Wa'awa'a and Pu'u Anahulu (hereafter PWW and PAH, respectively) game management areas on the island of Hawaii (Fig. 1). The combined area of both sections was approximately 254 km^2 in size. There was a network of roads to facilitate travel throughout PWW, but PAH was only partially accessible by road. Topography is characterized by an incline in elevation from 640 m to 2000 m (Giffin, 2003). The southern boundary of PWW stops short of Mount Hualālai's summit. Although Hualālai is an

active volcano, no lava flows down the northern slopes into PWW (Giffin, 2003). Climate in PWW and PAH is relatively dry in comparison to the mesic forests found throughout Hawaii (Giffin, 2003). Updrafts caused by the warming Hualālai slopes encourage cloud cover during most afternoons (Giffin, 2003). There is limited seasonal heterogeneity, but a wet (Oct-Mar) and dry (Apr-Sep) season are generally identified (Giffin, 2003). Mean monthly temperatures are highest in September (86° F) and lowest in February (81° F) (https://w2.weather.gov/climate).

Vegetation varies between PWW and PAH. The majority of PAH is classified as montane dryland forest and grassland dominated by exotic fountain grass (*Cenchrus setaceum*). Lower elevations at PWW are also classified as montane dryland forest, with higher elevations on Hualālai considered more subalpine (Giffin, 2003). With roughly 90% of the flowering plant species native to the island of Hawaii, PWW is endemically diverse (Wagner et al., 1990) and many of those species are endangered. Subalpine forests in PWW are characterized by 'ohi'a trees (*Metrosideros polymorpha*) with shrub understories of pukiawe (*Styphelia tameiameiae*) and 'ōhelo 'ai (*Vaccinium spp.*) (Giffin, 2003). Among the many endemic and endangered plant species in the lower montane dryland forests are notably po'e (*Portulaca sclerocarpa*), a'e (*Zanthoxylum hawaiiense*), and narrowleaf stenogyne (*Stenogyne angustifolia*). Dry forests are dominated by 'ohi'a, naio (*Myoporum sandwicense*), and a'ali'I (*Dodonaea viscosa*) (Giffin, 2003). In addition to 'ohi'a, there are also small distributions of mamane and koa (*Acacia koa*) (Giffin, 2003).

Sheep Capture and Monitoring

With the assistance of the Hawaii Division of Forestry and Wildlife (DOFAW), we captured 80 sheep via aerial net-gunning and ground-herding in September 2016 and 32 sheep in October

2017. Sheep were aged by visual inspection of tooth wear and given a unique ear tag for identification. We fit either very high frequency (VHF) collars or Iridium GPS collars (Advanced Telemetry Systems, Inc., Isanti, MN) on randomly selected adults for a total of 16 VHF collars (10 rams and 6 ewes) and 47 GPS collars (17 rams and 30 ewes). The GPS collars were programmed to log location coordinates every 6 hours.

Both GPS and VHF collars were programmed to broadcast mortality alerts when they detected a lack of movement for more than 12 hours. Mortality alerts from GPS collars were sent via email along with the animal's most recently logged coordinates. Mortality alerts from VHF collars were broadcast over the collar frequency which could be heard with radio-telemetry. Attempts to listen for VHF collars were made according to the availability of labor, and only occurred a few times each year. Review of methods and procedures used in this project was provided by Brigham Young University's Institutional Animal Care and Use Committee (protocol number 160805).

Space Use Analysis

We estimated space use from data gathered by GPS collars. We assessed the accuracy of GPS data by checking the horizontal dilution of precision (HDOP) associated with each location and removed those with a value ≥20 (Dussault et al., 2001). We calculated home-range and core-area isopleths using a Brownian Bridge Movement Model (Horne et al., 2007), which we chose for its flexibility when dealing with heterogeneous movement patterns (Kranstauber et al., 2012). We determined the 6-hour interval between logged GPS coordinates was sufficient to calculate home-ranges and core-areas for all individuals (Horne et al., 2007; Sawyer et al., 2009).

We grouped coordinates by individual into 6-month subsets that correspond to the wet and dry seasons (October through March and April through September, respectively). Using the BBMM package (Nielson et al., 2013) within program R (R Core Development Team, 2016), we calculated 95% and 50% isopleths (home-range and core-area, respectively) for each subset. We then exported these isopleths for analysis within ArcGIS Pro® (ESRI®, Redlands, CA, 2017) and calculated the size of home-ranges and core-areas in square kilometers. We calculated summary statistics for both home-range and core-area size in.

Using the Shapiro-Wilk test for normality (Shapiro & Wilk, 1965), we addressed the non-normal distribution of home-ranges by selecting an appropriate transformation. We then assessed broad-scale factors impacting size of home-ranges, selecting variables such as season, sex, and location (Table 1). We attached these variables to home-range isopleths to model space use using a mixed-effects logistic regression with a random intercept for individual. We determined top models through model selection (Burnham & Anderson, 2002) in program R (R Core Development Team, 2016) and evaluated relative model support using Akaike's Information Criterion (Akaike, 1973). Upon encountering model uncertainty, we selected all models with ≤ 2 ΔAIC and derived model-averaged coefficients (Arnold, 2010).

Survival Analysis

We monitored survival remotely through GPS data, as well as sporadically with radio-telemetry. Mortality alerts sent by GPS collars were responded to as soon as possible to assess the cause of mortality and retrieve the collar. Mortality alerts broadcast by VHF collars were listened via radio-telemetry. Although attempts were made to visually confirm the status of sheep with VHF collars by the end of the year, we were confident that messages broadcast by the

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collars were reliable. Sheep with collars that were broadcasting mortality were assumed dead, and those that were broadcasting normal signals at the end of each year were assumed alive. Collars that had failed could not be confirmed alive or dead and were censored in the survival analysis.

We determined annual survival rates for both years with Program MARK (White & Burnham, 1999). We met assumptions of demographic closure for each year by censoring individuals who were not confirmed as alive or dead at the end of the period. Preliminary analysis of movement patterns through GPS data provided us with confidence that assumptions of geographic closure were sufficiently addressed.

RESULTS

Home-Range and Core-Area Estimation

Mean size of core-areas within PWW was 1.05 ± 0.14 km^2 ($n = 67$, range = 0.05—2.39 km^2). Mean size of core-areas within PAH was 1.62 ± 0.33 km^2 ($n = 47$, range = 0.18—4.57 km^2). Core-areas were generally larger within PAH compared to PWW ($P = 0.006$). Mean size of home-ranges within PWW was 5.77 ± 0.86 km^2 ($n = 67$, range = 0.31—13.30 km^2). Mean size of home-ranges within PAH was 9.81 ± 1.97 km^2 ($n = 47$, range = 1.48—34.59 km^2). Home-ranges were also generally larger within PAH compared to PWW ($P < 0.001$) (Fig. 2). We noted a strong correlation between core-area size and home-range size for both locations, though the correlation was generally stronger in PWW ($r = 0.86$) than in PAH ($r = 0.70$).

Home-Range Analysis

Home-ranges were non-normal in distribution ($W = 0.837$, $P < 0.001$). We applied a cube-root transformation to home-range size which significantly improved normality ($W = 0.988$, $P = 0.429$) preceding model-selection. Home-range sizes differed by study area. Home-ranges in PAH were generally larger than those within PWW. Area of home-ranges was also larger during the wet season compared to the dry season. Sheep released in the second year had larger home-ranges than those released in the first year. Our top three models held 0.71 model weight, with our fourth-ranked model (the null model) holding 0.05 model weight. The top model included only location, while the second and third-ranked models also included season. Additionally, the third model included capture year and survival year as well as the interaction between location and survival year. Sex did not influence home-range size, and neither did the three remaining interactions between location and capture year, season, and sex (Table 2).

Survival Analysis

There were 41 individuals with known fates at the end of the first year, and 48 individuals with known fates at the end of the second year. Five sheep died during the study: 3 were depredated by feral dogs during the first year, 1 succumbed to disease in the second year, and 1 was poached in the second year. Annual survival for the first year was 0.920 (SE = 0.044) and for the second year it was 0.930 (SE = 0.038).

DISCUSSION

Space Use

Our results suggest that there are spatial and temporal influences on space use, most likely in the form of location and season. This is most apparent when comparing space use between PWW and PAH. While we did not quantify forage availability, we did make assumptions on how the two distinct regions of PWW and PAH would differ by the amount of greenery observed from satellite imagery. Compared to the lush grass understories in PWW, the predominantly dry communities of fountain grass in PAH may supply forage with reduced quality. Furthermore, there is greater browsing opportunity in the diverse plant communities found in PWW. This pattern was corollary with the results of home-range model selection, as sheep in PWW are able to obtain sufficient resources from a smaller area, whereas sheep in PAH may need to cover more area, as is common with large herbivores (van Beest et al., 2011). We recognize this observation is large-scale and does not address fine-scale spatial variation, however we feel confident an analysis of habitat-selection would also reveal key differences between PWW and PAH. Our study provided Hawaii's first assessment of space use for hybridized sheep in Hawaii. Previous research on space use for mouflon sheep (Ciuti et al., 2009; Dubois et al., 1993; Dupuis et al., 2002; Marchand et al., 2015; Tablado et al., 2016) served to help us form expectations for how sheep may utilize Hawaiian habitat. For instance, space use of Mediterranean mouflon (*O. gmelini musimon*) is driven by hunting pressure and forage availability (Marchand et al., 2015).

Increased home-range size was correlated with an increased core-area size. This may simply be a result of spatial autocorrelation, since home-ranges and core-areas of each individual are calculated from the same dataset. We therefore expect some of the same processes driving formation of home-ranges to also drive formation of core-areas (Börger et al., 2006), albeit on a

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different scale. Since study area is a large-scale variable, it more readily models home-range size. Further research involving fine-scale differences between PWW and PAH could better describe mechanics of core-area formation of sheep, as studies involving habitat selection of other species of sheep have shown (Cransac & Hewison, 1997; Smith et al., 2015; Walker et al., 2007).

We predicted that abundant resources would result in smaller home-ranges during the wet season because increased precipitation is correlated with increased forage productivity (Bennett et al., 2003; Bukombe et al., 2019; Rafay et al., 2016; Sianga et al., 2017). Our results indicate, however, that home-range sizes increased during the wet season. We divided the year into wet and dry seasons since it was the only form of identifiable seasonal heterogeneity. That being said, the terms "wet" and "dry" may be misnomers, as rainfall and humidity differ only slightly. We believe the results of larger home-ranges during the wet season could be an artifact of the human-wildlife interactions caused by the capture process. Past research has shown how human interactions may alter ungulate behaviors and movement (Brambilla & Brivio, 2018; Found & St Clair, 2018; Stankowich, 2008). Côté et al. (2013) showed how mountain goats (*Oreamnos americanus*) had difficulty habituating to anthropogenic disturbance with partial habituation only occurring after more than 10-15 years of repeated exposure to helicopter traffic. Brambilla and Brivio (2018) demonstrated the lingering effects of human disturbance on Alpine ibex (*Capra ibex*) even after the perceived threat had dissipated. All of our capture events took place either in the beginning of the wet season (October), or at the very end of the dry season (September). The increase of stress-related activity related to capturing and handling may have increased movement through the beginning of the wet season, resulting in larger home-ranges.

Survival

We determined adult sheep have a high rate of survival (~90%) in our study area. The three mortalities in the first year were attributed to feral dog depredation while those in the second were either from poaching or disease. During the first year of the study, there were substantial trapping efforts conducted by the DOFAW to reduce numbers of wild dogs in order to improve game survival and quality of ecotourism. By the end of the first year, these efforts had successfully eliminated a majority of dogs, a result that was mirrored by the lack of dog depredation in the second year. With consistently high survival rates, managers would expect quickly rising population sizes. However, this expectation is not reflected by the observation of managers and technicians within the study area who have not observed rapid population growth. This could be due in part to a lack of reproductive success, or poor recruitment.

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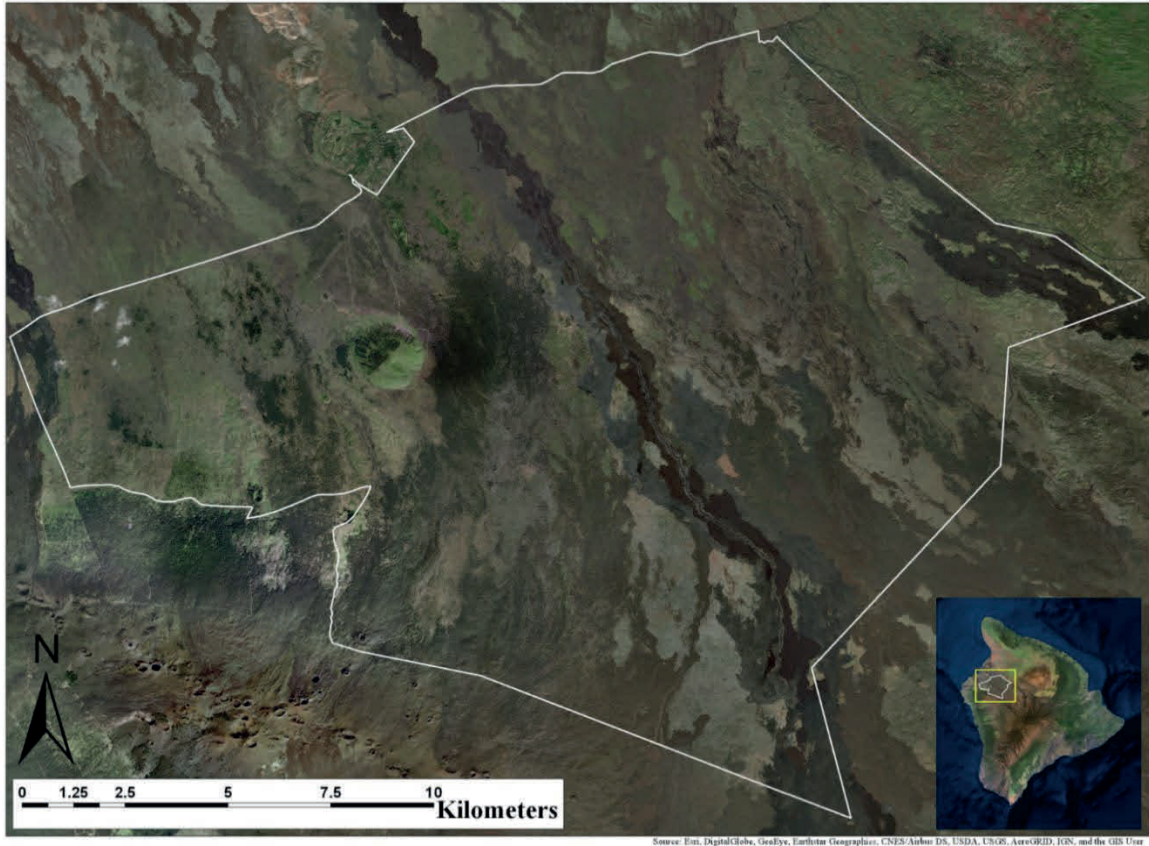
Figure 1- 1. The study area located on the island of Hawaii, encapsulating the Pu'u Wa'awa'a and Pu'u Anahulu management areas south of Mamalahoa highway, where survival and space use of feral sheep (*Ovis musimon* and *Ovis aries*) were analyzed during October 2016 through September 2018.
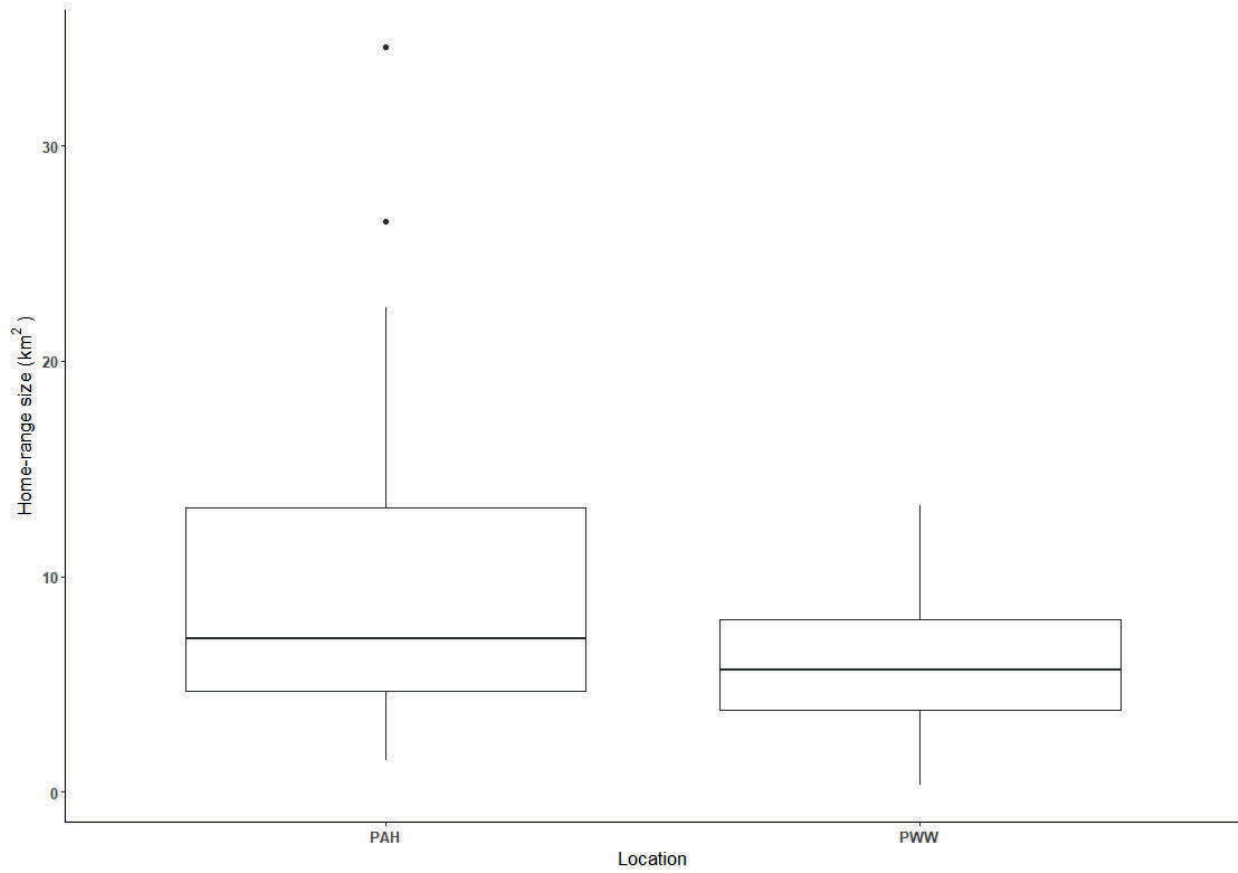
Figure 1- 2. Mean home-range size in km^2 of feral sheep (*Ovis musimon* and *Ovis aries*) calculated for two management areas (Pu'u Wa'awa'a and Pu'u Anahulu; PWW and PAH, respectively) on the island of Hawaii from October 2016 through September 2018.

Table 1- 1. Variables potentially associated with home-range size of feral sheep (*Ovis musimon* and *Ovis aries*) on the island of Hawaii.

Variable name	Description
ANID	Animal ID
CYEAR	Date of release referring to the year the animal was captured
LOC	Region of study area containing the animal home-range
SEASON	Wet or dry season
SEX	Male or female
SYEAR	Calendar year

Table 1- 2. Model results (≥ 0.01 model weight) for home-range size of feral sheep (*Ovis musimon* and *Ovis aries*) on the island of Hawaii, showing number of parameters (K), Akaike's Information Criterion corrected for small sample sizes (AICc), ΔAICc, model weight (ωi), and log likelihood (LL). Variable names match those in Table 1.

Model Number	Model Structure	K	AICc	ΔAICc	ωi	LL
5	LOC + (1|ANID)	2	118.53	0.00	0.30	-55.08
10	LOC + SEASON + (1|ANID)	3	118.79	0.27	0.26	-54.12
14	SEASON + LOC + SYEAR + CYEAR + LOC*SYEAR + (1|ANID)	6	119.89	1.36	0.15	-51.26
18	NULL	2	122.13	3.60	0.05	-57.96
11	SEASON + CYEAR + LOC + (1|ANID)	4	122.15	3.62	0.05	-54.68
1	SEASON + (1|ANID)	2	122.45	3.92	0.04	-57.04
9	LOC + SEX + (1|ANID)	3	122.70	4.17	0.04	-56.07
13	SEASON + LOC + SEASON*LOC + (1|ANID)	4	123.40	4.87	0.03	-55.31
4	CYEAR + (1|ANID)	2	123.41	4.89	0.03	-57.52
6	SEASON + SYEAR + (1|ANID)	3	125.54	7.01	0.01	-57.49
2	SYEAR + (1|ANID)	2	125.95	7.42	0.01	-58.79
12	SYEAR + SEX + LOC + (1|ANID)	4	126.11	7.58	0.01	-56.66
16	SEASON + LOC + SYEAR + CYEAR + SEX + (1|ANID)	6	126.44	7.91	0.01	-54.53
3	SEX + (1|ANID)	2	126.45	7.92	0.01	-59.04

CHAPTER 2

Instantaneous Sampling and Photographic Capture-Recapture: Comparing Estimates of
Population Size for Techniques Using Remote Cameras

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ABSTRACT

Accurate estimates of population size are highly beneficial to wildlife management. Remote
cameras have become increasingly popular as tools for estimating population size through
methods like photographic capture-recapture (CR). For many species, CR is not possible without
first capturing and marking animals for recapture. A recently developed technique addresses this
limitation by using imagery of unmarked animals to sample population density with replication,
otherwise known as instantaneous sampling (IS). However, IS has yet to be compared with a
robust method such as CR. Our objective was to estimate the size of an ungulate population
using IS, and compare it with estimates derived from CR. In September 2016 we captured 80
feral sheep (*Ovis musimon* and *Ovis aries*) on the island of Hawaii and marked them with ear
tags for photographic recapture. During the summers of 2017 and 2018 we deployed remote
cameras in randomly generated locations to detect sheep. We programmed cameras to trigger
every 15 minutes regardless of whether animals were present. Images taken in this manner acted
as samples of population density within the camera's field of view. We also programmed
cameras with infrared and motion detection during 2017 to build encounter histories of marked
sheep for CR. Through IS we estimated the population size to be 850 individuals, 95% CI [715,
984] in 2017, and 934 individuals, 95% CI [771, 1091] in 2018. Through CR we estimated
population size to be 919 individuals, 95% CI [544, 1552] in 2017. We observed that estimates of

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population size derived from IS and CR were comparable, and that the confidence intervals of IS were smaller than those of CR. Our results provide support for IS as an alternative method of estimating population size when compared to CR.

INTRODUCTION

Accurate estimates of population size are highly beneficial to wildlife management (Keever et al., 2017; Le Moullec et al., 2017; Murray et al., 2009). Estimates of population size are used by decision-makers to implement harvest quotas and set management goals for game species like ungulates (Hagen et al., 2018). Estimating the size of a population, however, can be challenging and is often influenced by spatial distribution and variable factors affecting detection probabilities (DeCesare et al., 2012; Duquette et al., 2014). In addition, current approaches to estimating population size can be both invasive and expensive. As managers seek accurate estimates of population size, methods for producing estimates undergo continuous revision, and new methods are intermittently added to the available toolset (Latham et al., 2018; Schuette et al., 2018; Witczuk et al., 2018).

One of the most common methods used by wildlife biologists to estimate population size are aerial surveys, which allow managers to cover large areas in a relatively short amount of time (Cumberland, 2012; Freddy et al., 2004; Peters et al., 2014; Terletzky & Koons, 2016). The accuracy of aerial surveys has improved with the development of more robust designs as well as the use of helicopters in lieu of fixed-wing aircraft (Anderson & Lindzey, 1996; Gosse et al., 2002; Poole et al., 2013). However, detection biases persist for most study designs which often require post-hoc correction to produce reliable results (Anderson & Lindzey, 1996; Cumberland, 2012; Peters et al., 2014; Rivest et al., 1995). Additionally, the high cost associated with aerial operations has long been a significant limitation for this method, particularly for those in under-

funded areas (Schuette et al., 2018). Alternative approaches to estimating population size can mitigate for expense and detection bias by reducing flight-time and improving sightability of animals (Franke et al., 2012; Moeller et al., 2018; Schuette et al., 2018).

Remote cameras, for instance, have garnered attention as a ground-based, non-invasive (Rowcliffe et al., 2008) tool for monitoring wildlife, due to their relatively low cost (Rovero & Marshall, 2009) and flexibility provided by a wide variety of available study designs (Burton et al., 2015; Keever et al., 2017). Since they are deployed at ground level, cameras provide a line of sight beneath canopy that can otherwise be obscured from an aerial view. Programming cameras to collect data automatically reduces frequency of potentially negative human-wildlife interactions. Cameras have also been adapted to data collection for existing study designs such as capture mark-recapture models (Burton et al., 2015; Curtis et al., 2009; Silver et al., 2004; Thorne et al., 1996).

Photographic capture-recapture (hereafter, CR) can be a reliable method for estimating population density, and subsequently population size, if species can be identified to the individual and then "recaptured" on camera (De Bondi et al., 2010; Karanth & Nichols, 1998; Marshal, 2017; Ryu et al., 2016). This assumption is met for species where unique pelage or morphology of individuals sets them apart from the rest of their cohort (Karanth & Nichols, 1998; Silver et al., 2004; Sreekar et al., 2013; Srivathsa et al., 2015). Ungulates however, do not commonly have unique marks that confidently identify them to an individual level, with the exception of some species (Marshal, 2017; Rahman et al., 2017) or demographics within species (Jacobson et al., 1997). In order to perform photographic CR analyses on these species, it is requisite to first capture and mark species to enable re-detection; thereby nullifying one of the primary advantages of monitoring with remote cameras.

Capture of animals for marking is often expensive as well as invasive, in many cases relying on aerial methods such as helicopter net-gunning. Among the potential consequences of handling animals are capture myopathy and negative behavioral-conditioning which can lead to the violation of CR's assumptions if detection heterogeneity is not properly modeled (Burton et al., 2015). These issues can potentially be addressed by models that do not use re-capture frequencies of individuals to estimate abundance, as some studies have attempted to demonstrate (Chandler & Royle, 2013; Evans & Rittenhouse, 2018; Keever et al., 2017; Parsons et al., 2017; Rowcliffe et al., 2008). Recent methodologies developed by Moeller et al. (2018) have used sampling theory to derive estimates of population size.

According to sampling theory, characteristics of a population such as density can be determined by taking random samples from that population (Cochran, 1977). With this foundation, one could theoretically estimate population size for a species within a calculable area by 1) estimating overall population density by extrapolating on random samples of population density and 2) using that estimate of density to calculate population size for an area with a known extent. Furthermore, sampling with spatial and temporal replication improves the accuracy of estimates (Johnson, 2002; Reilly et al., 2017). A recently proposed method referred to as Instantaneous Sampling (IS) (Moeller et al., 2018), uses remote cameras as a ground-based tool to sample population densities with spatiotemporal replication, and extrapolates on these samples over a defined area.

Estimates of population size derived from IS have been compared to estimates derived from aerial surveys to provide support for the viability of IS as an alternative technique for estimating population size (Moeller et al., 2018). In order to more critically assess the viability of IS, we proposed that further comparisons should be made using other methodologies from scientific

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literature. A method such as CR could provide a comparison with more inference due to its similar use of remote cameras as a tool for data collection. Furthermore, conducting multiple trials on the same population over time would demonstrate an ability to provide consistent results, given assumptions of closure are addressed between trials (Moeller et al., 2018).

Our first objective was to use IS to estimate the size of a population of feral sheep (*Ovis gmelini musimon* and *Ovis aries*; hereafter, sheep) within a defined study site and provide a comparison estimate of population size through a published methodology. We chose photographic capture-recapture (CR) as our comparison method due to its substantial support in the literature as a reliable method of estimating population size (Burton et al., 2015). Our second objective was to optimize IS methodology to determine temporal and spatial requirements for data collection; in other words, the minimum number of cameras that can be deployed within a given area in addition to the length of the deployment that result in consistently reliable and accurate estimates of population size. We predicted that confidence intervals generated by IS and CR would overlap, although we could not anticipate to which degree, as our study would provide a novel comparison between IS and a robust estimator such as CR.

METHODS

Study Area

The study area encompasses the southern extent of the Pu'u Wa'awa'a and Pu'uanahulu (hereafter PWW and PAH, respectively) game management areas on the island of Hawaii. Both sections were regarded as one continuous study area, approximately 254 km^2 in size. Mount Hualālai peaks near the southern boundaries of PWW, with a steady decrease in elevation from 2000 m to 640 m northwards (Giffin, 2003). The Pu'u Wa'awa'a Cinder Cone State Park is

located within the northeastern extent of PWW. Sheep represent the majority of free-ranging ungulates within the study area, with small populations of feral goats (*Capra aegagrus hircus*) near the cinder cone and northern boundary (Giffin, 2003). Wild pigs (*Sus scrofa*) are also present, but in smaller numbers distributed throughout PWW. With the exception of feral dogs, humans are the only source of predation on adult sheep populations (Scowcroft & Giffin, 1983).

Vegetation varies between the PWW and PAH areas. PAH is generally the drier of the two, classified as montane dryland forest with patches of grassland dominated by fountain grass (*Cenchrus setaceum*). Lower elevations at PWW are classified as montane dryland forest, and higher elevations on Hualālai classified as subalpine (Giffin, 2003). The dryland forests of PWW are much denser than those in PAH, and result in a greater amount of visual obstruction of sightlines. Subalpine forests in PWW are characterized by 'ohi'a trees (*Metrosideros polymorpha*) with shrub understories of pukiawe (*Styphelia tameiameiae*) and 'ōhelo 'ai (*Vaccinium spp.*) – all native to Hawaii. Among the many endemic and endangered plant species in the lower montane dryland forests are notably po'e (*Portulaca sclerocarpa*), a'e (*Zanthoxylum hawaiiense*), and narrowleaf stenogyne (*Stenogyne angustifolia*). Dry forests are dominated by 'ohi'a, naio (*Myoporum sandwicense*), and a'ali'I (*Dodonaea viscosa*). In addition to 'ohi'a, there are also small distributions of mamane (*Sophora chrysophylla*) and koa (*Acacia koa*) (Giffin, 2003).

Data Collection

With the assistance of the Hawaii Division of Forestry and Wildlife, we captured 80 sheep throughout the study site via helicopter net-gunning and funnel-trapping in September 2016. Sheep were marked with ear tags to enable identification and a random sample was fitted with

radio collars for auxiliary monitoring purposes. We fit either very high frequency (VHF) collars or Iridium GPS collars (Advanced Telemetry Systems, Inc., Isanti, MN). We programmed collars to log coordinates every 6 hours. The GPS collars facilitated measurements of survival and movement that would be critical in meeting assumptions of demographic and geographic closure when modelling population size through CR and IS.

Survival was monitored remotely, with GPS collars programmed to send an alert when they sensed an animal had not moved for an extended period of time. Technicians confirmed mortalities as soon as possible, as well as tracking VHF collars with radio telemetry. The actual number of individuals that were visually confirmed as alive were considered part of the CR dataset. Additionally, animals that moved outside of the study area were considered non-detectable and also removed from the dataset.

Our objectives of calculating population size through CR and optimizing IS for a follow-up trial required a large first sampling period. We therefore maximized the amount of cameras that would be required, as well as the length of time they should be deployed for our 2017 trial. A total of 95 remote cameras were deployed for a time period spanning the end of June through October of 2017 (Fig. 1). Optimization of these methods are detailed shortly hereafter, and resulted in a reduction in number of cameras deployed, as well as a shorter sampling period. We deployed 48 cameras for the duration of August 2018 in the same study area. We determined locations for the deployment of cameras by randomly generating points within the bounds of the study area using ArcGIS Pro® (ESRI®, Redlands, CA, 2017). Due to variable terrain limitations, we generated a 400m buffer around these points to allow for flexible placement of cameras. All cameras faced a general SW azimuth to minimize sun glare. Where possible, cameras were anchored to available trees, otherwise, cameras were anchored to t-posts. We

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deployed cameras 3-5 feet above the ground at a downward angle to maximize visibility and prevent animals going undetected should they walk beneath the camera's viewable area (Fig. 2). We estimated the size of each camera's viewable area in order to calculate population density for each photo taken.

We used remote cameras capable of multiple trigger settings (PC900; Reconyx®, Holmen, Wisconsin, USA) to collect two sets of data simultaneously in 2017. Cameras automatically took pictures every 15 minutes for the duration of the study. Cameras also triggered upon infrared and motion detection, taking a burst of three pictures separated by a 1 second delay. Motion triggers had a 60 second quiet period in between events. Based on results from 2017, we did not perform a CR analysis in 2018 and the cameras were only programmed with a 15 minute time-lapse.

Data Analysis

Upon retrieval of cameras, images were analyzed for sheep counts which provide estimates of population density within a camera's viewable area. Images comprising the IS dataset had a large number of empty images as expected. Empty images were counted as having a population density of zero. Sheep with ear tags or collars were identified to an individual level where possible to build encounter histories for CR. Due to camera failure before a sufficient number of images could be taken, some cameras were removed from each dataset.

Estimates of population size were derived from the IS estimator described by (Moeller et al., 2018). In short, IS estimates overall population density by calculating the sum of all samples of density (sheep counts over the camera's sampled area) and dividing by the number of samples taken. We calculated variance around this estimate of density with a non-parametric bootstrap of our dataset (Efron & Tibshirani, 1993) with 2000 repetitions. We then used population density to

calculate population size within our study area, given that abundance can be described as a function of area and population density.

We addressed the assumptions of demographic and geographic closure required by CR before analyzing encounter histories. To determine the number of marked animals within the population that were alive and available for recapture, we analyzed the status of deployed GPS and VHF collars. For GPS collars, this process was simplified by frequent data uploads that confirmed animals were moving and alive. For VHF collars, we listened for signals with radio-telemetry to determine if animals were in a state of mortality. We also met assumptions of geographic closure by evaluating movement patterns of GPS collars. Sheep that were outside of the study area during the duration of the camera deployment were not considered available for recapture. We used model selection and a zero-inflated unidentified marks Poisson robust design to analyze encounter histories with program MARK (White & Burnham, 1999). We evaluated relative model support using Akaike's Information Criterion (Akaike, 1973) to estimate population size for a closed population.

Optimization of IS methodology was performed on two levels: spatial and temporal. To determine the optimal length of deployment for cameras, we grouped continuous camera data from the 2017 dataset into weeks of incrementally larger size. We analyzed the estimates of population size derived from these datasets to look at variation between 1 week datasets, 2 week datasets, and son on until we reached the maximum length available. We calculated the coefficient of variation (CV) for each distribution of deployment length. We then analyzed the relationship between CV and length of camera deployment to determine the optimal length of deployment.

We optimized the number of cameras deployed in a similar fashion by grouping camera imagery into datasets of incrementally larger size. We selected 5 cameras at random from the total number of available cameras and used that data to calculate an estimate of population size. We repeated this process 1,000 times for random draws increasing by 5 each time until we reached the maximum amount of cameras available. We then calculated the CV for each distribution of random draw and analyzed the relationship between CV and number of cameras deployed to determine the optimal number of cameras we could deploy.

RESULTS

Through IS we calculated estimates of population density which we converted to population size given the 254km^2 area. In 2017 we estimated the size of the sheep population at 919 individuals [95% CI (544, 1552)] through CR. We also estimated the population of sheep at 850 individuals [95% CI (715, 984)] through IS in the same year. In August 2018, we estimated the population of sheep at 934 individuals [95% CI (771, 1091)] through IS (Fig. 3).

We observed a decrease in CV as length of camera deployment increased (Fig. 4). The most notable change in CV occurred between 1 week (CV = 34.76%) and 4 weeks (CV = 10.61%) of deployment, after which CV varied between 1-10%. A similar decrease in CV occurred as the number of cameras used to estimate population size increased (Fig. 5), improving from a random draw of 5 cameras (CV = 130.65%) to 85 cameras (CV = 3.20%). The inclusion of more cameras always resulted in an increase in CV, whereas an increased length of camera deployment did not always reduce CV after 4 weeks.

By reducing the spatial and temporal requirements of data collection, we were able to drastically reduce the number of images that needed to be analyzed. In 2017 we analyzed over

750,000 time-lapse images alone. This number was reduced to just over 130,000 images in 2018. Processing time of time-lapse imagery from 2017 took roughly 200 hours, whereas processing time in 2018 took roughly 40 hours. An additional 400,000 motion-detection images were analyzed in 2017 in order to build encounter histories for CR.

DISCUSSION

Our results provide support for IS as a viable technique for estimating population size. Estimates derived from IS were similar to CR and had more narrow confidence intervals. Additionally, confidence intervals of IS fell entirely within those of CR. We observed that requirements for duration of deployment were also reduced from CR to IS. In order to obtain more accurate estimates of population size, we needed to maximize the number of individuals that were recaptured from the available pool of marked animals (White, 2008; White & Burnham, 1999). This required data from the full length of camera deployment, or a total of 18 weeks.

We provided two estimates of population size through IS. The confidence intervals around each estimate suggest our optimized number of cameras and length of deployment were acceptable for our study area. However, we encourage a conservative approach when determining the duration of deployment and number of cameras deployed. Some studies refer to CVs within 10-20% as having "little" to "moderate" variation (Gaillard et al., 2000; Ismail et al., 2003). Our results suggest that deploying cameras for a minimum of 3 weeks at a density of 1 camera per ~4 km^2 should consistently estimate population size with acceptable levels of variation.

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The concept of having reliable frameworks for estimating the population size of unmarked wildlife is not new (Murphy & Noon, 1991; Rabe et al., 2002). With recent developments both technological and methodological, techniques for monitoring unmarked wildlife are becoming more repeatable and are thus subjected to increased scrutiny (La Morgia & Focardi, 2016; Terletzky & Koons, 2016). We anticipate interest in IS will increase as managers continue searching for methods that are repeatable and cost-effective. With this in mind, we provide the following insight for those interested in using the IS estimator.

Ideally, fixed-area counts are re-randomized after each sampling occasion (Moeller et al., 2018). In a real world setting, logistics normally preclude a systematic re-deployment of cameras across a landscape. Thus, it is crucial when using this IS estimator to provide estimates of variance around mean population density to address spatial autocorrelation which we accomplished through a non-parametric bootstrap (Efron & Tibshirani, 1993). Additionally, the sensitivity of IS to rigorous collection methods is evident when calculating population density. Inaccurate counts of animals are a common source of error throughout study designs (Glass et al., 2015; Nuno et al., 2015; Rivest et al., 1995; Terletzky & Koons, 2016). We noted that factors such as weather, camera resolution, time of day, and animal behaviors affected the quality of pictures (Fig. 6). While the majority of our cameras had short view distances which did not suffer as much from these factors, other cameras sample larger areas and animal counts were accompanied with lower certainty in some instances. Another more significant source of error could be the improper measurement of camera sampling area, as this area is used to calculate every measure of density for a given camera for the duration of its deployment. Such an error repeated throughout a camera's deployment can result in estimates of density that skew either low or high, and can drastically impact the estimates returned by IS. We suggest a systematic

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approach to calculating view area to reduce the frequency of this error, such as measuring view distances with stakes or flagging to ensure counts always occur over the same view area.

Another consideration should be given to the labor required in analyzing high-volumes of pictures. Studies involving remote cameras are often limited by the sheer amount of data that is collected (Fegraus et al., 2011; Krishnappa & Turner, 2014; Swanson et al., 2015). Analyzing cumbersome datasets of imagery may additionally lead to human error due to fatigue (Krishnappa & Turner, 2014). While we were able to reduce the amount of hours required to analyze images from 200 to 40, our study area may be considered small-scale (254 km^2) when compared to larger management areas on the mainland. Large-scale monitoring efforts may therefore be limited by expectedly larger datasets (Swanson et al., 2015).

There are some distinct advantages of the IS estimator. Using time-lapse programming, we eliminate uncertainty stemming from variable detection associated with each camera. Additionally, many studies assume variable detection rates with varying distance from the camera (Parsons et al., 2017). Cameras that take pictures regardless of animal presence all assume the same rate of detection when line-of-sight is un-inhibited (Burton et al., 2015; Moeller et al., 2018). By deploying cameras and defining a view area, we assume perfect detection and ignore animals that are present outside of the view area.

It is also worthy to mention recent technological advancements as applied to the field of ecology. With an increased focus on camera data, methods for processing imagery have been explored. Automatic classification of imagery through machine learning, for instance, may prove to be an effective way of classifying imagery by eliminating the manual burden associated with analyzing large datasets (Chen et al., 2014; Gomez Villa et al., 2017; Tabak et al., 2018). This

can lead to more rigorous sampling techniques without a sacrifice in cost-effectiveness, or enable sampling over larger extents.

The flexibility offered by IS may be one of its most desirable advantages. The data provided by the collection process is permanently archived and can be reviewed for detection error post-hoc, whereas counts taken by technicians in the field cannot be replicated. Furthermore, cameras are capable of replicating samples over time more consistently than humans. While still in a developmental stage, the IS estimator demonstrates promise as an effective technique for monitoring wildlife populations.

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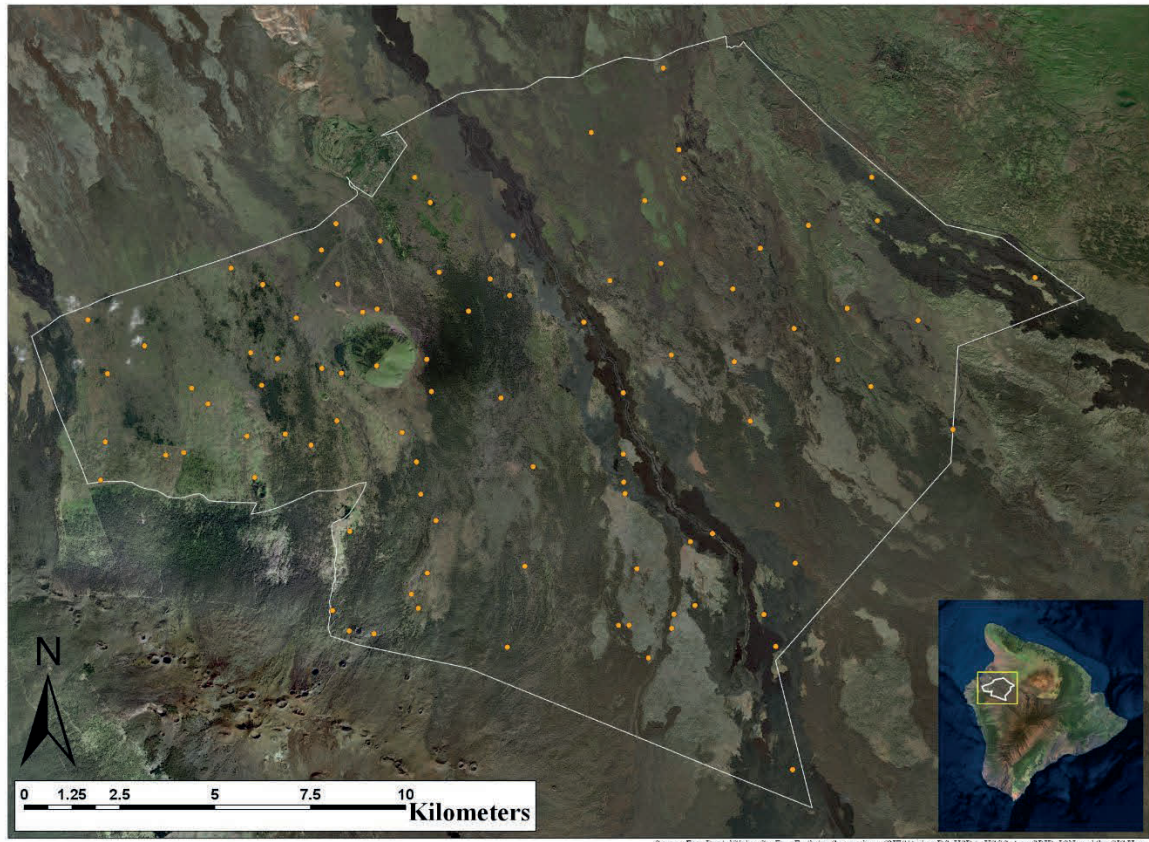
FIGURES

Figure 2- 1. Locations where we deployed remote cameras in 2018 to estimate population size of feral sheep (*Ovis musimon* and *Ovis aries*) through Instantaneous Sampling. The study site encompasses two areas managed by the Hawaii Division of Forestry and Wildlife on the island of Hawaii. Camera locations are represented by orange dots.

Figure 2- 2. A camera deployed in Pu'u Wa'awa'a Game Management Area on the island of Hawaii during 2017. Remote cameras were anchored to trees to photograph wildlife and estimate population size of feral sheep (*Ovis musimon* and *Ovis aries*) through Instantaneous Sampling.
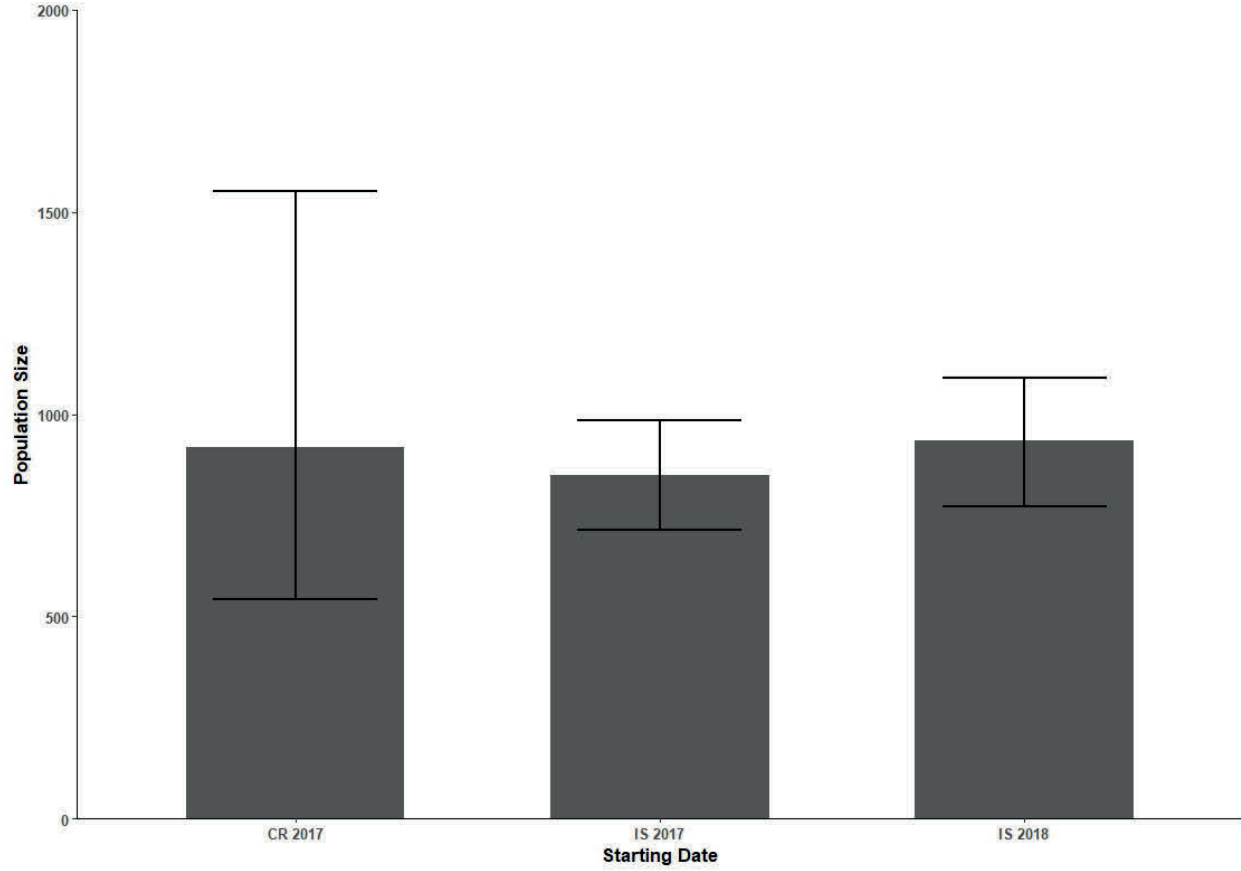
Figure 2- 3. Estimates of population size derived from Photographic Capture-Recapture (CR) and Instantaneous Sampling (IS) for a population of feral sheep (*Ovis musimon* and *Ovis aries*) on the island of Hawaii during 2017 and 2018.
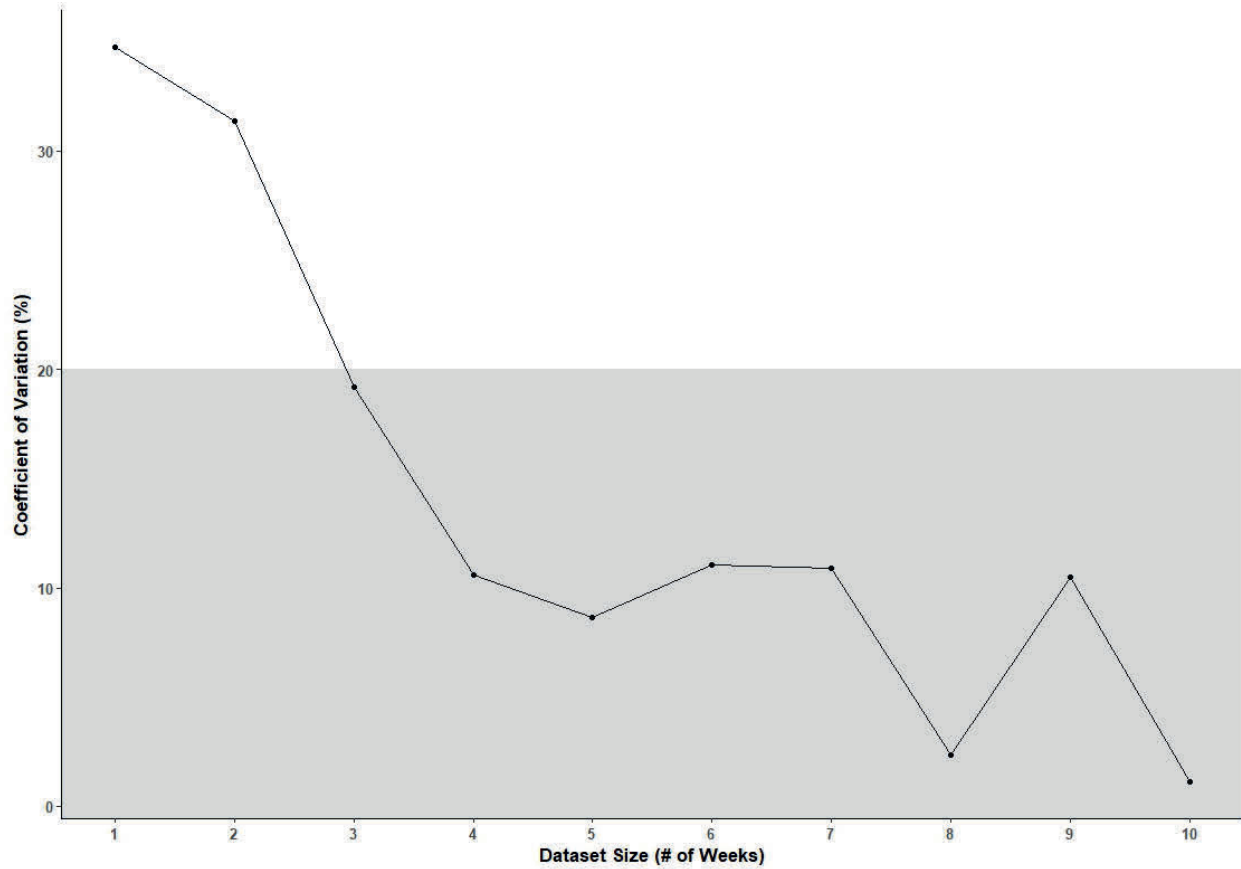
Figure 2- 4. Coefficient of variation (CV) for estimates of population size of feral sheep (*Ovis musimon* and *Ovis aries*) on the island of Hawaii during 2017. Estimates were derived through Instantaneous Sampling using increasing sample sizes corresponding to length of deployment in weeks. The grey section refers to a target CV of 20%.
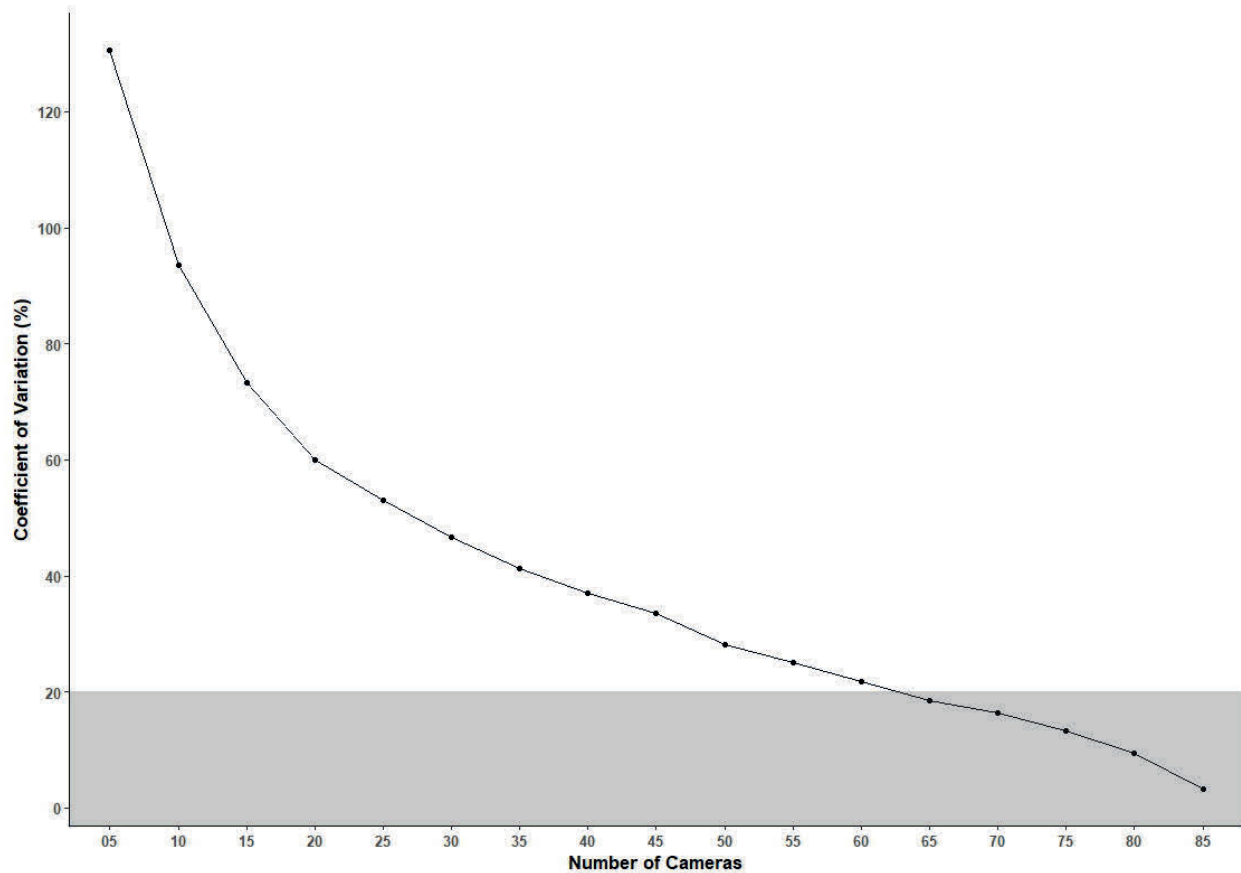
Figure 2- 5. Coefficient of variation (CV) for estimates of population size of feral sheep (*Ovis musimon* and *Ovis aries*) on the island of Hawaii during 2017. Estimates were derived through Instantaneous Sampling using increasing sample sizes corresponding to number of cameras deployed. The grey section refers to a target CV of 20%.

Figure 2- 6. Pictures demonstrating impacts of behavior, weather, and time of day on image quality which may impact accuracy when counting animals. Pictures were taken on the big island of Hawaii during 2017 and used to estimate population size of feral sheep (*Ovis musimon* and *Ovis aries*).