

Mesopredator release facilitates range expansion in fisher

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Abstract

Some central and eastern populations of fisher *Pekania [Martes] pennanti* are expanding their ranges following historic range contractions, while many western populations have yet to do so. We investigated whether expanding fisher populations are benefiting from a mesopredator release following reductions in their carnivore predator communities. This hypothesis posits that local extinctions of the largest predators ‘release’ mesopredator populations from direct predation and competition, leading to an increase in their abundance, expansion of their range and potentially to shifts in their morphology and ecological niche. Our comparison of the conservation status and predator communities of fishers across four geographic regions of their range supports the mesopredator release hypothesis, especially in their eastern range. Our meta-analysis of fisher diet also suggests that released fisher populations may benefit by complementing their diverse diets with more large-bodied prey species, whereas those with more specialized diets (e.g. northwestern populations) or diverse diets with small amounts of large-bodied prey (e.g. populations within California) have experienced little range expansion. Further, measurements of museum specimens suggest that individuals within released populations have evolved a larger body size since the time of their most contracted range, which may help them hunt larger prey species that are expected to be more available in the absence of larger carnivores. Collectively, these data support the hypothesis that a reduced predator community is contributing to the geographic variation in modern fishers’ range expansion. In addition to harvest restrictions, habitat protection and translocations, future conservation plans should consider the potential effects of the predator community, emphasizing the need to quantify fisher mortality sources and fisher–predator interactions.

Introduction

Anthropogenic forces, such as habitat fragmentation, habitat loss, overharvest and direct persecution, have resulted in severe range contractions of many apex predator species (Channell & Lomolino, 2000; Gittleman *et al.*, 2001; Laliberte & Ripple, 2004; Hemerik, Hengeveld & Lippe, 2007). The loss of large predators can have widespread and complex effects on ecosystems (Estes *et al.*, 2011), including allowing populations of smaller predators to increase (i.e. mesopredator release; Crooks & Soulé, 1999; Prugh *et al.*, 2009; Ritchie & Johnson, 2009; Ripple *et al.*, 2013). In turn, the ‘released’ mesopredators may benefit from reduced interspecific killings (Palomares & Caro, 1999), reduced competition for prey (Polis, Myers & Holt, 1989) or from reduced habitat selectivity because of a lower ‘fear’ of predation (Laundré, Hernández & Altendorf, 2001). Released mesopredators may then increase in abundance, expand their range or both.

Fishers *Pekania [Martes] pennanti* are mesopredators (females 2.0–2.5 kg; males 3.5–5.5 kg) native to the northern forests of North America (Powell, 1993). Their range contracted northward following the Euro-American colonization of North America and the subsequent land conversion, timber and fur harvesting, leaving fishers in the southern portion of their range surviving in isolated refugia (Lewis, Powell & Zielinski, 2012). By the early 20th century, however, agricultural land abandonment increased and forest clearing eased within much of their southeastern range (Pimm & Askins, 1995). Across the US, fisher trapping seasons were closed, first in Wisconsin (1921) and finally in California (1946), reducing the harvest pressure on fisher populations (Powell, 1993). Fisher populations have since expanded their central and eastern ranges southward, aided by successful translocations (Lewis *et al.*, 2012), and have begun colonizing suburban woodlands in parts of their southeastern range (Brown *et al.*, 2012; LaPoint *et al.*, 2013). However, fishers still have the fourth most contracted

geographic range of the 32 North American carnivores investigated by Laliberte & Ripple (2004). Regional variation in fisher range expansion exists, with greater success in the east than west. Their range is restricted along the western coast of the US, despite harvest bans and five translocation efforts (Lofroth *et al.*, 2010; Lewis *et al.*, 2012). In contrast, fisher translocations and subsequent range expansion in their eastern range have been largely successful (Lewis *et al.*, 2012). Lewis *et al.* (2012) suggested that the success of a fisher translocation effort was partially predicted by whether the release occurred within the eastern or western range, and acknowledged that predator–prey communities may be a contributing factor.

Large predators may hinder fisher populations through both indirect (e.g. behavioral avoidance) and direct (e.g. mortality) effects. Records of adult fisher mortalities from predation events are rare, but noteworthy, and illustrate the important mortality risk posed by larger predators. Coyotes *Canis latrans* killed a female fisher in Maine (Krohn, Arthur & Paragi, 1994). In Montana, Roy (1991) documented eight fisher mortalities attributed to predators: three males to cougar *Puma concolor*, one male and two females to coyote, one male to a wolverine *Gulo gulo* and one female to a lynx *Lynx canadensis*. A lynx in British Columbia killed an adult female fisher (Weir & Corbould, 2008). A fisher in Minnesota was killed by a female wolf *Canis lupus*, but was the only report of such an event known to the authors (Palacios & Mech, 2011). Cougars and bobcat *Lynx rufus* have been documented as the most frequent natural mortality sources for male and female fishers, respectively, in California, Oregon and Washington (Wengert *et al.*, 2014). Interspecific killings are common, but often undocumented among carnivores (Palomares & Caro, 1999), and are important factors that affect community structure (Donadio & Buskirk, 2006). Apex predators may also hinder fisher populations through indirect effects, such as increased competition for resources, or by active avoidance of the apex predators and the areas within which they occur (Ritchie & Johnson, 2009). This ‘landscape of fear’ (Laundré *et al.*, 2001) imposed by the apex predators can affect mesopredator behavioral responses, such as changes in activity times and habitat use, thereby reducing prey and habitat availability.

The regional variation in fisher range expansion makes them a suitable species to explore the factors that affect range expansion in carnivores. We investigated whether expanding fisher populations are benefiting from a reduced potential carnivore predator community. We first partitioned the fishers’ geographic range into regions and quantified their range expansion in each region since the date of their most contracted range. We then quantified the overlap of the fishers’ current range with the historic and current ranges of potential predators. If fishers have experienced a reduction in their predator community, then they may expand their ecological niche (Hutchinson, 1957). Fishers could do this by consuming a greater diversity of food items, especially larger-bodied prey (Moreno, Kays & Samudio, 2006), thereby increasing their energy intake efficiency

(Gittleman & Harvey, 1982; Carbone, Teacher & Rowcliffe, 2007). Thus, we predicted that released fisher populations should have more diverse diets that also contain more large-bodied prey than fisher populations who have not experienced a release from their predators. Additionally, larger fishers should be better suited for targeting larger-bodied prey, as these individuals can reduce their prey handling time (Powell, 1979) and should be better suited to defend their cache from interspecific and intraspecific competitors (Arnott & Elwood, 2009). Therefore, we investigated temporal trends in fisher size (i.e. condylobasal length) across their range, predicting that the body size of released fisher populations should increase over time. We tested these hypotheses with available data and highlight areas requiring additional study to help guide conservation practitioners working to re-establish fishers and other carnivore species.

Materials and methods

Fisher range regional divisions

We divided the fishers’ current geographic range (Lewis *et al.*, 2012) into four regions with boundaries delineated based on ecoregions (U.S. Environmental Protection Agency, 2010), genetics (Hall, 1981; Drew *et al.*, 2003) and probable range discontinuities (Lewis *et al.*, 2012) (Fig. 1). The Pacific region includes fisher populations within California and Oregon, corresponding to the probable subspecies (*Pekania pennanti pacifica*) range within the northwestern forested mountains ecoregion, but does not include neither the reintroduced population within northwestern Washington nor the ongoing translocations occurring in the northern Sierra Mountains of California, as the amount of time since individuals were released in these areas (2011 and ongoing, respectively) is insufficient to determine their re-establishment (Lewis *et al.*, 2012). The northwest region includes fishers within western Montana and northern Idaho and extends to the northern and westernmost extent of their current range, ending at the easternmost extent of the northwestern northern forests. The Central region includes the fishers’ range east of the northwest region boundary, ending within Ontario at a probable range discontinuity during the species most contracted range (Lewis *et al.*, 2012), including the states of Minnesota, Wisconsin and Michigan. The eastern region includes areas east of the Central region to the Atlantic Coast and southward along the Appalachian Mountains to West Virginia and including the satellite population introduced in Tennessee.

Predator range overlap

For each region, we compared percentage overlap of the current fisher geographic range with the historic and current geographic ranges of their documented carnivore predators: bobcat, lynx, cougar, coyote, wolf and wolverine. We digitized the current fisher range from Lewis *et al.* (2012) using ArcGIS (version 10.1; Environmental Systems Research

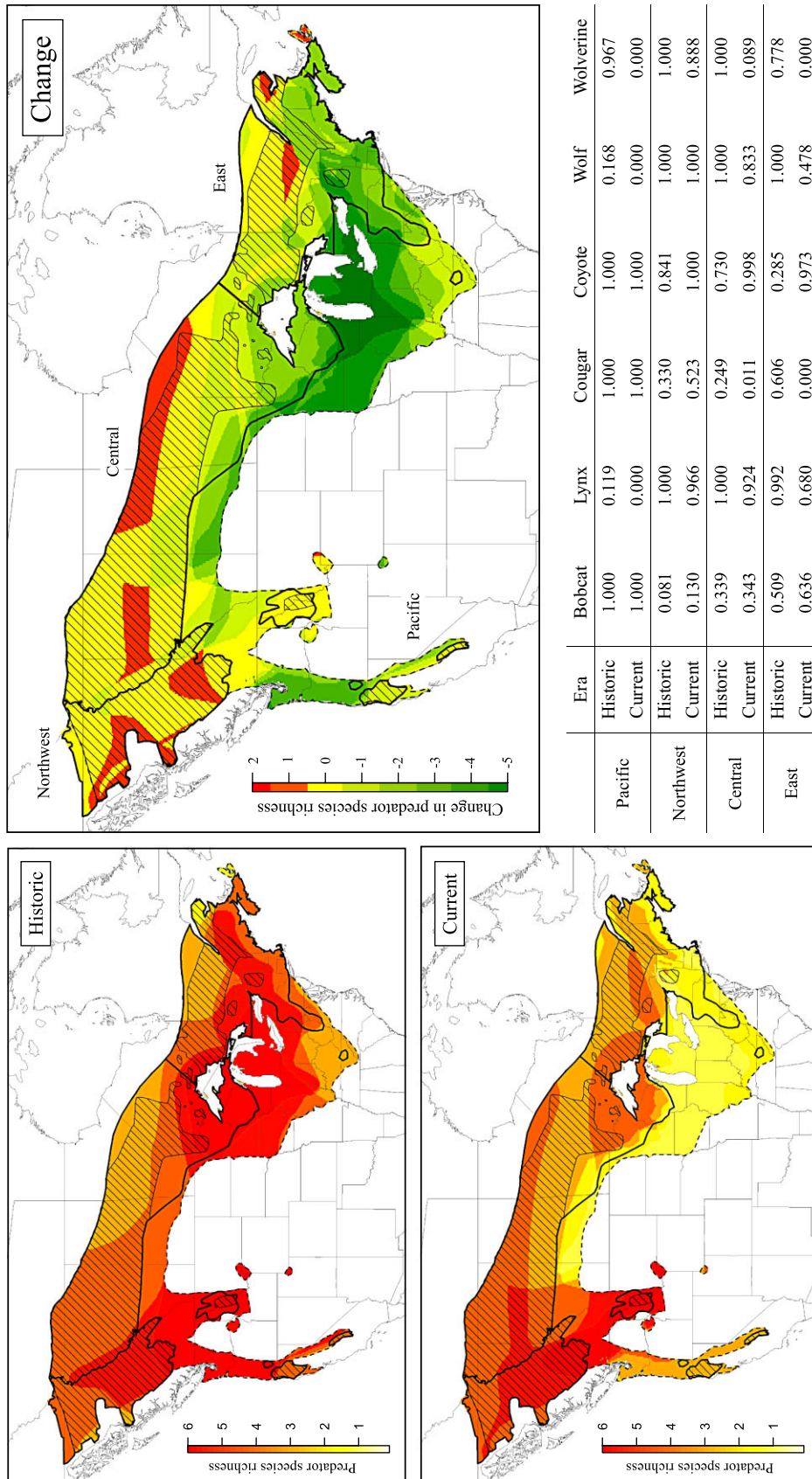


Figure 1 Historic (i.e. 19th century), current and the change in predator species richness across the current and historic ranges of fishers. Dashed line indicates fisher historic range and diagonal lines indicate refugia. Table values indicate the historic and current proportion of each predator species range overlap with the current range of fishers, per region.

Institute, 2012). For the predator historic range maps, we used data from Laliberte & Ripple (2004) and Prugh *et al.* (2009) which are based on field observations from the 18th and 19th century (Hall & Kelson, 1959). We used shapefiles available from the International Union for the Conservation of Nature (2012) as our source for predator current ranges. To quantify changes in the predator community, we first calculated the proportion of overlap of the fisher's current range with each predator's historic range and each predator's current range. We also mapped the change in species richness over time by subtracting the current predator species richness from the historic to visualize the changes experienced by fishers. All spatial analyses were conducted using packages for program R (R Core Team, 2013, version 3.0.1): *maptools* (version 0.8-25; Bivand & Lewin-Koh, 2013), *PBSmapping* (version 2.66.53; Schnute *et al.*, 2013), *raster* (version 2.1-49; Hijmans, 2013), *sp* (version 1.0-11; Pebesma & Bivand, 2005) and *rgeos* (version 0.2-19; Bivand & Rundel, 2013).

Fisher diet

The disappearance of larger carnivores should allow fisher populations to exploit prey species that are now more available because of reduced competition and exclusion with larger carnivores, particularly larger-bodied prey (McKinney & Lockwood, 1999; Gehring & Swihart, 2003; Bowman, Donovan & Rosatte, 2006; Prugh *et al.*, 2009; Clavel, Julliard & Devictor, 2010; Hüner & Peter, 2012). Thus, we hypothesized that the diets of fisher populations experiencing a mesopredator release should contain greater proportions of larger-bodied prey items (i.e. mammals with mass > 1 kg) within their diets than those populations that have not experienced a release. To test this hypothesis, we quantified the diversity and generality of fisher diets by region and compared the proportion of larger-bodied prey within their diets.

We conducted a literature survey, yielding 20 published studies, theses and agency reports, including the 12 studies reviewed by Martin (1994) (Table 1). The diet studies varied in their method for reporting fisher diet composition, so it was necessary to standardize fisher diet compositions. We did this by calculating the % occurrence ($%O_i$) as the number of samples that contained food item i , divided by the total number of occurrences of all food items when raw data were reported (van Dijk *et al.*, 2007). When raw data were not available, we converted reports of % frequency ($%F_i$) (i.e. the number of times food item i was present divided by the total number of analyzed samples) to $%O_i$ by dividing F_i by the sum of frequencies for all food items. Because studies also varied in the level of specificity of their food item identification (e.g. Golightly *et al.*, 2006 vs. Powell, 1977), we reclassified diet components into 13 broad food item categories: insectivores, mice and voles (including bats and *Ochotona* spp.), arboreal rodents, ground squirrels (excluding species with mass > 1 kg), lagomorphs (including *Sylvilagus* spp. and *Lepus* spp.), porcupine *Erethizon dorsatum*, carnivores, other large mammals (including

'carrion', beaver *Castor canadensis*, muskrat *Ondatra zibethicus*, *Odocoileus* spp., moose *Alces alces*, reindeer *Rangifer tarandus*, elk *Cervus canadensis* and woodchuck *Marmota monax*), bird (including eggs), reptiles and amphibians, insects, fruit and vegetation (Table 1). We excluded 'unknown', 'remainder', 'other', 'rock' and 'trace materials' that were listed as diet items within studies. We then calculated the diet diversity of each study using the % occurrence values of these reduced food item categories with the Shannon-Weiner diversity index (H'_{red}) (Zar, 1996). After using a Shapiro-Wilk normality test to find that H'_{red} was not normally distributed, we used Wilcoxon rank sum tests to compare diet diversity among regions.

To facilitate interpretation of fisher diet specialization related to the prevalence of large-bodied prey, we calculated Kendall's coefficient of concordance (W) on the reduced food item categories. This allowed us to quantify the variability of food item contribution rankings within fisher diets and also to investigate whether these contributions varied between and within regions (Legendre, 2005). To estimate Kendall's W , food items (rows) are arranged by study (columns) and each food item is ranked by their proportion within each study. These rankings are then summed for each food item (row) and the variance of these ranking sums is estimated. For example, if the food item rankings are consistent across all studies, then the variance of the ranking sums (i.e. W) will be high, suggesting the diet is specialized. As W approaches 0, the food item rankings across diet studies approach dissimilarity (food item rankings are variable; i.e. opportunist or generalist diet), and as W approaches 1, the food item rankings become more similar (i.e. specialized diet) (Legendre, 2005).

Fisher body size

We measured condylobasal length data on museum specimens across North America to investigate whether fisher body size has changed since their most contracted range. Earlier work suggested that fisher skull size varies geographically, with the pacific and the eastern populations having the smallest skulls (Hagmeier, 1959). However, data from more recent specimens were required to test our hypotheses. Condylobasal length is a commonly used body size metric as it is invariant with body condition and age in adults, and is associated with low measurement error (Meiri, Dayan & Simberloff, 2005; Meiri *et al.*, 2009). Condylobasal length measurements were taken by natural history museum staff or the authors using digital calipers to at least 0.1 mm precision. We only included sexed, adult (i.e. fused cranial sutures), wild caught specimens with locality data. When coordinates were not available, we georeferenced the center of the town or city, excluding specimens whose spatial data contained a courser resolution (see Supporting Information Appendix S1). For female specimens, we excluded individuals with condylobasal lengths greater than the 95% confidence interval, and for males, we excluded condylobasal lengths that were less than the 5% confidence interval, under the assumption that these

Table 1 Fisher diet studies (sample size, time of year) listed by region and date with the number of occurrences per food category (arranged alphabetically), total occurrence (O), diversity of the full food item list (H') and the reduced food item list (H'_{red}) we created to be more comparable between studies, and the proportion of the diet comprised of large-bodied prey (i.e. mammals with mass > 1 kg; indicated with '**' within food categories). Unless reported as 'bait' within the study, 'large mammal' includes beaver, muskrat, deer, moose, reindeer, elk and woodchuck

	Arboreal rodent	Bird	Carnivore*	Fruit squirrel	Ground squirrel	Herptile	Insect	Insectivore	Large mammal*	Mice & voles	Porcupine*	Rabbit*	Vegetation	O	H'	H'_{red}	Large prey
Pacific ($W = 0.401$)	106	315	39	61	128	169	440	111	133	105	7	105	377	2096	2.923	2.272	0.135
Grenfell & Fasenfest, 1979 (8, winter)	1	0	0	0	0	0	0	1	2	3	0	1	4	12	2.120	1.633	0.250
Zielinski et al., 1999 (201, year)	24	90	2	18	13	41	113	9	8	41	0	1	0	360	2.233	1.877	0.031
Aubry & Raley, 2006 (387, year)	18	109	10	0	66	25	99	16	42	8	7	87	53	540	2.407	2.164	0.270
Golightly et al., 2006 (388, year)	63	116	27	43	49	103	228	85	81	53	0	16	320	1184	2.571	2.175	0.105
Northwest ($W = 0.719$)	95	23	47	0	3	0	3	32	143	115	43	95	33	632	2.603	2.069	0.519
Jones, 1991 (25, year)	5	4	2	0	3	0	3	0	13	10	1	11	33	85	2.860	1.858	0.318
Weir, Harestad & Wright, 2005 (215, winter)	90	19	45	0	0	0	0	32	130	105	42	84	0	547	2.617	1.928	0.550
Central ($W = 0.579$)	21	45	9	0	0	6	3	7	32	21	12	188	20	364	1.950	1.689	0.662
Powell, 1977 ^a (35, winter)	5	0	0	0	0	0	0	3	7	7	7	11	2	42	1.828	1.834	0.595
Leonard, 1980 (120, winter)	14	22	1	0	0	1	0	4	20	12	5	43	0	122	2.484	1.771	0.566
Raine, 1987 (159, winter)	2	23	8	0	0	5	3	0	5	2	0	134	18	200	1.347	1.202	0.735
East ($W = 0.528$)	281	214	34	171	19	3	59	293	473	380	168	294	340	2729	3.145	2.276	0.355
deVos, 1952 (66, winter)	5	2	4	4	0	0	14	4	15	6	20	26	0	100	2.416	2.015	0.650
Hamilton & Cook, 1955 (60, winter)	11	6	1	14	0	0	2	8	12	14	5	8	6	87	2.625	2.233	0.299
Coulter, 1966 (369, winter)	53	34	18	26	3	3	12	34	152	58	74	82	0	549	2.790	2.114	0.594
Stevens, 1968 ^a (490, year)	83	18	6	0	13	0	21	182	83	134	5	65	131	743	2.381	1.999	0.214
Clem, 1977 (176, winter)	3	47	2	10	0	0	0	19	34	33	30	26	0	204	2.473	1.952	0.451
Kelly, 1977 (40, winter)	8	4	0	4	0	0	0	5	0	17	0	3	0	41	2.275	1.586	0.073
Brown & Will, 1979 ^a (332, winter)	73	10	3	0	3	0	10	10	87	57	20	40	203	516	2.094	1.801	0.291
Arthur, Krohn & Gilbert, 1989 (69, winter)	17	9	0	25	0	0	0	4	5	6	14	12	0	92	2.197	1.918	0.337
Giuliano, Litvaitis & Stevens, 1989 (331, winter)	28	84	0	88	0	0	0	27	85	55	0	32	0	399	2.308	1.835	0.293
<i>Pekania pennanti</i> ($W = 0.314$)	503	597	129	232	150	178	505	443	781	621	230	682	770	5821	3.455	2.372	0.313

^aStudy details taken from table 8 of Powell (1993).

individuals may have been incorrectly sexed. We used a generalized linear model to determine whether fisher skull lengths have changed over time. We ran these models per sex for each region separately, with no interaction terms, an alpha of 0.05 and assumed skull lengths had a Gaussian distribution. We searched for non-normality in the residuals and used Cook's distance (D) to verify that no specimens had undue influence on the final model (i.e. specimens with potential measurement error) (Zar, 1996).

Results

Fishers have extended their range by 57% from their most contracted range, but the amount of range expansion varied among regions. Fishers in the eastern and central regions have increased their geographic ranges by 119% and 46%, respectively, although they do not yet fully occupy their historic ranges (Fig. 1). In contrast, fishers in the pacific and northwestern regions have expanded their ranges by only 15% and 18%, respectively. Fishers have also experienced changes in the members of, and overlap with, their predator communities (Fig. 1). The expanding eastern fisher populations have experienced a 34% reduction in their predator species overlap, including the complete loss of cougar and wolverine and large range overlap reductions in lynx and wolf (Fig. 1). The Central region has experienced a 25% reduction in their predator range overlap, with large reductions again in both cougar and wolverine. Fishers within the northwest region, however, have experienced a 6% increase in their predator co-occurrence with only small reductions in their overlap with lynx and wolverine. However, changes in the pacific fisher predator community (29% reduction) are not consistent with the mesopredator release hypothesis. Pacific fishers have experienced the complete loss of lynx, wolf and wolverine, but continue to have complete overlap with bobcat, cougar and coyote.

Two diet studies (Kuehn, 1989; Roy, 1991) were excluded from our analyses because they did not report values from which we could calculate % occurrence. We were not able to replicate the exact H' values reported by Martin (1994), but our H' values were positively correlated with those reported by Martin (1994) ($r_s = 0.74$, $P = 0.008$) and our H'_{red} and H' estimates were also correlated ($r_s = 0.74$, $P < 0.001$). For the remaining 18 diet studies, we found no differences in the dietary diversity (H'_{red}) between fisher population regions (Wilcoxon tests; $P > 0.3$) nor in their variances (F-test of variance; $P > 0.176$). Fishers were generalist predators across their range ($W = 0.314$), but again we found no differences in W between regions (Wilcoxon tests; $P > 0.1$) (Table 1). The proportion of large-bodied prey did vary between regions, with the diets of central fishers containing more large-bodied prey than eastern ($t = 3.455$, $P = 0.009$) and pacific fishers ($t = 6.022$, $P = 0.002$), and eastern fishers consuming more large-bodied prey than pacific fishers ($t = 2.295$, $P = 0.047$) (Table 1).

Condylobasal lengths for male fishers were 17% larger than those for females ($n = 180$, 115.89 mm, $SD = 3.81$ mm and $n = 203$, 99.43 mm, $SD = 2.61$ mm, respectively)

(Supporting Information Appendix S1). As predicted, both male and female eastern fisher condylobasal lengths have increased since the late 19th century whereas northwest female skull lengths have decreased over the last century (Fig. 2). We found no significant patterns for central and pacific fishers or for northwest male fishers. Although the general linear model suggested pacific male fisher skulls have increased in length, we consider this result inconclusive as we were only able to measure five specimens that were collected since 1930 in this region.

Discussion

The fishers range expansion varied geographically with the greatest expansion occurring southward in their eastern range, while their western populations have expanded their ranges considerably less. The fisher's predator community has also changed in both composition and area of co-occurrence between regions during this time. The fishers range expansion in the eastern and central regions appears coincident with reductions in the predator species richness and with reduced predator co-occurrence, particularly within the southern extents of these regions, thus supporting our predictions. Further, the relatively small amount of range expansion experienced by the northwestern fishers may support our predictions as these fishers have experienced an increase in range overlap with their predator community. Thus, it appears that reductions in the predator community are either facilitating or correlated with fisher population range expansion, particularly within the southern extents of the central and eastern regions. Apex predators have been reported to reduce abundance of mesopredators (e.g. Levi & Wilmers, 2012; Pasanen-Mortensen, Pyykonen & Elmhagen, 2013) that in turn could influence mesopredator range expansion (Ripple *et al.*, 2013). The limited range expansion of the pacific fishers does not match our predictions, despite reductions in their predator community, bans on their harvest and five translocation efforts (Lewis *et al.*, 2012). The cause of limited range expansion for pacific fishers is unclear, but could be influenced by multiple factors including variation in abundance of fishers and other predators compared with other regions, anthropogenic pressures and multiple bottom-up processes (Casanovas *et al.*, 2012; Kennedy *et al.*, 2012; Pasanen-Mortensen *et al.*, 2013; Schuette *et al.*, 2013). Recent mortality data suggest that predation by cougars and bobcats are frequent in pacific fisher populations, further underscoring the importance of larger predators to fisher population dynamics (Wengert *et al.*, 2014).

Fisher diets should contain food items that provide the greatest ratio of energy provided per unit effort, such as carrion or rabbits (Charnov, 1976). Shifts in species' niche breadth often occur in the absence of, or reduction in, competitors (e.g. Ginger *et al.*, 2003; Mesquita, Colli & Vitt, 2007). Released mesopredators may capitalize on the now relatively more available food items, particularly large-bodied prey species (Moreno *et al.*, 2006), despite the potential for simultaneous increases in other mesopredator

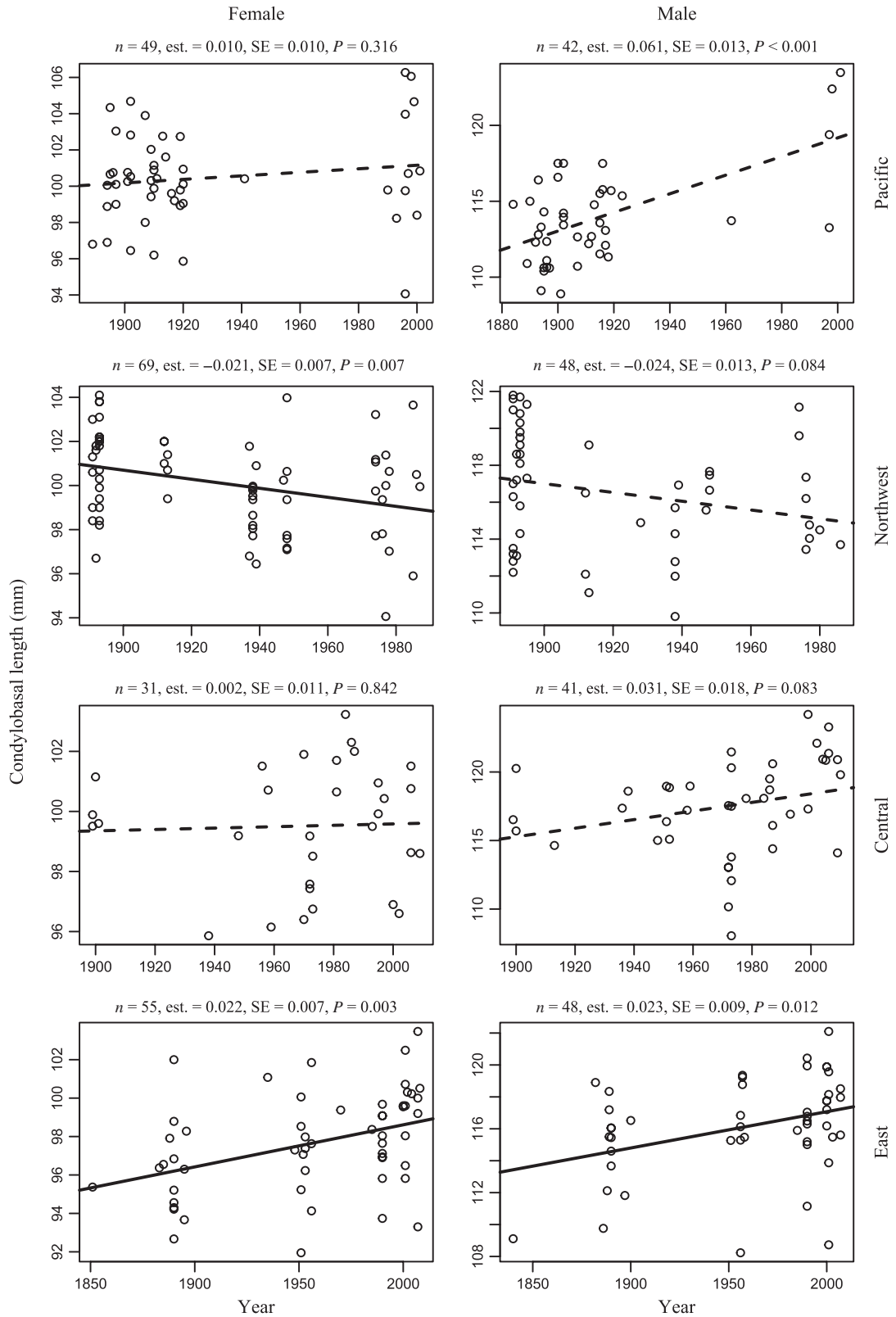


Figure 2 General linear model results showing changes in fisher skull size (condylobasal length) over time. Sample sizes (n), model estimates ($est.$), standard error (SE) and P -values (P) indicated, with significant ($P < 0.05$; solid) and non-significant (dashed) trend lines.

species abundance. Consuming these larger-bodied prey species could facilitate range expansion for fishers as these species provide more energy per unit of effort (Powell, 1979) and can be cached for future consumption (Kuehn, 1989; Powell, 1993; Bowman *et al.*, 2006; Hüner & Peter, 2012). This is especially advantageous for dietary generalists, such as fishers, that are able to add large-bodied prey species to their already general diets (McKinney & Lockwood, 1999; Gehring & Swihart, 2003; Prugh *et al.*, 2009; Clavel *et al.*, 2010). The reduced predator community in the eastern region may be especially beneficial to the fishers in this region as they consumed a diversity of food items including large-bodied prey, particularly rabbits and other large mammal species, possibly in the form of carrion. Fisher diets that contained more low-ranked food items could suggest that the population is experiencing high competition for these high-ranked food items.

A mesopredator release is also predicted to select for an evolution of larger body size in the 'released' species (Dayan & Simberloff, 1994; Simberloff *et al.*, 2000) as these larger individuals can more efficiently kill larger prey species (Powell, 1979) and are more able to defend their cache from interspecific and intraspecific competitors (Arnott & Elwood, 2009). Supporting this, we found that the size of the released eastern fishers, as indexed by condylobasal length, has increased over the last century. Central male fishers show a similar, but non-significant, trend ($P = 0.083$). Interestingly, the skull size of female northwestern fishers (who have experienced an increase in predator overlap) has decreased significantly; northwestern male fishers show a similar but non-significant negative trend ($P = 0.084$). We believe these results are authentic and are not an artifact of translocation efforts because the source population and destination for most translocations (15 of the 17 eastern and five of the seven northwestern translocations) were from within the same region (Lewis *et al.*, 2012). Further, because condylobasal length is invariant with age of adults, and is unaffected by seasonal changes, animal health and food abundance (Meiri *et al.*, 2009 and citations within), we were able to limit our risk of type I and II errors that may otherwise be more likely with an analysis of body mass, for example. Unfortunately, our interpretation from the Pacific fishers is limited due to the low number of specimens collected between 1930 and 1990, and we strongly encourage the continued deposition of specimens to natural history museum collections.

Although our results are correlational, all three analyses partly support the predictions of the mesopredator release hypothesis and suggest some insightful patterns. For example, coyote co-occur with fisher nearly completely, but do not appear to greatly hinder their populations given that both species have robust populations in the east (Kays, Gompper & Ray, 2008). Cougar populations, however, were extirpated from the eastern half of North America, yet co-occur with Pacific fisher completely, have expanded their northwestern range and are the most frequent documented predator of adult male fishers within the Pacific States (Wengert *et al.*, 2014). These killings are not well

predicted by the species relative body sizes alone (Donadio & Buskirk, 2006); however, cougars seem prone to interspecific killings across their range including hog-nosed skunk *Conepatus humboldtii* (Johnson & Franklin, 1994), wolverine (Krebs *et al.*, 2004), ocelot *Leopardus pardalis* (Nuñez, 1999), culpeo fox *Pseudalopex culpaeus* (Novaro, 1997), chilla fox *Pseudalopex griseus* (Yañez *et al.*, 1986) and gray fox *Urocyon cinereoargenteus* (Logan & Sweanor, 2001). The degree of intraspecific killing among carnivores is varied and in addition to body size, can be influenced by diet, predatory habits and taxonomy (Donadio & Buskirk, 2006).

Future directions

Numerous natural and anthropogenic drivers are likely affecting the current range of fishers. Translocation efforts have facilitated their range expansion, yet efforts to explain why translocations have been more successful in the east than in the west were inconclusive (Lewis *et al.*, 2012). The chronology of and time since Euro-American settlement across North America may be a factor, as fisher populations in their eastern range may be receiving a twofold advantage from this temporal effect: more time for their forests to recover and more time for the fishers themselves to adapt to human activities. Differences in fisher habitat selection across their range could also be important and should be explored, given the differences between the ecological landscape and current land management regimes (Pimm & Askins, 1995; Lofroth *et al.*, 2010). Such an effort would have to overcome the variety of methods used to record fisher movement patterns and to quantify their habitat use and availability (but see Aubry *et al.*, 2013). Rodenticide poisoning is a threat to fishers in California (Gabriel *et al.*, 2012), yet has not been reported elsewhere (e.g. Stone, Okoniewski & Stedelin, 1999) and warrants continued vigilance. Given the results of our large-scale comparisons, we advocate for additional fine-scale research into interactions between fishers and co-occurring carnivore species to provide direct information on potential mesopredator release effects, including food web dynamics, resource partitioning, behavioral responses, predator-prey dynamics and especially, cause-specific mortality.

Conclusion

The mesopredator release hypothesis has typically been explored on species that are colonizing new habitats (e.g. raccoons *Procyon lotor* or domestic cats *Felis catus*) leading to associations with ecosystem collapse, local extinction and other negative phenomenon (Crooks & Soulé, 1999; Prugh *et al.*, 2009; Ritchie & Johnson, 2009). Here, however, we present an example of a once rare carnivore that appears to be benefiting from a reduced predator community. The fishers limited range expansion in its southwest range, despite its reduced predator community, suggests that future translocation efforts should target areas with lower predator densities and species richness, in addition to other documented factors (Lewis *et al.*, 2012; Powell *et al.*, 2012).

Elsewhere and for other species, future efforts to reintroduce mesopredators should consider the predator community at the release site and their potential threat to the released animals. Efforts to re-establish apex predators should consider the ecosystem stability of the release site and assess their potential impacts on already re-establishing species, especially if these species have yet to stabilize.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Specimens used in our analysis of fisher body size (i.e. condylobasal length; CBL).