Behavior as a rapid indicator of reintroduction and translocation success for a cryptic mammal, the New England Cottontail (*Sylvilagus transitionalis*)

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Interactions between animals and their environments are reflected in behavior, which is an indicator of perceived risk and habitat quality. Behavioral studies can therefore provide a rapid assessment of conservation actions. We evaluated the behavior of reintroduced and translocated New England cottontails (*Sylvilagus transitionalis*)– a species for which the benefits of habitat management, reintroductions, and translocations have been difficult to demonstrate via demographic studies. We first used a random forests model to create a behavioral library for the species using triaxial accelerometers deployed on captive animals that were also monitored with video. We then applied our library to compare time-activity budgets among wild catch-and-release rabbits, wild-caught translocated rabbits, and rabbits introduced into the wild from a captive population. Our library included six behaviors (feeding, grooming, vigilant, movement, resting, and investigating) with an overall classification accuracy of 96.63% and class error rates <14%. For all three groups of rabbits, resting, vigilance, and grooming were the most frequent behaviors; however, captive-bred and translocated rabbits spent significantly more time vigilant and moving than did catch-and-release rabbits. The results raise concern that time spent exploring a new environment may make reintroduced and translocated New England cottontails more vulnerable to predation than local wild rabbits and contribute to low survival rates in reintroduction programs. Our approach shows promise for developing behavioral studies as a rapid indicator of response to conservation efforts for cryptic mammals.

Key words: accelerometer, activity budgets, behavior, random forests, reintroduction, site familiarity, *Sylvilagus transitionalis*, translocation

Reintroductions and translocations are of great importance to imperiled species conservation; however, these efforts often fail to meet their objectives or lead to unclear outcomes (Fischer and Lindenmayer 2000; Letty et al. 2007; Resende et al. 2020). Success is influenced by a variety of factors, whether ecological (e.g., habitat quality, competition, predation) or nonecological (e.g., costs, long-term commitment, social factors; Fischer and Lindenmayer 2000), but the most cited causes of failure are low survival due to predation, habitat quality, or both (e.g., Moorhouse et al. 2009; Cabezas et al. 2011; Moseby et al. 2011; Bennett et al. 2013). Post-release monitoring has been increasingly incorporated into conservation strategies but has not always led to evaluation of success. In reviews of reintroductions and translocation studies, nearly half or more of the studies did not have information on the success or failure of the program (Fischer and Lindenmayer 2000; Resende et al. 2020). When success is measured, frequently it is evaluated based on the survival and reproduction and subsequent establishment of populations (IUCN/SSE 2013). However, it can take years before the demographic trends become apparent, and within that period little may be learned about immediate responses of relocated animals that may facilitate adaptive responses and promote the long-term success of these efforts. The initial stages of reintroductions and translocations can prove critical, and low

survival of released individuals may limit the efficacy of traditional evaluation metrics (i.e., survival analysis, reproductive output) in understanding the cause of high rates of post-release mortality (Grey-Ross et al. 2009; Bennett et al. 2012; Hardman et al. 2016). Tools that facilitate rapid understanding of animal responses to reintroduction and translocations, and support inference on the causes of low survival, could be used to refine these programs and improve overall rates of success.

Animals that have been translocated or introduced to the wild from captivity must acquire appropriate behavioral responses, such as antipredator behaviors, while exploring a new area (Zidon et al. 2009). The (site familiarity hypothesis') holds that animals in unfamiliar environments should have lower survival than those in familiar areas, presumably because they lack knowledge concerning effective escape routes, concealment cover, locations of high-quality forage, and how to respond to potentially unfamiliar predator communities (Clarke et al. 1993; Merkle et al. 2014; Forrester et al. 2015; Lafontaine et al. 2017; Gehr et al. 2020). As a result, animals in unfamiliar environments spend more time in exploratory behaviors than local animals as they locate resources (Burns 2005; Frair et al. 2007; Heidinger et al. 2009; Russell et al. 2010). These behaviors occur at the cost of maintenance behaviors like foraging and grooming, which support reproductive success (e.g., mate-seeking, mating, rearing young) and improve survival (Hart 1992; Alberts 2007). Further, increased movement, particularly in novel environments, can increase predation risk (Reinert and Rupert 1999; Yoder et al. 2004). For Ruffed Grouse (*Bonasa umbellus*), the effect of predation was 3–7.5 times greater while inhabiting or moving through unfamiliar areas than familiar areas (Yoder et al. 2004).

Evaluating behavior may allow for rapid assessment of species responses to novel habitat and aid in identifying release site characteristics that may impact success or failure of reintroductions. As an adaptive response to both internal and environmental stimuli, behavior directly influences the fitness of an individual (Kotler et al. 2007; Berger-Tal et al. 2011). In Australia, reintroductions of brown treecreepers (*Climacteris picumnus*) failed even with prior habitat restoration at release sites and one of the major reasons for failure was predation (Bennett et al. 2012). Bennett et al. (2013) found that a lack of high-quality ground foraging habitat and low density of refugia, which increased flight times, may have influenced predation rates. Frequently, the time that birds and mammals spend foraging—taxa that make up the majority of reintroduction and translocation efforts (Fischer and Lindenmayer 2000; Resende et al. 2020), negatively correlates with the quality and quantity of food resources (Lyons 2005; Weterings et al. 2018). Female prothonotary warblers (*Protonotaria citrea*) spent significantly more time foraging in lower-quality levee ecosystems than higher-quality swamp ecosystems (Lyons 2005), while both males and females attacked more prey in swamps, indicating greater availability of food resources, which also corresponded with higher breeding success.

Behaviors including vigilance and hiding in cover (i.e., predator avoidance), grooming, and foraging can all be indicative of habitat quality and risk, and often animals must make trade-offs among these behaviors. Antipredator behavior is an indicator of perceived risk and may correlate with the quality of cover features (Lindell 2008). Alleby's gerbils (*Gerbillus andersoni allenbyi*) harvested fewer seeds in the presence of owl predators than in their absence and had increased vigilance in open microhabitat (Kotler et al. 2004). For juvenile redshanks (*Tringa tetanus*), increased survival was associated with avoidance of high-risk areas, and for individuals in high-risk areas, likelihood of survival was related to increased vigilance and foraging success rate (Sansom et al. 2009). Grooming behavior can be effective in reducing ectoparasites like ticks and fleas (Hart and Hart 2018), and parasite load and time spent removing them is reflective of habitat characteristics. Impala (*Aepyceros melampus*) males had six times the number of ticks as females, presumably because they spent more time engaged in vigilance behavior and less time grooming than females (Mooring et al. 1995).

Given these associations, behavior can provide a rapid, sublethal indicator to help managers identify and address factors limiting success of reintroduction and translocation efforts including poor quality habitat, predation pressure, and risky behaviors (Kotler et al. 2007; Lindell 2008; Berger-Tal et al. 2011). In turn, these behaviors can be used to adjust management strategies; for example, practices such as conditioning and soft release can elicit antipredator behaviors, improve site fidelity, and reduce large movements upon release (Azevedo et al. 2017; Tetzlaff et al. 2019). In the past two decades, the emergence of accelerometers as bio-logging technology has permitted the characterization and quantification of behavior of species with cryptic characteristics (e.g., nocturnal, subterranean, camouflaged), or that inhabit challenging landscapes (e.g., rugged terrain, dense vegetation), which may preclude direct observation (Yoda et al. 2001; Shepard et al. 2008; Lush et al. 2016). Improved triaxial accelerometers that record acceleration along X, Y, and Z spatial axes are becoming a well-recognized method for quantifying behavior, especially when paired with powerful machine learning algorithms such as random forests (Breiman 2001) and have been successfully used to evaluate behaviors of many species of wildlife in aquatic and terrestrial systems (Nathan et al. 2012; Brown et al. 2013; Fehlmann et al. 2017; Studd et al. 2019a).

Our goal was to develop a behavioral approach to rapidly evaluate the reintroduction and translocation success of the New England Cottontail (*Sylvilagus transitionalis*; Fig. 1), an imperiled species that is difficult to observe directly in the wild due to cryptic coloration and densely vegetated habitat. The New England Cottontail is a shrubland obligate species that has experienced drastic population declines in the last century (Litvaitis et al. 2006; Rittenhouse and Kovach 2020). Extensive efforts have been made to conserve the species via habitat management, captive breeding and reintroduction, and translocation, but there has been no demonstrably clear benefit to population growth thus far as known occupied sites across the range of the species have declined by 50% in the past decade (Rittenhouse and Kovach 2020). The species continues to lose habitat to forest maturation and anthropogenic development (Litvaitis 1993; Litvaitis et al. 2006) and faces

Fig. 1.—New England Cottontail (*Sylvilagus transitionalis*) resting in mid- to late successional shrubland in New York, United States (2019).

widespread invasion of its historic range by eastern cottontails (*S. floridanus*), an introduced species that occupies similar habitat and competes for resources (Litvaitis and Probert 1996; Cheeseman et al. 2018). Studies of wild New England cottontails have suggested strong relationships between survival, habitat, and behavioral characteristics such as movement—with increased movement resulting in markedly lower survival rates and movement being closely tied to habitat characteristics (Cheeseman et al. 2019, 2021). New England cottontails have also been shown to sacrifice high-quality food, and even low-quality food, for the safety of cover, which resulted in the loss of body mass and increased rates of predation (Smith and Litvaitis 2000). Responses to habitat management have just begun to be assessed within an experimental framework, and there have been few published studies of long-term monitoring of reintroductions (Bauer et al. 2020). Success of New England Cottontail reintroductions is varied; reintroductions in New Hampshire resulted in a relatively stable population across a 5-year period (Bauer et al. 2020), while releases in Rhode Island have experienced low survival mainly due to predation (NEC Regional Initiative 2021).

A method for quantifying post-release behavioral response and comparing it to that of local wild rabbits in intact habitat could be a key tool for rapidly evaluating reintroduction efforts and aid in conservation of a difficult to observe, imperiled species. Our objectives were to (1) develop a behavioral library using captive animals, and (2) compare time-activity budgets among introduced captive-bred, translocated wild-bred, and caught-and-released on-site (hereafter local) wild-bred New England cottontails equipped with triaxial accelerometers. Based on the site familiarity hypothesis, we predicted: (a) that captive-bred rabbits would spend more time in movement and investigating behaviors, at the cost of maintenance behaviors including foraging, resting, and grooming compared to translocated and local rabbits; and (b) that the time spent in particular behaviors of translocated rabbits would be intermediate between that of captive-bred and local rabbits.
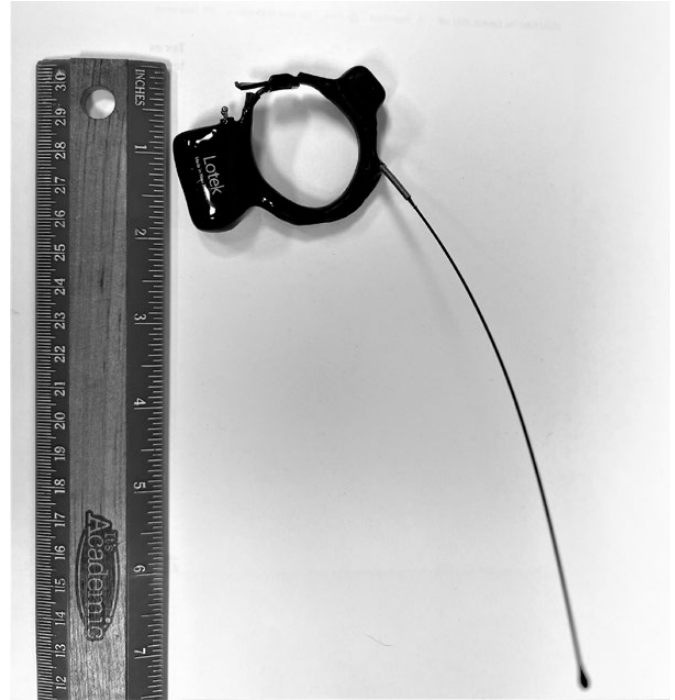

Fig. 2.—Lotek LiteTrack 20 RF collar.

Materials and Methods

Captive rabbit data collection.—To create a behavioral library for wild New England cottontails, we affixed GPS collars (LiteTrack 20 RF; Lotek Wireless Inc., Newmarket, Ontario, Canada; Fig. 2) equipped with triaxial accelerometers to four female New England cottontails in the captive breeding program at the Queens Zoo in Queens, New York during the breeding period. Although we developed the behavioral library on female New England cottontails in an effort to capture and quantify breeding and reproductive behaviors, nonsocial behaviors (i.e., feeding, grooming, movement, etc.) in cottontails have been described as not varying greatly between sexes (Marsden and Holler 1964; Bruch and Chapman 1983). Thus, we anticipated that nonbreeding behavioral signatures would be similar between males and females and between females in the breeding and nonbreeding seasons given previous observation and general physiology. GPS collars were attached by a zip-tie closure and total collar weight did not exceed 20 g, or <5% of the body mass for any individual. After collaring, each rabbit was released in a pen that was equipped with video cameras (Swann, Santa Fe Springs, California) and allowed to acclimate for 2–3 days. A male New England Cottontail was then introduced into the pen for breeding and we started accelerometer logging and video recording. Triaxial accelerometers recorded acceleration at 6 Hz saving every 6th sample. Accelerometer and video data were continuously recorded for the duration of the paired mating attempts (i.e., 5 days or until a rabbit was removed from the pen). After mating attempts, rabbits were moved to birthing pens that were equipped with a video camera. We programmed the start of accelerometer and video recordings to coincide with expected parturition (i.e.,

25–27 days after breeding attempts) and run continuously until the collar memory allocated for accelerometer data was full.

Captive rabbit data analysis.—We reviewed 15.2 h of video and recorded start and end times for each behavior. We selected 11 behaviors for further analysis that represented 93.8% of all observations and combined similar behaviors into broader categories (e.g., (movement') was a combination of running, hopping, and chasing; and (vigilant') was raised and crouched vigilance), resulting in eight behaviors (Table 1). However, we later removed birthing and grooming young from the training data, resulting in six behaviors for our study, and reran models. We removed these behaviors because our sample size for birthing and grooming young was too small to reliably generate predictions for those behaviors, and none of the free-ranging rabbits in the second part of the study were captured and collared during the breeding season. We aligned the accelerometer and video data for each individual by the second so that they were synchronized. Since internal clocks of devices can become out-of-sync over time, we adjusted the alignment of timestamps between the accelerometer and video data for each rabbit by identifying long bouts of behaviors such as resting, where the acceleration did not change and we could verify a lack of movement by the rabbit, followed by a sudden change such as running or hopping, which has a corresponding spike in acceleration (Studd et al. 2019b).

We used random forests-based classification (Breiman 2001) to build our behavior library (Cutler et al. 2007; Lush et al. 2016; Fehlmann et al. 2017; Studd et al. 2019a). Following methods by Fehlmann et al. (2017), we calculated 24 variables to assess movement within a smoothing window in the program R (Table 2; Shepard et al. 2008; Tatler et al. 2018; Studd et al. 2019a; R version 3.6.2, R Core Team 2019). Summarizing accelerometer data within sampling windows can aid in the classification accuracy of random forests models and reduce noise (Gjoreski et al. 2010; McClune et al. 2014; Lush et al. 2016; Fehlmann et al. 2017; Studd et al. 2019b). To determine the best smoothing window duration for predicting behaviors, we ran our random forests models with accelerometer data smoothed within five moving sample windows (6, 8, 10, 12, and 20 seconds) and chose the window that led to the best overall accuracy and lowest class error rates for the six behaviors. We split the data into training (70%) and validation (30%) sets to evaluate models (Studd et al. 2019a).

Random forests models using all 24 variables were run using the "randomForest" package in the program R (Liaw and Weiner 2002), with 500 trees "grown" and five variables split at each node of a tree. Random forests is a powerful classification method as it creates a specified large number of relatively uncorrelated decision trees using a randomly selected subset of both data and variable to build each tree. Comparison of tree performance using out-of-bag, unselected data are then used to evaluate performance and (vote') to select the prediction of the model (Breiman 2001). While not prone to overfitting, performance may be biased toward the majority class due to the uniform random sampling for each decision tree. Models were run with the full training data set as well as a (balanced') training data set to compare model accuracy and potential overfitting of behaviors with higher sample sizes (Chen et al. 2004). The balanced data set was developed using the down-sampling method, which entails the selection of a bootstrap sample from each class, where a subsample of larger classes is taken to ensure that they have the same sample size as the rare class, or a ratio sample size, as each tree is built (Chen et al. 2004). Since down-sampling does not always improve model accuracy (Freeman et al. 2012), we compared accuracy, precision, and recall for full (i.e., unbalanced) training models and balanced training models (Appendix I). We also validated each model and calculated per-behavior accuracy using the validation data set, before choosing the final model.

Wild rabbit data collection.—Wild rabbits were trapped and released on-site at two locations in Dutchess and Putnam Counties, New York (41.7650°, −73.7327° and 41.4264°, −73.7550°; Fig. 3). Sites consisted of old fields, successional shrublands, and forest, as well as areas recently managed to create early successional forest, which resulted in a mixture of mature forest and early to late successional patches. We used Tomahawk live traps (Tomahawk Live Trap, Hazelhurst, Wisconsin) placed near cover or rabbit sign and baited with apple slices to live trap New England cottontails. Traps were checked daily. Eastern cottontails are sympatric with New England cottontails in this area (Nielsen and Lanier 2019), necessitating genetic species confirmation. We captured, processed, and identified cottontail species in situ following protocols from Cheeseman et al. (2018). On initial capture, individuals were marked with a uniquely numbered metal ear tag, and a tissue sample was taken from the ear for species confirmation and stored in 100% ethanol for later genetic analysis. DNA was extracted from biopsied tissue using the Qiagen DNeasy Blood and Tissue Kit (Qiagen Inc., Valencia, California) and species of cottontail was identified using methods described by Whipps et al. (2020), which followed methods

Table 1.—New England Cottontail ethogram with eight behaviors and their definitions.

Behavior	Description
Resting	Crouched low to the ground, relaxed rather than alert
Movement	Combination of running, chasing, and hopping
Feeding	Crouched, head lowered with small movements, chewing or biting, head moves about
Investigating	Crouched, with head moving in small bouts around an object or along the ground
Vigilant	Combination of raised and crouched vigilance—sitting up with head raised or crouched low to ground with head raised, alert
Grooming (self)	Licking or scratching areas of the body
Grooming (young)	Licking young
Birthing	Giving birth to young

Table 2.—Predictor variable terms used in a behavioral classification model for New England Cottontail and their definitions.

| Predictor	Description
Static acceleration (st)—X, Y, Z	Running mean of raw acceleration for each axis
Dynamic acceleration (dy)—X, Y, Z	Raw acceleration—smoothed static acceleration for each axis
Average dynamic acceleration—X, Y, Z	Mean value of dynamic acceleration for each axis
Maximum dynamic acceleration—X, Y, Z	Maximum value of dynamic acceleration for each axis
Minimum dynamic acceleration—X, Y, Z	Minimum value of dynamic acceleration for each axis
Standard deviation dynamic acceleration—X, Y, Z	Standard deviation of dynamic acceleration for each axis
Overall dynamic body acceleration (ODBA)	$\|dyX\| + \|dyY\| + \|dyZ\|$
Vectoral dynamic body acceleration (VeDBA)	$\sqrt{dyX^2 + dyY^2 + dyZ^2}$
Smoothed vectoral dynamic body acceleration (VeDBA)	Running mean of VeDBA
Partial dynamic body acceleration (PDBA)—X, Y, Z	Absolute value of dynamic acceleration for each axis
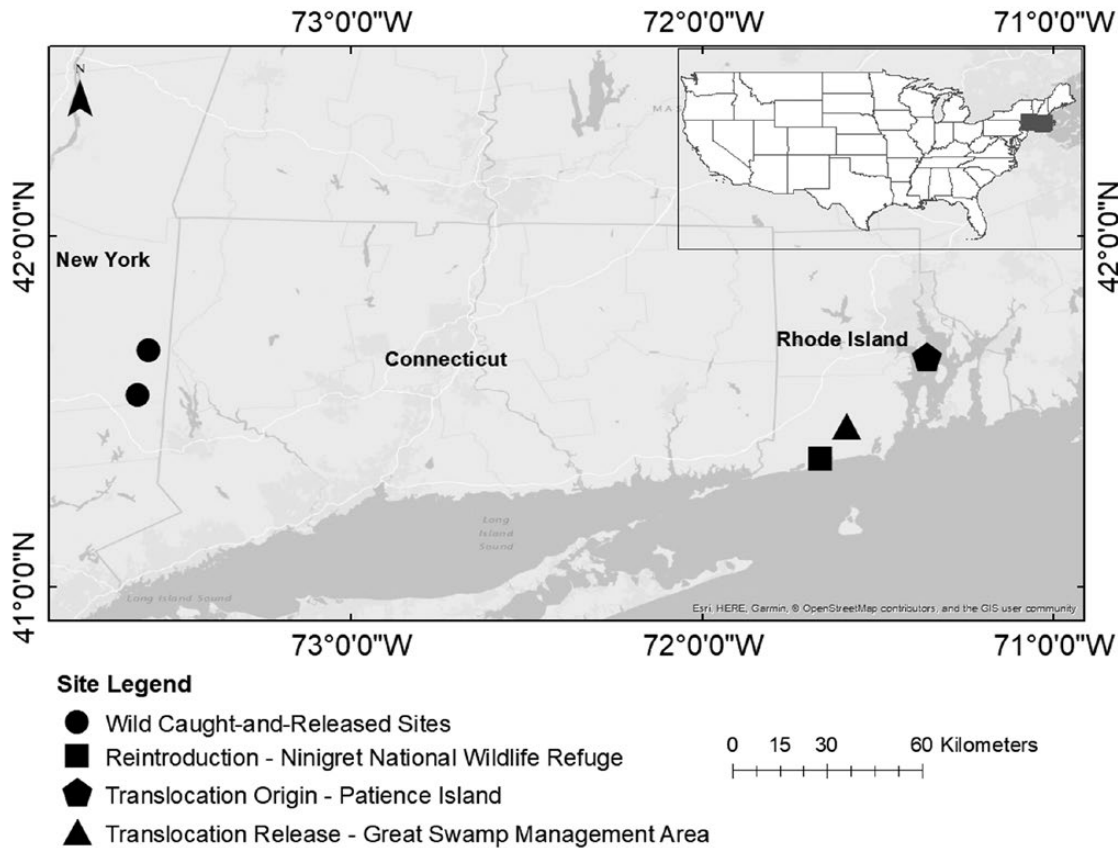
Fig. 3.—Map depicting: wild, caught-and-released New England Cottontail' (*Sylvilagus transitionalis*) trapping locations in Putnam and Dutchess Counties, New York (2019–2020); introduced captive-bred New England Cottontail release location at Ninigret Wildlife Refuge, Charlestown, Rhode Island (2019, 2021); translocated New England Cottontail trapping location at Patience Island, Rhode Island (2021); and release location at Great Swamp Management Area, West Kingston, Rhode Island (2021).

from earlier studies (Litvaitis and Litvaitis 1996; Kovach et al. 2003; Kilpatrick et al. 2013). Rabbits were outfitted with the same collar types used for establishing the behavioral library. GPS collars were attached by a zip-tie closure and total collar weight did not exceed 20 g, which was <5% of the body mass for any rabbit.

Accelerometers in the GPS collars were programmed to record activity beginning at 20:00 EST on the night of the capture to collect data on rabbit behavior post-collaring. Accelerometers ran continuously for the first 3 days after

capture in order to evaluate behavior immediately post-release, then on the 4th day the accelerometer schedule changed to recording 30 min of activity every 2 h for four more days. Due to collar memory limitations in the storage of accelerometer data, we chose this schedule to prioritize initial post-release behavior. We remotely downloaded accelerometer data weekly or when the collar was retrieved after a mortality or recapture.

Introduced captive-bred and translocated rabbit data collection.—Captive-bred and translocated New England cottontails were collared prior to release at designated sites (Fig. 3)

within their historic distribution. Captive-bred rabbits used for reintroduction were not used in development of the behavioral libraries; thus, all rabbits used for comparison under wild conditions are independent of those used to develop the models. Herein, we use (reintroduction') to identify the process of releasing captive-bred rabbits into a previously occupied wild landscape and corresponds to the captive-bred rabbit group, while (translocation') is the process of releasing wild-caught animals in a new location and refers to translocated rabbits. The sex of each captive-born individual used for reintroduction was visually checked and verified by polymerase chain reaction amplification using the SRY gene-specific primers for locus INRACCDDV0326 (Chantry-Darmon et al. 2005). After the captive-bred rabbits were weaned, they were transported to an enclosed, approximately 0.4-ha pen at the Ninigret National Wildlife Refuge (Charlestown, Rhode Island; Fig. 3). The pen was fenced, had an electric wire to deter mammalian predators, and was covered to protect against avian predation. The rabbits acclimated in the pen for approximately 1 month, were trapped from the pen for release into the wild at the refuge on 17 September ($n = 4$) or 2 October ($n = 3$) 2019, and provided with supplemental feeders that had cameras posted to detect use. Before release, all rabbits were treated with canine Revolution (Zoetis Services LLC, Parsippany, New Jersey) tick and flea topical medication and affixed with the same GPS collars using identical accelerometer schedules as used in New York. Data from GPS collars were remotely downloaded weekly.

New England cottontails intended for translocation were trapped from Patience Island in the upper Narragansett Bay (Fig. 3) and released directly on site the same day (30 March 2021) at the Great Swamp Management Area in West Kingston, Rhode Island (Fig. 3). Patience Island is an 85-ha island off the coast of Rhode Island that hosts an introduced breeding colony of New England cottontails. Mammalian predators on the island include Mink (*Neovison vison*), Coyote (*Canis latrans*), and Raccoon (*Procyon lotor*), along with a variety of avian predators. The sex of each individual was determined using the same methods as for captive-bred rabbits. Prior to release, all translocated rabbits were treated with the same type of tick and flea topical medication as were captive-bred rabbits, and fitted with the same type of GPS collar and accelerometer schedule as previously described. Translocated rabbits were not provided with supplemental feeders at the release site. Data from GPS collars were remotely downloaded weekly.

Rabbit behavior classification and activity budgets.—We processed accelerometer data for captive-bred, translocated,

and local rabbits following the procedure we used to develop our behavioral library. Using the random forests model created from the behavioral library, we classified each second of accelerometer data into one of the six behaviors. We compared multivariate median time-activity budgets among the three groups using Multi Response Permutation Procedure (MRPP), a nonparametric analog of MANOVA that is useful for small sample sizes, using the "Blossom" package in R (Talbert and Cade 2013). We also compared the multivariate median activity budget between each pair of groups using MRPP, in order to determine which budgets differed from each other. We used Bonferroni-corrected *P*-values and an experiment-wise α-level of 0.05 to evaluate the significance of pairwise differences.

All animal capture, handling, and other study procedures followed guidelines set by the American Society of Mammalogists (Sikes et al. 2016) and were approved by the State University of New York of Environmental Science and Forestry Institutional Animal Care and Use Committee (Protocol 180601), the Wildlife Conservation Society Institutional Animal Care and Use Committee (Protocol 19:01), or University of Rhode Island Institutional Animal Care and Use Committee (Protocol AN11-012-11), depending on the location of the research. Trapping was permitted under New York State Department of Environmental Conservation license 1402 and Rhode Island Department of Environmental Management Division of Fish and Wildlife license 2021-23-W.

RESULTS

Captive rabbit behavior classification.—The full data set (in which the training set contained 29,157 s of accelerometer data) with a 20-s smoothing window had the best classification accuracy (96.63%; Appendix I). Class error rates were below 10%, with the exception of investigating behavior (13.4%; Table 3). The average precision and recall for the model across the six behaviors were 96.2% (95% *CI* = 94.5–97.8) and 94.6% (91.2–98.0), respectively. A model run with the validation data set, comprising 12,496 s, had a classification accuracy of 96.75%, an average precision of 96.2%, and an average recall of 94.4%.

Behavioral classification and activity budgets for free-ranging rabbits.—We captured and collared six local New England cottontails, five males and one female, for behavioral monitoring across two sites. We collared 10 New England cottontails (seven males and three females) that were born to captive breeding programs at the Roger Williams Park Zoo ($n = 6$; Providence, Rhode Island) and the Queens Zoo ($n = 4$; Queens,

Table 3.—Confusion matrix and class error rates for a random forests model of New England Cottontail behavior, based on a training data set from accelerometers on captive animals, 2019–2020.

	Feeding	Grooming	Investigating	Movement	Resting	Vigilant	Class error
Feeding	3,654	16	15	1	0	107	0.037
Grooming	22	5,120	4	0	1	91	0.023
Investigating	45	38	857	2	5	43	0.134
Movement	0	4	15	514	0	17	0.065
Resting	12	26	4	0	6,170	216	0.040
Vigilant	73	135	29	13	47	11,854	0.024

New York) in 2019 and released at one site in Rhode Island. However, accelerometer data from only 7 of the 10 rabbits (four males and three females) were included due to three rabbits dying in under 48 h, making it difficult to accurately determine behaviors from their collar data. Six New England cottontails (four males and two females) were caught from Patience Island, collared, and translocated to one site in Rhode Island, which was different than the release site of the captive-bred rabbits. Approximately 5 million seconds of accelerometer data were collected and used from the captive-bred, translocated, and local rabbits. The activity budgets of the three groups of rabbits differed (MRPP test statistic = −5.10, $P < 0.001$), but there was no difference between the activity budgets of the introduced captive-bred and translocated rabbits (MRPP test statistic = −1.01, $P = 0.147$). However, the activity budget of local rabbits differed from that of both the introduced captive-bred group (test statistic = −4,86, $P = 0.001$) and the translocated group (test statistic = −3.81, $P = 0.004$). For all experimental groups, the majority of time was spent in resting, vigilance, and grooming (Fig. 4). However, introduced captive-bred rabbits spent 1.5 times more time vigilant, over 3.5 times more time moving, and 1.8 times more time investigating than local rabbits (Fig. 4). Translocated rabbits spent about 1.5 times more time vigilant and 3 times more time moving than local rabbits but spent about the same amount of time investigating (Fig. 4).

DISCUSSION

Our study resulted in the first behavioral library for use of accelerometer data with cottontails. The accuracy and very low-class error rates for most behaviors in our model were encouraging. Even the class error rate for investigating, which was the highest of any behavior in our study, was still relatively low when compared to other studies (Lush et al.

2016; Fehlmann et al. 2017; Studd et al. 2019b). Differences in behavior class errors could be due to variations in sample size or similarities in accelerometer data between behaviors, such that some behaviors were difficult to distinguish. Investigating, for example, is a behavior characterized by small movements such as sniffing at the ground and objects—and in the validation set it was mainly misclassified as feeding, which involves small movements of the head from the ground and up, or vigilance, where the head of the rabbit was positioned either low or high and remained still. Further, averaging accelerometer data within smoothing windows can increase the classification accuracy of larger movements or movements that often last for long bouts but can decrease accuracy of classification of finer scale movements that last only a few seconds (Lush et al. 2016; Studd et al. 2019b). Overall, however, the model performed similar to or better than other lagomorph-based models (Lush et al. 2016; Studd et al. 2019a).

Quantification of New England Cottontail behavior indicated that introduced captive-bred and translocated wild-bred rabbits had significantly altered behavioral patterns relative to local caught-and-released rabbits. Although all three groups spent most of their time either vigilant, resting, or grooming, captive-bred and translocated rabbits spent greater amounts of time in behaviors such as movement, investigating, and vigilance compared to local rabbits. Translocated and captive-bred rabbit activity budgets were similar, but we did observe slightly greater time spent resting and less time spent investigating in translocated than captive-bred rabbits, potentially suggesting greater familiarity with habitat features or predator avoidance knowledge for translocated rabbits. If our interpretation is correct, these results would support our predictions indicating that the introduction to a novel environment may result in shifts in behaviors that relate to fitness. However, the differences in
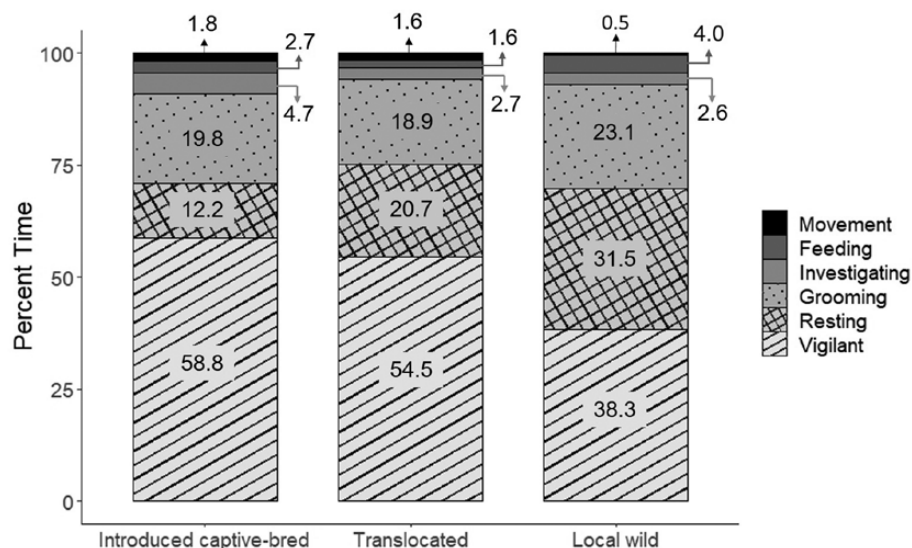

Fig. 4.—Multivariate median activity budgets for introduced captive-bred and translocated New England cottontails from Rhode Island, United States (2019–2020) and local wild-caught New England cottontails from New York, United States (2019–2020) with percent time spent in six behaviors: movement, feeding, investigating, grooming, resting, and vigilant.

behavior we observed also could be due to site-specific differences, which would require further investigation.

Over half of the activity budgets for captive-bred and translocated rabbits were devoted to vigilance, suggesting that unfamiliarity with a site may be an important determinant of vigilance, regardless of natal origin. Vigilance is an antipredator behavior, but it often comes at the cost of foraging effort (Kotler et al. 2004; Whittingham et al. 2004; Devereux et al. 2006). In addition, species in habitat with low visibility can experience a reduction in predator detection along with foraging efficacy (Whittingham et al. 2004; Devereux et al. 2006), which could have fitness consequences. European starlings (*Sturnus vulgaris*) not only had a reduction in food-searching bouts in obstructed habitat and an increase in vigilance, but when researchers simulated predator attacks, starlings were slower to respond (Devereux et al. 2006). The New England Cottontail is a cryptic mammal in coloration and a shrubland obligate, and its habitat often consists of dense thickets with low visibility; thus, rabbits may be dedicating greater amounts of time to predator detection overall, but captive-bred and translocated rabbits even more so in unfamiliar habitat.

Although the percent time spent in high-energy behaviors (i.e., movement and investigating) was low for all three of our study groups, the relatively greater amount of time spent in high-energy behaviors by recently introduced captive-bred or translocated rabbits than local wild rabbits may further indicate that New England cottontails in novel environments face elevated risk of predation. In familiar areas, animals are able to better avoid and escape predators (Clarke et al. 1993; Gehr et al. 2020)—conversely, unfamiliar areas can result in increased movement, which raises the risk of predation (Yoder et al. 2004). Movement and dispersal are often associated with lower survival (Sievert and Keith 1985; Moehrenschlager and Macdonald 2003; Cheeseman et al. 2021). Among translocated swift foxes (*Vulpes velox*), individuals that had small dispersal distances had greater survival and reproductive success than those with larger dispersal distances (Moehrenschlager and Macdonald 2003). Of 1,206 pygmy rabbits (*Brachylagus idahoensis*) reintroduced, only 176 individuals were detected near or on release sites, juvenile and adult median dispersal distances were 776 m and 471 m, respectively, and there was low apparent survival (13%; DeMay et al. 2017). Moreover, New England Cottontail survival is negatively correlated with distance moved (Cheeseman et al. 2021).

In our study, captive-bred rabbits were given time to acclimate in a pen at the release site, but based on our results, individuals may have been too naïve regarding predators or the acclimation period may not have been adequate due to increased time spent moving and investigating. Increased movement puts an individual at risk for predation, and a lack of predator avoidance knowledge for captive-bred individuals can be detrimental; however, several studies have shown that training individuals may help. Captive-bred juvenile black-tailed prairie dogs (*Cynomys ludovicianus*) were found to have greater survivorship 1 year after reintroduction if they were trained with experienced adults and exposed to different predators and nonpredators, compared to juveniles who were not trained with experienced adults (Shier and Owings 2007). In Australia, captive-bred rufous bettongs (*Aepyprymnus rufescens*) and quokkas (*Setonix brachyurus*) were trained to have a fear response to coyote and fox using live dogs (McLean et al. 2000). Further, in our study the pen at the reintroduction site was 0.45–0.6 km from the release sites, which could have limited its effectiveness as a training area because cottontail home ranges are typically small (0.84–1.81 ha; Cheeseman 2017) and, thus, the pen location may not have allowed rabbits to familiarize themselves with the location of forage and cover resources. Allowing more time for acclimation could reduce post-release movements and increase chances of survival; however, exposing captive-bred rabbits to predators via training could also increase chances of survival and should be an area of future research.

All three rabbit groups spent most of their time in low-energy behaviors (i.e., resting, vigilance, and grooming). Rabbits may spend much of the day resting to conserve energy or because food availability is high, thus reducing the need to search for high-quality forage, but doing so also confers predator avoidance benefits such as concealment and reduced movement (Tabor and Wurtsbaugh 1991; Llaneza et al. 2016). The majority of the activity budget of local rabbits was spent in vigilance and resting, followed closely by grooming. The high amount of time dedicated to resting compared to other behaviors may indicate a familiarity with their environment (e.g., location of cover and food resources). The moderately greater amount of time spent resting and slightly less time spent vigilant in translocated rabbits compared to introduced captive-bred rabbits may also suggest greater knowledge of key habitat characteristics (i.e., less naiveté). Similarly, translocated pygmy rabbits settled in sites with a higher amount of cover than where they were captured (Lawes et al. 2013), suggesting these individuals had knowledge of the ideal characteristics to use for cover. The slightly greater time spent grooming in local rabbits compared to captive-bred and translocated rabbits may be facilitated by lower movement or vigilance, but may also reflect parasite burden on local, wild rabbits as well as successful conservation procedures taken for captive-bred and translocated rabbits (e.g., flea, tick, and endoparasite medications). Wild New England cottontails in New York inhabit dense shrublands, which are often dominated by invasive shrub species, such as Japanese Barberry (*Berberis thunbergii*), that are known to harbor elevated tick densities (Williams et al. 2017). Grooming would be vitally important to survival and reproduction in that case, as tick burdens negatively affected survival of juvenile New England cottontails in New York (Cheeseman et al. 2021). However, captive-bred and translocated rabbits were treated with flea and tick medication prior to release, which may have slightly reduced the need for grooming to remove ectoparasites. Future studies might compare the impacts of parasite preventatives on activity budgets and resulting impacts on survival.

Our results suggest that a possible cause for low reintroduction and translocation success of New England cottontails could be a consequence of increased time spent in vigilance and movement at the expense of behaviors such as resting.

Increased movement may cause rabbits to be particularly vulnerable to predation when they are released from captivity or translocated among sites, due to naïveté concerning predator assemblages or lack of familiarity with available cover. Evaluating food and cover resources at release sites could aid in understanding factors influencing movement or dispersals immediately after release, and conducting soft releases with an acclimation period may be beneficial, but for New England cottontails the soft release technique may benefit from refinement. Ensuring that individuals are released where they have acclimated can aid in familiarity with available cover and food resources and reduce movement. In our study, introduced captive-bred rabbits had access to supplemental feeders while translocated rabbits did not. Managers might consider supplemental feeding, as increases in behaviors such as vigilance can come at the cost of foraging efficacy and feeding may aid in site fidelity (Bannister et al. 2016). Supplemental feeding placed near escape cover has been proven to aid eastern Cottontail winter survival, which was used as a proxy for the New England cottontail (Weidman and Litvaitis 2011). However, feeding stations could become ecological traps by attracting predators (Godbois et al. 2010; Turner et al. 2010)–thus, ensuring the habitat has high-quality forage may be safer. Cameras were posted at the feeding stations and detected the presence of released rabbits and predators (Ernst N., U.S. Fish and Wildlife Service, Charlestown, Rhode Island, personal communication, November 2020). In our study there was no difference in activity budgets between translocated rabbits without access to supplementary feeders and introduced captive-bred rabbits with feeder access. It is possible that supplementary feeding altered rabbit activity and compensated for hypothesized increased naiveté in reintroduced, captive-bred rabbits relative to translocated rabbits. However, due to concern with attracting predators, supplemental feeders in our study were only filled once or twice a month, which may have resulted in increased vigilance and movement for captive-bred rabbits due to the need to find forage. Supplemental feeding is an area for future study, and our study provides a method to formally evaluate the influence of supplemental feeding, release pens, and more in reintroduction and translocation programs.

Captive-bred and translocated rabbits were released at previously designated unoccupied sites as part of the ongoing recovery program. As a result, individuals comprising the local, translocated, and captive-bred groups were monitored at different sites. While all sites contained similar predator communities and habitat characteristics, site-specific differences in resources (e.g., availability and amount of food and cover) and predator distribution could influence spatial movements and behavior and could also be responsible for the trends observed herein. Formal examination of the impact of habitat quality and site factors on behavioral responses is needed to remove the confounding influences of habitat variability on activity budgets, but was not possible during our study due to collar memory limitations and constraints on releasing individuals as part of an ongoing recovery program. However, our evaluation of local rabbits at two distinct sites may lend supporting context. Local rabbits were trapped and released within two sites containing a diversity of habitat types representative of the study area, yet activity budgets did not differ between sites (see Supplementary Data SD1). Our findings of greater variability in behavior between local, reintroduced, and translocated groups than between sites for local cottontails are consistent with the notion that the described behavioral responses to novel environments are different from behavioral responses to resource variation within familiar environments. Future studies should prioritize collection of location data alongside accelerometer data at similar scales, as well as within site comparisons of reintroductions, translocations, and catch and release.

Reintroductions and translocations may fail due to the lack of knowledge of an individual in a novel environment (Frair et al. 2007; Berger-Tal et al. 2019)–however, understanding immediate behavioral responses of these individuals provides a way to improve conservation programs. Accelerometers, which are available with most GPS tracking technology, demonstrated promise in this case for assessing behaviors of a difficult to observe, imperiled species and gaining insight on their responses to these efforts. This method allows for the quantification of behavior and can collect behavioral data at large scales without direct observation, reducing disturbance from observers and facilitating behavioral data collection from cryptic, or hard to observe, mammals. Using it to rapidly determine responses to reintroduction and translocation efforts provides us with a way to aid our conservation efforts, such as evaluating and improving suitability of release sites or investigating the need for or improvement of site acclimation and supplemental feeding. We recommend that accelerometer data be incorporated into conservation assessment and adaptive management for New England cottontails and other species (e.g., pygmy rabbit, riparian brush rabbit, and other non-lagomorph species) that may be difficult to observe or capture and have sparse demographic data on response to reintroduction, translocation, and management programs.

CONFLICT OF INTEREST

The authors have declared no conflicts of interest.

Data Availability

Data and code for cottontail behavior library available at experts.esf.edu.

Supplementary Data

Supplementary data are available at *Journal of Mammalogy* online.

Supplementary Data SD1.—Average activity budgets for local wild-caught New England cottontails at two sites in New York, United States (2019–2020) with percent time spent in six behaviors: movement, feeding, investigating, grooming, resting, and vigilant.

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APPENDIX I

Results of (full') and (balanced') models for moving sample windows of 6, 8, 10, 12, and 20 s from random forests classification of four captive New England cottontail accelerometer data in New York, 2019. For (full') and (balanced') models, training model out-of-bag (OOB) estimate of error rate, model accuracy, and average precision and recall are shown, as well as the validation set model accuracy for each sampling window.

Window size	Model type	OOB error rate (%)	Accuracy (%)	Average precision (%)	Average recall (%)	Validation set accuracy (%)
6	Full	15.63	84.37	81.97	76.65	84.68
	Balanced	20.09	79.91	75.63	77.02	80.36
8	Full	11.88	88.12	86.50	82.00	87.61
	Balanced	17.53	82.47	78.52	81.45	81.75
10	Full	9.21	90.79	89.70	85.32	90.51
	Balanced	16.12	83.88	80.16	84.09	83.50
12	Full	7.48	92.52	91.50	88.32	92.50
	Balanced	14.83	85.17	81.56	86.32	85.11
20	Full	3.37	96.63	96.16	94.61	96.75
	Balanced	6.98	93.02	90.57	94.25	93.03