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Research Article

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Sex and age mediate the effects of rapid environmental change for a forest carnivore, the Fisher (*Pekania pennanti*)

Corbin C. Kuntze[1,*], M. Zachariah Peery[1], Rebecca E. Green[2,3], Kathryn L. Purcell[2], Jonathan N. Pauli[1],

[1]Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, United States
[2]USDA Forest Service, Pacific Southwest Research Station, 24075 Hwy 41, Coarsegold, CA 93710, United States
[3]National Park Service, Sequoia and Kings Canyon National Parks, 47050 Generals Highway, Three Rivers, CA 93271, United States

[*]Corresponding author: Department of Forest and Wildlife Ecology, University of Wisconsin, Madison, WI 53706, United States. Email: kuntze@wisc.edu
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Abstract

Rapid environmental changes—in climate, land use, and biotic interactions—are accelerating species extinctions and extirpations globally. Identifying drivers that threaten populations is essential for conservation yet can be difficult given the variable nature of the response of an organism to biotic and abiotic stressors. We analyzed a long-term monitoring data set to explore demographic responses of fishers (*Pekania pennanti*) to rapid environmental change in the southern Sierra Nevada, California, United States. Fisher survival was sensitive to both biotic and abiotic factors, although the strength and direction of these effects were ultimately mediated by age and sex. Specifically, male survival was lower among young individuals and decreased with increasing temperatures and fungi consumption. Female survival was resilient to age effects and diet but increased with greater forest heterogeneity and decreased with increasing temperatures and snow depth. Our findings suggest that continued climate change will likely have consequences for fishers through both incremental stressors and extreme weather events, but increasing forest heterogeneity may help to buffer against the impacts of such change. Further, we illustrate the importance of disentangling the effects of intrinsic and extrinsic factors on survival, especially among species with distinct sexual or ontogenetic differences. As global drivers of environmental change intensify in strength and frequency, understanding these complex relationships will allow practitioners to best manage for population persistence and habitat resilience concurrently.

Key words: carnivore conservation, environmental change, Fisher, forest management, sex differences, stable isotopes.

Rapid changes in climate are altering habitat conditions and biotic interactions to drive species extinct globally (Bellard et al. 2012). Understanding the proximate mechanisms underlying species responses to environmental change is essential for effective management (Bellard et al. 2012; Newbold 2018). However, identifying drivers that threaten individual species is difficult given the variable nature of exposure and sensitivity of an organism to changes in abiotic (e.g. temperature, precipitation) or biotic (e.g. vegetation cover, species interactions) conditions (Lenoir and Svenning 2015). Indeed, environmental stressors differ in space (Chen et al. 1999) and time (Trisos et al. 2020), while extreme weather events can trigger abrupt and unpredictable ecological responses (Harris et al. 2018). Multiple ecosystem stressors may have additive or even synergistic properties (Brook et al. 2008; Newbold 2018), and for populations that are genetically or geographically isolated, habitat loss, extreme weather, and decoupled trophic interactions may have unique consequences for persistence (Lenoir and Svenning 2015; Jones et al. 2018). Further confounding these relationships, organisms can exhibit great plasticity in morphology (Fox et al. 2019), physiology (Conradt et al. 2000), behavior (Chevin et al. 2010), and diet (Walsh and Tucker 2020), which can mediate adaptive capacity among conspecifics, especially in heterogeneous and changing environments (Chevin et al. 2010).

Intrinsic factors of the organism, such as sex and age, also facilitate different responses to environmental changes (Komoroske et al. 2014; Alonso et al. 2016). As an individual ages, ontogenetic differences in morphology and behavior can alter the strength and type of stressors encountered (Yang and Rudolf 2010; Komoroske et al. 2014). This is also true for sexually dimorphic species, for which differences in behavior and resource use (Barceló et al. 2022) can yield different responses to the same stressors (Fox et al. 2019). Thus, sex- or age-based differences may play a significant role in determining resilience to environmental change, with potential carry-over effects on population dynamics (Komoroske et al. 2014; Hangartner et al. 2022). However, quantifying effects of age, sex, and biotic interactions concurrently with broad,

regional-scale patterns in climate and habitat is logistically challenging and requires tracking of a large number of individuals over broad spatiotemporal scales. As a result, few studies have addressed differences in sensitivity and responses to rapid environmental change for species with apparent sexual or ontogenetic trait variation.

Between 2012 and 2015, the Sierra Nevada mountains, California, experienced the most extreme drought of the last 1,000 years (Crockett and Westerling 2018). This drought, in conjunction with an infestation of bark beetles, resulted in substantial forest mortality with up to hundreds of dead trees per square kilometer (Fettig et al. 2019). In contrast, even though average precipitation and annual snowpack have steadily decreased since the 1950s (Grundstein and Mote 2010), the region is also experiencing periods of extreme precipitation. Following the severe drought of 2012 to 2015, there was a record snowfall, with some areas receiving up to 186% of the statewide average (Hatchett et al. 2017). Such changes in climate and landscape composition will likely have numerous consequences for wildlife in the southern Sierra Nevada (Zielinski et al. 2013; Jones et al. 2018). For carnivores in particular, climate extremes and habitat loss can alter prey availability and mediate unique responses, including niche expansion and increasing dietary overlap among competing species (Manlick and Pauli 2020).

The Fisher (*Pekania pennanti*) is a mesocarnivore associated with dense, multilayered forests throughout North America (Zielinski et al. 2004), and occurs as a geographically and genetically isolated and federally endangered population in the southern Sierra Nevada (Tucker et al. 2012; USFWS 2020). Although fishers would have historically existed in a landscape with diverse topography and land cover (including natural openings and constrictions in forest cover), under current conditions there is concern that geographic barriers and habitat fragmentation may restrict connectivity and spatial recovery (Tucker et al. 2014; Thompson et al. 2021a), while mortalities from predation, disease, and anthropogenic threats including toxicants, incidental trapping, and vehicle collisions could limit population growth (Sweitzer et al. 2016a; Lewis et al. 2022). Fishers also possess relatively high foot loadings that can constrain movement in deep, uncompacted snow (Renard et al. 2008; Suffice et al. 2020), which exerts an energetic cost limiting occupancy and dispersal (Pauli et al. 2022). Fishers in this region have a complex history of dietary constraints; while fishers typically consume large-bodied Snowshoe Hare (*Lepus americanus*) and Porcupine (*Erethizon dorsatum*) across much of their distributional range (Kirby et al. 2018; Pauli et al. 2022), Fisher diet in the southern Sierra Nevada is primarily limited to small mammals (e.g. voles, mice, pocket gophers, tree and ground squirrels) and other forage such as reptiles, fungi, insects, and fruit (Zielinski et al. 1999). Recent work found that fishers in the southern Sierra Nevada exhibit a wide diversity of diet including nontrivial amounts of insects and especially fungi in addition to vertebrates (Smith et al. 2022). Increasing consumption of atypical or lower-calorie forage may affect the resilience of this endangered population to continued environmental change and has been suggested as a potential reason for reduced fecundity, recruitment, and juvenile survival rates relative to populations in the rest of their range (Green et al. 2018).

Sexual dimorphism among adult fishers—particularly within western populations—is striking, with males being up to 50% larger than females (Wengert et al. 2014). Male fishers also possess home ranges up to 3 times larger than females (Furnas et al. 2017; Kordosky et al. 2021). Differences in morphology, behavior, and energetic demands may present different risks for males and females. For example, while the predominant predator of fishers in this region are mountain lions (*Puma concolor*), females are also killed by smaller mammalian carnivores including bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), likely a result of their reduced body size (Wengert et al. 2014). Alternatively, mortality risk from disease, starvation, toxicants, and vehicle strikes is higher for males (Sweitzer et al. 2016a). Therefore, males typically exhibit lower survival rates than females across their distributional range (Sweitzer et al. 2016b; Lewis et al. 2022). Survival may also vary by age (Sweitzer et al. 2016b)—fishers disperse from natal areas before they reach sexual maturity (Matthews et al. 2013), and dispersal can have unique consequences for individual fitness. Younger carnivores typically have lower survival rates than adults (Farias et al. 2005; Manlick et al. 2017), although our knowledge of ontogenetic variation in responses to individual stressors remains limited (Sweitzer et al. 2015). Given the unique biotic and abiotic factors that threaten Fisher persistence in the southern Sierra Nevada, coupled with the potential for age- and sex-specific responses, it is important to consider both intrinsic and extrinsic factors when determining resilience to environmental stressors.

Herein, we explored whether age and sex mediate the demographic responses of fishers to rapid environmental change. We combined stable isotope analysis of diet with high-resolution climate and habitat data, along with spatial information collected from Fisher monitoring, to evaluate the proximate mechanisms driving spatiotemporal variation in Fisher survival. We hypothesized that the effects of environmental change—along both biotic and abiotic axes—affect Fisher persistence in the southern Sierra Nevada, but that the relative strength and direction of stressors are mediated by sex and age. First, we predicted that individuals within territories containing more features typical of Fisher habitat (i.e. dense, multilayered, late-successional forest) would exhibit high survival (Suffice et al. 2020). Second, we predicted that survival would decrease with increasing drought severity and forest mortality. We also predicted that survival would decrease with increasing snow depth (Suffice et al. 2020; Pauli et al. 2022), and that this effect would be stronger for males as larger body size, home range, and foot loading impose greater energetic costs (Renard et al. 2008). Finally, we predicted that increasing consumption of atypical foods, especially the consumption of fungi, would decrease survival for both males and females (Green et al. 2018; Kirby et al. 2018).

Materials and methods

Study system.

This study was conducted as part of ongoing research with the Kings River Fisher Project (KRFP) by the U.S. Forest Service, Pacific Southwest Research Station (PSW). The study area was located on the western slope of the southern Sierra Nevada, California, and encompassed roughly 435 km^2 of the Sierra National Forest (Fig. 1). The climate features warm, dry summers and cool, wet winters and the region is topographically complex, marked by steep slopes and river canyons. Most fieldwork occurred within elevation ranges of 915 to 2,385 m, within the primary range of Fisher occurrence in the area (Zielinski et al. 2004; Green et al. 2018). Here, mosaics of mixed pine, mixed fir, and montane hardwood forests are interspersed with pockets of chaparral, grasslands, and rocky outcrops throughout (Fites-Kaufman et al. 2007).

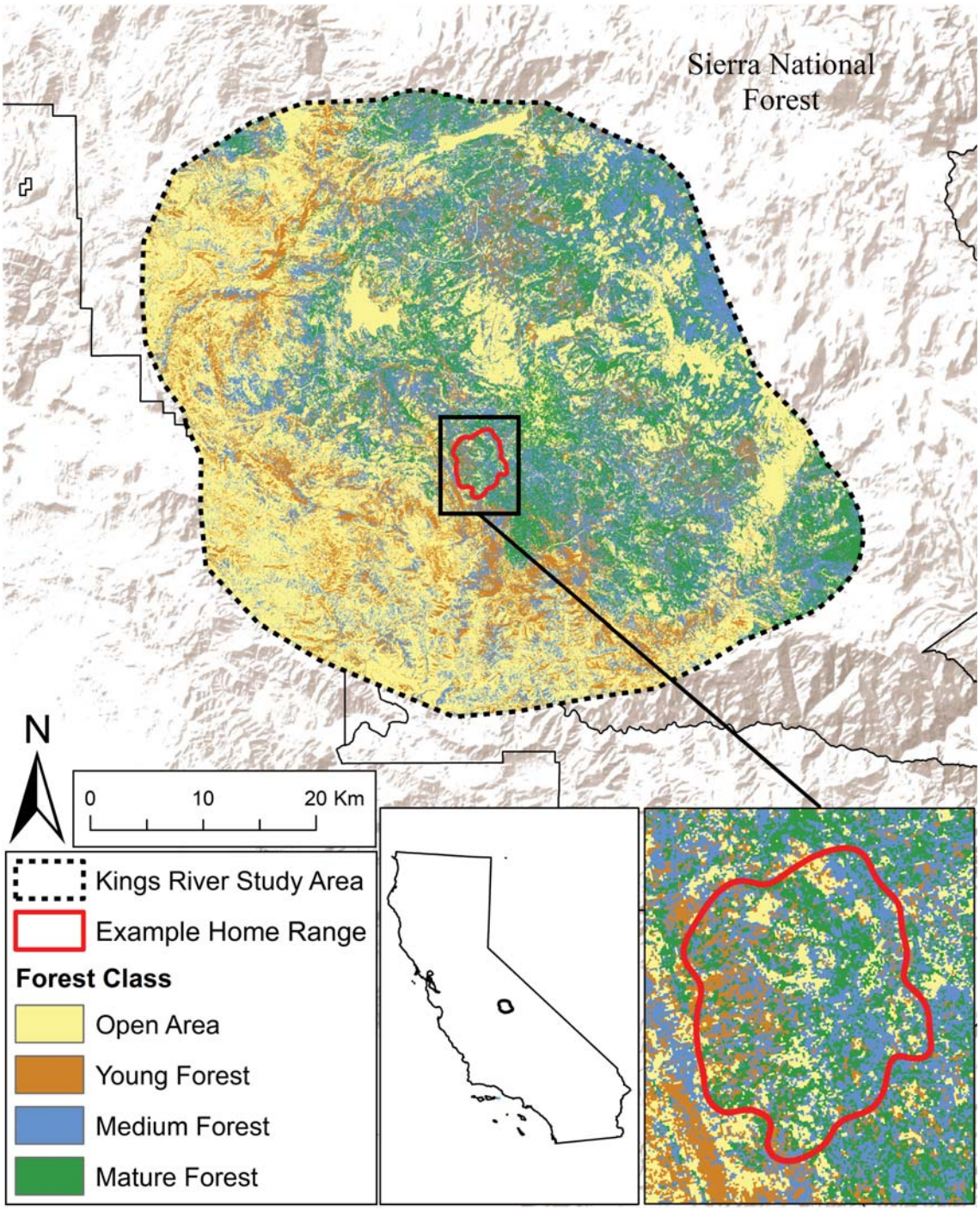

Fig. 1. Kings River Fisher Project study area visualized with forest class variables in the southern Sierra Nevada, California, United States, for monitoring Fisher (Pekania pennanti) diet and survival between 2007 and 2019. The inset map demonstrates an example of a typical 95% kernel home range for 1 female Fisher with a red outline.

Field methods.

For monitoring and sample collection, we trapped, handled, and collared fishers following established KRFP protocols (outlined in Green et al. 2018). We captured fishers in baited steel mesh traps (model 108; Tomahawk Live Trap Company, Hazelhurst, Wisconsin) outfitted with wooden cubbies. Trapping occurred primarily during fall and winter; we checked traps each morning and replenished bait when necessary. At capture, fishers were sedated with ketamine (22.5 mg/kg) mixed with Diazepam or Midazolam (0.125 mg/kg). We classified individuals by sex and age based on examination of genitalia, molar cusps, definition of sagittal crest—and for females, state of teats to provide evidence of breeding (Sweitzer et al. 2016b; Green et al. 2018). New individuals were marked with passive integrated transponder tags (Biomark, Boise, Idaho). During processing, we collected hair samples from both nape and tail. We fit fishers with VHF collars (Holohil model MI-2M, 31 g; Holohil Systems Ltd, Carp, Ontario, Canada, or Advanced Telemetry Systems model 1920, 38 g, ATS, Inc., Insanti,

Minnesota) or GPS collars (Lotek model LiteTrack 40, 45 g or model LiteTrack 60, 63 g; Lotek Wireless Inc., Newmarket, Ontario, Canada; Thompson et al. 2012). All collars were equipped with handmade breakaway devices to allow for growth and to avoid injuries. Captures were done under a combination of authorizations and permits over the years including California Department of Fish and Wildlife (Permit SC-2730), using techniques approved by the Institutional Animal Care and Use Committee of the University of California, Davis (IACUC #18022), and following guidelines of the American Society of Mammalogists (Sikes et al. 2016).

We initiated monitoring on the week of 3 June 2007, and recorded status (alive, dead, missing, or dropped collar) of all radio-collared fishers. Status was recorded from the first capture to either death, disappearance (collar drop or failure), or the end of the study (7 March 2020). We typically triangulated collared fishers 1 to 3 times per week by ground or air. Fishers that were missing or whose status was not recorded for >2 consecutive weeks were right-censored in our encounter histories. If these individuals were recaptured or regular monitoring was continued, they were added back to the data set from that point. We censored 39 individuals from our data set that were not recaptured; it is common for fishers to avoid detection for extended periods of time, and our approach follows previous studies (Sweitzer et al. 2016a; Lewis et al. 2022).

Quantifying environmental covariates.

We incorporated a set of spatially and temporally explicit environmental covariates classified into 3 subgroups: forest structure; landscape composition; and climate (Table 1; Supplementary Data SD1 to SD3). To calculate these, we first created 95% kernel density estimates of annual home ranges for individuals with a minimum of 16 relocations (158 individuals) obtained from captures, telemetry locations, and GPS fixes collected during our population year starting 1 June and ending 31 May the following year (Börger et al. 2006; Pauli and Peery 2012). After filtering out locations with suspect accuracy (i.e. for GPS relocations a Horizontal Dilution of Precision [HDOP] threshold of 10; for telemetry relocations a minimum of 3 bearings at least 20 degrees apart from each other), we generated these using the R package "adehabitatHR" (Calenge and Fortmann-Roe 2013). For individuals with <16 relocations (18 individuals), we buffered an area equal to the median adult activity area (46.08 km^2 males; 17.95 km^2 females) around the centroid of recorded locations of that individual from that year. We then extracted all environmental variables from these home ranges relative to the population year.

For climate, we used PRISM data to estimate monthly values for mean precipitation, as well as monthly and annual values for maximum and minimum temperature, averaged within individual annual home ranges (PRISM Climate Group; Oregon State University). We estimated mean and maximum land surface temperature in Fisher home ranges during summer (21 June to 21 September) at 30 m resolution (Ermida et al. 2020). We included values of mean and average maximum snow depth at 1 km resolution from 1 November until 30 April of the following year, obtained from the Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center) and calculated mean snow depth averaged over yearly (1 November to 30 April) and monthly timescales. Finally, we quantified annual and monthly drought conditions using the Palmer Drought Severity Index (PDSI; Palmer 1965; Mukherjee et al. 2018). For habitat, we included hardwood basal area, canopy cover, understory cover, and covariates of forest age class (open, young, medium, and mature) estimated within yearly Fisher home ranges from gradient-nearest-neighbor maps (LEMMA Lab; Oregon State University, Corvallis, Oregon). We also quantified yearly drought-mediated tree mortality from 2015 to 2018 from the Southern Sierra Nevada Fractional Land Cover Dataset (McGregor et al. 2021). For landscape composition, we included tree diameter diversity index and calculated forest heterogeneity (Shannon's Diversity Index [SHDI]) and patch adjacency (Interspersion and Juxtaposition Index) of our forest age classes, as well as dispersion (standard deviation) and disorderliness (entropy) of image texture pixel values from Enhanced Vegetation Index composites. For additional information on data sources and covariates, see Supplementary Data SD4.

Diet analysis.

To quantify Fisher diet, we analyzed samples for $\delta^{13}C$ and $\delta^{15}N$ ratios via stable isotope analysis following established protocols (outlined in Pauli et al. 2009 and Smith et al. 2022). We used Bayesian mixing models to quantify population- and individual-scale proportional diet of fishers in program MixSIAR (Stock et al. 2018). To represent source items in our mixing models, we used samples collected and analyzed during a previous study in the southern Sierra Nevada (Smith et al. 2022), then divided functionally similar dietary source items into 4 a priori categories (plants, fungi, insects, and vertebrates) and verified isotopic independence of these groups using a *K*-nearest-neighbor analysis (Rosing et al. 1998). We accounted for digestibility and elemental concentration for each source item (Smith et al. 2022), and addressed trophic discrimination by correcting for the digestibility of carbon and nitrogen by forage items ($\delta^{13}C \pm SD = 2.6‰ \pm 0.09$; $\delta^{15}N \pm SD = 3.4‰ \pm 1.2$; Supplementary Data SD5; Smith et al. 2022).

To evaluate individual diet, we ran a set of MixSIAR models with our 4 dietary source categories and an individual-year variable as a fixed factor. For each model, we used informative priors derived from a previous diet study that spatially overlapped with our study area (Smith et al. 2022; fungi 0.47, vertebrates 0.13, plants 0.16, insects 0.24) and ran 3 Markov chains (length = 1,000,000; burn-in = 500,000; thinning rate = 500). We also ran a second model set with uninformative priors (uniform across all source groups) to compare the influence of our priors on our dietary estimates. We confirmed model convergence by checking that Gelman–Rubin diagnostic values were <1.05 and <5% of Geweke diagnostics were outside ± 1.96 for each chain. We also calculated measures of individual specialization (Newsome et al. 2012)—the specialization index (ε) represents how much a consumer concentrates on a specific diet category, relative to the number of other diet items. Hair samples capture the period of isotopic incorporation during molting and hair growth (June–October; Pauli et al. 2009). Therefore, our estimates best represent the assimilated diet of fishers in our study area from summer through fall.

Survival analysis.

We estimated survival rates of fishers by constructing known-fate models in Program MARK (White and Burnham 1999), with a staggered entry design to allow introduction of individuals throughout the study. We used encounter histories from 3 June 2007 until 7 March 2020 and defined our population year from 1 June to 31 May the following year. We set 1 June as the start date to best align with the beginning of isotopic incorporation captured by Fisher hair growth (Pauli et al. 2009).

We analyzed 2 sets of models to explore interactions between demographic and environmental covariates. First, we constructed

Table 1. Covariates included in known-fate models to quantify changes in survival for fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, United States.

Category	Variable	Ecological description
Forest structure	Young forest	Proportion of home range with forest Quadratic Mean Diameter (QMD) < 30 cm and canopy cover > 40%
	Medium forest	Proportion of home range with forest with QMD 30 to 61 cm and canopy cover > 40%
	Mature forest	Proportion of home range with forest with QMD > 61 cm and canopy cover > 40%
	Open area	Proportion of home range with canopy cover < 40%
	Hardwood basal area	Mean basal area of hardwoods (m^2/ha)
	Understory cover	Percent of understory cover (between 2 and 4 m)
	Canopy cover	Percent of canopy cover
	Mean tree mortality	Percent of tree mortality within home range, averaged across 30 m pixels
Landscape composition	Interspersion and Juxtaposition Index	Evenness of patch adjacencies—represents intermixing of the 4 forest types (young, medium, mature, open)
	Forest heterogeneity	Shannon's Diversity Index calculated from the 4 forest types
	Entropy	Disorderliness in spatial distribution of image texture pixels from Enhanced Vegetation Index (EVI) data
	Standard deviation	Dispersion of image texture pixels from EVI data
	Diameter diversity index	Measure of forest structural diversity based on densities of different tree size classes. Increases with stand age
Climate—annual	Mean snow depth	Average snow depth in the winter (1 November to 30 April)
	Maximum snow depth	Maximum snow depth in the winter, averaged across all pixels at 1 km resolution
	Drought	Average yearly Palmer Drought Severity Index (PDSI) value at 4 km resolution
	Land surface temperature	Mean and maximum summer (21 June to 21 September) land surface temperature in Kelvin (K) at 30 m resolution
Climate—monthly	Minimum temperature	Average monthly minimum temperature, averaged across all pixels at 30 m resolution
	Maximum temperature	Average monthly maximum temperature, averaged across all pixels at 30 m resolution
	Snow depth	Average monthly snow depth, averaged across all pixels at 1 km resolution
	Drought	Average monthly PDSI value at 4 km resolution
	Precipitation	Average monthly precipitation, averaged across all pixels at 30 m resolution
Demography	Sex	Sex of individual. Two groups: male and female
	Age—A	Age class of individual. Three groups: juvenile (<12 months), subadult (12 to 24 months), adult (≥24 months)
	Age—B	Age class of individual. Two groups: young (<24 months), adult (≥24 months)
Diet	Fungi	Estimated dietary contribution from fungi (%)
	Specialization index	The degree to which an individual concentrates on a functional prey group

candidate models for all individuals including only demographic and seasonal effects. Here, we introduced covariates for sex, season (summer [1 May to 31 October]; winter [1 November to 30 April]), and age class with either 2 (young [<24 months]; adult [≥24 months]) or 3 (juvenile [<12 months]; subadult [12 to 24 months]; adult [≥24 months]) groups. We used the structure from the top model(s) in our first set (Table 2) to inform construction of our second model set. We derived estimates of monthly survival from our top-performing models and projected rates of annual survival relative to age and sex and 6-month survival relative to season.

We employed a secondary candidate set strategy (Morin et al. 2020) and constructed separate univariate model sets for males and females to compare covariates grouped within our environmental and diet subgroups (Table 1). We ranked models using Akaike Information Criterion adjusted for small sample sizes (AIC_c) and carried forward any covariate that outperformed the null and was within 2 ΔAIC_c of the top model (White and

Table 2. Top models (≤2 ΔAIC_C) for the first model stage of Fisher (*Pekania pennanti*) survival between 2007 and 2019 in the southern Sierra Nevada, California, United States. Information includes model covariates, ranked by AIC_C (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAIC_C (difference in AIC_C between a model and the top-ranked model), *w* (model weight), and *k* (number of parameters). Predictor variables shown include sex, age class (young [<24 months]; adult [≥24 months]), and season (summer [1 May to 31 October]; winter [1 November to 30 April]).

Covariate(s)	AIC_C	ΔAIC_C	*w*	*k*
Sex × Season + Sex × Age	795.93	0	0.30	6
Sex × Season	796.16	0.22	0.27	4
Sex × Season + Age	797.73	1.79	0.12	5
Sex × Season + Age × Season	797.75	1.82	0.12	6
Null	802.30	6.36	0.01	1

Burnham 1999; Morin et al. 2020). We considered other viable covariates (i.e. 95% confidence intervals [CIs] of coefficient estimates did not cross zero) if they were within 5 ΔAIC_C of the top model and were not correlated with other competitive variables. Given differences in morphology, life history events, and survival of fishers as a function of age, sex, and season (Wengert et al. 2014; Sweitzer et al. 2016b; Green et al. 2018), we also tested each univariate covariate with additive effects of age class and season. If the age- or season-additive form of a covariate outperformed the null model, the univariate form, and the univariate age or season model, it was also carried forward into the next stage of model construction. We also evaluated season interactions for several climate covariates and carried these forward if they were competitive.

With the top-ranking covariates from the univariate subgroups, we then constructed a set of a priori multivariate models for both males and females. We tested independent variables for collinearity using Spearman's rank coefficient and did not include highly correlated covariates ($r_s \geq |0.7|$) in the same model (Dormann et al. 2012). To evaluate temporal trends and effects, we modeled survival as either constant (.) or varying by categorical year (*t*), while the relative effect of our time-varying covariates was kept constant. Coefficients from our top-ranking and competitive models in both sets were examined and statistical significance was determined from 95% CIs.

Results

Between 3 June 2007 and 7 March 2020, we collared and tracked 170 fishers (91 females; 79 males). We compiled a total of 3,616 monthly monitoring records (2,262 females; 1,354 males). The number of monitoring months per individual ranged from 1 to 114 (females 1 to 114; males 2 to 67). We confirmed 84 mortalities over the course of our study (47 females; 37 males). Individual consumption of fungi, insects, and vertebrates was relatively equal across the population, with low overall consumption of plants (Supplementary Data SD6) and with moderate variability between and among years (Supplementary Data SD7).

Demographic and seasonal drivers of Fisher survival.

Fisher survival was associated with sex, age class, and season. The most supported model included an interaction between sex and age class, as well as an interaction between sex and season (Table 2). As we found more support for the age class covariate with 2 groups, we did not carry the age class covariate with 3 groups forward in the second stage of model construction. Yearly female survival ($\hat{s}$ = 0.781; 95% CI [0.720, 0.831]) was greater than male survival ($\hat{s}$ = 0.717; 95% CI [0.632, 0.786]), and this difference was greater when comparing survival of young females ($\hat{s}$ = 0.832; 95% CI [0.7173, 0.903]) and males ($\hat{s}$ = 0.643; 95% CI [0.521, 0.741]) to adult females ($\hat{s}$ = 0.759; 95% CI [0.683, 0.820]) and males ($\hat{s}$ = 0.803; 95% CI [0.680, 0.883]; Fig. 2A). Seasonal trends also differed by sex (Table 2). For females, seasonal (6-month) survival during the summer ($\hat{s}$ = 0.842; 95% CI [0.784, 0.886]) was lower than winter survival ($\hat{s}$ = 0.923; 95% CI [0.878, 0.952]), but for males, summer survival ($\hat{s}$ = 0.897; 95% CI [0.822, 0.942]) was greater than winter survival ($\hat{s}$ = 0.807; 95% CI [0.731, 0.865]; Fig. 2B).

Extrinsic drivers of Fisher survival.

The top model for female survival included the effects of maximum monthly temperature, mean winter snow depth, and SHDI of forest cover types (Table 3). Survival increased with greater forest heterogeneity (β = 2.08; 95% CI [0.06, 4.11]; Fig. 3A). For climate, survival decreased with increasing mean winter snow depth (β = –0.004; 95% CI [–0.005, –0.002]; Fig. 3B), as well as increasing minimum monthly temperature (β = –0.06; 95% CI [–0.11, –0.02]; Fig. 3C) and maximum monthly temperature (β = –0.05; 95% CI [–0.09, –0.02]; Fig. 3D). While understory cover (β = –0.03; 95% CI [–0.17, 0.10]) and canopy cover (β = –0.02; 95% CI [–0.07, 0.03]) were represented among competitive models, they did not affect survival.

The top model for male survival included the effect of season, age class, minimum monthly temperature, and the consumption of fungi (Table 4). Interestingly, survival decreased with increasing individual consumption of fungi (β = –0.15; 95% CI [–0.29, –0.01]; Fig. 4A). For climate, survival decreased with increasing minimum monthly temperature (β = –0.10; 95% CI [–0.19, –0.02]; Fig. 4C) but not maximum monthly temperature (β = –0.05; 95% CI [–0.14, 0.04]). However, when paired with a season interaction, survival decreased with increasing maximum monthly temperature in winter (β = –0.13; 95% CI [–0.25, –0.004]; Fig. 4D) but not in summer (β = –0.001; 95% CI [–0.12, 0.12]; Fig. 4D). Other variables from competitive models, including mean forest mortality (β = 0.04; 95% CI [–0.002, 0.09]), mean basal area of hardwoods (β = –0.17; 95% CI [–0.35, –0.001]), young forest (β = –0.91; 95% CI [–5.72, 3.91]), and PDSI (β = 0.047; 95% CI [–0.09, 0.18]), did not affect survival.

Discussion

Our work reveals that environmental factors associated with climate, habitat, and biotic interactions were important drivers of survival, but the direction and magnitude of individual responses were mediated by age and sex. Survival of male fishers was lower among young individuals and sensitive to changes in biotic and abiotic factors related to temperature and diet. Female fishers were vulnerable to changes in temperature, snow depth, and landscape composition, yet more resilient to diet and age effects. Our study adds to a growing body of literature emphasizing the importance of considering age and sex when assessing the impacts of environmental change (Yang and Rudolf 2010; Komoroske et al. 2014; Hangartner et al. 2022).

Temperature was a key determinant of Fisher survival, and the only covariate to affect both sexes. Survival of females decreased with both increasing minimum and maximum monthly temperature, while male survival decreased with increasing minimum

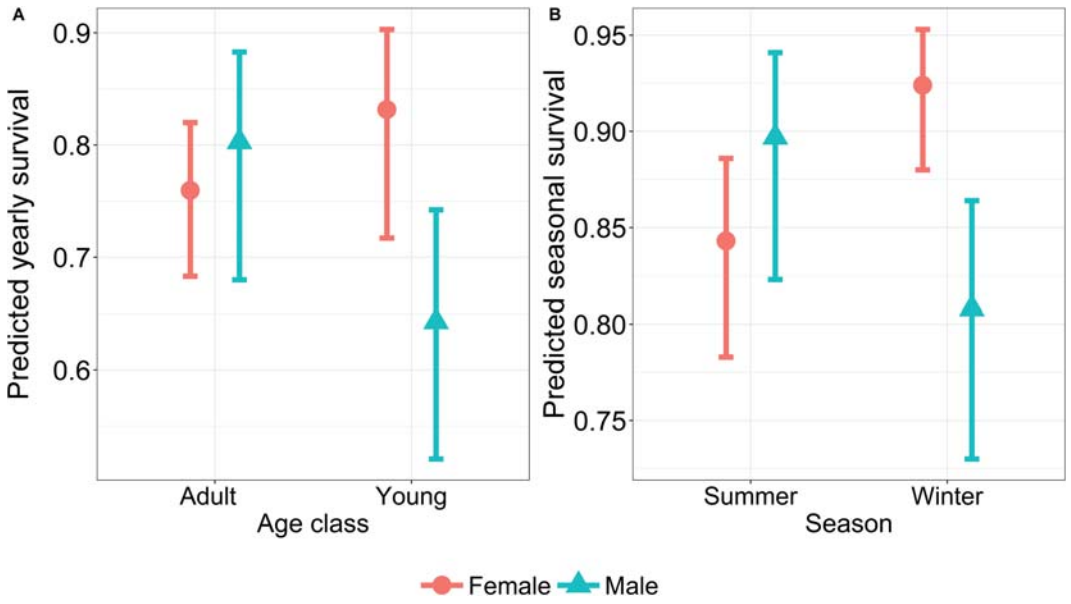

Fig. 2. Estimated survival rates (±95% CI) for male and female fishers (Pekania pennanti) between 2007 and 2019 in the southern Sierra Nevada, California, United States. Survival is shown relative to (A) age class (young [<24 months], adult [≥24 months]); and (B) season (summer [1 May to 31 October], winter [1 November to 30 April]). Survival rates were transformed from monthly model-derived estimates into (A) yearly and (B) seasonal 6-month rates.

Table 3. Top models (≤2 ΔAIC_c) for female Fisher (*Pekania pennanti*) survival between 2007 and 2019 in the southern Sierra Nevada, California, United States. Information includes model covariates, ranked by AIC_c (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAIC_c (difference in AIC_c between a model and the top-ranked model), w (model weight), and k (number of parameters). Predictor variables shown include max monthly temp (maximum monthly temperature), snow depth (mean winter snow depth), SHDI (forest heterogeneity, estimated with Shannon's Diversity Index of forest cover types), understory (mean understory cover), min monthly temp (minimum monthly temperature), and canopy (mean canopy cover).

Covariate(s)	AIC_c	ΔAIC_c	w	k
Max monthly temp + Snow depth + SHDI	448.21	0	0.20	4
Max monthly temp + Snow depth	449.39	1.17	0.11	3
Max monthly temp + Snow depth + SHDI + Understory	449.73	1.51	0.09	5
Min monthly temp + Snow depth + SHDI	449.98	1.77	0.08	4
Season + Max monthly temp + Snow depth + SHDI	450.22	2.01	0.07	5
Max monthly temp + Snow depth + SHDI + Canopy cover	450.221	2.011	0.07	5
Null	461.11	12.90	0	1

monthly temperature and maximum monthly winter temperature. During hot, dry periods, increasing temperatures compound the effects of heat stress and water loss (Alonso et al. 2016). Conversely, during cold winter months increasing temperatures should, in theory, benefit fishers by expediting snow melt (Grundstein and Mote 2010), and reducing energetic costs associated with locomotion and thermoregulation (Martin et al. 2020). However, increasing winter temperatures can also constrain availability of key prey. For example, fishers may change their diet in response to resource availability (Zielinski et al. 1999; Kirby et al. 2018), and mammal consumption typically peaks in winter when many other food groups are unavailable (Zielinski et al. 1999). For snow-adapted small mammals, winter conditions drive population cycles (Scott et al. 2022) and warmer ambient temperatures can reduce the insulating properties of the subnivium (Thompson et al. 2021b), with cascading effects for abundance and diversity (Scott et al. 2022). In turn, declines in seasonal prey resources resulting from warming winter temperatures can have consequences for Fisher persistence.

While decreasing annual snowpack may negatively impact Fisher survival via prey abundance, so too can events of extreme precipitation, which are likely to increase in frequency and severity with climate change (Hatchett et al. 2017; Harris et al. 2018). Snow can exert variable effects on organisms, mediated by physical characteristics such as depth, density, and surface hardness (Pozzanghera et al. 2016; Pauli et al. 2022). Indeed, while modest snowfall at regular intervals typically creates dense compacted snow, periods of heavy snowfall can create areas of deep, fluffy snow that limit occupancy and dispersal of many carnivore species (Pozzanghera et al. 2016). Among fishers, high foot loading is theorized to compound the energetic cost of movement through deep snow (Pauli et al. 2022), and male fishers exhibit a foot load up to 43% greater than females (Renard et al. 2008). However, while increasing snow depth had a negative effect on female survival, male survival was unaffected—which ran counter to our predictions. This suggests that morphology alone does not explain the relationship between snow and survival, and life history may also mediate differential demographic responses. It

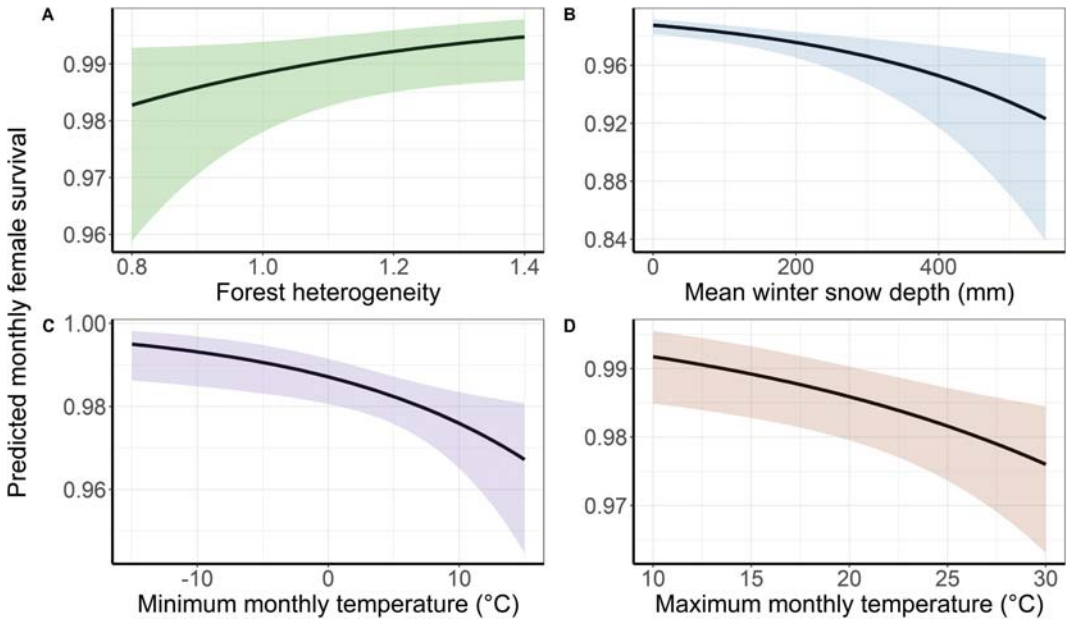

Fig. 3. Fitted values (±95% CI) representing monthly survival of female fishers (Pekania pennanti) between 2007 and 2019 in the southern Sierra Nevada, California, United States. Survival is shown relative to (A) forest heterogeneity, estimated with Shannon's Diversity Index (SHDI) of forest cover types, (B) mean winter snow depth, (C) maximum, and (D) minimum monthly temperature (°C). Values were derived from the top-ranked model for each covariate, with additional variables held constant at mean observed values.

Table 4. Top models (≤2 ΔAIC_c) for male Fisher (*Pekania pennanti*) survival between 2007 and 2019 in the southern Sierra Nevada, California, United States. Information includes model covariates, ranked by AIC_c (Akaike's Information Criterion adjusted for small sample size), and compared by ΔAIC_c (difference in AIC_c between a model and the top-ranked model), *w* (model weight), and *k* (number of parameters). Predictor variables shown include season, min monthly temp (minimum monthly temperature), age (age class), fungi (proportional consumption of fungi), tree mortality (proportion of tree mortality), PDSI (drought conditions), hardwoods (mean hardwood basal area), and young (proportion of young forest).

Covariate(s)	AIC_c	ΔAIC_c	*w*	*k*
Season + Age + Min monthly temp + Fungi	333.208	0	0.14	5
Season + Age + Min monthly temp + Tree mortality	333.210	0.002	0.13	5
Season + Age + Min monthly temp + Fungi + Hardwoods	334.46	1.25	0.07	6
Season + Age + Min monthly temp + Fungi + PDSI	334.74	1.53	0.06	6
Season + Age + Min monthly temp + Fungi + Tree mortality + Hardwoods	334.79	1.58	0.06	7
Season + Age + Fungi + Hardwoods	334.82	1.61	0.06	5
Season + Fungi + Hardwoods	334.87	1.67	0.06	4
Season + Age + Min monthly temp + Fungi + Tree mortality + Young	335.05	1.84	0.05	7
Age + Fungi + Hardwoods	335.24	2.03	0.05	4
Null	341.38	8.17	0	1

is possible that increased energy expenditure caused by higher foot loading could be offset by energy intake if males are able to forage on a food resource that females cannot, or that differences in body condition allow males to better survive these extreme weather events (Ross et al. 2021). Parturition among female fishers typically occurs in late winter or early spring (Green et al. 2018), coinciding with periods of high snow accumulation. The energetic demands of reproduction, lactation, and foraging for dependent offspring may expose females to increased risk (Powell and Leonard 1983; Green et al. 2018), and this has been corroborated by findings of reduced female survival from spring through summer (Sweitzer et al. 2016b). Therefore, even if movement through snow incurs a greater energetic cost for males, the ultimate impact may be stronger for females by compounding the effects of existing stressors. A baseline level of snow can benefit Fisher survival by increasing seasonal prey abundance (Scott et al. 2022) or reducing encounters with larger intraguild predators (Jensen and Humphries 2019), but during periods of extreme precipitation or reproductive stress, the net effect appears to be negative. Further, increasing winter temperatures may amplify the demographic consequences of deep snow by mediating the physical characteristics of snowpack. Specifically, by preventing the formation of an ice crust on snow surface, locomotion may be increasingly costly for fishers forced to move through deep, soft snow (Suffice et al. 2020; Pauli et al. 2022).We found that female survival increased with forest heterogeneity, highlighting the importance of both landscape composition and configuration. Heterogeneous landscapes increase niche availability (MacArthur 1972), which can promote prey diversity (Walsh and Tucker 2020) or facilitate carnivore coexistence (Manlick et al.

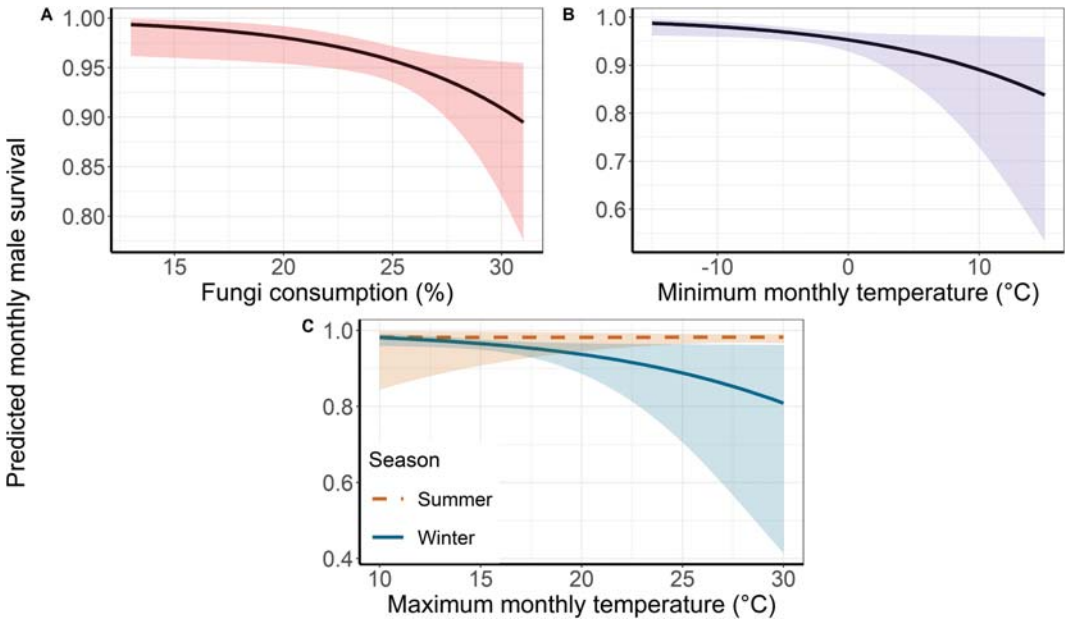

Fig. 4. Fitted values (±95% CI) representing monthly survival of male fishers (Pekania pennanti) between 2007 and 2019 in the southern Sierra Nevada, California, United States. Survival is shown relative to (A) dietary contribution of fungi (%), (B) minimum monthly temperature (°C), and (C) maximum monthly temperature (°C) with a season interaction during summer and winter. Values were derived from the top-ranked model for each covariate, with additional variables held constant at mean observed values.

2020). In the southern Sierra Nevada, Sweitzer et al. (2016a) found that intraguild predation accounted for 67% of Fisher mortalities, and anthropogenic change in forest structure driving increased interspecific contact may be responsible for high predation rates (Wengert et al. 2014). Intraguild predation generally decreases in habitats with greater structural complexity (Janssen et al. 2007), while female fishers are vulnerable to a more diverse predator guild (Wengert et al. 2014)—which may help explain the relationship between survival and forest heterogeneity unique to females. Heterogeneity also increases the availability of microclimatic refugia (Chen et al. 1999), which can dampen the effects of inclement or extreme weather (Latimer and Zuckerberg 2021). As both female and male fishers use a variety of habitat microsites as refugia throughout the year (e.g. tree cavities, hollows in logs; Green et al. 2019), habitat heterogeneity may help to buffer from the effects of both biotic and abiotic stressors.

Male fishers that consumed more fungi exhibited lower survival. In contrast, female survival was unaffected by diet. Mesopredators exhibit considerable dietary plasticity, both locally and across their distributional ranges (Manlick and Pauli 2020; Walsh and Tucker 2020), which is cited as a driver of resilience and contemporary range expansions (Prugh et al. 2009). However, reliance on atypical resources can incur fitness consequences, and among predators increasing consumption of low-quality forage has been linked to changes in space use (Hobart et al. 2019) and reproduction (Chevallier et al. 2020), although linking individual diet to survival is difficult for mesopredators given their ability to occupy multiple trophic levels (Prugh et al. 2009; Colborn et al. 2020). Diet limitations among fishers in the southern Sierra Nevada may explain small litter sizes (Green et al. 2018), and elsewhere reductions in preferred prey have been identified as a potential driver of poor body condition and population decline (Kirby et al. 2018). A modest level of fungi consumption may benefit Fisher persistence by providing nutrients and water during food shortages or periods of protracted drought (Claridge and May 1994; Smith et al. 2022). However, fishers have a relatively simple gut morphology (McGrosky et al. 2016), and in the absence of specialized digestive pathways or microbial communities, their digestive efficiency of fungi may be limited by enzymatic reactions (Claridge and May 1994). We found no differences in proportional diet between males and females, which corroborates prior findings (Kirby et al. 2018; Smith et al. 2022). Still, morphology, territory size, and life history strategies such as dispersal (Matthews et al. 2013) may drive increased energy expenditure and caloric requirements among male fishers—which was reported for closely related male Pacific martens (*Martes caurina*; Martin et al. 2020). Therefore, the risk of gut satiation, energetic deficiency, and associated demographic consequences may be greater for males consuming more fungi. Notably, our estimates of diet best reflect trends from summer and fall, which does not align with parturition or weaning among females (Green et al. 2018) or mate searching among males (Matthews et al. 2013). Given the potential for temporal changes in energy expenditure and food availability (Zielinski et al. 1999; Scott et al. 2022), we also recommend that future work quantify seasonal changes in Fisher diet and incorporates these estimates into demographic studies.

Our findings suggest that both biotic and abiotic factors are responsible for driving changes in Fisher survival, but individual responses are mediated by age and sex. We found that rapidly-changing climate may impact Fisher survival directly, by mediating temperature and snow depth, as well as indirectly, by shaping habitat conditions and resource availability. This work also highlights potential co-benefits in managing for Fisher persistence and forest resilience, objectives that have been viewed as complicated and at times, even diametrically opposed (Collins et al. 2010). Traditionally, wildfire has been a natural factor of the historical disturbance regime, maintaining habitat heterogeneity and creating complex, critical habitat elements (Steel et al. 2015). However, recent fires have both burned outside the natural range of variability and homogenized large sections of forest, removing many of the features that fishers depend on (Crockett and Westerling 2018; Green et al. 2019). While we did not explicitly

consider fire effects in this study, recent work on Fisher use of postfire landscapes found avoidance of areas dominated by high-severity fire, with greater use of low-severity or unburned islands (Thompson et al. 2021a). Therefore, future management designed around low-severity fire regimes, forest heterogeneity, and habitat connectivity may represent a solution that limits the risk of megafires while promoting Fisher survival. As the biotic and abiotic consequences of rapid environmental change threaten extinctions and extirpations globally, disentangling the intrinsic and extrinsic factors that mediate species responses will be critical in guiding effective conservation strategies.

Supplementary data

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

Supplementary Data SD1.—Spatial and temporal variation in climate variables. Figures represent climate variables averaged within an annual Fisher (*Pekania pennanti*) home range, including (A) Palmer Drought Severity Index (PDSI), (B) mean winter snow depth (mm), (C) mean summer land surface temperature (LST; °K), and (D) maximum summer land surface temperature (LST; °K). Gray circles represent values calculated within individual territories, whereas red circles and black lines represent yearly means and relationships.

Supplementary Data SD2.—Spatial and temporal variation in forest structure variables. Figures represent proportion of an annual Fisher (*Pekania pennanti*) home range containing (A) mature forest, (B) medium forest, (C) young forest, and (D) open habitat, as well as mean (E) hardwood basal area (m^2/ha), (F) canopy cover, (G) understory cover, and (H) percent of tree mortality. Gray circles represent values calculated within individual territories, whereas red circles and black lines represent yearly means and relationships.

Supplementary Data SD3.—Spatial and temporal variation in landscape composition variables. Figures represent composition of an annual Fisher (*Pekania pennanti*) home range quantified by (A) Interspersion and Juxtaposition Index (IJI), (B) forest heterogeneity calculated from Shannon's Diversity Index (SHDI) of forest cover types (mature, medium, young, and open), (C) standard deviation (SD) and (D) entropy of image texture pixels from Enhanced Vegetation Index (EVI) data, and (E) diameter diversity index (DDI). Gray circles represent values calculated within individual territories, whereas red circles and black lines represent yearly means and relationships.

Supplementary Data SD4.—Additional information on the specific environmental covariates used in known-fate models for fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, United States, including data sources, estimation methods, and spatial resolution.

Supplementary Data SD5.—Isotopic signatures of individual fishers (*Pekania pennanti*; females are shown as red points and males are shown as blue points) and trophic-corrected dietary source groups (means are shown as black points ± 95% CI).

Supplementary Data SD6.—Estimated means of proportional dietary contribution (95% credible intervals) for each functional prey group plus specialization index (ε) among fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, United States. Estimates are shown for all sampled individuals.

Supplementary Data SD7.—Estimated dietary contribution by source group and year among individual fishers (*Pekania pennanti*) in the southern Sierra Nevada, California, United States. Estimates are shown for all sampled individuals.

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Author contributions

CCK, JNP, MZP, REG, and KLP conceived the ideas and designed the methodology. CCK, REG, and KLP conducted the investigation process and curated data, while CCK performed the formal analysis. CCK and JNP led the writing of the manuscript, with key input from MZP. All authors contributed critically to the drafts and gave final approval for publication.

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Conflict of interest

The authors declare no conflict of interest.

Data availability

The data associated with this paper have not been provided due to the sensitive circumstances and endangered species status of the Southern Sierra Nevada Distinct Population Segment of Fisher.

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