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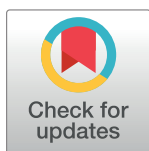
RESEARCH ARTICLE

Landscape of stress: Tree mortality influences physiological stress and survival in a native mesocarnivore

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Data Availability Statement: Wildlife observations collected by USDA Forest Service personnel are centrally stored in the Natural Resource Manager (NRM) Wildlife database. Data from the NRM databases are available to the public upon request to the U.S. Forest Service Region 5 T&E Species Coordinator (Patricia.Krueger@usda.gov), or the Regional Biologist (Gregory.Schroer@usda.gov). The authors did not have any special access privileges to gain access to the data.

Abstract

Climate change and anthropogenic modifications to the landscape can have both positive and negative effects on an animal. Linking landscape change to physiological stress and fitness of an animal is a fundamental tenet to be examined in applied ecology. Cortisol is a glucocorticoid hormone that can be used to indicate an animal's physiological stress response. In the Sierra Nevada Mountains of California, fishers (*Pekania pennanti*) are a threatened mesocarnivore that have been subjected to rapid landscape changes due to anthropogenic modifications and tree mortality related to a 4-year drought. We measured cortisol concentrations in the hair of 64 fishers (41 females, 23 males) captured and radio-collared in the Sierra National Forest, California. We addressed two main questions: (1) Is the physiological stress response of fishers influenced by anthropogenic factors, habitat type, canopy cover, and tree mortality due to drought in their home range? (2) Does the physiological stress response influence survival, reproduction, or body condition? We examined these factors within a fisher home range at 3 scales (30, 60, 95% isopleths). Using model selection, we found that tree mortality was the principle driver influencing stress levels among individual fishers with female and male fishers having increasing cortisol levels in home ranges with increasing tree mortality. Most importantly, we also found a link between physiological stress and demography where female fishers with low cortisol levels had the highest annual survival rate (0.94), whereas females with medium and high cortisol had lower annual survival rates, 0.78 and 0.81, respectively. We found no significant relationships between cortisol levels and body condition, male survival, or litter size. We concluded that tree mortality related to a 4-year drought has created a "landscape of stress" for this small, isolated fisher population.

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Introduction

The “landscape of fear” concept has been postulated to drive the behavioral responses of many species to perceived predation risk that cascades from individuals to ecosystems [1–4]. For example, the reintroduction of wolves (*Canis lupus*) has changed the behavior of elk (*Cervus elaphus*) in Yellowstone National Park with elk shifting their diel activity to using risky places during wolf downtimes [5]. Similarly, introduction of Tasmanian devils (*Sarcophilus harrisii*) to Maria Island, Tasmania, influenced the foraging behavior of their prey, the common brush-tail possum (*Trichosurus vulpecula*) with giving-up density being 64% higher than a devil-free site [6]. Even the fear of humans as the apex predator can influence wildlife communities [7]. We hypothesize that a “landscape of stress” also exists when environmental attributes place an animal in a state of chronic stress, and this stress response is subsequently linked to changes in components of fitness. The next challenge for stress research should be relating glucocorticoid secretion and measures of fitness [8].

Physiological stress in wildlife is often measured with cortisol concentrations, typically collected through blood, scat, feathers, and hair [9–12]. Cortisol is a glucocorticoid hormone released to mobilize energy in response to stress [13] and is incorporated in the hair shaft via passive diffusion during periods of active hair growth providing a long-term record (weeks to months) of both baseline physiological activity and stress responses [14]. The relationship between glucocorticoid concentrations measured in blood, hair, and scats, and animal stress is well established [15–18], and has been measured across numerous species, from garter snakes (*Thamnophis sirtalis*) to polar bears (*Ursus maritimus*) [18–20]. Past studies have found animals exposed to constant environmental stressors, such as predator abundance, weather, climate change, or human activity have elevated cortisol levels [12, 21, 22]. These elevated levels can negatively affect reproduction [23–25], increase vulnerability to diseases [26, 27], and reduce immune function [28, 29] causing mortality [30]. Stress can have indirect effects on survival as individuals with decreased fitness may have difficulty persisting in a “landscape of stress” [31].

Climate change and anthropogenic modifications to the landscape can have both positive and negative direct and indirect effects on wildlife [22, 32, 33]. As climate change and other anthropogenic influences impact the landscape, it is especially important to monitor the responses of small populations [34]. Extreme environmental characteristics, such as increased temperature or reduced precipitation, can act as chronic stressors that challenge physiological systems in animals [35, 36] and decrease measures of fitness such as survival and reproductive success [28, 37, 38]. Additionally, anthropogenic modifications to the landscape can influence stress levels for many species. For example, one study documented marine iguanas (*Amblyrhynchus cristatus*) had stress-induced elevations in plasma corticosterone among tourist-exposed populations relative to undisturbed populations [16].

Fishers (*Pekania pennanti*) are mesocarnivores dependent on dense, complex, multi-story forest [39–41]. Historically, fishers in California were distributed throughout the Sierra Nevada; however, due to trapping, habitat loss, and fragmentation, fisher densities are now lower than they were in the 1800s before these disturbances occurred [42–44]. In the 1940s, fisher populations in California declined and fishers were listed as a species of concern; as a result, a trapping ban was instituted in 1946 [45]. Due to the effects of overharvest, habitat loss, and landscape fragmentation, the fisher population in the southern Sierra Nevada has not recovered [43, 44]. In 1990, fishers were petitioned for listing as a threatened species under the Endangered Species Act. Currently, the southern Sierra Nevada population is small (<300 adults [46, 47]) and genetically isolated [47–49]. Factors which were identified as potentially limiting recovery of this fisher population include the influence of climate change (mainly

more frequent and longer droughts) and anthropogenic modifications (e.g., logging, development) to the landscape, since trapping has been banned for many years [50].

In the Sierra Nevada Mountains, California, a 4-year drought has affected the forest through mountain pine beetle (*Dendroctonus ponderosae*) infestation and tree mortality, as well as increased fire activity and severity [51]. Climate change will continue to increase the severity and frequency of droughts and insect outbreaks [52, 53], potentially influencing tree health and mortality. Additionally, anthropogenic modifications to the forest, such as continued development, logging, and prescribed burning, created a highly fragmented and constantly changing forest, further influencing the landscape [54, 55] which fishers must contend with when seeking suitable habitat. The increase in human activities in the Sierras led to the question of whether habitat changes associated with anthropogenic modifications and tree mortality related to a 4-year drought is directly or indirectly affecting the native fisher population through increased stress.

Concerns over low population numbers and conflicts with fuel reduction efforts led to the initiation of two studies beginning in 2007 that investigate the ecology and population dynamics of fishers in the Sierra Nevada [40, 41, 56, 57]. From 2007 to 2016, >250 fishers were radio-collared and monitored to determine their habitat use, survival, and reproduction. Results from these studies found that fishers preferred late-successional forests of dense tree cover within multi-layered old growth stands [40, 58], suggesting that altering the forest could negatively influence this isolated population. Our goal was to examine the influence of anthropogenic modifications, habitat, and tree mortality caused by a 4-year drought on the physiological stress response and fitness of Pacific fishers in the Sierra Nevada Mountains. Our objectives were to determine what anthropogenic modifications (silvicultural treatments, road and building densities), habitat (vegetative type, canopy cover), and tree mortality influenced cortisol concentrations among individual fishers. We also examined the relationship between cortisol and measures of fitness (body condition, survival, reproduction) to examine the effects of stress on fitness. We quantified metrics of anthropogenic modifications, habitat, and tree mortality across three home-range use scales (30, 60, 95% isopleths) for fishers in the Sierra Nevada, California. Results from this study can be used to inform forest managers and conservation practitioners, aiming to protect this small, isolated population of fishers.

Methods

Ethics statement

Fieldwork was approved by the United States Department of Agriculture, Forest Service, and the United States Department of Agriculture's National Wildlife Research Center. Permission to access land on the Sierra National Forest was obtained from the United States Forest Service, Bass Lake and High Sierra Ranger Districts.

We captured, immobilized, and handled animals under authorization of the United States Forest Service with permits from the California Department of Fish and Wildlife (Permit SC-2730), and review and approval of capture and handling protocols from the Institutional Animal Care and Use Committee at the University of California-Davis (IACUC #18022).

Study area

This study was conducted in the Sugar Pine (SP) and Kings River (KR) study areas located in the Sierra Nevada Mountains of central California, USA. The 800-km² SP study area (37° 19'29.5"N, 119° 31'31.8"W) was located near Oakhurst, California, while the 450-km² KR study area (37° 05'45.2"N, 119° 14'35.8"W) was located near Shaver Lake. The KR study area was located approximately 11 km southeast of the SP study area. Main habitats in the study areas [59, 60] included conifer forests at higher elevations dominated by ponderosa pine (*Pinus*

ponderosa), sugar pine (*P. lambertiana*), Jeffery pine (*P. jeffreyi*), white fir (*Abies concolor*), and incense cedar (*Calocedrus decurrens*). Lower elevations had hardwood forests dominated by California black oak (*Quercus kelloggii*) and canyon live oak (*Q. chrysolepis*) or a combination of conifer and hardwood forest. The understory often consisted of shrubs including manzanita (*Arcostaphylos spp.*), white thorn (*Ceanothus leucodermis*) and bear clover (*Chamaebatia foliolosa*). During summer, precipitation was rare with maximum temperatures averaging 23° C and minimum temperatures averaging 9° C (<https://weather.com/weather/monthly/l/Shaver+Lake+CA+93664:4:US>). During winter, snow accumulation was typical throughout the Sierras, with both study areas having snow cover from November–April. Winter temperatures averaged a high of 7° C and a low of -4° C. Both areas were similar in elevation from 1,000 to 2,400 m. The region was impacted by a 4-year (2012–2015) drought, resulting in high levels of tree mortality due to a combination of the drought and mountain pine beetle infestation [61].

Capture and monitoring

Cortisol levels in hair are an accumulation of physiological stress responses over several months, and can therefore be used as a measure of chronic stress [20, 62–66]. Hair hormone concentrations can be used as a minimally invasive alternative to serum concentrations, which must come from animal captures. Hair samples also provide a long-term average measurement of hormone concentrations that is not influenced by short-term fluctuations like that of serum. However, recent evidence has also suggested cortisol may also enter the hair from peripheral sources via glandular secretions or locally from the hair follicle [67, 68]. Therefore, cortisol levels in the hair may represent a combination of chronic and acute timeframes as well as central and peripheral cortisol release [14, 69], but is currently unknown in the fisher. Cortisol concentrations from hair has been shown to be a viable alternative for many animals [14, 70], including several species of mammals [10, 71, 72]. Unfortunately, due to the low numbers of this threatened species, we were unable to perform a physiological validation for this species to directly link stimulation of the hypothalamic-pituitary-adrenal axis to cortisol levels in the hair [69, 73].

During 3 trapping seasons (2014–2015, 2015–2016, 2016–2017), U.S. Forest Service personnel collected hair samples from fishers from the KR and SP study areas during capture and radio-collaring operations (mid-October to late February). We followed capture and monitoring techniques described by Green et al. [74]. During processing, we measured body length (cm), weight (kg), tail length (cm), teeth length (mm), and reproductive status through teat condition and testicular size. We shaved an area on the neck for blood sampling, and this shaved hair was collected for analysis; the same area was shaved on each fisher to standardize the area of hair collection [66]. Fishers were fitted with a VHF radio-collar weighing 31 g (Holohil model MI-2M, Holohil Systems Ltd., Carp, Ontario, Canada) with a handmade breakaway [40]. We injected each fisher with a Passive Integrated Transponder (Biomark, Boise, ID) for future identification and tracking [74]. At capture, we measured body mass (kg) and body length (cm) from the tip of the nose along the back of the spine to the base of the tail to determine BMI. We captured and handled animals under authorization of the U.S. Forest Service with permits from California Department of Fish and Wildlife (Permit SC-2730) with Institutional Animal Care and Use Committee review and approval from the University of California-Davis (IACUC #18022), and followed capture and handling protocols recommended by the American Society of Mammalogists [75].

Sample extractions and radioimmunoassay

Protocol for hair processing and extraction followed [10, 20]. The mass of hair samples ranged from 35 to 200 mg; sample mass was used to adjust for final cortisol sample concentration of

each individual sample. We washed hair samples three times for 3 minutes each with HPLC-grade methanol to remove any dirt and waste. We air-dried and weighed the hair samples, then placed the sample in a 25-ml chamber with a 7-mm steel grinding ball (Restch ball mill, Verder Scientific, Germany). The hair sample was ground for 20 min at 30 Hz. We collected and assayed a subsample of each of three washes to assure no hormone was lost during washing. We then weighed the ground hair and transferred the hair to a 5-ml Eppendorf tube. We added 3 ml of methanol to the ground hair samples and they were placed on a vortexer for a 24-hr period to facilitate extraction of the hormone from the ground hair to the methanol. We then centrifuged the ground hair samples for 10 min at 914 g, and 1.5 ml of supernatant was removed and placed in a clean glass tube. This volume was chosen so as to not remove any of the hair during separation of the supernatant. The supernatant was then dried under a stream of nitrogen and re-suspended in 0.2 ml of PBS buffer. We assayed samples using a radioimmunoassay in duplicate for cortisol 3 antibody [16]. Species validation was performed to test for non-specific binding, binding interference, and parallelism prior to running all samples. The assay included a 10-point standard curve run in triplicate with known values of cortisol. The intra-assay variation was 4.0%. All assayed samples fell within the standard curve for the assay. We performed a species validation for the radioimmunoassay and antibody prior to study samples and found good parallelism with an $R^2 = 0.986$, and no significant interference using tests with known high and low spikes of cortisol which yielded an average recovery of 94.8%.

Home range estimates

Cortisol in hair indicates an accumulation of physiological responses over months depending on growth and molt cycles [64], suggesting hair can be used as a measure of chronic stress. Fishers molt and replace their fur from September through early November [39], thus accumulation of cortisol from the body into the hair occurs during this molting period and active hair growth [14, 66]. Hair collected in February will still represent cortisol accumulation between September through early November when the hair is growing. Whether the hair follicles of fishers stop growth by early November is unknown [76], but 93% (59 of 64) of the hair samples were collected after November 1. A comprehensive meta-analysis of the literature supported hair cortisol analysis as a sensitive measure of central hypothalamic-pituitary-adrenal axis function and a biomarker of persistent or ongoing stressors [77].

To associate the level of cortisol in a hair sample with the time when cortisol was accumulated in the hair, we used the annual home range prior to when the hair sample was collected; all hair samples were collected during trapping operations from mid-October to late February. Home ranges from the year before the sample was collected were associated with the hair samples because the location the individual inhabited the year before would influence the individuals' chronic stress levels. Essentially, animals were initially captured and radio-collared, then recaptured approximately a year later and a hair sample collected which represented an accumulation of cortisol from the prior year. Therefore, the previous annual home range was used as a conservative measure of space use and reflected exposure to activities and landscape changes within their home range during the previous year.

We determined annual home ranges using radio-telemetry locations, rest sites, aerial locations, and den sites [74]. Rest sites were defined as a single structure in which an individual was located (i.e., tree, snag, burrow). Rest areas were defined as an area (within 50 m) in which an individual was located, but could not be narrowed down to one specific structure [74]. Locations (triangulations, rest sites, and rest areas) of female fishers were obtained approximately every 3 days, with rest site locations and rest areas were collected opportunistically when searching an area. Den locations were added into the data set once for every 3 days a

female was at a den; this was based on how often female fishers are typically relocated, and these locations were subsampled as to not skew the home range estimators towards these den sites. The telemetry error for each location type varied but were similar among fishers and therefore any bias was weighted equally among individuals. We analyzed females and males separately since males use a larger area and do not use dens, while females have smaller home ranges and restrict their movements when raising young; males do not assist with raising young [78]). We used program R (adehabitatHR package; version 3.3.0) in R studio (version 1.0.136, [79]) and ArcGIS 10.5 (ESRI, Redlands, CA, USA) to determine annual home ranges with 30%, 60%, and 95% isopleths [80]. These three spatial scales were used to determine whether individuals experienced different stressors in the core (30%) of their home ranges/areas of use versus larger areas (60%) and the entirety of their home ranges/areas of use (95%). We examined these three scales because the levels of anthropogenic influences varied among the three home range scales [81]. We calculated area-observation curves for each fisher and determined 25–30 points were needed to estimate the home ranges of females. We defined the areas the males inhabited as “areas of use” because the area-observation curves for males never reached an asymptote.

Anthropogenic modifications

We obtained data layers of known and mapped silvicultural treatments on the study areas for each year from the Forest Service Activity Tracking System (FACTS) database (<https://data.fs.usda.gov/geodata/edw/datasets.php>); data layer had a spatial resolution of 1 m. Management activities included (a) thinning of natural fuels, (b) commercial thinning, (c) full planting without concurrent site preparation, (d) fill-in re-planting without concurrent site preparation, (e) individual tree release and weeding, and (f) pre-commercial thinning of individual or selected trees. We calculated the area of each activity for each female home range or male area of use at the three kernel sizes, and converted to the proportion (m^2 of activity/ km^2 of home range or area of use) of each activity in each home range during each year. We used m^2 instead of km^2 because some management activities were very small. The U.S. Forest Service provided locations of buildings and roads in each study area; spatial resolution of 1 m. Using GIS, we determined building density (# buildings/ km^2) and road density (m of roads/ km^2) within each female's home range, or each male's area of use at all three kernel sizes. We used meters for road length instead of km because some roads were <1 km. Road density consisted of paved, dirt, and decommissioned roads; the available data layer combined all of these roads into one category.

Habitat characteristics

In addition to anthropogenic modifications, we examined two habitat characteristics (canopy cover, vegetation type) on both areas for each year as a measure of habitat quality. We obtained canopy cover and vegetation data from the LANDFIRE database (U.S. Forest Service; U.S. Department of Interior) which has a native spatial resolution of 30 m. We delineated eight vegetative types: conifer forest, hardwood forest, mixed hardwood-conifer forest, granite, water, developed land, shrubland, and sparse cover. We measured the percent of each habitat type available in each home range or area of use at each kernel estimator. Prior research in the study areas characterized dense canopy as $\geq 60\%$ canopy cover [40]. Therefore, canopy cover was divided into 3 classes: $\geq 60\%$ (dense), 41–59% (moderate), and $\leq 40\%$ (low). Our goal in dividing canopy cover into these three categories was to determine whether any of these canopy cover levels influenced cortisol, and which levels may be more tolerated by fishers. In the future, these canopy classes could be used to determine a canopy cover threshold that fishers

prefer. We calculated the percentage of each canopy class for each home range or area of use at each kernel estimator.

Tree mortality

We obtained tree mortality data from the U.S. Department of Agriculture Remote Sensing Lab (www.fs.usda.gov/detail/catreemortality/toolkit/?cid=fseprd498067) and intersected this data layer with the home ranges and areas of use using ArcGIS; data was measured as the number of dead trees per hectare. We reported tree mortality as the number of dead trees per acre. Data on levels of tree mortality were available for the years 2015 and 2016 only; measurable tree mortality was not recorded in 2014.

Components of fitness

We examined how levels of cortisol influenced three fitness parameters (body condition, survival, reproduction). For allometric body condition, we calculated a body mass index (BMI) as the ratio of body mass (kg)/body length (cm) [82]. We used linear regression to examine the relationship between cortisol and BMI. We determined survival intervals for the time when the individual was radio-collared until September 15 of the year following their capture. We used September 15 as the end-point for the interval each year because this was when new hair began to grow [39]. However, for animals captured during the 2016–2017 trapping season, we used May 1, 2017, when project monitoring ended. We calculated male and female survival rates and 95% confidence intervals for each year using the program MICROMORT [83]. To examine the influence of cortisol on survival rates, we divided animals into three classes of cortisol (low: <0.12 pg/mg, medium: 0.121–0.189 pg/mg, high: >0.190 pg/mg); classes were chosen by dividing the animals into thirds based on the distribution of cortisol values. We performed a z-test to determine differences in survival rates among years and classes of cortisol levels.

Denning season for females and their kits occurs in April–June. Once we identified the natal den tree via telemetry, we placed remote cameras to monitor the tree until the female moved her kits to the next den tree; we used these photos to determine litter size [74]. We climbed den trees after the female moved her kits to document mortality or abandonment. To investigate the influence of cortisol on reproduction, we examined the relationship between cortisol and litter size during the denning season before and after the sample was collected. This analysis examined (a) whether the number of kits a female produced was associated with her cortisol level, or (b) whether her cortisol level was associated with the number of kits produced the following year. As we were examining chronic stress instead of acute stress, cortisol accumulating in the hair during molting season could be influenced by the previous reproductive season, or could influence the following reproductive season. We used analysis of variance to examine the relationship between cortisol and the number of kits produced by a female for the year before and the year after the cortisol sample was collected.

Statistical analysis

We used R (version 3.3.0) in R studio (version 1.0.136; [79]) for statistical analysis. When the data did not conform to a normal distribution, we would log or square root transform the data. We used generalized linear mixed models (GLMM) with normal distribution followed by Akaike Information Criterion (AIC_c) model selection [84] due to our small sample sizes to determine which measures of anthropogenic modifications, habitat, tree mortality, and the additive and interactive combination of these factors, influenced cortisol levels in female and male fishers at each of the home range estimators (30, 60, 95% isopleths). Due to different life

histories and space use patterns, we analyzed female and male fishers separately. Because we often sampled fishers from more than one year, we included ‘individual’ as a random effect. Data on tree mortality was only available for 2015 and 2016, thus we could only use these years for model selection. To reduce the number of models, we analyzed models in a sequential process or phased-modeling approach [85–89]. The sequential process was used to create a more rigorous and thoughtful approach to the analysis instead of incorporating every variable into the final model. In the first phase, we analyzed canopy cover, management activity, and vegetation type as univariate models and all possible additive and interactive combinations of these covariates. With the sequential approach, the variables from the top model in each group (canopy cover, vegetation type, management activity) were then moved to the global model. In the next phase, we then added road density, building density, and tree mortality to the global model for final model analysis. Any variables that were correlated ($r > 0.6$) through the *cor* test function in program R were not included in the same model. The global model included all possible additive and interactive combinations. We did not include study area or year in the models because we were examining all these variables within each individual fishers’ home range on a yearly basis (i.e., these categorical variables were presented by the continuous variables for each individual fisher). Models with a weight ≥ 0.1 were considered significant and model weight aided in model inference. For statistical tests, we reported the *P*-values and considered $P < 0.10$ as an indicator of significance.

Results

In 2014–2016, we captured 23 male (KR: 10, SP: 13) and 41 female (KR: 22, SP: 19) fishers. We captured some individuals more than once contributing to 32 hair samples obtained from males (KR: 19, SP: 13) and 68 hair samples from females (KR: 44, SP: 24). During each trapping season, each individual was only captured and measured once; animals recaptured in the same trapping season were immediately released without sampling. Home range size for female fishers averaged 1.92 ± 1.88 (SD), 5.92 ± 5.58 , and 21.82 ± 18.16 km², for the 30%, 60%, and 95% isopleths, respectively. Areas of use for male fishers averaged 9.28 ± 7.30 , 26.33 ± 19.65 , and 88.56 ± 54.79 km², respectively. The percent of the home range impacted by management activities was very small for both female and male fishers (Table 1). Cortisol levels averaged 0.182 ± 0.103 (SD) pg/mg (range: 0.0609–0.7922 pg/mg) for females, and 0.163 ± 0.066 pg/mg (range: 0.0878–0.2863 pg/mg) for males ($t_{131} = -1.3384$, $P = 0.183$). Cortisol levels of both males and females were relatively similar in the first two years, but increased in the third year (Fig 1; $F_{2, 130} = 25.96$, $P < 0.001$). Cortisol levels averaged 0.188 ± 0.099 pg/

Table 1. Metrics (mean \pm SD) of building density, road density, tree mortality, and percent of the home range affected by management activities in the 95% kernel home ranges of female and male fishers, Sierra National Forest, California, 2014–2016.

| Variable | Females | Males |
|---|-----------------------|-----------------------|
| Building density (#/km ²) | 0.54 \pm 0.79 | 2.38 \pm 2.85 |
| Road density (m of road/km ²) | 2,052.79 \pm 633.99 | 2,000.89 \pm 601.97 |
| Tree mortality (# dead trees/acre) | 20.48 \pm 21.47 | 16.93 \pm 12.76 |
| % thinning of natural fuels | 0.0005 \pm 0.0029 | 0.0003 \pm 0.0033 |
| % commercial thinning | 0.0054 \pm 0.0342 | 0.0002 \pm 0.0004 |
| % full planting without concurrent site preparation | 0.0038 \pm 0.0141 | 0.0001 \pm 0.0002 |
| % fill-in re-planting without concurrent site preparation | 0 | 0.0011 \pm 0.0021 |
| % individual tree release and weeding | 0.0075 \pm 0.0316 | 0.0068 \pm 0.0085 |
| % precommercial thinning of individual or selected trees | 0.0229 \pm 0.0699 | 0.0046 \pm 0.0068 |

<https://doi.org/10.1371/journal.pone.0253604.t001>

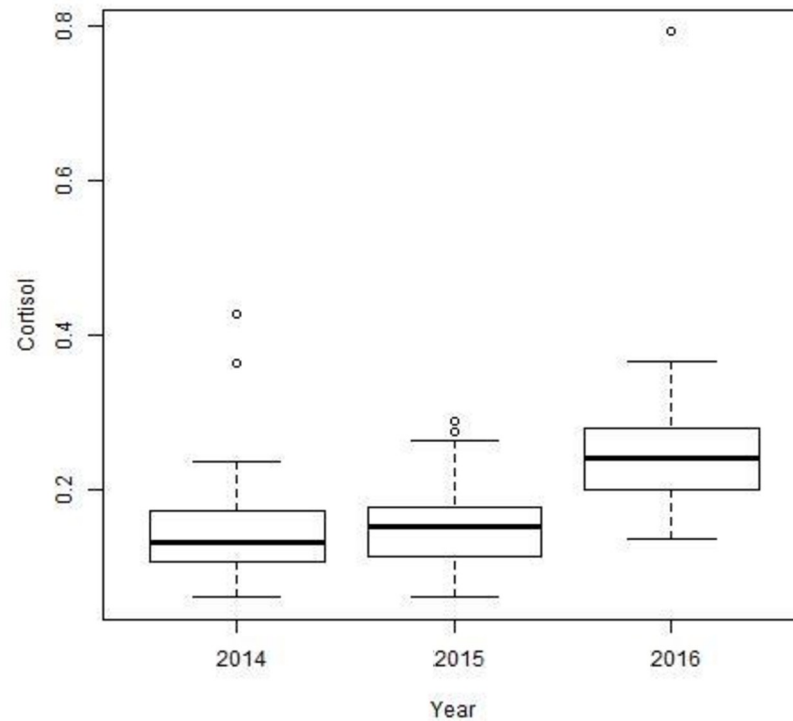


Fig 1. Cortisol levels (pg/mg) for female and male fishers combined in 2014, 2015, and 2016, Sierra National Forest, California, USA.

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mg (range: 0.0899–0.7922 pg/mg) in the Kings River study site, and 0.146 ± 0.056 pg/mg (range: 0.0609–0.2877 pg/mg) in the Sugar Pine study site.

Influence of anthropogenic modifications, habitat, and tree mortality on cortisol levels in female fishers

We collected 68 hair samples from 41 females during 2014–2016, but only used 40 hair samples collected from 30 females during 2015–2016 to examine model selection in the years that had tree mortality data. After removing models with correlated variables (different variables were correlated at different spatial scales for each sex), we constructed 36 models examining the influence of various anthropogenic modifications, habitat, and tree mortality within the 30% isopleth on cortisol levels of females. For females, a model containing only tree mortality had the highest influence on cortisol (Table 2) with increasing cortisol related to increasing tree mortality ($r = 0.49$; Fig 2). A second model containing tree mortality and percent developed habitat added an additional 10.5% model weight, with the 2 top-ranked models carrying 35.4% of the model weight (Table 2). Although both models were over the threshold of weight ≥ 0.1 , tree mortality was the only significant variable with all other variables considered uninformative (variable coefficients had P -values > 0.1 ; [90]). Tree mortality was present in all of the 10 top-performing models, with these 10 models containing tree mortality having a combined model weight of 80.0%. The one apparent outlier was a female with high cortisol (Fig 2), but there was no apparent error in lab analysis, thus we retained this data point. However, removing this possible outlier produced similar model results with the 2 top-ranked models containing tree mortality as the only significant variable having a combined weight of 24.7%. Tree mortality was still in all of the 10 top-performing models with these 10 models having a combined weight of 69.9%.

Table 2. Models with weight ≥ 0.1 examining metrics of anthropogenic modifications, habitat, and tree mortality in the 30, 60, and 95% kernel home range of individual female fishers and the influence on hair cortisol levels, Sierra Nevada Mountains, California, 2014–2016.

| Model | $\Delta AICc$ | Weight | P-value for variables |
|--|---------------|--------|---|
| 30% kernel | | | |
| Tree mortality | 0.0 | 0.248 | 0.0013 |
| Tree mortality + % developed | 1.7 | 0.105 | Tree mortality: 0.0017 % developed: 0.4031 |
| 60% kernel | | | |
| Tree mortality | 0.0 | 0.210 | 0.0024 |
| Tree mortality + % hardwood_conifer | 0.3 | 0.184 | Tree mortality: 0.0103 % hardwood_conifer: 0.1555 |
| 95% kernel | | | |
| Tree mortality | 0.0 | 0.538 | 0.0011 |
| Tree mortality + Pre-commercial thinning of individual or selected trees | 2.0 | 0.197 | Tree mortality: 0.0017 Pre-commercial thinning of individual or selected trees: 0.5114 |
| Tree mortality + Building density | 2.4 | 0.159 | Tree mortality: 0.0013 Building density: 0.8428 |

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For the 60% isopleth, we constructed 48 models after removing models with correlated variables. The top-ranked model influencing cortisol in females included only tree mortality (Table 2) with cortisol increasing as tree mortality increased ($r = 0.47$; Fig 2). The second-

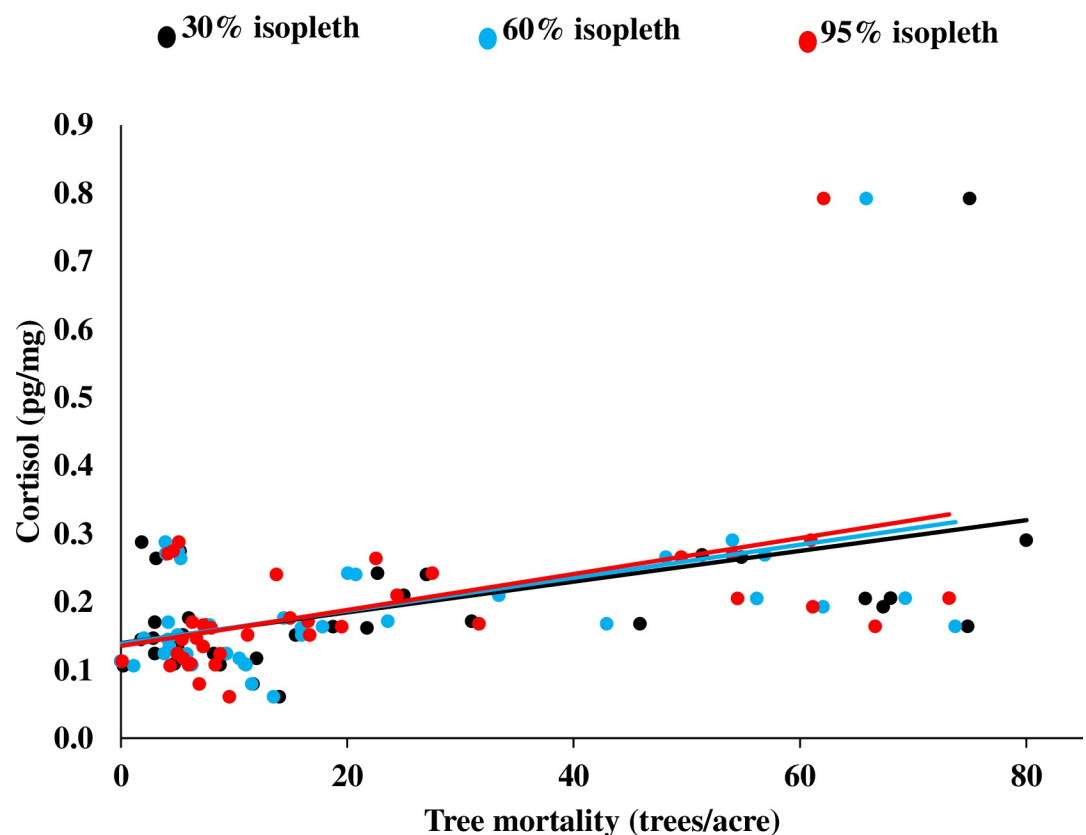


Fig 2. Relationship between cortisol (pg/mg) in hair and the amount of tree mortality (trees/acre) in the 30%, 60%, and 95% kernel home ranges for female fishers, Sierra National Forest, California, USA, 2014–2016.

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ranked model included tree mortality and percent hardwood-conifer, with the 2 top-ranked models carrying 39.4% of model weight (Table 2). Although these models were over the threshold of weight ≥ 0.1 , again only tree mortality was significant with all other variables considered uninformative [90]. Tree mortality was present in all top-10 performing models, with these 10 models containing tree mortality having a combined weight of 77.0%. Similar to the results for the 30% isopleth, removing the one possible outlier produced similar model results with tree mortality in 9 of the 10 top-performing models with these 9 models having a combined weight of 62.2%.

For the 95% isopleth, we constructed 19 models after removing models with correlated variables. The top-ranked model again contained only tree mortality as influencing cortisol of females (Table 2) with cortisol increasing with increased tree mortality ($r = 0.50$; Fig 2). Two additional models that included tree mortality, pre-commercial thinning of individual or selected trees, and building density with model weights >0.1 weight had a combined model weight of 89.5% (Table 2). Although these models had weights ≥ 0.1 , tree mortality was significant in the 3 top-ranked models and all other variables were considered uninformative [90]. Tree mortality was present in only 4 of the 10 top-performing models, but these 4 models containing tree mortality having a combined weight of 94.5%. Again, removing the one possible outlier produced models with tree mortality in 6 of the 10 top-performing models with these 6 models having a combined weight of 86.0%.

Influence of anthropogenic modifications, habitat, and tree mortality on cortisol levels in male fishers

We used 32 hair samples collected from 20 males during 2015–2016 to develop 48 models (after removing models with correlated variables) examining the influence of anthropogenic modifications, habitat, and tree mortality within the 30% isopleth area of use on cortisol levels of male fishers. The top-ranked model for males contained tree mortality, percent sparse cover, and pre-commercial thinning of individual or selected trees (Table 3) with cortisol increasing in areas with increased tree mortality ($r = 0.52$; Fig 3), as well as areas of use with increased sparse cover and increasing pre-commercial thinning of individual or selected trees. Two other models containing tree mortality, percent low canopy cover, and amount of pre-commercial thinning of individual or selected trees had model weights >0.1 with these 3 top-ranked models having a combined model weight of 55.0% (Table 3). Although these models had model weight ≥ 0.1 , tree mortality and the amount of pre-commercial thinning were the only significant variables with all other variables considered uninformative [90]. Tree mortality was present in all of the 10 top-performing models, with these 10 models having a combined model weight of 81.8%.

For the 60% isopleth, we constructed 40 models after removing models with correlated variables and found the top-ranked model contained only tree mortality (Table 3) with cortisol increasing as tree mortality increased ($r = 0.72$; Fig 3). Three other models containing tree mortality, the amount of pre-commercial thinning of individual or selected trees, percent sparse cover, and percent low canopy cover had model weights >0.1 , with these 4 top-ranked models carrying 65.6% of the model weight (Table 3). Although these models had model weights ≥ 0.1 , only tree mortality was significant with all other variables considered uninformative [90]. Tree mortality was present in all of the 10 top-performing models with these 10 models having a combined model weight of 90.1%.

For the 95% isopleth, we constructed 26 models after removing models with correlated variables. We found the top-ranked model contained the variables of tree mortality and road density (Table 3) with cortisol increasing as tree mortality and road density increased (Fig 4). A

Table 3. Models with weight ≥ 0.1 examining metrics of anthropogenic modifications, habitat, and tree mortality in the 30, 60, and 95% kernel areas of use for individual male fishers and the influence on hair cortisol levels, Sierra Nevada Mountains, California, 2014–2016.

| Model | $\Delta AICc$ | Weight | P-value for variables |
|---|---------------|--------|---|
| 30% kernel | | | |
| Tree mortality + % sparse + pre-commercial thinning of individual or selected trees | 0.0 | 0.219 | Tree mortality: 0.0063 |
| | | | % sparse: 0.0876 |
| | | | Pre-commercial thinning of individual or selected trees: 0.0181 |
| Tree mortality + pre-commercial thinning of individual or selected trees | 0.1 | 0.204 | Tree mortality: 0.0083 |
| | | | Pre-commercial thinning or individual or selected trees: 0.0252 |
| Tree mortality + % low canopy cover + pre-commercial thinning of individual or selected trees | 1.1 | 0.127 | Tree mortality: 0.0056 |
| | | | % low canopy cover: 0.1495 |
| | | | Pre-commercial thinning of individual or selected trees: 0.0338 |
| 60% kernel | | | |
| Tree mortality | 0.0 | 0.264 | 0.0004 |
| Tree mortality + pre-commercial thinning of individual or selected trees | 1.2 | 0.147 | Tree mortality: 0.0016 |
| | | | Pre-commercial thinning of individual or selected trees: 0.2001 |
| Tree mortality + % sparse | 1.2 | 0.144 | Tree mortality: 0.0009 |
| | | | % sparse: 0.2045 |
| Tree mortality + % low canopy cover | 1.9 | 0.102 | Tree mortality: 0.0001 |
| | | | % low canopy cover: 0.3067 |
| 95% kernel | | | |
| Tree mortality + road density | 0.0 | 0.338 | Tree mortality: 0.0069 |
| | | | Road density: 0.0131 |
| Tree mortality + road density + building density | 0.6 | 0.250 | Tree mortality: 0.0028 |
| | | | Road density: 0.0113 |
| | | | Building density: 0.1259 |

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second-ranked model containing tree mortality, road density, and building density added an additional 25% of model weight, with the 2 top-ranked models having a combined model weight of 58.8% (Table 3). Both tree mortality and road density were significant variables with all other variables considered uninformative [90]. Tree mortality was present in 7 of the 10 top-ranked models with these 7 models having a combined model weight of 85.1%.

Influence of cortisol level on fitness

We examined the relationship between BMI and cortisol concentrations using samples from the 68 females and 32 males collected during 2014–2016, and found no relationship between cortisol and individual BMI estimates ($F_{1, 117} = 0.356$, $P = 0.552$). There was no significant correlation between individual cortisol levels and BMI for females ($r = 0.131$, $P > 0.40$) or males ($r = -0.078$, $P > 0.50$).

We examined 37 females to determine if the number of kits produced influenced the subsequent cortisol level of an individual female fisher after giving birth. We found no difference in cortisol concentrations among females after they produced 0, 1, 2, or 3 kits ($F_{3, 33} = 0.354$, $P = 0.786$). We also examined if cortisol influenced the subsequent litter size for 54 females where we were able to obtain kit counts and found no difference in cortisol prior to giving birth and whether they subsequently produced 0, 1, 2, or 3 kits ($F_{3, 50} = 1.251$, $P = 0.301$). The

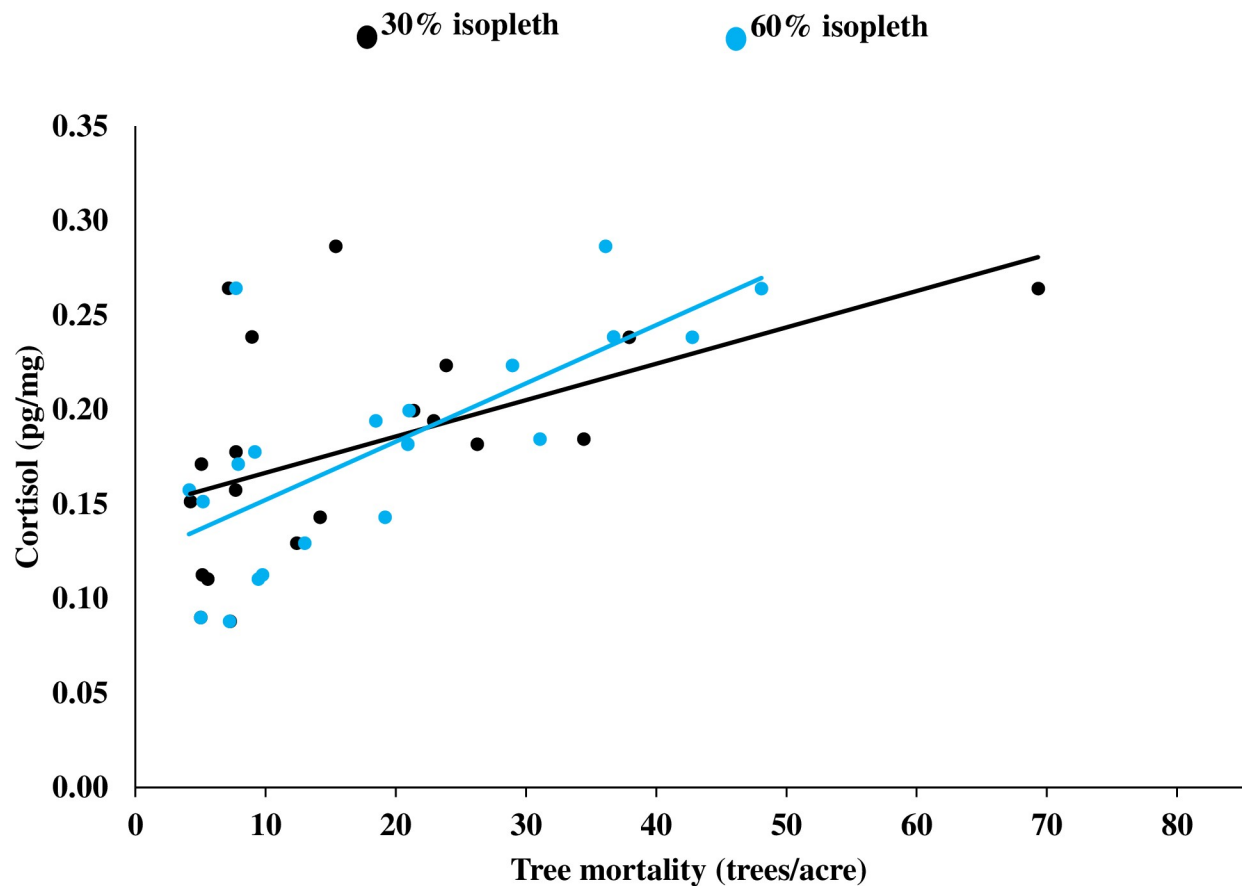


Fig 3. Relationship between cortisol (pg/mg) in hair and the amount of tree mortality (trees/acre) in the 30 and 60% kernel areas of use for male fishers, Sierra National Forest, California, USA, 2014–2016.

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average litter size across the two study areas was 1.57 kits per female [74] with 25%, 33%, 32%, and 10% of females having litters of 0, 1, 2, and 3 kits, respectively.

Using 17,664 radio-days for females, annual survival rates showed an increasing trend over the 3 years, but there was no difference among years (all z-tests had $P > 0.26$). When we examined the relationship between cortisol levels and annual survival rates (Fig 5), females with low cortisol concentrations had the highest annual survival rates (0.94) compared to females with medium (0.78; $z = 1.56$, $P = 0.06$) or high (0.81; $z = 1.44$, $P = 0.07$) cortisol concentration. Annual survival rates for females with medium and high levels of cortisol did not differ ($z = 0.27$, $P = 0.39$).

Using 9,373 radio-days for males, annual survival rates generally increased over time, but there was no difference amongst years (all z-tests had $P > 0.30$). Among the 3 classes of cortisol levels, males exhibited a similar trend as females with males with low cortisol levels having higher survival (0.81), and medium and high cortisol levels having lower survival, 0.74 and 0.71, respectively. However, there was no statistical difference in annual survival rates among males with low, medium, and high levels of cortisol (all z-tests had $P > 0.17$; Fig 5).

Discussion

This is the first study documenting a link between increased tree mortality and increased cortisol levels in fishers. For female and male fishers, tree mortality was the most important variable

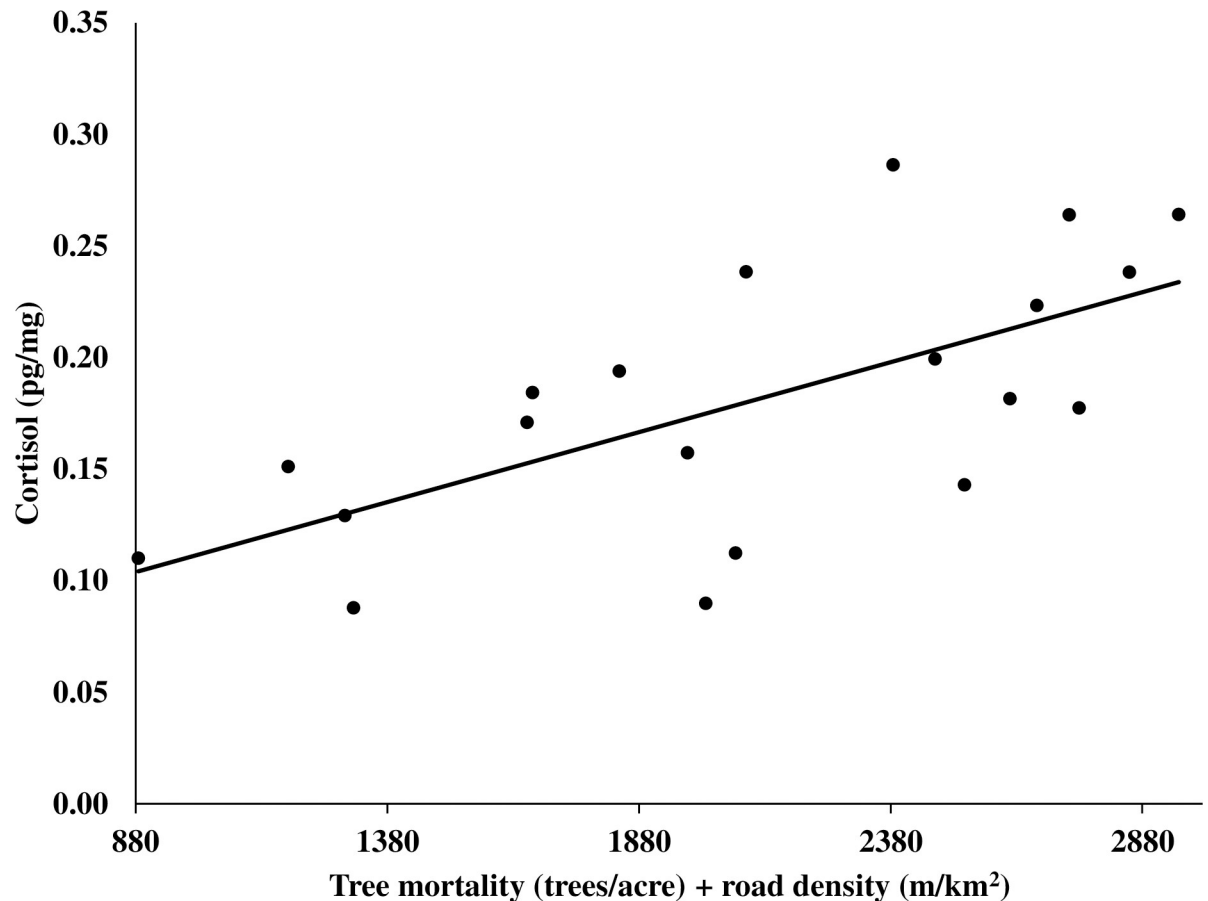


Fig 4. Relationship between cortisol (pg/mg) in hair and the amount of tree mortality (trees/acre) and road density (m/km²) in the 95% kernel areas of use for male fishers, Sierra National Forest, California, USA, 2014–2016.

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influencing cortisol levels at all spatial scales, such that increased cortisol was associated with increased tree mortality. Our results showed tree mortality, as related to the effects of the 4-year drought, is the principle driver creating a “landscape of stress” for fishers in the Sierra Nevada Mountains. Tree mortality could influence fishers by reducing thermoregulatory cover, loss of escape terrain, or decreased prey base. Loss of canopy cover (escape terrain) may lead to increased predation risk from other carnivores. Decreased canopy cover due to tree mortality may increase the outside temperature or reproductive den temperature due to lack of shade. Kilpatrick and Rego [78] reported fishers selected rest sites in part due to thermoregulation. If the amount of late-successional forest continues to decrease with increased tree fall [91], these animals will also have fewer trees to use for shelter and dens. With the loss of trees and decreased cone production, small mammals will likely decline during subsequent years. Numerous studies have shown prey declines can lead to changes in reproduction and reduced body condition in carnivores [92, 93]. If the small mammal prey base declines, this isolated fisher population could be adversely impacted.

Levels of tree mortality have increased in the Sierras due to the recent 4-year drought and increases in mountain pine beetles attacking the already struggling trees [94] with high tree mortality (>80% of stands) observed throughout the area. Tree mortality due to drought and pine beetle infestation will likely continue to increase as climate change increases the severity of droughts and insect infestations [52, 53]. Although the winter of 2016–2017 experienced greater than average levels of precipitation, the high levels of tree mortality were irreversible

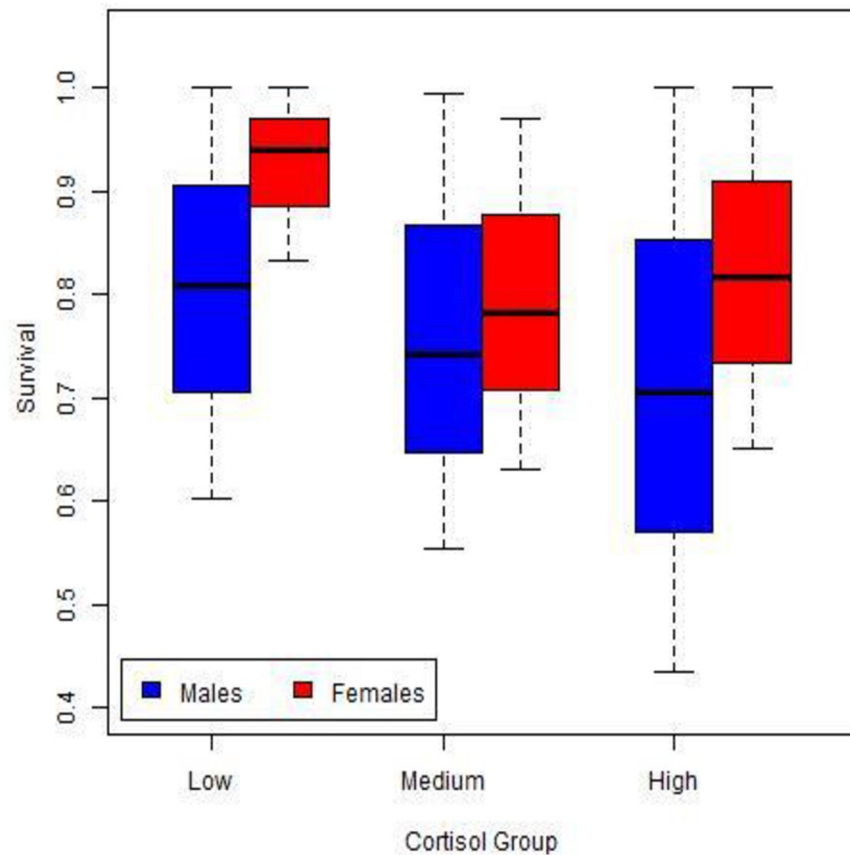


Fig 5. Annual survival rates of male and female fishers in relation to their level of cortisol, Sierra National Forest, California, USA, 2014–2016. Cortisol classes were low (<0.12 pg/mg), medium (0.121 – 0.189 pg/mg), and high (>0.190 pg/mg); error bars represent 95% confidence intervals.

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[94]. If tree mortality continues to increase with the resulting increase in tree fall, the amount of late-successional forest that fishers prefer will also continue to decrease [91].

Within the 95% isopleth for male fishers, we found the combined effect of tree mortality and road density had the greatest influence on cortisol. The additive effect of road density likely reflects the life history of male fishers. Mountain lions (*Puma concolor*), which prey on fishers [56, 95], frequently use roads to hunt, and given the male fishers' widespread movement, increased road density may increase encounter rates with mountain lions, which could lead to increased cortisol in males and potentially decrease survival.

Pre-commercial thinning of individual or selected trees was the only management action contained in the top-ranked models suggesting fishers in the study areas were not negatively influenced by most management actions. This supports other studies reporting animals can adapt and may even benefit from anthropogenic modifications [96]. Levine [97] showed environmental stressors that are controllable or predictable may not be perceived as stressful. Anthropogenic modifications can usually be avoided compared to widespread tree mortality. The areas impacted by human activities were very selective in placement and small in area, while tree mortality occurred across the landscape. One study [41] showed fishers may tolerate small amounts of management on the landscape, and another study [44] documented resident fishers responded to management activities within their territory by travelling around impacted areas but did not alter their overall home range. In contrast, tree mortality was severe

in both areas, with mortality of Ponderosa pines $\geq 80\%$ [94]. The effects of tree mortality were unavoidable amongst individual fishers, whereas anthropogenic modifications which were low in density and occurred in small patches may allow the animals to concentrate their activity to areas devoid of human activities and anthropogenic modifications.

Average cortisol levels for fishers sampled in the KR area were generally higher than in the SP area likely due to differences in tree mortality in the two areas. In the SP area, males had an average of 10.45 dead trees/acre and females averaged 7.5 dead trees/acre. In contrast, in the KR area, males had an average of 19.71 dead trees/acre, and females averaged 26.04 dead trees/acre. The large difference in tree mortality between the two areas is likely influencing the level of cortisol levels in the individual fishers across these two study populations. Topographic and microclimatic differences between these sites likely influenced different rates of pine beetle infection and subsequent tree mortality.

Most importantly, we found female fishers with low cortisol levels had higher annual survival rates than females with medium and high cortisol levels. Although females with high cortisol had slightly higher survival than females with medium cortisol levels, these two groups did not differ in survival. Decreased survival in females could greatly influence the future of this small, isolated population. Although not statistically significant, the trend among males was similar to the females with decreasing survival rates as cortisol levels increased; lack of significance was likely due to small sample size. This is the first study linking a physiological stress response to changes on the landscape to subsequent fitness (i.e., survival rate) among female fishers. Similarly, Rakotoniana et al. [98] reported that high levels of hair cortisol was associated with reduced survival probabilities in grey mouse lemurs (*Microcebus murinus*). In boreal woodland caribou (*Rangifer tarandus caribou*), individuals with more of their home range having been logged best explained the variance in hair cortisol concentrations [99]. Lavergne et al. [100] reported a relationship between stress profiles and risk avoidance behavior among snowshoe hares (*Lepus americanus*). Linking anthropogenic changes in an animal's home range to physiological stress responses and subsequent fitness consequences is important for future management and conservation.

Conclusion

Tree mortality, in response to the 4-year drought, is creating a “landscape of stress” within this fisher population. This study is the first to show a link between tree mortality and physiological stress in fishers. Even more significant was the link between increased cortisol and decreased female survival. During this study, cortisol increased over the 3 years which could cause fitness to decline if tree mortality continues to increase and decreases the amount of late-successional forest [40]. Climate change is continuing to increase the average temperatures of this region [101]. If cortisol levels continue to increase, we may begin to see greater impacts of physiological stress on the fitness and health of individuals in this population. With anticipated increases in drought severity due to climate change, the landscape of stress will likely continue to persist and expand. By understanding how climate change is influencing this sensitive species, forest managers may be able to conserve the late-successional forest this fisher population occupies. Additionally, the methods of determining the physiological stress response to landscape change has important applications to other forest carnivores in this region. Two other meso-carnivores (ringtails, *Bassariscus astutus*, and pine marten, *Martes americana*) in this region could also be equally impacted by changes in forest structure.

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