Conservation translocations of Hawaiian monk seals: accounting for variability in body condition improves evaluation of translocation efficacy

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Abstract

To assess the efficacy of conservation translocations, survival of released individuals is typically compared to that of control groups. Such comparisons assume that treatment groups consist of otherwise equivalent individuals. When that assumption is unmet, incorporating physiological parameters may improve assessment of translocation programs. During 2012-2014, 19 weaned female Hawaiian monk seal pups were translocated to sites where survival prospects were expected to be more favorable than at their natal locations. We compared survival from weaning to age two years of translocated pups to two control groups; pups remaining at source sites and pups native to destination sites. To account for the known relationship between weaning girth and survival, we generated probability distributions of the number of survivors at source and destination sites given the weaning girths of translocated seals. Data were available to calculate girth-adjusted survival probabilities for 13 of the translocated pups. Of these, we estimated that only one pup would have been expected to have survived had the translocated pups remained at their natal site. Seven of the 13 translocated seals survived, a value just below the median (eight) expected to have survived at the destination site. Thus, translocation substantially improved survival. Had we not accounted for weaning girth effects on survival, we would have erroneously concluded that the translocation program had yielded no survival benefit. Identifying and integrating correlates of survival into quantitative analyses associated with conservation translocations can reduce bias and lead to greater success.

Keywords: Conservation translocation, survival, Hawaiian monk seal, body condition, Monte Carlo methods

Introduction

The science of conservation translocation is well established. Gone are the days when ill-conceived reintroductions (and other conservation translocations) were conducted with little or no post-release monitoring or documentation (Seddon & Armstrong, 2016). The accepted standards for every step of the process are embodied in the IUCN Guidelines for Reintroductions and Other Conservation Translocations (IUCN, 2013).

Evaluating post-release survival is a critical element in assessing the efficacy of conservation translocations (Armstrong *et al*., 2017). Drawing meaningful conclusions from post-release survival monitoring of translocatees may depend on the availability of appropriate control groups. For example, survival of released individuals may be compared to that of natives at the release location and others left behind at a source population (e.g., Lloyd *et al*., 2019). In making such comparisons among treatment groups, however, one assumes that the groups consist of otherwise equivalent individuals. A variety of factors such as the age, mass, sex, behavioral traits, and experience of individuals can influence post-translocation survival (Bremner-Harrison, Prodohl, & Elwood, 2004; Attum *et al.*, 2010; Frair *et al.*, 2010; Cabezas, Calvete, & Moreno 2011; Day, Westover, & McMillan, 2013; Mathews, Coates, & Delehanty, 2016; West *et al.*, 2018; Hare *et al.* 2019). Failing to account for such factors may render comparison of treatment and control groups invalid. Incorporating physiological parameters, both pre- and post-translocation, may especially improve assessment of translocation programs (Tarszisz, Dickman & Munn, 2014), though this can be challenging in the context of real management (Pinter-Wolman, Isbell & Hart, 2009).

In the endangered Hawaiian monk seal, translocation has been successfully applied for 35 years to mitigate shark predation and conspecific male aggression, reduce human–seal interactions, and take advantage of favorable foraging habitats (Baker *et al*., 2011). The Hawaiian monk seal meta-population comprises eight Northwestern Hawaiian Islands (NWHI) subpopulations and one in the main Hawaiian Islands (MHI) (Fig. 1). These subpopulations exhibit varying degrees of demographic independence but are linked through migration and regional environmental variability (Baker & Thompson, 2007; Schultz *et al*., 2011; Baker, Howell & Polovina, 2012; Johanos *et al.*, 2014). Total abundance in 2016 was approximately 1400 monk seals, with individual subpopulation totals ranging from 70 to roughly 250 seals (Carretta *et al*., 2019).

In the late 2000s, abundance at the six most closely monitored subpopulations in the NWHI (from Kure Atoll to French Frigate Shoals, Fig. 1) was declining with no indication that trajectory was likely to change. The decline was due primarily to poor juvenile survival (particularly to age 2 years). Prey limitation, shark predation and entanglement in marine debris were known contributors to juvenile seal mortality (Craig & Ragen, 1999; Henderson, 2001; Bertilsson-Friedman, 2006; Baker, 2008). Faced with this grim situation, an experiment was conducted to evaluate whether conservation translocations from a subpopulation with low juvenile survival to a site where survival prospects were likely better might be an effective tool to mitigate early mortality. Thus, in 2008-2009, a total of 12 weaned pups was removed from French Frigate Shoals (where juvenile survival was especially poor) and released at Nihoa Island at the eastern end of the NWHI (Norris *et al.*, 2017). Nihoa was chosen as the destination for the translocation experiment because recent increasing trends in index counts of seals at this site suggested that juvenile survival was likely favorable (Harting, Baker & Johanos, 2017).

Norris *et al*. (2017) compared translocated and resident Nihoa Island seals' clinical health status, disease exposure, foraging behavior and habitat use. However, results regarding post-release survival of translocatees relative to seals remaining at French Frigate Shoals and residents at Nihoa were inconclusive for two reasons. First, Nihoa Island is a small (<1 km^2), isolated, steep-sided basalt volcanic remnant (Evenhuis & Eldredge, 2004) upon which it is difficult to safely land with a small boat. Due to these logistical, as well as unforeseen funding constraints, planned surveillance to resight seals at Nihoa was less than anticipated and insufficient to reliably estimate survival rates. Further, it is well-established that condition (specifically axillary girth) of Hawaiian monk seal pups at weaning is strongly correlated with post-weaning survival to age two years (Craig & Ragen, 1999; Baker, 2008). As it happened, translocated pups were fatter on average than those remaining at French Frigate Shoals and comparable in girth to Nihoa resident pups. Norris *et al*. (2017) found that girth was the only significant predictor of minimum survival rates, such that whether the survival of translocated seals was enhanced remained uncertain. Despite the inconclusive results regarding survival benefits, Norris *et al*. (2017) demonstrated that translocations of weaned monk seal pups between subpopulations could be safely conducted and that translocated pups adapted well to their new home and developed normal foraging behavior.

Baker *et al.* (2013) developed and modeled a translocation scheme for Hawaiian monk seals designed to circumvent a juvenile survival bottleneck while maintaining metapopulation structure. During 2012-2014, we further experimented with implementing the initial stage of that scheme by translocating weaned female pups from subpopulations with low juvenile survival to subpopulations where survival prospects were judged to be much higher. In the conservation translocation lexicon, this activity falls under the category of reinforcement, "…*the intentional movement and release of an organism into an existing population of conspecifics. Reinforcement aims to enhance population viability, for instance by increasing population size, by increasing* *genetic diversity, or by increasing the representation of specific demographic groups or stages*" (IUCN 2013). The monk seal translocations meet this definition both in terms of the activity (moving individuals among existing populations) and intent (increasing the species population size and viability, with a focus on young females). The term "reinforcement" implies a primary objective is specifically to benefit the receiving population, and in practice that is typically, but not always (*e.g.,* Menkhorst *et al.,* 2019) the motivation for this type of translocation (Seddon 2010). The Hawaiian monk seal translocations analyzed here are somewhat distinct. While the receiving populations arguably benefit from augmentation, thereby becoming more resilient, the primary motivation to preserve the lives of young females in order to fortify the entire metapopulation.

Here, we report on the efficacy of the 2012-2014 conservation translocations of monk seal pups. We employed a novel method for comparing survival amongst treatment groups that accounts for the fact that weaning condition influences subsequent survival. We demonstrate that failing to account for such physiological correlates of survival may lead to erroneous conclusions about the efficacy of conservation translocations.

Materials and Methods

Monk seal long-term monitoring and life history

The NWHI is a remote region of the Hawaiian Archipelago, comprising atolls and small islands spanning 1800 km, all but one of which (Midway Atoll, where there is a functioning airport) can only be reached by sea-going vessels. Monk seal populations are monitored by researchers manning seasonal field camps at six NWHI sites: Kure Atoll, Midway Atoll, Pearl and Hermes Reef, Lisianski Island, Laysan Island and French Frigate Shoals (Fig. 1). Camps are typically deployed in late spring or early summer and demobilized in late summer or early autumn.

Parturition in Hawaiian monk seals is asynchronous, occurring at all times of year with a broad peak from March to August (Johanos, Becker & Ragen, 1994). Females give birth to a single pup, which they subsequently nurse for five to seven weeks (Johanos *et al*., 1994). Pups are weaned abruptly, and as in other phocids, commence a prolonged post-weaning fast during which they live off the blubber reserves they accumulated while nursing (Bowen, 1991). The duration of the post-weaning fast for Hawaiian monk seals is not well characterized, but Henderson & Johanos (1988) found that pups were seen on the beach nearly every day for approximately 8 weeks after weaning, suggesting they likely are not foraging appreciably during that time.

As soon as possible after weaning, monk seal pups are tagged on each rear flipper with plastic tags bearing unique identifiers and also marked with an injected passive integrated transponder (PIT) tag. Their axillary girth (measured just posterior to the insertion of the pectoral flippers) and dorsal straight length are also measured when the pups are captured for tagging (Johanos, 2018a). Subsequent annual visual monitoring and re-identification using applied tags and natural marks generate long-term capture-recapture data, which are analyzed to estimate age- and site-specific survival rates (Harting, Baker & Becker, 2004; Baker & Thompson, 2007; Johanos, 2018b).

Translocation

Consistent with the IUCN translocation guidelines (IUCN, 2013), we use the terms *source* and *destination* to denote the populations or locations, respectively, whence animals were taken and where they were delivered for release. During 2012-2014, we experimented with translocating weaned female pups from source subpopulations where anticipated juvenile survival was low, to destination subpopulations where the pups were expected to fare better. The selection of source and destination subpopulations was evaluated each year by evaluating the difference in average survivorship amongst subpopulations from weaning until age three years (denoted as l_{w3}) observed during the preceding three years. Weaning was chosen as the beginning of the survival interval because it is the earliest point when translocation could occur without disrupting maternal investment. Three years of age was selected as the end point of the juvenile survival interval, consistent with Baker *et al.* (2013), because the species tends to exhibit high adult survival rates beyond age three years. Because there is considerable temporal and spatial variation in juvenile monk seal survival rates, we averaged l_{w3} over the most recent three years, rather than simply using the most recent year, in order to dampen the influence of a transitory good or poor year. Thus, for example, to determine source and destination sites for translocations conducted in 2012, we estimated survivorship using resighting data for each age class (from weaning to age three years) from 2010, 2011, and 2012. In this example, the 2010-2011 estimates were generated using Cormack-Jolly-Seber (CJS) models as described in Baker & Thompson (2007), whereas minimum survival rates were calculated from the 2012 resighting data, which were being reported in real time right up until translocations were conducted.

Once source and destination sites were identified, candidates for translocation were identified based on several criteria. To maximize the demographic impact of improving survival, only females were considered for translocation. Based upon past experience indicating that recently weaned translocated pups tended to stay near the release site, we preferentially selected candidates that had weaned within 60 days of scheduled transport (Baker *et al.*, 2011). Finally, candidates were screened to ensure they were generally healthy (methods comparable to Norris et al., 2017). Toward the end of each field season, a ship was dispatched from Honolulu with the dual purpose of picking up field researchers and transporting pups among subpopulations. Up to three days prior to the ship arriving at a source site, researchers already on site would capture any candidate seals that could be located and hold them in temporary shore pens. When the ship arrived, candidates were health screened by an attending veterinarian, taken in a small boat to the ship, transported to the destination site and released on shore.

During 2012-2014, between eight and 38 pups were born at each of the potential source subpopulations. Some of these died before weaning, and because parturition is asynchronous, many of the pups were not candidates for translocation because they were either still nursing or had weaned several months prior to the transport ship arriving. These circumstances meant that the available seals meeting the criteria for translocation may not have been representative of their cohorts, for example, in terms of their weaning girths. Because weaning girth is strongly related to post-weaning survival (Craig & Ragen, 1999; Baker, 2008), this metric was accounted for when evaluating post-weaning survival of tranlocatees relative to control seals.

Estimating weaning girth

During the post-weaning fast, monk seal pups' axillary girths decline as they deplete blubber reserves. Weaning is the most appropriate point at which to compare body condition amongst pups because it represents a consistent developmental stage (the end of maternal investment) regardless of the date when it occurs. In order to obtain accurate estimates of girth at weaning, we corrected post-weaning girth measurements to account for this loss between weaning and measurement. To do so, we required three values: Weaning date, measurement date, and rate of girth decline during fasting. Measurement dates were obviously known. Weaning dates were estimated from visual survey records in the following way. Pups were considered weaned when they were no longer observed in association with a lactating female. Weaning date was treated as known if the weaning was either witnessed or if the pup had been observed with a mother on the day immediately preceding the first day it was observed weaned. Because surveys did not occur daily at all locations, in many cases a range of weaning dates was determined. This range was bounded by the day after the pup was last observed with a lactating female and the first day the pup was observed weaned. For our analysis we estimated weaning date as the median of this date range. There were two scenarios in which weaning date was treated as unknown. First, some pups were already weaned when researchers arrived at an island or atoll so that there was no reliable information on the earliest possible weaning date. Second, some pups were still nursing when researchers departed at the end of a field season, so that latest possible weaning date was not known.

To estimate the rate of decline in girth post-weaning, we analyzed repeat measurements of individual free-ranging, live weaned pups recorded over the past three decades. In these cases, the secondary measurements were opportunistically collected when the pups were captured for research purposes or conservation interventions. To ensure that our estimate of rate of girth change reflected only fasting pups, we limited the analysis to pups whose final measurements were within 60 days of estimated weaning. This was based on Henderson & Johanos' (1988) findings that that monk seal pups were nearly always found on shore for at least eight weeks after weaning and subsequently began to spend more time in the water, and presumably gradually began to forage. We calculated the proportional change in axillary girth per day for each serial measurement and used linear models to determine whether this parameter varied by sex and whether it was constant. The latter was evaluated using a model with the median days from weaning to the mid-point of two serial measurements as an independent variable.

Once an estimate for proportional rate of change in girth (r) was obtained from serial measurements, post-weaning girth measurements at time t (g_t) of translocated pups and controls (non-translocated pups at the source and destination sites) were back-corrected to obtain estimated girth at weaning (g_0) in the following manner. Let the proportional change in girth per unit time be

$$r = \frac{(g_t - g_0)}{g_0 \cdot t}.$$

Rearranging the above equation yields

$$g_0 = \frac{g_t}{(rt + 1)}.$$

Estimating expected survival

To evaluate whether the translocations carried out during 2012-2014 were successful in improving the survival of the individuals involved, we compared the observed post-release survival of the translocated seals to their expected survival had they remained in their natal sites. For this comparison, seals which were born and remained at the source sites during 2012-2014 served as controls for the translocated seals.

Elevated mortality following animal translocations, so-called “post-release effects”, are common and important to quantify when modeling or planning translocation actions (Armstrong & Reynolds, 2012). Here, we evaluate whether such post-release effects occurred and used native pups born at the destination sites in 2012-2104 as a second set of controls. Survival of translocated and both classes of control seals was evaluated from weaning until age two years, which encompassed the remainder of the seals' birth year and the subsequent year. We chose this metric because we expected that post-release effects of translocation, should they occur, would not persist beyond two years of age.

To evaluate survival of the study cohorts (2012-2014), we simply tallied the proportions that were observed to have survived to at least two years of age. This approach required high confidence that seals which survived to age two years would be resighted at that, or an older, age. Using resighting data collected through 2019 meant that there were up to four (2014 cohort) to six (2012 cohort) years of surveillance to resight those that survived to at least age two years. Baker & Thompson (2007) estimated that probabilities of observing monk seals given that they were alive exceeded 0.90 at most subpopulations and years. In this study, we conducted intensive resighting effort with the intention of resighting all living seals every year. To evaluate the degree to which this was achieved, we estimated resighting probabilities (p) by fitting CJS models to the capture histories of translocated and control seals from 2012 to 2019 in Program MARK (White & Burnham, 1999) with RMark (Laake, 2013) as an interface. Factors known (from Baker & Thompson, 2007) to influence Hawaiian monk seal survival (age, subpopulation, time) and resighting probabilities (subpopulation, time) were included in candidate models. Whether or not seals were translocated was also treated as a potential explanatory factor. Model selection was based on small sample Akaike Information Criterion (AIC_c).

To account for the known relationship between weaning girth and survival, we used Monte Carlo methods to generate probability distributions of the number of seals that would have survived both at their natal sites and at the destination sites *given* the weaning girths of translocated seals. These distributions were based upon estimated girths and survival outcomes of non-translocated seals at the source and destination sites. We began by fitting logistic regression models with a binary response variable (survived to age two years or not) using weaning girth as a predictor. Separate models were fitted to the available data for seals which were born and remained at the source and destination sites in 2012-2014. Year and sex were included as factors in candidate models to determine whether the relationship varied significantly during the study years or by gender.

The following example demonstrates how we generated a probability distribution for the number of seals (of the same cohort and with the same weaning girths as the translocated seals) that would have survived had the translocated seals in question been left at their source (natal) site.

1) Randomly draw a sample parameter set from the multi-variate normal distribution specified using the logistic regression parameters and associated variance-covariance matrix fitted to the girth and survival data from seals that remained at the source site.
2) For each translocated pup with an estimated weaning girth, calculate the fitted logit scale response using the parameter set drawn above.
3) Calculate the inverse logit of the preceding results to transform them to probabilities.
4) Conduct a binomial “coin flip” for each pup using its randomly drawn survival probability.
5) Sum up how many simulated pups “survived” and store this value.

Repeating steps 1 through 5 10,000 times results in the desired probability distribution. The approach described above accounts for uncertainty in the relationship between girth and survival (by randomly drawing fitted model parameters) and random chance given a binomial survival probability. An analogous procedure was used to generate distributions for the number of survivors at the destination sites assuming translocated pups experienced the same survival probabilities as native born seals at those sites.

We did not have estimated weaning dates (and consequently no estimates of weaning girth) for some translocated seals. Additionally, other translocated seals had weaning girth estimates, but the girth and survival information of non-translocated seals from their respective source and destination sites were insufficient to fit logistic regression models. In these cases, we could not account for girth when evaluating the success of translocation. Instead, we simply generated probability distributions of numbers surviving using the observed proportions of survivors at the respective source and destination sites as binomial probabilities and conducted steps 4 and 5 above.

Results

Translocations

A total of 19 weaned Hawaiian monk seal pups were translocated during 2012-2014 based on the estimated differences in survivorship from weaning to age three years that were available at the time translocation decisions were being made (Table 1). Fifteen pups were taken from French Frigate Shoals to Laysan Island, and two each were taken from Kure and Midway Atolls to Lisianski Island. All the translocated seals were females and passed their health screenings. The entire process of capture at the source subpopulation, transport and release into the destination subpopulation required from two to four days. The time from weaning to arrival at the destination subpopulation ranged from six to more than 71 days. Four pups had unknown weaning dates. All surviving translocated seals remained at the subpopulation where they had been released for up to six years and were not sighted elsewhere. This included those who were the oldest when translocated, suggesting there may be no need to give preference to recently-weaned translocation candidates.

Estimating weaning girths

A total of 92 live, free-ranging pups were measured at two times after weaning, 54 (21 females and 33 males) of which were measured the second time within 60 days of their estimated weaning date. Weaning date was known exactly for 40 of those 54 pups, and within a four-day range for another 13. The final pup's weaning date occurred within a six-day range. The proportional rate of girth loss did not vary significantly among the sexes (p = 0.88), and did not vary with the length of time from weaning to the median of the two measurement dates. Consequently, we used the mean rate of proportional girth change (-0.0019/d) to back-correct all measurements to estimated weaning dates. There was considerable variability in this rate (s = 0.0016, CV -0.836); however, it was less variable as the interval between measurements increased (Fig. 2). Because the loss of girth while fasting is cumulative over time, estimates measured over longer intervals should be more precise. Given that the mean rate was quite stable with increasing measurement interval, we chose to use the mean of all 54 observations for back correction. Further, while limiting the calculation to include only measurements made within 60 days post-weaning was prudent to ensure the measurement interval represented fasting, this criterion made little difference in the mean rate. Increasing this cutoff value from 60 days in intervals up to the maximum of 197 days resulted in means ranging from -0.0018/d to -0.0019/d.

A total of 183 pups were either translocated or were controls born and remained in the source (French Frigate Shoals, Midway and Kure Atolls) or destination subpopulations (Laysan and Lisianski Islands) during 2012-2014. Weaning date was not known for 80 of these. Of the remaining 103, weaning date was known exactly for 39 and within a five-day range for 62 others. Two pups had weaning date ranges spanning 29 and 30 days, respectively. Twenty-two pups were measured on their known weaning date; thus their girths did not require correction. Fifty-four pups were measured within a week, and 22 others were measured up to 53 days after their median estimated weaning dates. The girths from pups measured a day or more after weaning were back-corrected using the above mean proportional rate of girth change.

Efficacy of translocations

Several CJS models were fitted to assess whether resighting probabilities (*p*) were sufficiently high to assume that seals which survival to age two years were detected at that age or older. The best fitting model had a single constant *p* parameter estimated at 0.992 (95% confidence interval 0.980 to 0.997). Given this very high resighting probability, the chances of having incorrectly judged whether a seal survival to age two years are extremely small (see Supplementary Material). We therefore proceeded with the assumption that seals died prior to age two years if they were not resighted at that age or older.

We accounted for the influence of weaning girth when evaluating the survival outcomes of 13 translocated seals, all of which were born at French Frigate Shoals and taken to Laysan Island during 2012 to 2014. Four of the remaining six translocated seals had no estimated weaning dates. The other two were measured at weaning but there were insufficient girth data available for non-translocated seals at their source and destination sites to fit logistic regressions relating survival to girth.

Among non-translocated seals at both French Frigate Shoals and Laysan Island, survival from weaning to age two years was strongly associated with weaning girth. At both sites, the models with the lowest AIC_c values contained only girth as a predictor of survival. Null models as well as those with year or sex in addition to girth had less statistical support (Table 2). The fitted relationships differed markedly between subpopulations; at French Frigate Shoals the curve was shifted to the right and the curve was more steeply inclined compared to Laysan Island (Fig. 3). The weaning girths of pups selected for translocation tended to be on the low end of the distributions for non-translocated seals at both source (French Frigate Shoals) and destination (Laysan Island) in 2012-2014 (Fig. 4), the exception being that those translocated in 2014 were comparable in weaning girth to pups born at Laysan Island.

Monte Carlo sampling yielded estimated distributions of the number of pups that would have survived to age two years at both French Frigate Shoals and Laysan Island, from a group of 13 pups with weaning girths identical to those of the pups actually translocated (Fig. 5(a)). Of these 13, the median number that would be expected to have survived at French Frigates Shoals was just one, with an upper 97.5th percentile of three. In fact, seven of 13 translocated pups survived to age two at Laysan Island, a number just below the median (eight) expected at that location. This strongly supports the conclusion that these 13 translocated pups fared far better than they would have if they had remained at French Frigate Shoals.

As noted previously, we could not account for weaning girth effects on survival of six of the 19 translocated seals. This group, translocated in 2014, included two pups taken from French Frigate Shoals to Laysan Island, and two each taken from Midway and Kure Atolls and delivered to Lisianski Island (Table 1). For these, sampling the observed proportions of survivors at the respective source and destination sites as binomial probabilities yielded distributions of the numbers expected to have survived. The Monte Carlo results for these six seals revealed that the median expected number of survivors at both source and destination sites was four, whereas the number of translocated seals that actually survived was three (Fig. 5(b)). While this outcome was one seal lower than the median expected at the destination sites, it was well within the center 95th percentile interval (from one to six expected survivors). By combining these distributions with those generated previously for the 13 pups whose survival prospects were adjusted according to girth, we obtained an evaluation of the entire translocation experiment. Thus, we found that of the 19 translocated pups, the median expected to have survived at the source site had they been left in place was six, with a 95th percentile of eight. In fact, ten of the translocated seals survived, one less than the median (11) expected to have survived at the destination sites (Fig. 5(c)).

Finally, we explored how our conclusions about the efficacy of the translocations might have changed had we not accounted for girth effects on survival to the degree possible. We did so by simply sampling the observed proportions of survivors at the respective source and destination sites as binomial probabilities, without applying girth-adjusted survival probabilities to any of the of the 19 translocated seals. The median expected number surviving at the source sites was nine with an upper 95th percentile of 13. The actual number surviving (ten) was solidly in the middle of the distribution (Fig. 5(d)). In contrast, the median expected to survive at the destination sites was 14 with a 2.5th percentile of ten.

Discussion

Our analysis demonstrated that translocations of Hawaiian monk seals between subpopulations during 2012-2014 achieved the objective of improving survival outcomes. The strongest evidence supporting this conclusion derives from the 13 seals whose survival prospects were informed by their weaning girths and location-specific relationships between girth and survival. Seven of these seals survived to at least age two years, whereas only one (median of the distribution) would have likely survived had they remained at their natal site. While seven survivors exceed the entire distribution of expected survivors at the natal site, it falls squarely in the middle of the distribution generated for the destination site (Fig. 5(a)), suggesting the translocated seals fared about as well as would natives at the destination with comparable girths. This seven-fold increase in survival was probably in part due to good luck. The decision to translocate seal pups from French Frigate Shoals to Laysan Island was based on differential survivorship that had been observed among those subpopulations in the preceding three years (Table 1). That was not luck; rather it followed the decision framework outlined in Baker *et al.* (2013). The apparent good fortune was related to which specific individuals happened to be available and met the general criteria for translocation candidates when a ship arrived at French Frigate Shoals to collect them. Most of these pups happened to have weaning girths that fell within the range of maximum differential survival between the two subpopulations (Fig. 3). Ideally, individuals should be chosen precisely in this way to maximize the survival benefits of translocation. Practically, the ideal candidates are not always going to be available at the time when translocations are scheduled. Still, it would be wise to choose not to translocate weaned pups at the upper end of the girth range, if they have high probability of surviving at their natal sites.

While the efficacy of the translocation effort was most apparent among the 13 seals discussed above, there was also strong statistical support that the entire experiment involving all 19 seals was beneficial (Fig. 5(c)). Among the six seals for which girth-adjusted survival could not be analyzed, the resulting three survivors was one fewer than the median for both distributions generated for source and destination subpopulations. Thus, for this subgroup of six seals, translocations appeared to provide no benefit nor convincing evidence of harm. It is possible that had we been able to account for these seals' girths, the efficacy may have been revealed to be either greater or lesser. Regardless, the conclusion of no benefit was at least partially due to the fact that survival at the source sites subsequent to translocations was considerably higher than had been expected based on the previous three years, while survival was somewhat lower than expected at the destinations. This highlights a risk of basing translocation decisions on past survival performance at prospective source and destination sites.

A key finding of this study is that had we not accounted for the girths of translocated seals and the girth/survival relationships, we would have erroneously concluded the translocations did no good; rather they essentially 'broke even'. That is, if all seals born at source and destination subpopulations had equal prospects for survival as assumed in the scenario depicted in Fig. 5(d), the observed outcome of 10 survivors would be just above the median expected for the source sites. In fact, because the translocated seals tended to be on the low end of the girth ranges among their respective cohorts, their survival prospects were relatively diminished, and the realized outcome constituted a considerable improvement.

Failing to properly account for post-release survival effects can bias short- and long-term assessment of the efficacy of conservation translocations (Armstrong *et al*., 2017). In simulating potential benefits of a particular translocation scenario, Baker, Harting & Littnan (2013) applied a multiplier (0.90) to affect a reduction in survival of translocated weaned monk seal pups during the first year post-release compared to natives at the destination site. This was based on an *ad hoc* comparison of mean girth at the source subpopulation and a single point estimate from a fitted girth and survival relationship at the destination. The present study's results allow us to evaluate post-release effects associated with the translocation independent of body condition (girth). To do so, we simply divided the number of survivors (seven among the 13 translocatees for which survival was adjusted according to girth) by the distribution of expected number of survivors at the destination site. The resulting distribution was right skewed with median 0.875 and mean 0.996, and with a center 95th percentile overlapping 1 (0.636 to 1.75). Thus, there is no compelling evidence of post-release survival effects for translocated weaned monk seal pups. This result has high associated uncertainty and additional experience could yield greater precision. Baker *et al.* (2011) reviewed all Hawaiian monk seal translocation cases available at that time and also found no consistent evidence of post-release survival effects.

Health and disease screening has long been recognized as a critical element of wildlife translocation programs, with a primary objective of minimizing disease transfer among affected populations (Leighton, 2002). More recently, health surveillance has also been recognized as an important element in identifying predictors of survival and in the design of translocation programs (Mathews *et al*., 2017). Tarszisz *et al*. (2014) make a case for measuring physiological parameters at every stage of the translocation process. Here, we demonstrate that failing to account for a factor related to survival also may lead to erroneous conclusions about the efficacy of translocations.

In the context of species reintroductions, selection of especially healthy and robust individuals improves the chances of establishing a new population. However, the optimal approach for selecting individuals varies with the goal of the conservation translocation program. In this study, we sought to improve survival outcomes for the translocated group to the greatest degree. The benefit in this context is maximized by selecting monk seal pups whose girth-adjusted survival differential is greatest between source and destination populations (Fig. 3). Selecting the fattest individuals would achieve little as these seals would have high probability of surviving no matter where they resided. Thus, appropriate selection criteria for specific physiological attributes, including body condition and others, such as tolerance to climate conditions at the release location (e.g., Cooper *et al*., 2018), will vary with the particulars of conservation translocation schemes. What remains consistent is that information about the relationships between those parameters and fitness, and measuring them in candidates for translocation as well as source and destination populations at large will improve the design of translocations and unbiased assessment of their efficacy.

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Table 1.

Summary of weaned Hawaiian monk seal pup translocations between Northwestern Hawaiian Islands subpopulations, 2012-2014. Source and destination subpopulations are identified. Estimates of source and destination survivorship from weaning to age three years (l_{w3}) averaged over the three most recent years are shown.

Year	Source	Source survivorship	Destination	Destination survivorship	Number of pups
2012	French Frigate Shoals	0.21	Laysan Island	0.56	2
2013	French Frigate Shoals	0.24	Laysan Island	0.60	6
2014	French Frigate Shoals	0.28	Laysan Island	0.60	7
2014	Midway Atoll	0.28	Lisianski Island	0.67	2
2014	Kure Atoll	0.29	Lisianski Island	0.67	2
Total					19

Table 2.

Logistic regression modelling results with Hawaiian monk seal survival from weaning to age two years at French Frigate Shoals and Laysan Island as the dependent variable. Predictors include weaning girth, year (2012, 2013, 2014), and sex. *k* is number of estimated parameters. Null model results are also shown. Models at each location are sorted by AICc.

Model	*k*	*AICc*	Δ*AICc*
FFS (n=35)			
girth	2	29.863	
girth + sex	3	32.161	2.298
girth + year	4	33.084	3.221
null	1	47.125	17.262
LAY (n=43)			
girth	2	44.242	
girth + sex	3	45.016	0.774
girth + year	4	48.943	4.701
null	1	48.740	4.497

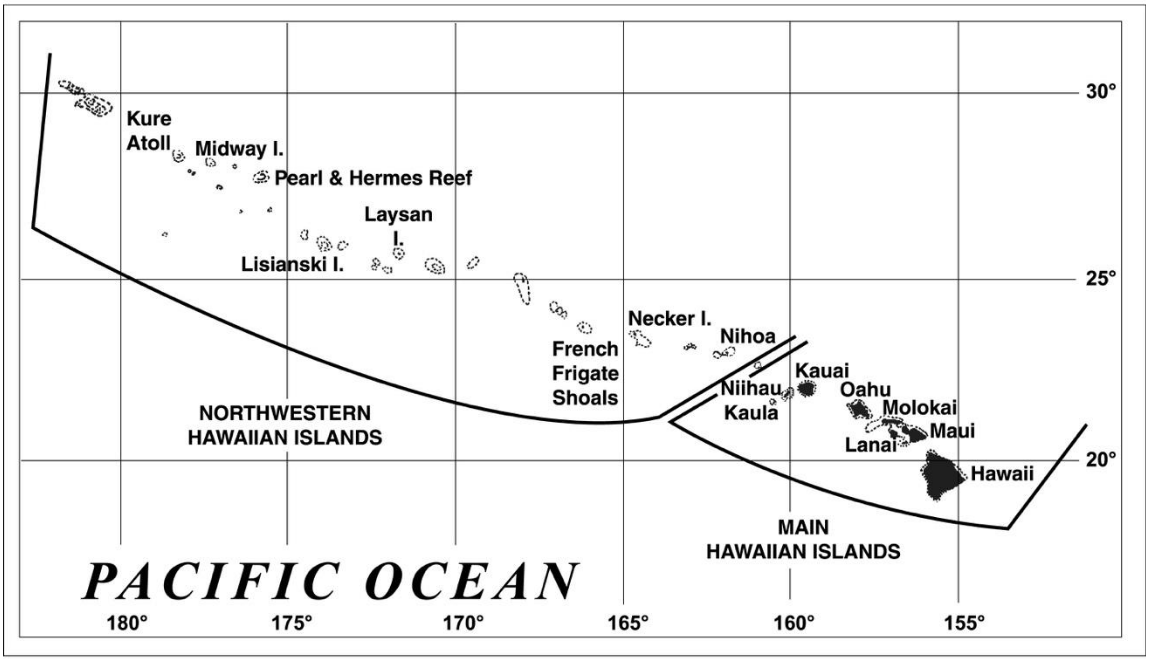

Figure 1. The Hawaiian Archipelago and range of the Hawaiian monk seal.

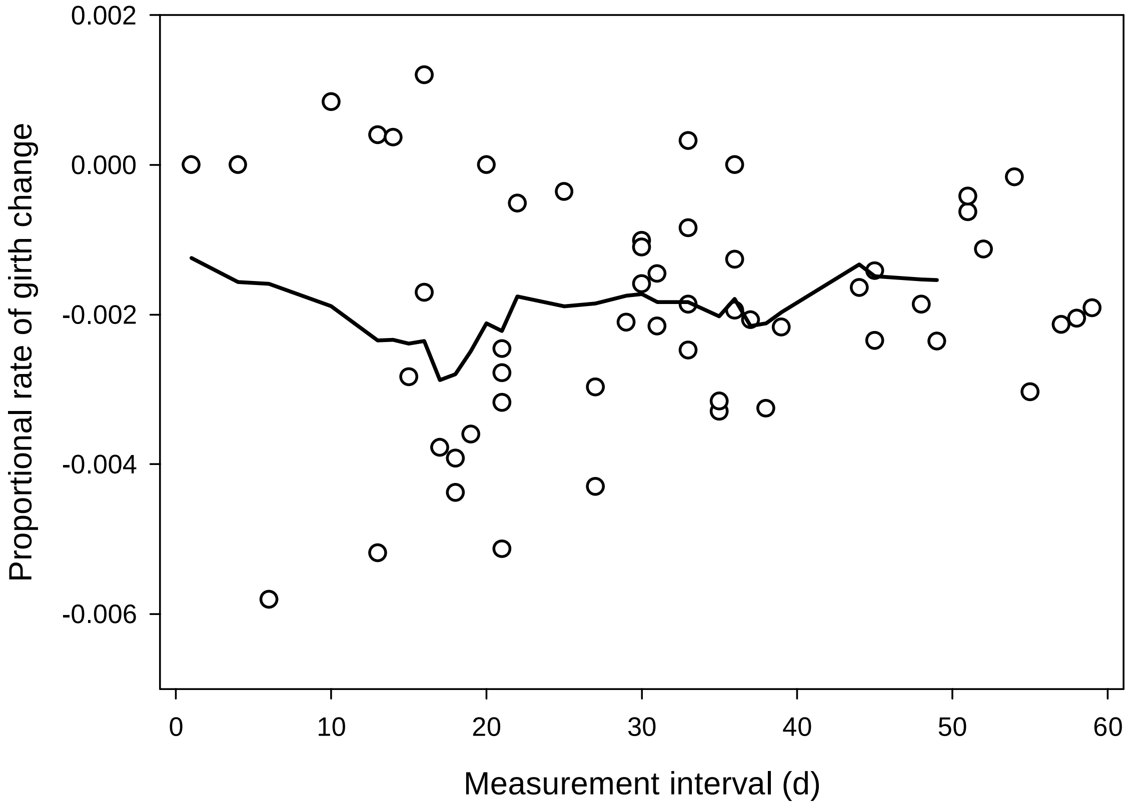

Figure 2. Estimates of proportional daily rate of axillary girth change in post-weaning Hawaiian monk seals plotted against the duration of the interval between sequential measurements. While the variability in the proportional rate of girth change declined with increasing measurement interval (circles indicate individual observations), the mean was quite stable (solid line indicates 10-day running mean).

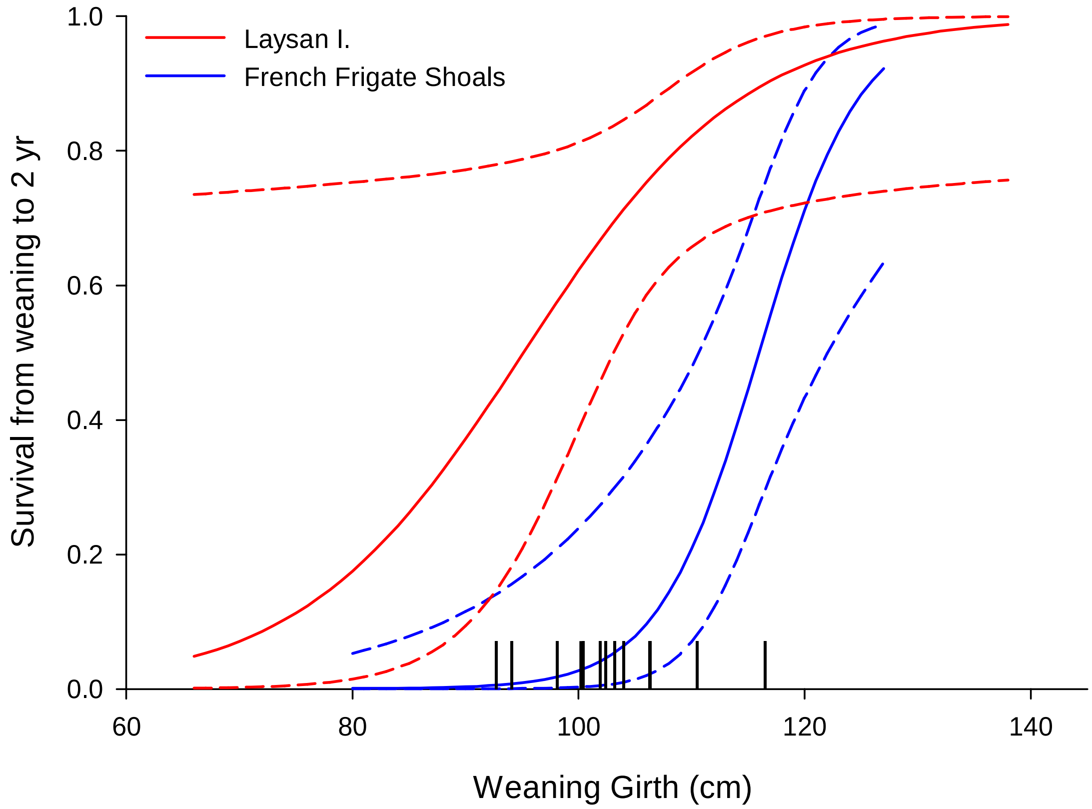

Figure 3. Relationship between survival from weaning to age two years and weaning girth of non-translocated Hawaiian monk seals during 2012-2014 at Laysan Island and French Frigate Shoals. Fitted logistic regression curves with 95% confidence intervals are shown. Vertical black lines indicate the weaning girths of pups translocated from French Frigate Shoals to Laysan Island during those same years.

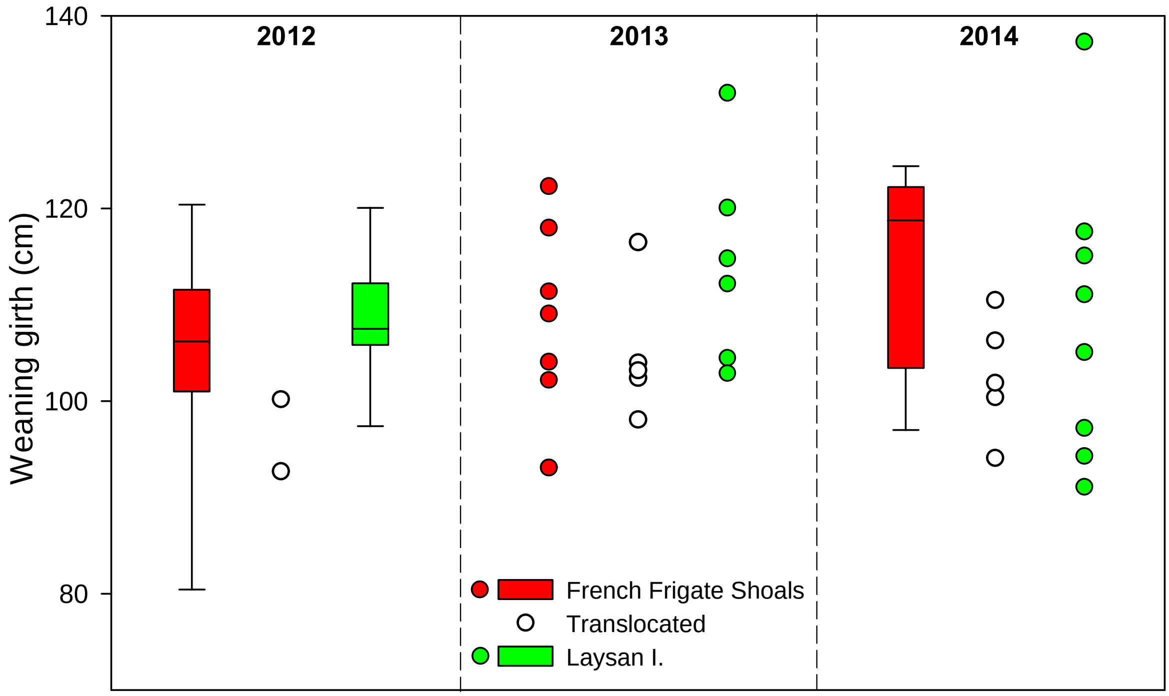

Figure 4. Distributions of estimated weaning girths of Hawaiian monk seal pups in 2012-2014. For each year, non-translocated pup girth distributions at French Frigate Shoals (red, source subpopulation) and Laysan Island (green, destination subpopulation) are plotted flanking the girths of translocated pups (open circles). Box plots are shown when sample sizes exceeded ten pups (boxes are bounded by the 25th and 75th percentiles, whiskers indicate 10th and 90th percentiles, and the medians are denoted by black lines within the boxes).

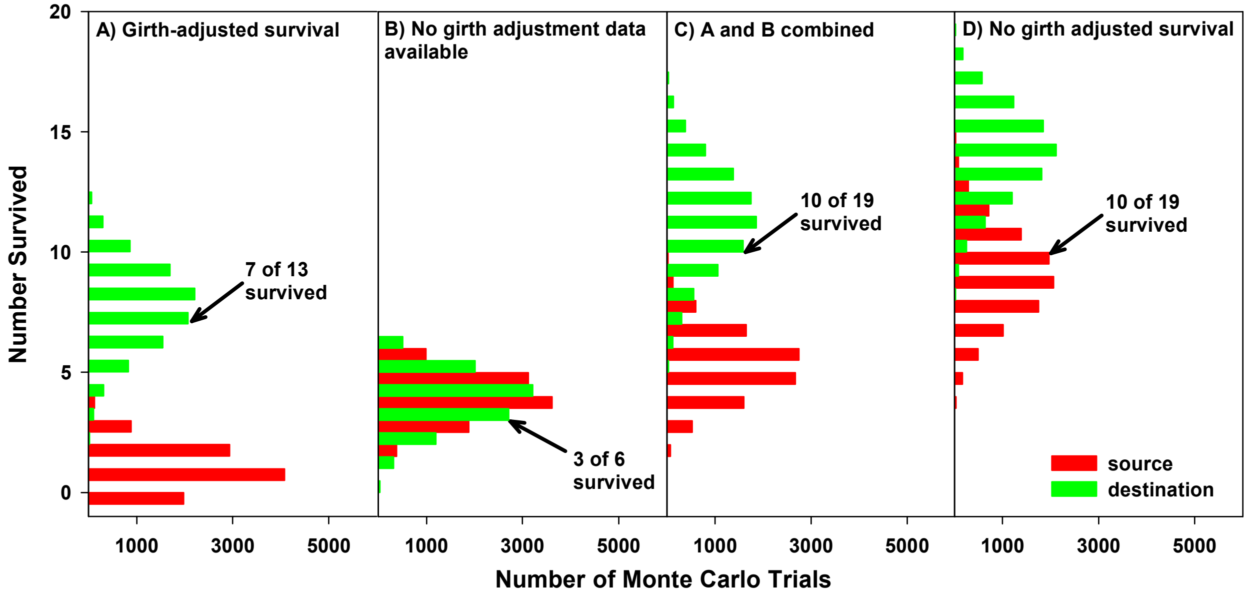

Figure 5. The number of Hawaiian monk seals that would be expected to survive from weaning to age two years at source (red) and destination (green) sites among (A) a group of 13 pups with weaning girths matching those that were translocated during 2012-2014, and accounting for location-specific relationships between girth and survival (and associated uncertainty); (B) a group of 6 pups for which adjustment of survival according to girth was not possible due to data deficiencies; (C) the combined distributions from A and B for all 19 translocated pups; (D) all 19 translocated pups with no adjustment of survival according to girth. For each plot, the number of translocated pups that actually survived is shown (black arrows and text). All distributions were generated by Monte Carlo sampling of survival distributions as described in the text.

Figure Captions

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