

Timing of translocation influences birth rate and population dynamics in a forest carnivore

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Abstract. Timing can be critical for many life history events of organisms. Consequently, the timing of management activities may affect individuals and populations in numerous and unforeseen ways. Translocations of organisms are used to restore or expand populations but the timing of translocations is largely unexplored as a factor influencing population success. We hypothesized that the process of translocation negatively influences reproductive rates of individuals that are moved just before their birthing season and, therefore, the timing of releases could influence translocation success. Prior to reintroducing fishers (*Pekania pennanti*) into northern California and onto the Olympic Peninsula of Washington, we predicted that female fishers released in November and December (early) would have a higher probability of giving birth to kits the following March or April than females released in January, February, and March (late), just prior to or during the period of blastocyst implantation and gestation. Over four winters (2008–2011), we translocated 56 adult female fishers that could have given birth in the spring immediately after release. Denning rates, an index of birth rate, for females released early were 92% in California and 38% in Washington. In contrast, denning rates for females released late were 40% and 11%, in California and Washington, a net reduction in denning rate of 66% across both sites. To understand how releasing females nearer to parturition could influence population establishment and persistence, we used stochastic population simulations using three-stage Lefkovich matrices. These simulations showed that translocating female fishers early had long-term positive influences on the mean population size and on quasi-extinction thresholds compared to populations where females were released late. The results from both empirical data and simulations show that the timing of translocation, with respect to life history events, should be considered during planning of translocations and implemented before the capture, movement, and release of organisms for translocation.

Key words: California; carnivore; delayed implantation; fisher; life history; Olympic Peninsula; *Pekania pennanti*; population extinction; reintroduction; reproduction; timing; translocation; Washington.

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INTRODUCTION

Timing is important in nature. The life histories of organisms are often timed to cues from

their environment that increase survival and reproduction through specific mechanisms such as exploitation of important or seasonally abundant resources (Siekman et al. 2001, Ryan et al. 2007,

Love et al. 2010, Fletcher et al. 2013, Lodge et al. 2013). The timing of specific life history traits (e.g., migration or reproduction) spans a continuum temporally from invariant to highly plastic to account for environmental change (Smith et al. 2010, Monteith et al. 2011), and the alteration in one trait, such as reproduction, may have cascading effects on other traits or interactions with other species (Mitchell et al. 2012, Touchon et al. 2013). Mistiming of key life history events may reduce individual fitness and lead to population decreases or even collapse (Seeley and Visscher 1985, Boonstra 2004). Failure to consider how timing influences management actions may reduce effectiveness, or result in total failure, of efforts to restore species or populations (Stüwe and Nievergelt 1991).

Translocation has become an often used management tool aimed at the establishment, augmentation, or reestablishment of functional populations of imperiled animal and plant populations (IUCN 2013, Seddon et al. 2014). Throughout history, humans have translocated wild animals (reviewed by Bolen and Robinson 2003, Powell et al. 2012) and plants, but researchers have begun only relatively recently to examine factors that influence the success of such conservation actions (Griffith et al. 1989, Reading and Clark 1996, Sarrazin and Barbault 1996, Wolf et al. 1996, Armstrong and Seddon 2008). Several factors consistently predict population establishment and persistence following translocations, including the size of the founding population, habitat quality at the release sites, and the release location relative to the historical and contemporary range of the species (Griffith et al. 1989, Lomolino and Channell 1998, Wolf et al. 1998, Lewis et al. 2012, Powell et al. 2012). The reproductive potential of the translocated individuals or the presence or abundance of potential consumers (predators or herbivores) and diseases are also important for some species (Cunningham 1996, Griffin et al. 2000, Letty et al. 2000, Sarrazin and Legendre 2000, Cabezas and Moreno 2007). Despite advances in recognizing the primary attributes that influence translocation success, many modern translocations still fail, which has led to a demand for rigorous scientific methods in their planning and implementation to deduce the mechanisms affecting success (Miller et al. 1999, Seddon et al. 2007).

The initial numbers of founder individuals in a translocated population are nearly always small relative to naturally occurring, self-sustaining populations (Hayward et al. 2007). Small populations are vulnerable to extinction due to demographic and environmental stochasticity and negative density-dependence (Allee effects; Allee and Bowen 1932, Shaffer 1981, 1987, Courchamp et al. 2008). Thus, minimizing mortality and maximizing the reproduction of translocated organisms is particularly important because they have a disproportionate effect on persistence of small populations.

The process of translocating animals likely depresses reproduction of individuals through a variety of physiological, ecological, and behavioral mechanisms. Physiologically, translocation elevates the stress responses of animals through multiple, often additive, mechanisms including capture, time in captivity, handling, and releasing individuals into unfamiliar environments (Teixeira et al. 2007, Dickens et al. 2009, 2010, Scarlata et al. 2013). Elevated stress in animals affects gonadotropins directly and, ultimately, impairs or curtails reproduction (Teixeira et al. 2007, Busch and Hayward 2009, Breuner 2011, Scarlata et al. 2012). Additionally, animals released into new environments are unfamiliar with the locations and types of important resources, thus affecting their energetic balances and, potentially, reproduction (Armstrong and Perrott 2000, Kemink and Kesler 2013, Lodge et al. 2013). Stress in combination with the challenges experienced within new environments may reduce or curtail short-term reproductive success individually or interactively (Busch and Hayward 2009). The effects of stress may last for many weeks but are likely to be highly variable based on individual species as well as the circumstances of translocations (Dickens et al. 2010).

Translocations, and specifically reintroductions (release of animals into areas once occupied by members of the species; IUCN 2013), have been used extensively to restore populations of martens (*Martes* spp.) and fishers (*Pekania pennanti*) throughout North America and Eurasia (reviewed by Powell et al. 2012). Fishers (Fig. 1) were reintroduced often to restore populations that were extirpated due to overharvesting and habitat alteration (Lewis et al. 2012, Powell et al. 2012). Many of these reintroductions succeeded



Fig. 1. Female fisher moving her approximately 3-month-old kit to a new den in the northern Sierra Nevada of California.

in the eastern portion of the fisher's range but in California, Oregon, Washington, and western Canada more than 50% of reintroductions have failed (Lewis et al. 2012). To increase the success of translocations of fishers and martens, researchers have experimented with release-based effects, such as hard vs. soft releases (allowing for a period of adjustment before release). Proulx et al. (1994) found that translocating fishers during summer increased site fidelity, but did not link this observation to the long-term success of the reintroduction. The reasons most reintroductions fail are unknown and, moreover, few novel mechanisms that may affect population establishment and persistence are hypothesized or tested (Powell 1993a, Lewis et al. 2012, Powell et al. 2012). Here, we use a rigorous approach to consider how translocating fishers during critical periods of their reproductive cycle affects reproduction and population establishment.

Fishers have relatively low rates of reproduction and population growth. Females can give birth for the first time on or near their second birthdays, in late March or April, and they produce at most one litter per year of 1–4 kits. Natal dens are always cavities in trees or standing snags. Kits depend on their mothers until autumn of their first year (Powell 1993a, Frost 1994, Frost et al. 1997). Within several days to 2 weeks after giving birth, female fishers breed and their blastocysts suspend development (delayed implantation) until winter of the following year, at which time blastocysts implant concurrent with increasing day length, followed by a normal pregnancy of ~32 d (Enders and Pearson 1943, Enders and Enders 1963, Wright and Coulter 1967, Mead

1971, Frost et al. 1997). Generally, fisher translocations occur in autumn and through late winter, with late releases coinciding with the time when blastocysts implant and active gestation occurs (Proulx et al. 1994, Frost et al. 1997). Trapping fishers for translocation cannot easily begin before autumn for many reasons, but the chief concern is that adult females have dependent young that are difficult to locate and to trap, introducing an unacceptable risk of mortality to kits if mothers are captured and translocated (Proulx et al. 1994). By and large, managers translocating fishers have not considered that moving female fishers during late winter could prevent implantation of blastocysts, leading to complete reproductive failure, or could affect maternal stress *in utero*, reducing the total number of kits born.

In planning the reintroduction of fishers in northern California, we hypothesized that fishers translocated just prior to or during the period of implantation would have lower reproductive success immediately following translocation than females that were captured and released earlier (autumn or early winter). We were concerned enough with these potential effects that we proposed to move all fishers prior to January 1 in each of the 3 yr of reintroduction (Callas and Figura 2008). In our concurrent, but independent, reintroduction of fishers in Washington, we also attempted to release fishers early (Lewis and Hayes 2004, Lewis 2006). In both cases, however, the logistics of planning and capturing enough fishers necessitated the capture and movement of individuals across a range of dates from November through March. Here, we test our *a priori* hypothesis that the timing of the release of female fishers affected their abilities to give birth in the first spring after their release. Furthermore, through simulation we evaluated the consequences of a depressed reproductive rate, as the result of releases in late winter, on reintroduction success.

METHODS

Fisher reintroductions

We reintroduced fishers to both California and Washington as independent efforts to restore fishers to unoccupied portions of the species' historical range (Lewis and Hayes 2004, Lewis 2006, Callas and Figura 2008). Many of

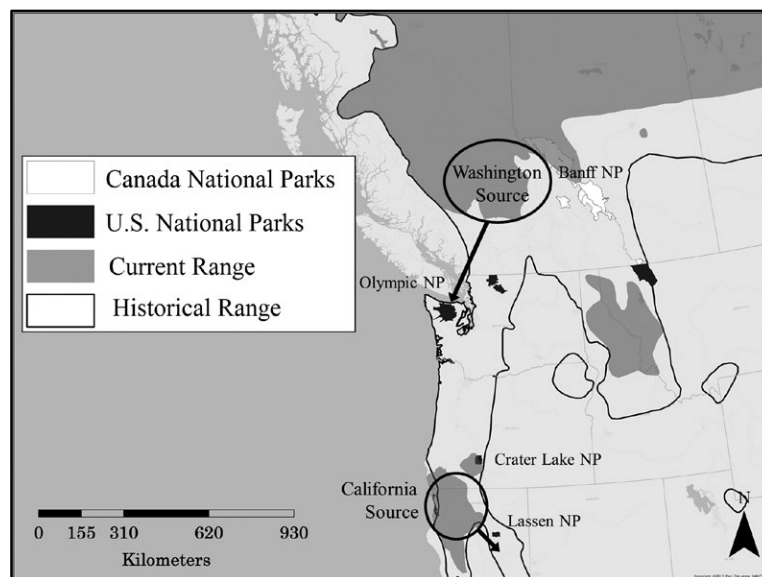


Fig. 2. General locations of source (labeled circles) and release areas (arrows) of fishers for both the California and Washington reintroduction projects, 2008–2011 compared to the current range of fishers in western North America (gray shading) and their historical range (thin black outline; Lewis et al. 2012).

the approaches and methods used during these reintroductions, though similar, varied in meaningful ways. For example, source populations and the duration that we held fishers in captivity differed. Additionally, the final release locations are found in different ecoregions with presumably different biotic and abiotic influences (Olson et al. 2001). For both projects, we immobilized fishers chemically to fit transmitters and to obtain information on sex, reproductive status in previous years, general condition, body mass, and morphological measurements. We immobilized fishers with tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Animal Health, Fort Dodge, Iowa) in California, and in Washington with a combination of ketamine hydrochloride (Ketaset, Zoetis, Florham Park, New Jersey) and detomidine hydrochloride (Dormosedan, Zoetis, Florham Park, New Jersey). We outfitted female fishers with either Telonics (IMP-310 or MOD-125; Mesa, Arizona, USA) or Holohil (MI-2i, Carp, Ontario, Canada) Very High Frequency transmitters. We removed one of the first premolars from each fisher to estimate age by counting cementum anuli (Arthur et al. 1992). We released fishers into the wild with no acclimation period (i.e., hard releases). The

Institutional Animal Care and Use Committee from North Carolina State University (09-007-O) approved the handling protocol for the California reintroduction, whereas the translocation and monitoring conducted during the Washington project were approved by the Animal Care and Use Committee of the Wildlife Science Division of the Washington Department of Fish and Wildlife. For both projects, handling of fishers was consistent with the guidelines of the American Society of Mammalogists for the use of wild mammals for research (Sikes and Gannon 2011).

In California, we reintroduced 40 fishers (24 F; 16 M) from early November 2009 to December 2011 to the region where the southern Cascades and northern Sierra Nevada mountain ranges meet (Fig. 2). We live-trapped fishers from across a large source area in northern California (Fig. 2). At least one field biologist and one wildlife veterinarian evaluated each fisher to determine its suitability for reintroduction. In California, we sought to reintroduce only individuals that were old enough to reproduce (females anticipated to give birth the next spring, males able to breed), and those that had body mass at or above average and appeared in good general health. To decrease the likelihood that we would inadvertently

move diseases or parasites to the reintroduction site, we vaccinated all candidate fishers for canine distemper virus and rabies and treated them for both ecto- and endo-parasites. We held all fishers selected for reintroduction in captivity for 3–14 d, while we tested them for previous exposure to distemper and canine parvovirus (Larkin et al. 2011, Keller et al. 2012). We transported individual fishers that passed this disease quarantine period to their release sites within 2 d, whereas fishers that tested positive for previous exposure to distemper were returned to their original capture locations. We released all fishers onto the Stirling Management Area (Lat 39.9 Lon -121.5°) owned by Sierra Pacific Industries. We released fishers across Stirling to encourage a widely distributed population and to reduce potential intra-sex conflict (Powell 1979). Our goal was to release all fishers from October through December so that females could overcome stress responses incurred during translocation and become familiar with the release site well before blastocyst implantation and active gestation began. Nevertheless, we released some fishers in January and February because we were unable to trap sufficient numbers of fishers before January 1 (Fig. 3).

We reintroduced 90 fishers (50 F; 40 M) onto the Olympic Peninsula in northwestern Washing-

ton (Lewis et al. 2010). We captured and housed fishers in central British Columbia, where we assessed their general health and vaccinated them for canine distemper and rabies (Lewis et al. 2010, Fig. 2). In Washington, our goal was to introduce ~100 fishers, and our relatively low rates of capture necessitated accepting all apparently healthy fishers regardless of age. Because of the high costs of transportation associated with the long distance from the capture site to the release site, we held fishers in captivity until ~10 were available to move to Washington. Mean duration of captivity was 21 ± 12 d (range 2–55), but we held five fishers for 32–55 d for special medical treatment (e.g., treatment of wounds, impacted canine teeth). We released fishers across sites in Olympic National Park (lat 47.9° lon -123.4°; Lewis et al. 2010), usually in groups of 3–7 that included both males and females of variable ages. Originally, our intent was to release all fishers as early as possible (late fall or early winter) but limited capture success during this period necessitated a greater duration of trapping effort (into January and February) and resulted in late releases (as late as early March; Fig. 3).

Documenting reproduction

We tracked all female fishers 1–5 times per week in California using a combination of ground and aerial telemetry, whereas in Washington we located females ~1 time per week using aerial telemetry. In Washington, we located females 1–3 times weekly during the breeding season (March–June) to identify denning sites. At both sites, a female was suspected of having given birth in a den when she was repeatedly located in a restricted area, especially in the same tree, in late March and early April. We confirmed reproduction by placing three remotely triggered cameras (PC800 Hyperfire Professional, Reconyx, Inc., Holmen, Wisconsin, USA) within 6 m, and facing the base, of a suspected den tree to photograph kits (Fig. 1; e.g., Matthews et al. 2013). Photographs showing repeated use of a tree indicated that a female was attending kits, and photographs of females with kits confirmed reproduction as well as provided documentation of minimum litter size (Fig. 1). If kits were not photographed, we deduced that a female had given birth if we observed her, through

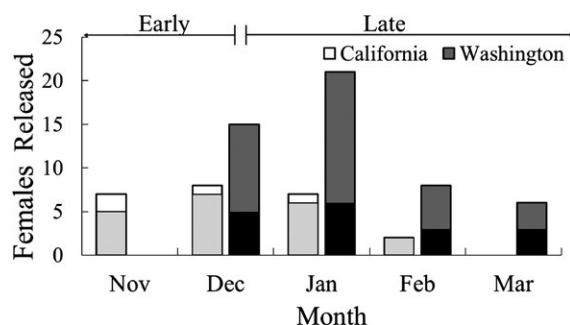


Fig. 3. Full column lengths show the total numbers of female fishers released at each site in each month (total is 24 for California and 50 for Washington), whereas the darker portions represent the numbers of adult females for whom we could confidently assess denning status and that were used in our analysis. Females released prior to January were considered early releases, whereas fishers released in January or later were considered late releases.

pictures or telemetry, returning to the same locality for several weeks. As we tracked females regularly, we could confidently identify patterns of location indicating that a female was using a confined area more often than was normal for prereproductive location patterns. A female that we never photographed with kits and who was never found in a confined portion of her home range for a 2–4 week period we designated as non-parous. Our analyses did not include females <2 yr old ($n = 18$) that could not have given birth or those whose denning status could not be determined. We only evaluated birth rate, as indicated by the denning rates of females, and thus we did not remove females from the analysis that died after we confirmed that they had denned.

Analysis

We analyzed whether a female denned (yes or no) as a binary response using logistic regression (PROC LOGISTIC, Statistical Applications Software, Cary, North Carolina, USA). We modeled the response of denning rate to covariates that we hypothesized *a priori* might affect the probability that a female would establish a den (i.e. give birth). We categorized females into two groups based on the time we released them: “early” (November or December release) or “late” (January, February, or March release). We compared the proportions of early- vs. late-released females that denned in each study area. Additionally, we compared these proportions to the mean denning rate for reintroduced females (California only) that denned in the years subsequent to translocation and to the mean denning rate for resident (not reintroduced) female fishers studied elsewhere in western North America (Aubry and Raley 2006, Weir and Corbould 2008, Matthews et al. 2013). Proulx et al. (1994) found that the distance that female fishers traveled after release had stabilized after 2–4 weeks, suggesting they had established home ranges. Moreover, the lengths of time that stress responses last and influence fishers are unknown but are likely to be on the order of several weeks (Dickens et al. 2010). We reasoned that fishers released before January 1 had at least 1 month to establish home ranges and overcome stress responses before blastocysts implanted. Therefore, we used January 1 as

the dividing line between early and late releases. This dividing date also bisected our releases into two relatively equivalent periods (Fig. 3). We considered these two periods as reasonable proxies for evaluating the effect of release time on birth rate; nonetheless, we also recognized that if our hypothesis was correct we might observe a continuous decline in denning rate with later dates of release. Consequently, we included in our analysis a continuous variable quantifying the number of days beyond November 1 on which we released a female. We predicted that denning rate would decrease as date progressed. Our discrete and continuous variables evaluated the same effect and, therefore, we did not include both in the same models.

We tested several other covariates that we hypothesized might influence denning rate. The two reintroduction projects differed in many ways such as the source locations of fishers, biotic and abiotic differences at the source and release locations, and our protocols for handling fishers while in captivity. Therefore, we hypothesized that project differences could influence denning rate. We included the project variable in both additive and interactive models for both discrete and continuous time analyses. We also hypothesized that a female’s body condition influenced denning rate. Because fishers from British Columbia were heavier than those from California, we standardized female body mass relative to the mean body mass of each study area (i.e., [(body mass – mean body mass)/standard deviation]). We hypothesized that a female’s age and the variation in conditions associated with the year of release affected denning rate.

We evaluated and ranked our candidate models using Akaike’s information criterion adjusted for small sample size (AIC_c , Burnham and Anderson 2002). We followed the general approach and suggestions of Burnham and Anderson (2002) and considered the model with the lowest AIC_c value to be the hypothesis best able to describe our data. Our main objective was to evaluate the hypothesis that the timing of release influenced denning rate; hence, we summed the AIC_c weights (w) for individual variables across models to quantify their relative importance (Burnham and Anderson 2002).

We examined the direction and magnitude of covariate effects on denning rate with both parameter estimates from the top-ranked model (containing a specific covariate), and with estimates from model averaging across all models in the candidate set (Burnham and Anderson 2002). We used an exponential transformation (e^β) to convert both the model-estimated, and model-averaged, beta parameters to an odds ratio, with the associated 95% confidence interval (Hosmer and Lemeshow 2004).

We hypothesized that the time a female spent in captivity would be highly correlated with the stress she endured and, therefore, would explain some amount of the variation associated with the project variable (Teixeira et al. 2007). Consequently, we tested this covariate (days in captivity) within our analysis but did not consider it *a priori*; nevertheless, we compared it with other variables and models to evaluate this hypothesis and how it explained observed project differences.

Simulating effects of release date on population growth and probability of extinction

We evaluated the potential effects of release timing on population size, population growth rate, and the likelihood of extinction of reintroduced fisher populations using stochastic simulation in MATLAB (The Mathworks Inc., Natick MA). We constructed a three-stage Lefkovitch matrix (Lefkovitch 1965) that described the life history pattern of fishers (Fig. 4). Because the number of animals released affects the probability of success for a reintroduction (Lewis et al. 2012, Powell et al. 2012), we simulated reintroductions of 9, 30, and 60 female fishers over 3 yr with 1/3 of those totals released each year (Powell et al. 2012). We chose 20 yr for the length of each simulation because it is a common period of time for evaluating success of reintroductions for fishers and martens (Lewis et al. 2012, Powell et al. 2012). For each number of females released, we simulated two release strategies, one in which all females were released early with no effect on their denning rate in the first year and a second strategy in which all females were released late and denning rate was diminished in the first year. For the late strategy we simulated a small (34% reduction), medium (66% reduction, matching our field

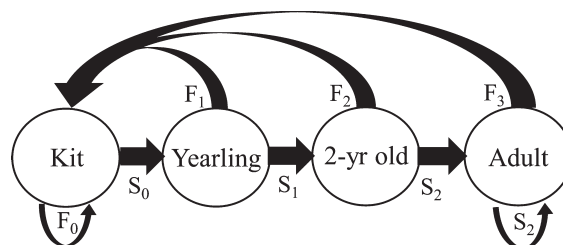


Fig. 4. Life-stage model of the fisher life cycle used to construct projection matrices to simulate reintroductions. Each circle represents the discrete life-stage of a female fisher with the kit life-stage consisting of all females aged 0 to <1 yr old, the yearling life-stage is females 1 to <2, 2-yr olds aged 2 to <3, and the adult life-stage is all females aged 3 and older. The arrows connecting the circles represents the transition values between the life-stages: S_0 = probability of surviving from birth until 1st birthday, S_1 = probability of surviving between 1st and 2nd birthday, S_2 = probability of surviving from 2nd to 3rd birthday and annually after 3rd birthday, F_0 = probability of a newborn giving birth (always 0), F_1 = the probability of a yearling female denning (also always 0), F_2 = the probability of a 2-yr-old female denning (giving birth) $\times$ the number of her female offspring, and F_3 = the probability of an adult female denning (giving birth) $\times$ the number of her female offspring.

data), and large (90% reduction) effect of late releases on denning rate (Table 1). All other population parameters were unaffected by the timing of release and the effect on denning rate applied only to females the first year immediately following their releases.

We generated model parameter values as random deviates from distributions based on estimated vital rates reported from other populations of fishers (Powell 1993a, Higley and Matthews 2006, Buskirk et al. 2012, Matthews et al. 2013, Table 1). We evaluated many different combinations of mean vital rates but ultimately used three sets of mean values for vital rates that simulated habitat quality as poor, fair, or good. For each life stage, we randomly generated survival and denning rates using the beta distribution (betarnd function of MATLAB) where the alpha and beta parameters define the shape of the distribution and are transformations from the means and standard deviations taken from the empirically derived distributions (Morris and

Table 1. Mean values $\pm$ SD for life history parameters used to simulate fisher populations resulting from releases where the habitat quality was poor, fair, or good.

Parameter	Life stage	Poor	Fair	Good
Apparent survival	Kit	0.25 ± 0.20	0.35 ± 0.30	0.35 ± 0.20
Apparent survival	Yearling	0.60 ± 0.10	0.70 ± 0.10	0.70 ± 0.10
Apparent survival	2-yr old and adult	0.84 ± 0.10	0.84 ± 0.10	0.84 ± 0.10
Den rate	2-yr old	0.50 ± 0.12	0.50 ± 0.12	0.70 ± 0.12
Den rate	Adult	0.90 ± 0.08	0.90 ± 0.08	0.90 ± 0.08
Litter size	2-yr old and adult	1.80 ± 0.41	2.1 ± 0.41	2.4 ± 0.41
Sex ratio	2-yr old and adult	0.50 ± 0.05	0.50 ± 0.05	0.50 ± 0.05
Low den rate†	2-yr old and adult (Low)	0.34 ± 0.00	0.34 ± 0.00	0.34 ± 0.00
Moderate den rate†	2-yr old and adult (Med)	0.66 ± 0.00	0.66 ± 0.00	0.66 ± 0.00
High den rate†	2-yr old and adult (High)	0.90 ± 0.00	0.90 ± 0.00	0.90 ± 0.00

†The percent reduction on reproduction of releasing female fishers in the late period.

Doak 2002). Litter size was similarly generated randomly using the normal distribution (normrnd function) and parameterized by the mean (μ) and standard deviation (σ) from the empirically derived distribution. Each vital rate was randomly generated (random number seeded by the computer clock) independently for each year of the simulation without correlation among years or vital rates. We set the maximum number of home ranges available after establishment at 200 and after these home ranges were occupied reproduction and juvenile survival fell to 0, but survival of animals ≥ 1 -yr old was unaffected.

We replicated each 20-yr reintroduction 1000 times for each combination of release size, time of release strategy (including the three effect sizes for late releases), and three levels of habitat quality. For all simulations, we calculated the percent of 1000 replicates in which the population fell below each of three quasi-extinction thresholds of 5, 10, and 20 female fishers during years 4 through 20 (Morris and Doak 2002). We calculated the geometric mean of population size and population growth rate at each time step of the reintroduction to evaluate the average response to the simulated release scenarios and effect sizes.

RESULTS

Denning rate

We released 24 females in California and 50 females in Washington from 2008 to 2011 (Fig. 3). Because some female fishers were too young and because we could not document

denning for all females, we included only 37 of these 74 females in our analyses. Twenty-three of 24 (95%) and 33 of 50 (66%) fishers released in California and Washington were old enough to give birth in the April following their releases. We determined the denning status of 87% (20 of 23) and 52% (17 of 33) of the potentially parous females in California and Washington. We could not determine the denning status of one adult female in California because her VHF transmitters failed prematurely and two others died prior to the denning season. In Washington, we could not determine the denning status of 18 adult females. Six died prior to the denning season and the others we could not confidently designate due to our inability to track them thoroughly in the National Park. In California we released 12 adult females, whose denning status we could determine, early and 8 late, whereas in Washington we released 5 early and 12 late. Photographs of kits from cameras set at den sites confirmed reproduction for 80% and 86% of females we suspected of denning in California and Washington, respectively. For the remaining females, we documented that denning by observing them repeatedly at the same tree via remote cameras.

The date when we released female fishers was the most important variable influencing denning rate in both California and Washington (Table 2, Fig. 5). Our seven highest ranking models included either the discrete or the continuous *date of release* variable. The best supported model included the discrete *date of release* variable with

Table 2. Metrics used to compare 17 models hypothesized to explain the initial denning success of female fishers in their first year following reintroduction to California and Washington in 2008–2011, where the $-2\log$ likelihood (not shown), the number of estimable parameters (k), number of observation ($n = 37$ for all) are used to construct Akaike’s information criterion corrected for sample size (AIC_c) and calculate the difference between top model and other models (ΔAIC_c), the model likelihood, and model weight (w).

Model description	k	AIC_c	ΔAIC_c	Likelihood	w	$\bar{R}^2$
Date _D [†] + Project	3	42.73	0.00	1.00	0.42	0.45
Date _D	2	45.40	2.67	0.26	0.11	0.32
Date _D + Body mass	3	46.04	3.31	0.19	0.08	0.37
Date _C [‡] + Project	3	46.08	3.35	0.19	0.08	0.37
Date _C	2	46.40	3.67	0.16	0.07	0.29
Date _D + Days held captive [§]	3	47.06	4.33	0.11	0.05	0.34
Date _D + Year	6	47.10	4.37	0.11	0.05	0.47
Project	2	47.34	4.61	0.10	0.04	0.27
Date _D + Age	3	47.77	5.04	0.08	0.03	0.32
Date _C × Project	4	48.57	5.84	0.05	0.02	0.37
Date _C + Days held captive	3	48.71	5.98	0.05	0.02	0.30
Date _D × Day held captive	4	48.95	6.22	0.04	0.02	0.36
Date _C × Days held captive	4	51.20	8.47	0.01	0.01	0.30
Days held captive	2	52.36	9.63	0.01	0.00	0.11
Body mass	2	53.35	10.62	0.00	0.00	0.05
Age	2	55.58	12.85	0.00	0.00	0.00
Year	4	56.44	13.71	0.00	0.00	0.14

[†]Date_D is a discrete variable that places females into two release groups, those that were released prior to January (early) and during or after January (late).

[‡]Date_C is a continuous variable that was defined as the number of days after November 1 when a female was released.

[§]The number of days a female was held in captivity (Days Captive) was a post hoc variable used to test the idea that variance between projects was associated with this factor. All models with the variable are not considered *a priori* tests of our central hypotheses.

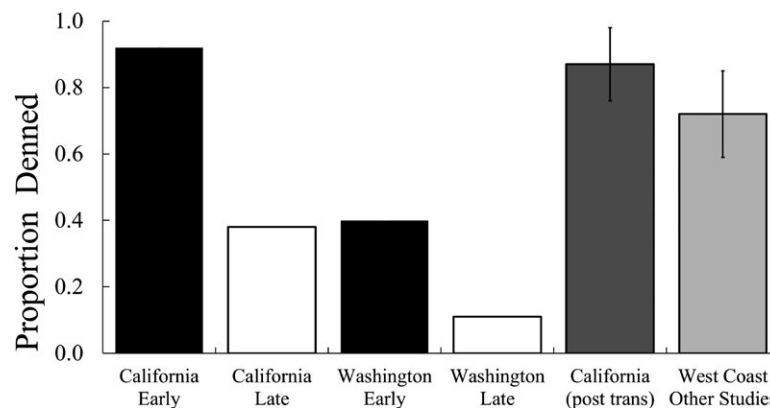


Fig. 5. The percent of female fishers released early or late and confirmed to have denned in their first year following reintroduction to California and Washington, 2008–2011. The dark gray bar shows the average percent $\pm$ SD of females that denned in all years, excluding their first, following their reintroduction at the California site while the light gray bar shows a mean value $\pm$ SD for denning rate in non-reintroduced fisher populations in the western United States (Aubry and Raley 2006, Weir and Corbould 2008, Matthews et al. 2013).

an additive effect of *project* differences (Table 2 and Fig. 5). Models that did not include an effect of release date received nearly no support ($\Delta AIC > 4$). The discrete *date of release* variable had

the highest summed Akaike’s weight (Table 3) indicating that, relative to other variables tested, it was able best to describe denning rate across models. Additionally, differences between the

Table 3. Summary statistics for variables included in logistic regression models including the summed Akaike weight (Σw) for each variable, the odds-ratio estimates from the top-ranked model that included the variable (OR_{Top}) and the model-averaged value (OR_{avg}) and their associated 95% confidence intervals.

Variable	Σw	OR_{Top}	95%CI $_{Top}$	OR_{avg}	95% CI $_{avg}$
Date _D (Late vs. Early)	0.76	0.124	0.024, 0.637	0.429	0.003, 52.060
Project (Wash vs. Cal)	0.56	0.164	0.032, 0.849	0.610	0.008, 43.320
Date _C	0.20	0.966	0.941, 0.991	0.994	0.893, 1.106
Days held captive	0.10	0.970	0.900, 1.045	0.997	0.828, 1.199
Body mass	0.08	1.799	0.705, 4.588	1.049	0.206, 5.320
Year 2008 vs. 2011	0.05	0.069	0.004, 1.180	0.923	0.093, 9.107
Year 2009 vs. 2011	0.05	0.250	0.015, 4.198	0.982	0.102, 9.377
Year 2010 vs. 2011	0.05	1.058	0.114, 9.781	0.951	0.118, 7.658
Age	0.03	0.989	0.540, 1.811	1.000	0.506, 1.974

projects and the continuous *date of release* variables had relatively high weight compared to other factors we tested (Table 3). We found good support that the date of release influenced denning rate but little support that *body mass*, *year* effects, and female *age* beyond reaching maturity influenced denning rate (Tables 2 and 3).

Denning rate across both sites for adult females released early was 76% (13 of 17) whereas that for females released late was only 25% (five of 20). Compared to females released early, the denning rate for late-released females was reduced by 58% in California and 73% in Washington, respectively, demonstrating similar patterns at both sites (Fig. 5). Females released early had similar rates of denning to those of females that survived and denned beyond their first year after reintroduction in California (similar data were not available for Washington), and were similar to the rates of naturally occurring populations of fishers in western North America (Fig. 5). All candidate models that included either a discrete or a continuous *date of release* variable indicated a negative influence of late release on denning rate (Table 3). Females released late were only 12% as likely to den compared to females released early indicating a negative relationship between denning rate and the number of days from November 1 a female was released (Table 3 and Fig. 6). Evaluation of the odds ratio for females released 100 d from November 1 indicate they had only a 3% (0.04% to 41%) probability of denning compared to females released on November 1.

The *project* variable was included in our top model, indicating a difference in denning rates between the projects. Additionally, an effect due

to the *project* had the second highest summed Akaike's weight, indicating a relatively high importance (Table 3). Nonetheless, the *project* variable as a single-variable model was less well supported than either of the single-variable *date of release* models. Females released in California denned at a higher rate than in Washington, and this pattern was apparent in both early and late-released females, consistent with models with additive effects and ranking higher than those with interactive effect (Table 2, Fig. 5).

As a single-variable model, the number of *days in captivity* had a lower AIC_c value, as well as a higher adjusted R^2 value, and thus described our data better, than did either *body mass* or *age* (Table 2). When combined with a *date of release* variable, *days in captivity* described only 75% of the variation compared to our top model. The longer a female was held in captivity the lower the denning rate, but the estimated 95% confidence intervals for both the beta and odds-ratio estimates bounded 1, indicating a weak relationship (Table 3).

Population simulations

Our reintroduction simulations demonstrated an effect of release date on average population size (Fig. 7). For all simulations, reintroductions based on an early release strategy showed higher average population sizes compared to reintroductions where females were released late (Fig. 7). Average population sizes tended to converge through time between early and late strategies when the simulated population occurred in poor habitat yielding negative population growth. The differences in mean

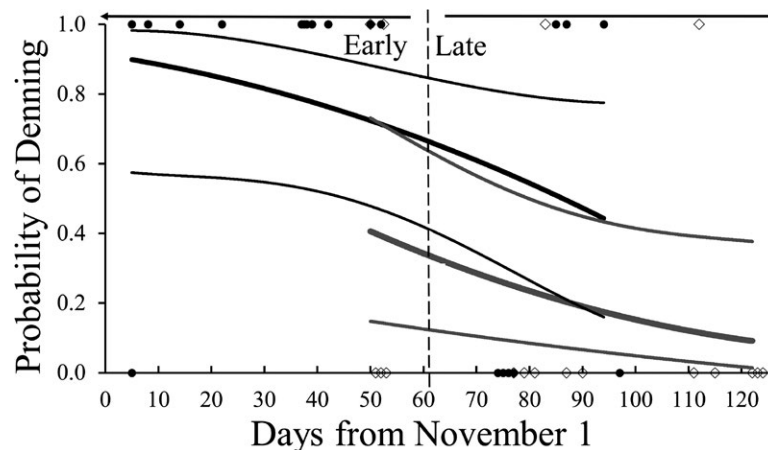


Fig. 6. Estimated logistic relationship between the time of a female fishers' release (days after November 1) and the probability that she denned (gave birth) after reintroduction for two studies, 2008–2011 where heavy solid lines represent the California (black lines) and Washington (gray lines) study sites with thinner solid lines as the 95% confidence intervals, and the vertical dotted line is January 1 which divided the transition between early and late releases. Black-filled circles represent females reintroduced in California, whereas open diamonds represent females reintroduced to Washington that were included in the analysis and whether they denned (value = 1) or did not (value = 0).

population sizes were greater for large founder populations living in fair or good habitats. Population growth was most strongly affected by reintroduction time during the first 4 yr of simulated reintroductions (Fig. 7). In fact, for simulations with large reductions in denning rates, the average population size decreased in the first 2 years after release. Subsequent to the final releases of all animals, simulated populations stemming from both early and late reintroduction strategies had nearly identical average rates of growth (Fig. 7), which only makes sense because they had the same mean values for life history rates.

Within our simulations, the reduction of the denning rate associated with releasing females late resulted in small increases in the probability that a population edged toward extinction (Fig. 8). Late releases and small founder group sizes caused populations to fall closer to extinction on more occasions than did reintroductions with early releases. The number of animals released and the population growth rate had the largest effects on whether a reintroduction fell below any quasi-extinction threshold (Fig. 8). Yet, the effect of releasing females late did increase the number of times we observed a reintroduction to fall below these thresholds (Fig. 8).

Scenarios with high effect sizes, as the result of late release, had a concordant influence on the probability of extinction (Fig. 8). In general, the effect of timing of release on the probability of extinction was small relative to the population release size and the quality of the release habitat but did increase the risk of extinction for reintroduced populations (Fig. 8).

DISCUSSION

The female fishers that we released late denned at a lower rate in the spring following their release than did females we released early. For the California and Washington projects, we observed decreases in denning rates of 58% and 73% for females that we released after January 1 compared to females released prior to this date (Fig. 5). A discrete model (early vs. late release) described our data better than did a continuous model. We interpret the strong support for the models including a discrete date to suggest that individual female fishers either have a discrete threshold for when denning would be affected (such as implantation of blastocysts) or that other unrecognized factors influenced denning rate during these distinct periods. Releasing females late affected females

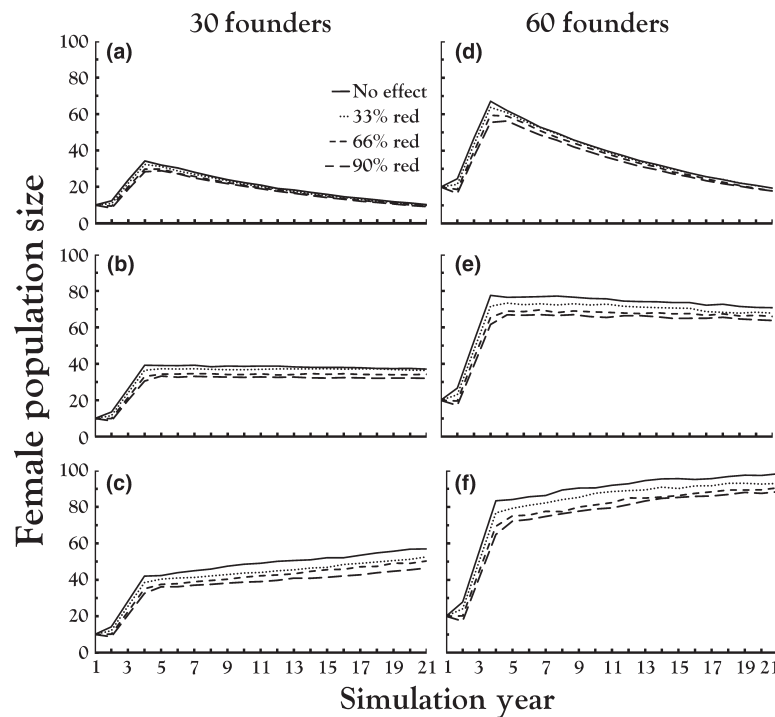


Fig. 7. Mean population sizes for female fishers over time from 1000 replicates of stochastic simulations of reintroduced populations for founding sizes of 30 and 60 females with 1/3 released in each of 3 yr. We simulated growth rates for reintroduced populations in poor (panels a and d), fair (panels b and e), and good (panels c and f) habitat after the final release (year 3). We simulated early releases of females (solid line), which did not reduce denning rates, and we simulated late releases with a 34% reduction in denning rate (dashed lines), a 66% reduction in denning rate (dotted lines), and a 90% reduction in initial denning rate (long-dashed line) in the year following translocation.

in all years, irrespective of a female's age, body mass, or other potentially confounding factors we tested. These results support our hypothesis that late releases, just prior to or during the time when dormant blastocysts were implanting and active gestation was beginning, had a substantial effect on the reproduction of adult female fishers.

Many factors may affect whether translocations succeed but the timing for releasing animals is heretofore unconsidered in analyses or planning (Griffith et al. 1989, Wolf et al. 1998, Armstrong and Seddon 2008). In the few instances when timing, in any capacity has been discussed or studied it has related to the time animals spend either in captivity or the mistiming of vital rates as a consequence of the reintroduction, rather than a product of when animals were released (Stüwe and Nievergelt 1991, Teixeira et al. 2007).

In contrast, we demonstrate that the timing of the release of fishers produced changes in their reproductive rates and that those short-term changes have the potential for long-term consequences. Our results are explicit for this effect on reproduction by fishers but the timing of specific life history traits affects vital rates of individuals in non-translocated populations of other animals (Seeley and Visscher 1985, Siekmann et al. 2001). Thus, it makes sense that other species may be influenced by translocations that coincides with important times in their natural history. If the untimely release of animals occurs during a period when they are acquiring important resources, reproducing, migrating, or entering torpor, they may experience subsequent effects on their general health or rates of survival or reproduction (Monteith et al. 2011, Mitchell et al. 2012). Our observations implicated the timing of release on

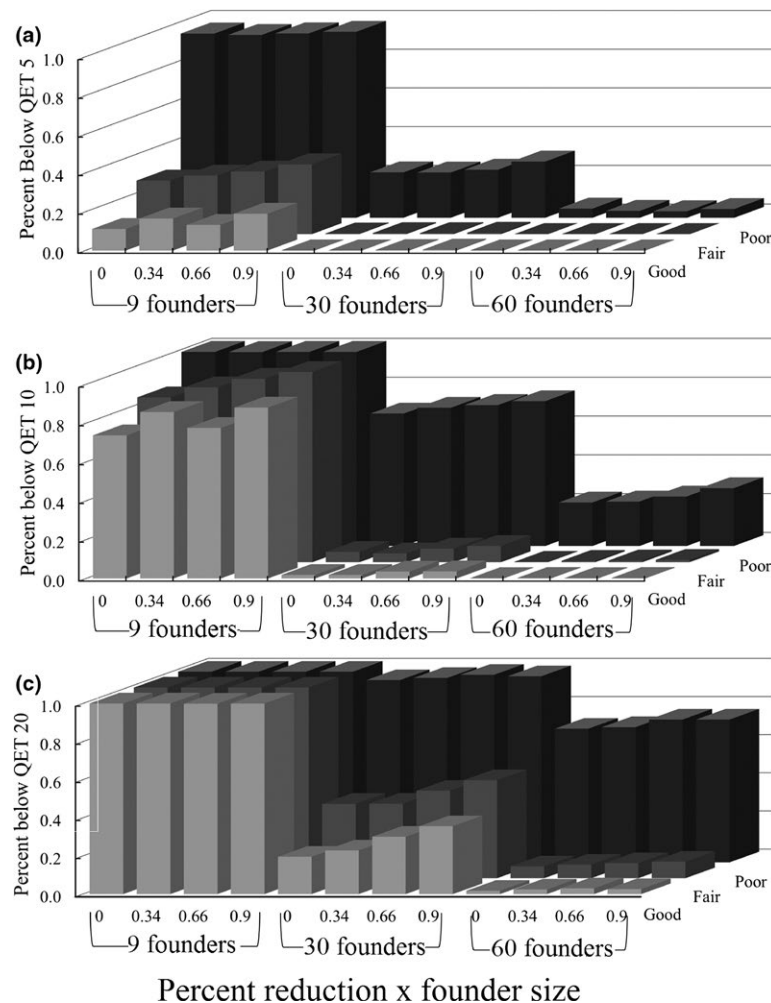


Fig. 8. Percent of simulated, reintroduced fisher populations monitored for 20 yr and that fell below a quasi-extinction threshold of 5, 10, and 20 fishers (panels a, b, and c). These scenarios depict different founding populations (9, 30, and 60 fishers), different habitats (good, fair, and poor), and an early release strategy (no effect on reproduction the first year following release) and a late release strategy (reduced reproduction of 0.34, 0.66, and 0.90).

reproduction directly but we hypothesize that such direct effects may not always be obvious. Rather, the effects of release may be cryptic or influence aspects of life history occurring at later times for some organisms. For example, animals released late (or early, depending on the species) may be at competitive disadvantages to animals released early or may miss critical resources prior to events like migration or hibernation (Monteith et al. 2011). Intra-species comparisons of translocations that occurred within and outside of hypothetically important periods may pro-

vide insight into if, and how, timing has affected the outcomes of translocations. Researchers and managers considering translocation should carefully consider a species' life history to determine an optimum season to release animals.

The effect of translocation timing on reproduction is important and warrants further consideration; nonetheless, we view the actual moving of fishers as a proximate mechanism for our observations. Many mechanisms can alter reproductive rates of animals and may correlate with translocation, and of these we

hypothesize that stress incurred from trapping, handling and transport as well as the novelty of new environments as the most important and ultimate mechanisms. Stress is a ubiquitous by-product of translocating animals, and though we did not measure stress directly, we assume that our fishers had stress responses that are similar to those of other species (Teixeira et al. 2007, Dickens et al. 2009, 2010). Because stress can affect reproduction directly (Breuner 2011, Scarlata et al. 2013), we expect that female fishers experiencing the highest levels of stress at the time when reproductive was re-activated had a concordant depression in reproduction during that year. Stress responses are advantageous because they modulate different aspects of the life history of animals (Busch and Hayward 2009). Newly released individuals are unfamiliar with the landscape, its potential resources, and the threats that occur there (Dickens et al. 2010, Powell and Mitchell 2012). With respect to reproduction by fishers, females released in autumn should have an advantage compared to females released in late winter and spring because they will be better acquainted with, and able to exploit, resources in the new landscape when reproduction re-activates. For example, fishers have unique denning habitat requirements and give birth only in tree cavities (Powell 1993a, Weir et al. 2012). Female fishers that are released just before the denning season will have less time to find suitable den sites and their kits may be more vulnerable to severe weather conditions or predation if females select poor-quality den sites due to time constraints. Trade-offs, as the result of translocations, between survival and reproduction could also have important consequences for both individuals and populations and warrant investigation in future theoretical and empirical work.

Our analyses documented clear differences in denning rates between our two projects. The two projects used different drugs to immobilize fishers. All three of the main drugs used for sedation are contraindicated for use during pregnancy (Plumb 2011). Yet, adverse effects on reproduction from these drugs appear most likely during late embryonic development rather than during implantation of blastocysts and no evidence suggests that these drugs are teratogens (Plumb 2011). Regardless, the role that sedatives play in

reproduction of mammals is largely unknown and should be investigated more.

Additionally, the logistics of tracking fishers in California differed from those in Washington. The California study site had extensive road networks that provided relatively close access to females. In Washington, road access was limited because Olympic National Park made up a large portion of the study area and it is largely without roads. These differences may have contributed to identifying the denning status of fewer females that could have given birth and, thus, affected the estimated rates of denning in Washington. We emphasize that these potential differences occur between projects but not among females based on when they were released. Moreover, errors that occurred in designating a female parous or not would have been distributed randomly among females and unlikely to influence the pattern related to timing, though such errors could influence the precision of our estimates.

The length of time that females spent in captivity described some variation between projects. In Washington, we held fishers in captivity longer (mean = 21 ± 23 d) than in California (mean = 6 ± 13 d) because they had to be transported farther and, therefore, more individuals were transported at any one time to reduce expenses. We assumed that females captured in British Columbia and northern California had similar numbers of fertilized but un-implanted blastocysts, but if this assumption was incorrect it could describe some of the differences we observed between projects (Wright and Coulter 1967, Frost et al. 1997). Another factor that may have contributed to differences between release sites is the variation in the respective environments between source and release locations. The source sites for both California and Washington existed within ecoregions that differed from the release locations (Olson et al. 2001), and differed in climate, vegetation and, potentially, prey type, and availability. Though we have not quantified these differences for either project, the California source sites were closer to the release site and we hypothesize more similar, and therefore familiar, to newly reintroduced fishers. We hypothesize that fishers released in Washington were less familiar with their new environments compared to fishers in California,

which may have resulted in energetic, or other unknown, deficits. How animals select and respond to their release environments remain key questions in studies on translocations that may relate to how and when management activities, like translocation, should take place (Seddon et al. 2007, Stamps and Swaisgood 2007, Mabry and Stamps 2008).

We recognize that releasing animals early vs. late has only a secondary effect on potential reintroduction success relative to factors like founder population size and habitat quality. Nevertheless, it represents a non-trivial influence on how a population may establish or thrive. The simulations we used here demonstrate that releasing animals late may increase the likelihood of extinction. We note that these simulations likely underestimated the extinction rate because the variation in vital rates, and population change, was potentially low because we did not include scenarios in which vital rates were correlated temporally. Nor did we include unexpected, random catastrophes (e.g., wildfires). Incorporation of such dynamics in reintroduced populations may increase the likelihood of extinction for populations where fishers are released late.

Timing of translocation of animals should be considered in conjunction with other risks and the time of life history traits of the animals during the planning of any translocation effort. In particular, reproductive phenology should be considered when species are proposed for translocation. Releases should be scheduled at times most advantageous for maximizing rapid reproduction of the founding members of the population. Maximizing reproduction in early years of a translocation is important because founding populations are typically small, additional source animals may be limited, and relatively rapid initial population growth should increase the probability of establishment. We contend that this research has important implications for timing and management that extend beyond translocations. Management activities like logging or trapping for research may also induce stress responses or change foraging behaviors in animals, and specifically fishers (Powell 1993b). If these activities occur during the birthing season then effects on reproduction may occur similar to those we observed. Additionally, we contend that timing of

translocations may have impacts on factors other than reproduction and, therefore, should be evaluated for life stages that are crucial for the species of interest. We suggest that, for species with life histories similar to fishers, consideration for the time at which they are captured, moved, or released may decrease negative effects on their reproduction and, thereby, increase the viability of populations, especially small populations typical of translocations.

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