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# Forest structure provides the income for reproductive success in a southern population of Canada lynx

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*Abstract.* Understanding intrinsic and extrinsic drivers of reproductive success is central to advancing animal ecology and characterizing critical habitat. Unfortunately, much of the work examining drivers of reproductive success is biased toward particular groups of organisms (e.g., colonial birds, large herbivores, capital breeders). Long-lived mammalian carnivores that are of conservation concern, solitary, and territorial present an excellent situation to examine intrinsic and extrinsic drivers of reproductive success, yet they have received little attention. Here, we used a Canada lynx (*Lynx canadensis*) data set, from the southern periphery of their range, to determine if reproductive success in a solitary carnivore was consistent with capital or income breeding. We radio-marked and monitored 36 female Canada lynx for 98 lynx years. We evaluated how maternal characteristics and indices of food supply (via forest structure) in core areas influenced variation in body condition and reproductive success. We characterized body condition as mass/length and reproductive success as whether a female produced a litter of kittens for a given breeding season. Consistent with life-history theory, we documented a positive effect of maternal age on body condition and reproductive success. In contrast to predictions of capital breeding, we observed no effect of pre-pregnancy body condition on reproductive success in Canada lynx. However, we demonstrated statistical effects of forest structure on reproductive success in Canada lynx, consistent with predictions of income breeding. The forest characteristics that defined high success included (1) abundant and connected mature forest and (2) intermediate amounts of small-diameter regenerating forest. These attributes are consistent with providing abundant, temporally stable, and accessible prey resources (i.e., snowshoe hares; *Lepus americanus*) for lynx and reinforce the bottom-up mechanisms influencing Canada lynx populations. Collectively, our results suggest that lynx on the southern range periphery exhibit an income breeding strategy and that forest structure supplies the income important for successful reproduction. More broadly, our insights advance the understanding of carnivore ecology and serve as an important example on integrating long-term field studies with ecological theory to improve landscape management.

*Key words: capital breeding; felids; habitat quality; habitat–fitness relationship; income breeding;* Lepus americanus; Lynx canadensis; *maternal effects; reproductive strategy; reproductive success.*

## Introduction

Individual reproductive success is an essential component of population dynamics, population persistence, as well as lifetime fitness (Stearns 1992). Therefore, ecologists and conservation biologists are keenly interested in evaluating the relative importance of intrinsic and extrinsic factors affecting reproductive success (Frederiksen et al. 2014). Intrinsic factors include many attributes such as cohort, genotype, maternal condition, or age, whereas extrinsic factors include climate, weather, population density, or the availability and distribution of food. Many of these factors exhibit spatial or temporal variation and thus provide opportunities to evaluate how their variation is linked to individual reproductive success (e.g., Clutton-Brock and Sheldon 2010). Moreover, a central mechanism to the conservation of endangered and threatened species is the designation of critical habitat (e.g., U.S. Endangered Species Act and Canada Species at Risk Act), which requires an understanding of habitat quality through the characterization of habitat–fitness relationships (e.g., via reproductive success, survival, or both) despite the challenges of doing so (e.g., Van Horne 1983, Mosser et al. 2009). Indeed, the insights generated from assessing intrinsic and extrinsic drivers of individual reproductive success are vast for both ecological theory and policy-relevant decision making. Unfortunately, however, the current state of understanding on factors driving individual reproductive success is disproportionately influenced by the particular groups of organisms where long-term studies have been conducted (e.g. birds, social mammals, large herbivores, capital breeders; Hamel et al. 2010, Clutton-Brock and Sheldon 2010, Saether et al. 2013, Uboni et al. 2017).

Reproduction is constrained by trade-offs associated with resource acquisition and the allocation of those resources to

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offspring production and rearing (Stearns 1992). Capital- and income-breeding strategies, and combinations thereof, represent the gradient of potential solutions to these trade-offs, which are distinguished based on how an organism applies stored energy to finance the cost of reproduction (Jönsson 1997). An organism employing a capital breeding strategy acquires its resources in advance and stores (i.e., capital) them until needed to finance reproductive costs (Jönsson 1997). In mammals, capital breeders generally exhibit a strong association between pre-pregnancy body condition and reproductive success (e.g., Ozgul et al. 2010, Rode et al. 2010, Monteith et al. 2014), whereby individuals in better condition exhibit higher success. In addition, the maternal investment associated with producing and rearing young often impacts the condition of females that exhibit a capital breeding strategy (e.g., Clutton-Brock et al. 1989, Festa-Bianchet et al. 1998, Monteith et al. 2013). In contrast, an income breeder adjusts its food intake (i.e., income) during the prenatal period to finance reproductive costs, with little reliance on stores (Jönsson 1997). Consequently, pre-pregnancy body condition does not mediate the effects of food on reproductive success, nor capture the investment in previous reproductive effort as with a capital breeder. Mammals that are required to engage in complex movements to capture agile prey might rely on an income breeding strategy because of (1) the burden of storing excessive body reserves (e.g., Houston et al. 2006), and (2) the unpredictable nature of prey populations (vs., for example, the waves of plant green-up in spring; Merkle et al. 2016). Evaluating the reproductive strategies of organisms not only informs life-history theory, but also provides guidance on how animals might navigate environmental changes influencing food resources (e.g., Kerby and Post 2013).

Mammalian carnivores that are solitary and territorial present an excellent situation to examine factors driving individual reproductive success. These organisms are generally long lived, reproduce once a year, have short gestation periods, and exhibit high maternal investment in rearing young (Bekoff et al. 1984, Proaktor et al. 2007, Balme et al. 2017). In addition, they exhibit intrasexual territoriality (e.g., Bischof et al. 2016) and do not navigate seasonal migrations (e.g., Squires et al. 2010) allowing variation in environmental resources to be linked to individual females. Furthermore, many species of carnivores are also globally at risk (Ripple et al. 2015), which underscores the conservation relevance of understanding drivers of their reproductive success and ultimately population persistence. However, despite these characteristics, relatively few studies have simultaneously evaluated the intrinsic and extrinsic drivers of reproductive success for solitary and territorial carnivores beyond the family Ursidae (e.g., Atkinson and Ramsay 1995, Samson and Huot 1995, Rode et al. 2010), although other studies have examined mostly extrinsic (Mowat et al. 1996, Walton et al. 2017) or intrinsic drivers (Atkinson and Ramsay 1995, Zedrosser et al. 2009, Nilsen et al. 2012, Gaillard et al. 2014). In a recent study, however, Rauset et al. (2015) demonstrated that female wolverines (*Gulo gulo*) exhibited age-specific reproductive output that was impacted by prior breeding activity as well as food limitation, reflecting aspects of both income and capital breeding. Additional work characterizing drivers of reproductive success in solitary mammalian carnivores, and particularly those that are of conservation concern, is warranted for both theory development and informing critical habitat designations.

Within the contiguous United States, Canada lynx (*Lynx canadensis*) are a federally threatened forest carnivore (USFWS 2000) and the management of lynx habitat is a contested topic (e.g., lawsuits reaching the U.S. Supreme Court; Howard 2016). Given the need to characterize critical habitat for recovery planning processes (according to the U.S. Endangered Species Act), coupled with the lack of studies examining drivers of reproductive success in solitary carnivores, the Canada lynx presents an excellent study system. Furthermore, lynx along the southern range periphery (vs. the northern range) offer additional benefits in terms of characterizing drivers of reproductive success. For instance, lynx and snowshoe hares (*Lepus americanus*) are relatively acyclic along the southern range and densities of lynx are comparatively lower (Aubry et al. 2000, Murray et al. 2008), both of which somewhat control for spatiotemporal variation that may confound assessments of reproductive success (e.g., McLoughlin et al. 2006, Gaillard et al. 2010).

Here, we evaluated the influence of intrinsic and extrinsic factors on reproductive success in female Canada lynx using a long-term (i.e., 14-yr), individually based data set collected along the southern periphery of the lynx's range. Our research objectives were to (1) test whether Canada lynx exhibited a reproductive strategy consistent with income or capital breeding (Jönsson 1997; Fig. 1), and (2) understand the effects of forest structure (and thus forest management and wildfire) on reproduction. We hypothesized that Canada lynx would exhibit a reproductive strategy closer to income breeding than capital breeding (Fig. 1) because (1) the cost of storing excessive body reserves is high for a solitary predator that relies on catching elusive prey (e.g., Houston et al. 2006), (2) maternal investment might be plastic as in other felids (e.g., Balme et al. 2017), which would be difficult to achieve under a strict capital breeding strategy, and

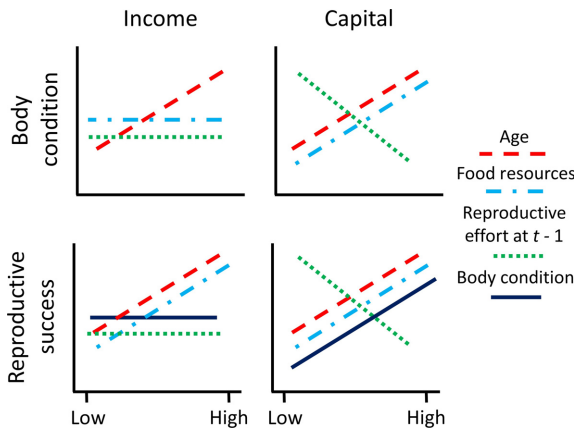


FIG. 1. Predictions we evaluated to test income and capital breeding in female Canada lynx (*Lynx canadensis*) in northwestern Montana, USA. Body condition was defined as mass/length and reproductive success was whether a female produced a litter of kittens during a given breeding season. We indexed food resources (see Table 1) through measures of forest structure and arrangement in 50% core use areas for each female lynx. See Table 2 for how we measured age and reproductive effort.

(3) the acquisition of prey during the breeding season is relatively stochastic (vs., for example, plant green-up in the spring) for female lynx that become central place foragers when denning (e.g., Olson et al. 2011, Gaillard et al. 2014). Based on this hypothesis, we tested the following predictions: (1) pre-pregnancy body condition would improve with maturation but be unrelated to food resources (assuming individuals are not starving) and reproductive effort in the previous year, (2) reproductive success would increase with accessible food resources and maturation (e.g., Mowat et al. 1996, Slough and Mowat 1996, O'Donoghue et al. 1997, Reynolds et al. 2017), and (3) reproductive success would be unrelated to pre-pregnancy body condition and reproductive effort in the previous year (Fig. 1). To our knowledge, our work is the first assessment of income and capital breeding in Canada lynx, and more broadly serves as an important example on integrating long-term field studies with ecological theory to improve land management.

## Methods

### *Study area*

Our research occurred on two study areas in northwestern Montana, USA, which is on the southern range periphery for Canada lynx. Our study areas were located in the Swan and Mission Mountains near Seeley Lake, Montana, and in the Purcell Mountains near Yaak, Montana (Fig. 2). Elevations ranged from 1,200 to 2,400 m in the Seeley Lake study area (hereafter Seeley) and 800 to 2,300 m in the Yaak study area (hereafter Yaak). Both study areas featured a diversity of montane habitats ranging from low to mid-elevation ponderosa pine (*Pinus ponderosa*) and dry Douglas-fir (*Pseudotsuga menziesii*) forests to high-elevation forests dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmanii*), and lodgepole pine (*Pinus contorta*). The Yaak consisted almost entirely (>95%) of federal lands, whereas Seeley contained approximately 48% federal lands, 37% Plum Creek Timber Company lands (although most Plum Creek lands were transferred to state and federal agencies during the study in 2009–2010), and lesser amounts of state, tribal, and private land (Squires et al. 2010). Additional details characterizing our study locations are presented in previous work (e.g., Squires et al. 2010, 2013, Holbrook et al. 2017*b*).

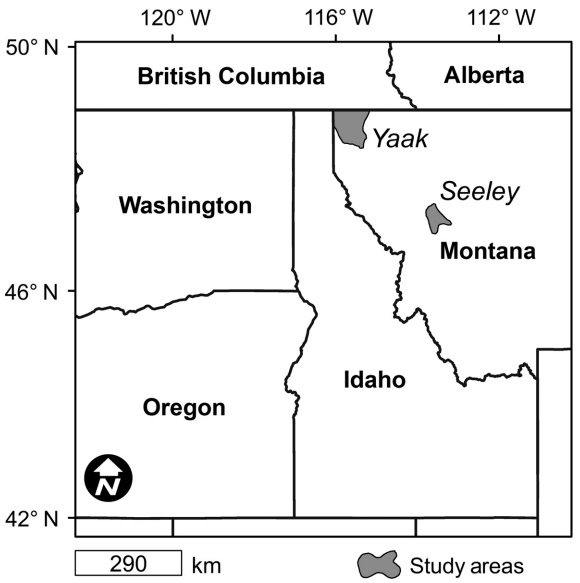


Fig. 2. Our study areas (Yaak and Seeley) in northwestern Montana, USA, where we monitored female Canada lynx (*Lynx canadensis*) during 1998–2012.

### *Female spatial data and reproductive success*

We trapped and radio-collared female lynx in Seeley and Yaak from 1998 to 2012. We captured, handled, and collected morphological data (according to Squires et al. [2008]) using methods approved by the Institutional Animal Care and Use Committee (IACUC permits 4–2008 and TE053737–1). We collared females with Very High Frequency (VHF) radio collars (Advanced Telemetry Solutions, Isanti, Minnesota, USA) from 1998 to 2004, and with store-on-board GPS collars (Lotek Wireless, Newmarket, Ontario, Canada and Sirtrack, Havelock North, New Zealand) from 2005 to 2012. We located females with VHF collars every 1–2 weeks using aerial telemetry and GPS collars collected a location every 30 min for 24 h, every other day for 6–8 months. We monitored females until they died, disappeared from the study area, radio-collars failed, or until the end of the study period. We used telemetry to locate females each spring and recorded whether the female produced kittens or not. Litter production for a given reproductive season was our measure of reproductive success, which is sensitive to food resources and by definition correlates with kitten recruitment (e.g., Brand et al. 1976, Mowat et al. 1996). We did not assess variation in litter sizes because, in contrast to lynx populations in the northern boreal forests (Mowat et al. 1996), litter size in our data set was mostly invariant (e.g., females 2 yr old, 3 yr old, and >3 yr old all produced approximately 2.5 kittens/litter; $n$ = 4 litters, 6 litters, 43 litters, respectively). Further, while litter production correlates with kitten recruitment in lynx (e.g., Mowat et al. 1996), we were unable to directly monitor kitten recruitment to independence. We recognize the recruitment process is an important aspect of reproductive success and should be evaluated in the future.

Female lynx exhibit distinctive central place foraging behavior from natal (parturition) and maternal (rearing) dens during the first 6–8 weeks of the kittens' lives (Olson et al. 2011, Vashon et al. 2012). Therefore, we likely detected all reproductive events of radio-collared females where kittens survived >1–2 weeks of age because we could intensively search a comparatively small area increasing the probability of detecting a litter. However, we could have missed brief attempts at reproduction if females abandoned their kittens <7 d after parturition.

### *Maternal state and age*

We analyzed variation in body condition and reproductive success relative to multiple measures of maternal condition. We recorded pre-pregnancy body condition (i.e., mass/length), an individual's reproductive effort the previous year

(i.e., produced a litter or not at $t - 1$), and maternal age. Parker et al. (1983) demonstrated a positive correlation between body mass and fat storage for Canada lynx, suggesting our measure of condition is associated with stored capital. In addition, body mass has been applied previously to evaluate how condition influenced litter size of Eurasian lynx (*Lynx lynx*; Gaillard et al. 2014). We only considered body condition measurements that were collected during a few months (i.e., January–March, but mostly January–February) prior to parturition (generally early May; Olson et al. 2011), which coincided with the pre-pregnancy period or the early phases of pregnancy. This allowed us to address two questions: (1) how does producing young in the previous ($t - 1$) spring affect year $t$ winter body condition and (2) what is the effect of winter body condition on subsequent spring reproductive success? Consistent with income breeding, we predicted litter production and body condition at year $t$ would be independent of the reproductive success in year $t - 1$ (Fig. 1). Further, we expected pre-pregnancy body condition would be unrelated to spring reproductive success (Fig. 1), which has been demonstrated in Eurasian lynx (Gaillard et al. 2014) but remains untested in Canada lynx (Reynolds et al. 2017).

We assigned females to three ordinal ages (2, 3, and >3 yr old) based on known age for females first observed as kittens, or an analysis of tooth annuli (Matson's Laboratory, Bonner, Montana, USA) collected from mortalities. We assigned unknown aged females to the >3 yr old age category after we had monitored a female >3 yr. We selected these age categories based on our ability to distinguish age in the field and for comparison with other studies (Mowat et al. 1996, Slough and Mowat 1996, Palomares et al. 2005, Nilsen et al. 2012, Gaillard et al. 2014). We predicted body condition and reproductive success would be positively related to age based on female maturation, a common relationship observed in mammals (Clutton-Brock 1984, Hadley et al. 2007, Nussey et al. 2007, Saether et al. 2013). Our prediction does not account for senescence, however, because our age categories did not include an "old" stage.

### *Forest structure as an index of food resources*

To establish the spatial boundaries of our forest structure analysis, we estimated core use areas of annual female territories (Fig. 3). We used ArcGIS 9.3.1 (Environmental Systems Research Institute [ESRI], Redlands, California, USA) and the Home Range Tools Extension (HRT; Rodgers et al. 2007) to estimate 50% annual home ranges (hereafter, core areas) using the fixed-kernel density method (Worton 1989) and a reference smoothing factor (href; Worton 1995) of 1.0. We focused on core areas because (based on previous analyses) they were more strongly related to demographic responses than were 90% home ranges, which indicated similar patterns but displayed more variation (Kosterman 2014). We only considered females with ≥30 locations to ensure reasonable estimates of home ranges (Seaman et al. 1999). Detailed methods for core area estimation are presented in Appendix S1.

To characterize the spatial distribution of forest structural classes, we developed a forest structure map for our study areas. First, we used the U.S. Forest Service's Vegetation Mapping Program (VMap) layer (Brewer et al. 2004) to delineate boundaries of homogeneous forest patches within female core areas. We then visually assigned five forest structural types to these patches using temporally coincident aerial imagery: open, sparse forest, small-diameter regenerating forest, medium-diameter regenerating forest, and mature forest (see descriptions in Table 1). We were unable to identify a very small-diameter structural stage that was different from our open or sparse categories because this resolution of classification was inconsistent with the coarse nature of aerial imagery. We expected our forest structure classes to relate directly to the abundance, distribution, and accessibility of snowshoe hares for Canada lynx (Table 1). For example, previous work has demonstrated that open and sparse forest structural stages generally produce low densities of snowshoe hares (Griffin and Mills 2009, Holbrook et al. 2017*b*), while small–medium diameter stands, as well as mature stands, produce high densities of snowshoe hares (Griffin and Mills 2009, Ivan et al. 2014, Holbrook et al. 2017*b*). To evaluate the accuracy of our imagery-based classifications, we ground truthed (using an independent observer) 187 random locations stratified by study area and structure type. Overall accuracy was 93% with 87 of 93 locations classified correctly in Seeley and 87 of 94 locations classified correctly in the Yaak.

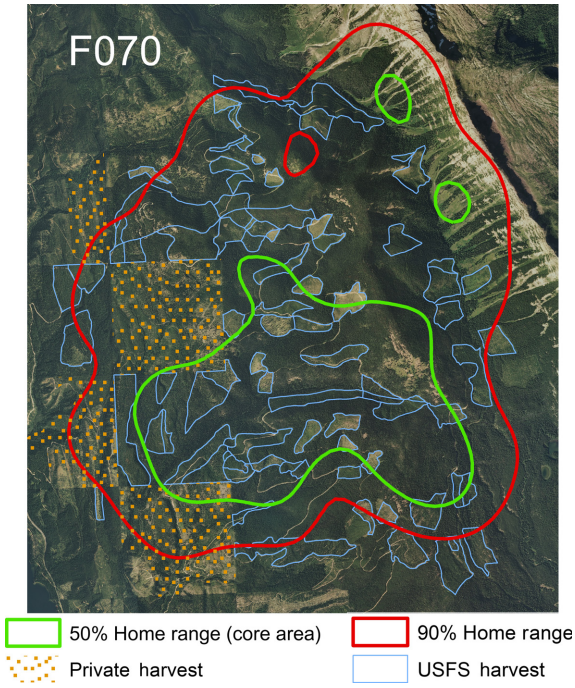


FIG. 3. Example core area and home range of a highly productive female (i.e., F070) Canada lynx (*Lynx canadensis*) in the Seeley study area during 2001–2007 in northwestern Montana, USA. F070 produced seven litters of kittens out of seven years of monitoring within a landscape managed for multiple use, including timber extraction. Timber harvest during the 1960s–1990s from the United States Forest Service (USFS) and private companies (Private) are indicated.

We used Fragstats software (v.4.2; McGarigal et al. 2012) to quantify landscape metrics that described forest structure composition and spatial configuration within female core use areas. Landscape composition describes the variety and

TABLE 1. Description of forest structural classes within the Canada lynx (*Lynx canadensis*) study areas in northwestern Montana, USA.

| Forest structure class | Stand description | Relationship to snowshoe hares |
|---|---|---|
| Open | No trees or canopy present, low horizontal cover. | Low density of snowshoe hares (Griffin and Mills 2009, Holbrook et al. 2017*b*) |
| Sparse forest | Naturally sparsely stocked or mechanically thinned stands with a discontinuous canopy and a visible forest floor, low horizontal cover. | Low density of snowshoe hares (Griffin and Mills 2009, Holbrook et al. 2017*b*) |
| Small-diameter regenerating forest | Regenerating forests generally due to forest management with smaller sized (~10–15 cm DBH) trees, intermediate canopy cover, and high horizontal cover. | Capable of producing high density of snowshoe hares over a limited time frame, but hares are potentially difficult to access and kill for lynx because of high stem densities (Griffin and Mills 2009, Lewis et al. 2011, Ivan et al. 2014, Cheng et al. 2015, Ivan and Shenk 2016, Holbrook et al. 2017*b*) |
| Medium-diameter regenerating forest | Regenerating forests from forest management with medium sized (~15–20 cm DBH) trees and continuous canopy and high horizontal cover. | Capable of producing high density of snowshoe hares over a limited time frame, but hares are somewhat accessible because of intermediate stem densities (Griffin and Mills 2009, Lewis et al. 2011, Ivan et al. 2014, Cheng et al. 2015, Ivan and Shenk 2016, Holbrook et al. 2017*b*) |
| Mature forest | A multistoried or uneven-aged stand with a median DBH of 26 cm (10 inches). This DBH is reflective of the multistoried nature of the structure class, but despite this DBH, there was a comparatively high proportion (i.e., 22%) of large trees (≥38 cm in DBH). Common attributes in this class were substantial understory (e.g., seedlings and saplings) and horizontal cover, continuous canopy, and no evidence of recent disturbance. | Capable of producing medium density of snowshoe hares over a long time frame, and kill rates are higher for lynx because stem densities are lower than regenerating classes (Griffin and Mills 2009, Squires et al. 2010, Ivan et al. 2014, Ivan and Shenk 2016) |

*Note:* We characterized our predicted relationship between forest structure and snowshoe hare densities using literature from the Northern and Southern Rocky Mountains, USA.

abundance of forest structure types (McGarigal et al. 2012). We characterized landscape composition by simply calculating the percent composition of small- and medium-diameter regenerating forest in each female's core area (Table 2). Consistent with income breeding, we generally predicted body condition of female lynx would be unrelated to food resources. However, we expected reproductive success by lynx to be positively related to small- and medium-diameter regenerating forest because snowshoe hares (i.e., food resources) tend to reach the highest densities at intermediate structural stages (e.g., Ivan et al. 2014, Cheng et al. 2015).

A novel metric we used to characterize amount and configuration of mature forest patches was "area-normalized correlation length" (Table 2). Correlation length is a landscape metric based on the average extensiveness of connected patches of a focal habitat type within a given landscape (McGarigal et al. 2012). This can be interpreted as the average distance an animal could travel within each female's core area without leaving mature forest, starting from a random point and moving in a random direction. Because this metric is sensitive to area, we area-normalized the correlation length (S. Cushman and K. McGarigal, *personal communications*) by (1) quantifying the "potential" correlation length for each core area if the entire core area was one contiguous patch of mature forest; (2) quantifying "realized" correlation length for each core area, or the ability for the female to traverse her core area without exiting mature forest given the existing forest mosaic; (3) then dividing the "realized" by the "potential" for each core area. This resulted in a mature forest connectivity index (MFCI) scaled 0–1, with values closer to 0 representing low connectivity and values closer to 1 representing high connectivity. Similar to the previous predictions consistent with income breeding, we expected body condition of female lynx to be unrelated to mature forest connectivity, but predicted reproductive success would be positively related with high connectivity of mature forest. Mature forest provides abundant, temporally consistent, and accessible snowshoe hares for Canada lynx in the Rocky Mountains (Table 1; Griffin and Mills 2009, Ivan et al. 2014, Holbrook et al. 2017*b*) and lynx are more successful at killing snowshoe hares in mature forest than regenerating forest (Ivan and Shenk 2016). In addition, lynx exhibit strong selection for mature forest and use this structural stage twice as much as any other during both winter and summer seasons (Holbrook et al. 2017*a*).

### *Statistical analyses*

We used generalized linear mixed-models (GLMM; Bolker et al. 2009) to assess our predictions on income vs. capital breeding in Canada lynx (Fig. 1). We used a Gaussian and binomial distribution (with a logit link) for our analysis of body condition and reproductive success, respectively. We included the identity of individual females as a random effect to control for repeated measures of the same individual over time (Bolker et al. 2009). Initially, we assessed the effect of each covariate on body condition and reproductive success and determined if there was support for a curvilinear relationship based on the Akaike information criterion corrected for sample size ($AIC_c$; Burnham and Anderson 2002). For each assessment, we reported unstandardized regression coefficients (β), standard errors (SE), *P* values, and sample sizes (*n*). If multiple covariates were characterized as important based on Hosmer and Lemeshow (2000) criteria (e.g., $\alpha = 0.20$) and were uncorrelated

TABLE 2. Covariates used in evaluating the evidence for income and capital breeding by female Canada lynx (*Lynx canadensis*) in northwestern Montana, USA, during 1998–2012.

| Covariates | Description |
|---|---|
| Maternal characteristics | |
| Body condition index | mass/length (kg/cm) from nose to the tip of tail |
| Age at parturition | three ordinal categories: 1 = 2 yr olds, 2 = 3 yr olds, and 3 = >3 yr old |
| Reproductive effort at $t - 1$ | reproductive cost of producing a litter of kittens the previous year ($t - 1$); 0 = no litter at $t - 1$, 1 = litter of kittens at $t - 1$ |
| Forest structure (index of food resources) | |
| Percentage of small-diameter regenerating forest | percentage of core area |
| Percentage of medium-diameter regenerating forest | percentage of core area |
| Mature forest | mature forest connectivity index (MFCI), which is an area normalized correlation length (index ranging from 0 to 1) |

($|r| < 0.70$), we combined them into a multivariate model. If a multivariate model was constructed, we assessed the fit of the Gaussian model using Spearman's correlation coefficient ($r_S$) between predicted and observed values and used the area under the curve of a receiver operating characteristic for the binomial model (AUC of ROC; Hosmer and Lemeshow 2000). All statistical analyses were performed in program R (R Core Team 2013) using the following libraries: lme4 (Bates et al. 2014), effects (Fox 2003), and ROCR (Sing et al. 2005).

## RESULTS

We monitored 36 females (Yaak = 17, Seeley = 19) of reproductive age (≥2 yr old) for an average of 2.7 ± 1.9 yr of observation per female (mean ± SD, range = 1–7 yr). This resulted in a total of 98 lynx years monitored over the study (1998–2012). Females produced 61 litters (150 kittens), which resulted in a raw parturition percentage of 62%. Mean female body mass was 9.04 kg (range = 7.25–11 kg) and the body condition index (mass/length) ranged from 0.20 to 0.31 with a mean of 0.24.

Composition of structure classes within female core areas was variable and ranged from relatively contiguous mature forest among a mixture of other forest structure types, to those typified by smaller and more isolated mature forest patches surrounded by different forest structures (Fig. 4). Mature forest was the dominant forest structure type in core areas, comprising 49% ± 13% (mean ± SD, range = 7–79%; see Appendix S2 for forest metrics associated with mature forest). Mature forest was multi-storied with a substantial understory and a dense canopy. For instance, tree sizes for mature forest were approximately distributed as follows: 2.0–12.7 cm DBH (11%), 12.7–25.4 cm DBH (37%), 25.4–38 cm DBH (30%), and >38–72 cm DBH (22%; Appendix S2). Medium-diameter regenerating forests comprised an average 24% ± 18% (range 1–54%) and small-diameter regenerating forests comprised 13% ± 6% (range = 1–26%) of core areas. Open and sparse forest structure types comprised the remaining area (4% ± 4%, range 0–12%; 10% ± 7%, range 3–24%, respectively).

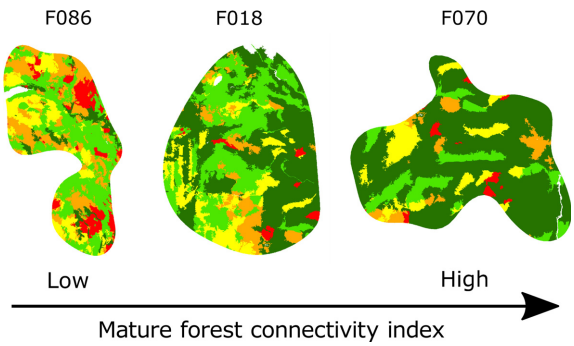


FIG. 4. Example core areas of female Canada lynx (*Lynx canadensis*) in the Yaak and Seeley study areas in northwestern Montana, USA. Core areas of females that produced litters had higher connectivity of mature forest (dark green) and ~12–20% composition of small-diameter regenerating forests (yellow). Forest structure categories include mature forest (dark green), medium-diameter regenerating forest (light green), small-diameter regenerating forest (yellow), sparse forest (orange), and open areas (red).

### *Body condition*

Consistent with our predictions, only maternal age was related to changes in female body condition (Table 3). We observed a positive effect of age on body condition, with female lynx >3 yr old exhibiting better condition than 2-yr olds (Fig. 5). Neither reproductive effort at $t - 1$ nor indices of food resources (i.e., forest structure classes) were statistically related to variation in female body condition (Table 3). We did not develop a multivariate model because only female age was statistically related to body condition in our univariate analyses.

### *Reproductive success*

Based on univariate analyses, reproductive success of female lynx was positively related to maternal age and the connectivity of mature forest (Table 3). However, reproductive success was negatively related to medium-diameter regenerating forests and exhibited a curvilinear relationship with small-diameter regenerating forest (Table 3). Neither body condition nor reproductive effort at $t - 1$ was statistically related to reproductive success of female lynx.

We developed a multivariate model characterizing reproductive success of female Canada lynx, which included a linear effect of maternal age, medium-diameter regenerating forest, and mature forest connectivity. Additionally, we included a curvilinear effect of small-diameter regenerating forest. Once combined, the effect of maternal age and

TABLE 3. Marginal coefficients from our GLMM univariate assessment of factors influencing variation in body condition and reproductive success of female Canada lynx (*Lynx canadensis)* in northwestern Montana, USA, during 1998–2012.

| Covariates | β | SE | *P* | *n* | Females |
|---|---|---|---|---|---|
| Body condition | | | | | |
| Age | **0.015** | 0.005 | 0.001 | 43 | 28 |
| Reproductive effort at $t-1$ | 0.001 | 0.012 | 0.948 | 24 | 15 |
| Percentage of small-diameter regenerating forest | −0.001 | 0.001 | 0.335 | 44 | 22 |
| Percentage of medium-diameter regenerating forest | 0.000 | 0.001 | 0.451 | 44 | 22 |
| Connectivity of mature forest | −0.006 | 0.018 | 0.732 | 44 | 22 |
| Reproductive success | | | | | |
| Body condition | −18.227 | 16.381 | 0.266 | 52 | 30 |
| Age | **0.794** | 0.416 | 0.056 | 85 | 34 |
| Reproductive effort at $t-1$ | 0.456 | 0.989 | 0.645 | 61 | 23 |
| Percentage of small-diameter regenerating forest | **0.832** | 0.240 | 0.001 | 78 | 23 |
| (Percentage of small-diameter regenerating forest)$^2$ | **−0.026** | 0.008 | 0.001 | 78 | 23 |
| Percentage of medium-diameter regenerating forest | **−0.076** | 0.038 | 0.042 | 78 | 23 |
| Connectivity of mature forest | **2.719** | 1.787 | 0.128 | 78 | 23 |

*Notes:* Unstandardized beta coefficients (β), standard errors (SE), *P* values, sample sizes (*n*), and number of females are identified. Univariate tests suggesting a statistical effect (α = 0.20; Hosmer and Lemeshow 2000) are highlighted in boldface type.

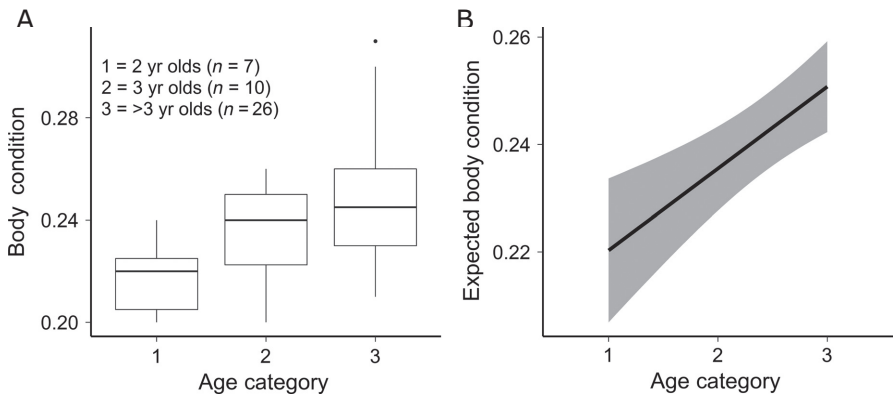


FIG. 5. (A) Box plot characterizing the positive relationship between body condition and maternal age for female Canada lynx (*Lynx canadensis*) northwestern Montana, USA. Middle line, median; box edges, interquartile range (IQR); whiskers, ≤ 1.5 x IQR beyond the box. (B) Predicted relationship from our GLMM highlighting the marginal effect of maternal age on body condition. Gray bands indicate the 90% CIs.

medium-diameter regenerating forest became statistically insignificant ($P > 0.60$, $n = 68$ seasons, females = 22), while the effect of small-diameter regenerating forest and mature forest connectivity remained significant ($P = 0.002$–$0.052$, $n = 68$ seasons, females = 22). The connectivity of mature forest and the amount of small-diameter regenerating forest were the most important covariates influencing reproductive success of female lynx. The AUC for our multivariate model indicated reasonable predictive performance (AUC = 0.85).

The probability of producing a litter was highest for females that had core-use areas with ~12–20% of small-diameter regenerating forest ($\beta_{\text{small-diameter}} = 1.57$, SE = 0.59; $\beta_{\text{small-diameter}}^2 = -1.01$, SE = 0.33), and increased with increasing connectivity of mature forest ($\beta_{\text{MFCI}} = 1.45$, SE = 0.75; Fig. 6). The influence of small-diameter forests on female productivity was mediated by the connectivity of mature forest patches. In core areas with high connectivity of mature forest, the probability of producing a litter increased from 0.5 to 1.0 as the proportion of small-diameter regenerating forest increased from ~5% to ~10%. The probability of producing a litter remained consistently high up to ~20% of small-diameter forest within core areas, and then declined slightly beyond ~20% (Fig. 6B, lower right quadrant). Conversely, in core areas with low connectivity of mature forest, the optimal was ~17% for small-diameter regenerating forest; however, the probability of producing a litter did not exceed 0.80 (Fig. 6B, upper left quadrant) emphasizing the importance of connected mature forest (i.e., lower right quadrant where probability of producing a litter reaches 1.0).

## DISCUSSION

Consistent with our hypothesis, our analyses support the notion that Canada lynx on the southern range periphery exhibit a strategy of income breeding (Jönsson 1997, Houston et al. 2006). First, the main drivers of reproductive success for females were the combined effects of highly connected mature forest and intermediate amounts of small-diameter regenerating forest within core use areas (Fig. 6). The most likely mechanism associated with these findings was food limitation, which has been demonstrated in many

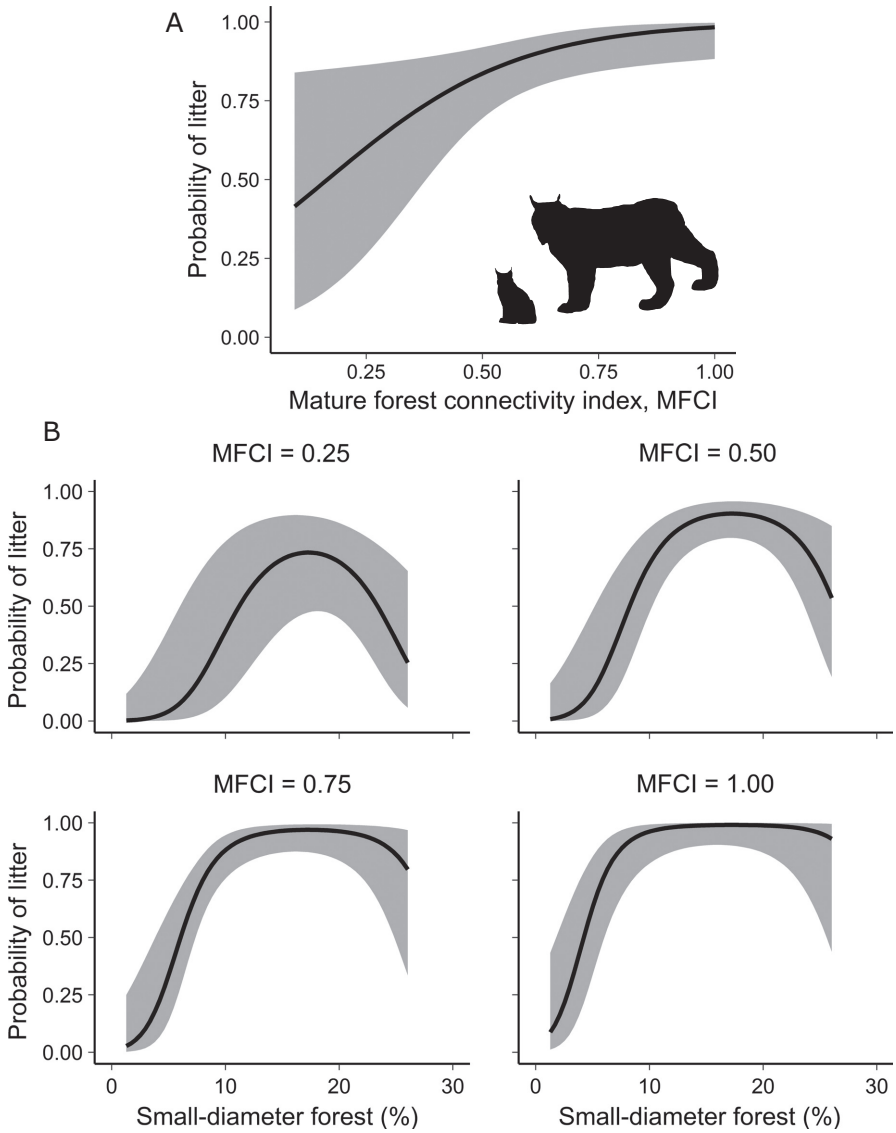


FIG. 6. Predicted relationship from our multivariate GLMM characterizing the marginal effect of connectivity of mature forest (A; mature forest connectivity index; MFCI) and small-diameter regenerating forest (B; percentage of small-diameter forest) on the probability of producing a litter for female Canada lynx (*Lynx canadensis*) in northwestern Montana, USA. We held small-diameter forest, medium-diameter forest, and maternal age at their mean values to generate panel A. We evaluated the effect of small-diameter forest across the gradient of mature forest connectivity (MFCI = 0.25–1.00) in panel B, while holding medium-diameter forest and maternal age at their mean values. Gray bands indicate the 90% CIs.

studies of Canada lynx from the northern portion of their geographic range (e.g., Brand et al. 1976, Brand and Keith 1979, Parker et al. 1983, Mowat et al. 1996, Slough and Mowat 1996, O'Donoghue et al. 1997, Reynolds et al. 2017). Second, despite observing a food limitation signature via forest structure, we did not identify a relationship between pre-pregnancy body condition and reproductive success in female lynx. Thus, our results are similar to Eurasian lynx, which were recently suggested to exhibit an income breeding strategy (Gaillard et al. 2014). Finally, in contrast to predictions of capital breeding, we observed no effect of reproductive effort in the previous year on pre-pregnancy body condition or reproductive success in the current year, nor did we observe an effect of forest structure on body condition. Indeed, our results support an income breeding strategy for Canada lynx on the range periphery as well as provide tangible habitat targets for land managers that are consistent with lynx reproduction (i.e., habitat–fitness relationships).

The reproductive success for female Canada lynx was largely associated with forest structure and configuration. Mature forest was the most dominant structural class within core areas and connectivity of mature forest was positively related to producing a litter. Mature forest with a dense understory supports abundant and accessible snowshoe hares for Canada lynx in the Rocky Mountains (Squires et al. 2010, Ivan et al. 2014, Ivan and Shenk 2016, Holbrook et al. 2017b), which are their primary prey source (Squires and Ruggiero 2007). We assume not all Canada lynx behavior affords fitness benefits, but coupling our

results with recent landscape-level analyses (e.g., Squires et al. 2013, Holbrook et al. 2017a) indicates that broad-scale selection of mature forest results in higher reproductive success of females. Previous studies have provided compelling evidence that prey resources influenced selection behavior (e.g., Hopcraft et al. 2005, Balme et al. 2007, Holbrook et al. 2017a) and reproductive success of carnivores (e.g., Mowat et al. 1996, Nilsen et al. 2012, Rauset et al. 2015, Walton et al. 2017). Our analyses suggest that mature forest in a connected configuration creates an energetically efficient context for Canada lynx to acquire snowshoe hares and successfully reproduce.

While mature forest was an important forest structure type for reproductive output, our findings also suggest small-diameter regenerating forest aids reproductive success of female lynx. This is similar to results from Franklin et al. (2000), who showed that, while mature forest was important for Spotted Owls (*Strix occidentalis*), some juxtaposition with early-seral forest was also beneficial. Small-diameter regenerating forest was generally sparse in core areas, but intermediate levels (e.g., ~12–20%; Fig. 6) positively influenced reproductive success of female lynx. Squires et al. (2010) demonstrated that resource selection by lynx broadens in the summer, with more use and selection for smaller-diameter stands. Forests in a small-diameter and regenerating structural stage can produce the highest densities of snowshoe hares (e.g., Cheng et al. 2015), particularly in the summer, but hares in these areas may be difficult to access for lynx because of high stem densities (Fuller et al. 2007, Ivan and Shenk 2016). Previous studies have indicated Canada lynx exhibit high hunting success in areas with dense horizontal cover (Squires et al. 2010), but that success can decrease at the highest stem densities (Ivan and Shenk 2016). However, having intermediate levels of small-diameter regenerating structural stages (i.e., higher stem densities) might provide additional snowshoe hares resources within an accessible context of mature forest (i.e., lower stem densities). Previous work on other felids (e.g., leopards and lions; *Panthera pardus* and *Panthera leo*) has also demonstrated the importance of prey accessibility relative to absolute abundance (Hopcraft et al. 2005, Balme et al. 2007). Alternatively, small-diameter regenerating forests might provide important habitat for alternative prey, such as Columbian ground squirrels (*Urocitellus columbianus*) or Ruffed Grouse (*Bonasa umbellus*), for lynx during the spring and summer months (but this remains unknown). If true, small-diameter regenerating forest might be particularly important immediately prior to parturition and during the kitten neonatal stage (i.e., spring and summer), and thus have substantial consequences on the physiology and behavior of an income breeder (e.g., Stephens et al. 2014). Additional work examining how variation in food resources during this narrow time period influences reproductive output for species such as Canada lynx would be a useful line of inquiry.

We also demonstrated a positive effect of maturation on female body condition and reproductive success (Table 3). Previous work has identified a positive relationship between age and the amount of fat in Canada lynx, and our results are consistent with those studies (e.g., Brand and Keith 1979, Parker et al. 1983). Older females also produced a litter more frequently than younger females, which was consistent with previous work on Canada lynx from northern populations (Mowat et al. 1996, Slough and Mowat 1996). This indicates that prime-aged females might be disproportionately contributing to population growth and therefore the survival of females to >3 yr old is likely important for long-term persistence of Canada lynx on the range periphery. In similar studies on Eurasian lynx, Nilsen et al. (2012) documented that older females produced litters more frequently than younger females, and Gaillard et al. (2014) demonstrated that experienced mothers tended to recruit more kittens. Indeed, many studies on long-lived, iteroparous mammals have highlighted the positive effects of prime-aged females on reproductive output (e.g., Côté and Festa-Bianchet 2001, Crocker et al. 2001, Hadley et al. 2007, Zedrosser et al. 2009, Monteith et al. 2014, Rauset et al. 2015).

The remainder of our analyses provided little support for maternal attributes influencing reproductive success, rejecting the capital breeding hypothesis. We found no evidence that pre-pregnancy body condition influenced reproductive success, despite body condition being positively related to age (Table 3, Fig. 5). Numerous studies have demonstrated that maternal body mass or condition is related to reproductive output in long-lived, iteroparous mammals (e.g., Atkinson and Ramsay 1995, Crocker et al. 2001, Monteith et al. 2014), but these organisms generally exhibit a capital breeding tactic (e.g., Jönsson 1997, Houston et al. 2006). Additional work evaluating effects of pre-pregnancy condition on reproductive output is needed, particularly for solitary mammalian carnivores that may exhibit income breeding (e.g., non-social Felidae spp.). Finally, we observed no detectable cost of reproductive effort at year $t - 1$ on reproductive performance at year $t$ in Canada lynx. Many studies have demonstrated the reproductive consequences of previous reproductive events in mammals (e.g., Koivula et al. 2003, Hamel et al. 2010, Monteith et al. 2013, 2014, Rauset et al. 2015). However, we were limited in our ability to detect the cumulative costs of reproduction because we could not fully characterize the total amount of maternal investment up to kitten independence. Therefore, it would be fruitful to evaluate the recruitment process to better evaluate the fitness consequences of reproduction in Canada lynx.

### *Generalizations on reproductive strategies*

We have demonstrated that Canada lynx on the southern periphery of their range exhibit a reproductive strategy consistent with an income breeder, which is largely driven by food resources mediated by forest structure. Theoretically, an income breeding strategy makes sense for lynx because there is a substantial cost of storing reserves for a solitary felid that is required to chase and capture elusive prey (i.e., snowshoe hares in this case; Houston et al. 2006). Moreover, recent work has identified flexibility in maternal care within leopards, whereby mothers invested more time into offspring rearing when prey abundance was low relative to when prey resources were abundant (Balme et al. 2017). Flexibility in maternal care is a "bet-hedging" strategy that may be pervasive in Felidae (as well as other solitary carnivores) to deal with environmental heterogeneity. If true, it would be difficult to execute this plasticity of care under a strict capital breeding tactic (Stephens et al. 2014), where only a fixed

amount of reserves can be stored leading up to parturition. For instance, a capital breeder might be forced to hedge their bets when resources are poor and discontinue care for offspring because of the risk associated with depleting capital that is important for survival and future reproduction (e.g., Monteith et al. 2014). Because income breeders are not reliant on stored capital for survival or future reproductive events, they might exhibit more plasticity in maternal care when conditions are poor (e.g., Balme et al. 2017).

Alternatively, the income breeding strategy we observed within Canada lynx may be reflective of a latitudinal gradient in food resources. For instance, snowshoe hares are acyclic across the southern periphery of the lynx's geographic range and generally occur at low densities relative to northern populations in the boreal forests of Canada (Aubry et al. 2000, Murray et al. 2008). Consequently, southern populations of Canada lynx might not experience the gradient in food resources necessary to implement a capital breeding strategy at snowshoe hare peaks. In other words, food resources are consistently low (relative to northern populations) and therefore lynx are unable to gather enough resources to acquire the capital necessary for the cost of late-gestation–early-lactation (Clutton-Brock et al. 1989). This might explain our seemingly narrow range in body condition and relatively invariant litter sizes (~2.5 kittens/litter). However, Canada lynx in the northern boreal forests may experience the snowshoe hare resources necessary to implement aspects of the capital breeding strategy, especially during peaks of the hare cycle, which might be associated with their larger litter sizes (e.g., up to 7 kittens/litter; Mowat et al. 1996). For example, Brand and Keith (1979) identified an increase in body fat indices of Canada lynx carcasses during the high phase of the snowshoe hare cycle, suggesting there may be some attempt to store capital. Moreover, Mainguy and Thomas (1985) indicated that northern populations of non-migratory Canada geese (*Branta canadensis*) had higher body fat percentages than their southern counterparts, suggesting a latitudinal gradient in food storage and perhaps reproductive strategies. Future work evaluating the relative reliance on capital vs. income to finance the cost of reproduction within Canada lynx across a latitudinal gradient might be particularly insightful for understanding the reproductive ecology of carnivores.

### *Conservation implications*

We report the first study linking individual reproductive success and forest characteristics for Canada lynx. We found substantial support for forest-dependent reproductive output for female lynx and older females tended to produce kittens more frequently. Based on our results, the highest quality core area for female lynx is provided within a habitat mosaic that includes (1) mature forest in a connected configuration and (2) intermediate amounts of small-diameter regenerating forest (e.g., F070 in Figs. 3 and 4). Importantly, the amount of small-diameter regenerating forests that is optimal for female lynx is dependent on the landscape context; that is, the optimal quantity broadens as mature forest becomes more connected (Fig. 6). However, despite the curvilinear relationship between litter production and small-diameter forests, the peak of the relationship does not reach a probability of 1 unless mature forest is well connected (Fig. 6). Thus, mature forest in a connected configuration is particularly important for core use areas of lynx, which aligns with landscape-level habitat selection exhibited by Canada lynx (Squires et al. 2013, Holbrook et al. 2017a).

Further, the spatiotemporal dimensions of mature and small-diameter forest structures are of central importance. For example, hypothetically, if the stage of small-diameter forest lasts for around 10 years after disturbance, and the mature forest stage takes at least 40 years to establish, managing for 20–30% small-diameter regenerating forest in isolation would facilitate a predominately young forest structure throughout the core area over a short time frame (e.g., within 40 years). Coupling this example with the spatial variation in forest structures from our most productive female (F070 in Fig. 3) highlights the spatiotemporal complexity of forest management in the context of Canada lynx habitat–fitness relationships. This does not preclude forest management activities and indeed F070 contained substantial amounts of historical manipulation and management in her home range (Fig. 3). Combining this collective understanding with general forest metrics (Appendix S2) should assist land managers in applying our results to on-the-ground decision making. Characterizing the intrinsic and extrinsic drivers of reproductive success for long-lived mammals is a difficult and onerous task (Gaillard et al. 2010), the benefits are great for both animal ecology and land management as demonstrated here for Canada lynx.

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## Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1707/full

## Data Availability

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pp06m3k