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Many demographic parameters of imperiled fishers (Martes pennanti) in the Pacific Northwest remain poorly understood but are necessary to develop conservation strategies; herein we report on fisher reproduction, recruitment, and dispersal on the Hoopa Valley Indian Reservation, California, to help fill key knowledge gaps. Forty radiocollared, breeding-age females exhibited denning behavior on 80 (87%) of 92 opportunities between 2005 and 2011. Twenty-eight female fishers weaned offspring in 55 (65%) of 85 adequately monitored denning opportunities. Two-year-old female fishers were less likely than older females to den and wean kits. We counted 52, and extracted and marked 51, kits comprising 28 litters of 19 females between 2005 and 2008. Average litter size was 1.9 kits (27 females, 24 males, and 1 unknown) 4–12 weeks postbirth. Mean distances between natal dens and centroids of newly established ranges for 7 juvenile females was 4.0 km (range = 0.8–18.0 km); this distance for 1 male was 1.3 km. The recruitment rate of juveniles that successfully established a home range per adult female was 0.19 (0.16 for females and 0.02 for males). Our results suggest that managers should work toward increasing female survival rates and consider translocations to increase and expand existing fisher populations.

Key words: dispersal, fisher, Martes pennanti, recruitment, reproductive rates, vital rates

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Fisher (Martes pennanti) populations in the Pacific states have suffered significant declines and range contractions over the last 2 centuries (Lewis et al. 2012). In California, fishers occur in less than 50% of their historical range in 2 isolated populations (Zielinski et al. 1995, 2005). These declines have been linked to overtrapping for furs; predator- and pest-control campaigns; and loss and fragmentation of forested habitats by logging, fire, and farming (Douglas and Strickland 1987; Powell 1993; Powell and Zielinski 1994).

Small and isolated populations have been identified as the most challenging threat to the conservation of fishers in the Pacific states (Lofroth et al. 2010), and the 2 extant fisher populations in California have failed to recover from range contractions (Aubry and Lewis 2003; Matthews et al. 2011; Spencer et al. 2011; Zielinski et al. 1995, 2005). Thus, current sizes and distributions of fisher populations in the Pacific states place them at inherently higher risk of extinction due to potential stochastic phenomena (Lofroth et al. 2010; Shaffer 1981). Lofroth et al. (2010) suggest the most effective conservation strategy to reduce extinction risk involves protecting existing populations and encouraging them to expand beyond their current boundaries (Lofroth et al. 2010).

Rates of reproduction, recruitment, and dispersal are needed to adequately model population dynamics, sub- and metapopulation extinction risk, the ability of populations to recolonize suitable habitat, and gene flow (Brown and Kodric-Brown 1977; Hanski 1999; Krebs 2009; Levins 1970). These are particularly important variables to understand when considering subpopulations that are increasingly isolated by habitat change and fragmentation (Hanski 1999; Levins 1970; Macdonald and Johnson 2001; Stephens et al. 2004). Only 1 study (Reno et al. 2008) has reported on denning rates for northern California fishers. However, samples sizes were small (n ≤ 14 female fishers) and variation among the 2 years of the
Our goal was to quantify reproduction, recruitment, and dispersal of fishers in managed, Douglas-fir (*Pseudotsuga menziesii*)–dominated forests on the 366-km² Hoopa Valley Indian Reservation in northwestern California (hereafter, Hoopa; Fig. 1) to inform conservation efforts. In 2005, fisher density in Hoopa declined to about 14 individuals/100 km² from 52 individuals/100 km² in 1998 (Matthews et al. 2011). The causes of the decline are unknown. Examination of mark–recapture data anecdotally suggested the population had stabilized or was increasing by 2006. Thus, we hypothesized that Hoopa fishers would exhibit higher reproductive, higher recruitment, and lower dispersal rates than other unharvested fisher populations as the Hoopa population recovered and available habitat was reoccupied.

**MATERIALS AND METHODS**

**Study area.**—Our study area was located within the Klamath physiographic province (Kuchler 1977) in northwestern California (Fig. 1); elevations ranged between 98 and 1,170 m. Mean daily maximum and minimum temperatures were 22°C and 6°C, respectively, and mean annual precipitation, primarily rain, was 138 cm (National Climate Data Center 2011). Hoopa supported a human population of approximately 2,600 (U.S. Census Bureau 2002), to whom fishers are culturally significant and not harvested outside rare harvest for ceremonial regalia (Cooperrider et al. 2000).
Forests within the study area generally had an overstory dominated by Douglas-fir and a midstory dominated by hardwood trees including tanoak (Lithocarpus densiflorus), madrone (Arbutus menziesii), Oregon white oak (Quercus garryana), California black oak (Q. kelloggii), and canyon live oak (Q. chrysolepis). Hardwood stands occurred in localized areas, whereas at higher elevations Douglas-fir was replaced by white fir (Abies concolor) and pine (Pinus spp.). Hoopa was bisected by the Trinity River into eastern and western portions (Fig. 1).

Past and current timber harvests created a mix of mature old-growth and early second forests. Prior to 1990, clear-cuts averaged 12–20 ha, although cuts up to 276 ha occurred. From 1960 to 1980, 30% of Hoopa was harvested, averaging over 500 ha/yr across multiple clear-cuts averaging 19 ha. Between 1994 and 2010, under the direction of the Hoopa Tribe’s Forest Management Plan, tribal forest managers averaged 12–20 ha, although cuts up to 276 ha occurred.

We used ground-based radiotelemetry techniques using a handheld receiver (model TR-4; Telonics, Inc.; or model R1000; Communications Specialists, Inc., Orange, California) and a 4-element antenna (model RA-14; Telonics, Inc.) to estimate locations of fishers and identify den structures. Locations of inactive fishers were obtained using the loudest-signal method and by hiking to the source of the signal (Springer 1979). The observer circled the collared fisher until an individual tree or other structure was isolated and identified as the most likely position of the transmitter. The location of the structure was recorded using a handheld global positioning system unit (Garmin Rino 120; Garmin International, Inc., Olathe, Kansas) with a 3-dimensional fix with an estimated error ≤10 m.

We calculated the proportion of monitored adult female fishers that exhibited denning behavior and the proportion that weaned at least 1 kit. We defined “denning opportunities” as the total number of individual, breeding-age (≥2 years old) female fishers monitored across all den seasons (March–June—Powell 1993). We defined a den as a structure used ≥2 times in succession over ≥3 days by an adult female within the den season for birthing and nursing kits (Aubry and Raley 2006; Truel et al. 1998). We classified dens as natal (location where parturition took place) or preweaning (any den used after the natal den and before the kits were weaned [Lofroth et al. 2010]). We considered kits weaned at 10 weeks of age or by 31 May if no parturition date was established (Powell 1993). We determined if denning and weaning rates were independent of adult female age class using Fisher’s exact tests using the BASE package in program R version 2.13.2 (R Development Core Team 2011).

We investigated dens 4–12 weeks after kit parturition when the adult female was not present. Den investigations involved climbing the den tree using a single-rope technique or tree-climbing spurs and a flip rope (Jepson 2000). The presence and number of kits were determined visually, often with the aid of a Burrow Camera System (Sandpiper Technologies, Inc., Manteca, California). We extracted kits from dens without physically altering the den structure. Kits were not anesthetized and were handled for <60 min. We warmed kits with a towel and heat packs if necessary. We marked kits with a passive integrated transponder tag for future identification. Tissue, ectoparasites, and swabs of ocular exudate, nasal exudates, and feces were collected for genetic and disease analyses. Morphometric measurements, an assessment of overall body condition, and condition of eyes (open or closed) were recorded. After handling, we placed kits back at their site of capture.

Locating and investigating dens.—During the early den season (1 March–15 April) we attempted to locate inactive female fishers 4 or 5 days/week to observe reuse of sites indicating den establishment. Denning behavior was identified by a sudden change in activity from using numerous rest sites per week across the majority of the home range to more restricted movements in a small portion of the home range and repeated use of the same structure while inactive (Aubry and Raley 2006).
Our capture and handling methods followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Institutional Animal Care and Use Committee of Humboldt State University (protocol 04104.W.42.A). Our den investigation techniques were approved under a National Environmental Policy Act compliance checklist (in cooperation with G. Falxa, United States Fish and Wildlife Service, Arcata, California), which specified that we were to immediately terminate den investigations if we detected signs of litter abandonment.

Recruitment.—We calculated recruitment rates (number of juveniles/adult female) at 3 time intervals: at weaning, after the fall–winter livetrapping period, and at home-range establishment (often by April of their 2nd year).

Dispersal.—We determined the timing of dispersal movements, dispersal distance, and fate by conducting telemetry monitoring of each radiocollared juvenile. We used ground-based and aerial telemetry techniques to track fisher movements and dispersal patterns within and outside the mother’s home range, which we defined as the natal range. We located all radiocollared animals 1 or 2 days/week from the ground. We used a Cessna 182 plane, a model 1000 receiver (Advanced Telemetry Systems, Inc., Isanti, Minnesota), and 4-element yagi antennas (Advanced Telemetry Systems, Inc.) in aerial telemetry efforts within 30 days following our inability to locate a radiocollared animal from the ground.

We plotted juvenile locations collected on a weekly basis and measured dispersal distances using ArcGIS 9.3 (ESRI, Redlands, California). We measured dispersal distances as the straight-line distance between the natal den (or the 1st preweaning den if the natal den was not located) and the most distant location recorded for each fisher (Arthur et al. 1993; York 1996) and between the natal den and the centroid, or geometric center, of each fisher’s 95% minimum convex polygon home-range estimate. We calculated home-range estimates using an average of 55 locations/fisher (range = 39–61 locations) that were limited to diurnal, ground-based telemetry and capture locations collected between 1 April and 31 March of the fisher’s 2nd year (Bennett et al. 2001; Weir and Corbould 2008). We used 95% minimum convex polygon home ranges so that we could compare our results to those from previous studies. We calculated home-range estimates and centroids using Home Range Extension and Tools (Blue Sky Telemetry, Aberfeldy, Scotland) and XTools Pro Shapes to Centroids tool (Data East, LLC, Novosibirsk, Russia) in ArcGIS 9.3. We selected the date range based on spatial data that indicated that fishers in Hoopa finished dispersing and began establishing a home range by mid-March of their 2nd year. We categorized these distances as follows: juveniles that lived to their 2nd birthday and established a home range, juveniles that died prior to establishing a home range, and juveniles that we failed to locate and never detected again with radiotelemetry during dispersal (Arthur et al. 1993).

RESULTS

We captured 179 individual fishers (94 females and 85 males) on 839 occasions during 15,215 trap-nights between 2004 and 2011. Forty radiocollared, breeding-age (≥2 years old) female fishers exhibited denning behavior in 80 (87%) of 92 opportunities to produce offspring during 7 den seasons from 2005 to 2011 (Table 1). The average start and end dates that female fishers exhibited denning behavior were 22 March and 25 May, respectively. Female fishers started denning as early as 9 March and as late as 7 April. Eighteen (23%) of 80 whelping and rearing episodes failed prior to kits being weaned (Table 1). Five of the failures were the result of the denning female being killed by a predator, and a 6th was the result of the denning female dying of either disease or poisoning. The ultimate cause of the remaining 12 failures could not be determined. Additionally, we were unable to adequately monitor 5 females closely enough during 7 denning opportunities to determine their fate because of limitations in field staffing (Table 1). Thus, 55 (65%) of 85 adequately monitored denning opportunities of 28 adult female fishers were successful in weaning at least 1 kit. Denning and weaning rates were not independent of adult female age class (P < 0.001; Table 1). Two-year-old females were less likely than expected to den and wean. Females 3–5 years old were more likely than expected to den, and weaned kits in accordance with expectations. Females ≥6 years old were more likely than expected to den and wean.

Female fishers monitored from den initiation until weaning (n = 28) used a mean of 3.1 dens per den season (n = 53 denning opportunities, range = 1–6 dens). Successive dens were located an average of 385 m apart (n = 138, range = 18–1,728 m). Females monitored until weaning moved an average total distance between successive dens of 873 m (n = 52, range = 0–2,459 m).

We counted 52 kits in 28 litters born to 19 females during 4 den seasons between 2005 and 2008. Average litter size at the time of extraction from the den was 1.9 kits (27 females, 24 males, and 1 unknown). We documented the deaths of 6 kits (3 females and 3 males) prior to weaning in 4 litters. Necropsy of a dead female kit from a litter of triplets suggested death due to starvation. We suspected that a female kit we marked in a den had died when we could not locate her during the marking of 2 male littersmates 12 days after marking the female. We found 2 male kits dead in their den and presumed a male and female kit died following the death of their mothers from predation. We successfully rescued a female kit from another litter from its den after her mother was predated upon. We raised her in captivity and subsequently released her within her mother’s home range. Data on the dispersal patterns of this kit are not reported here. We surveyed 1 other litter, from which we extracted and marked 1 female kit but were unable to extract and mark its littersmate. Additionally, we were unable to monitor the adult female to determine the success of weaning.

We believe 43 kits (22 females and 21 males) were weaned from 24 adequately monitored litters of 16 adult female fishers after accounting for known and suspected adult and kit
mortalities (Table 2). We captured 14 passive integrated transponder–tagged juveniles (12 females and 2 males) of the 43 kits and radiocollared during fall livetrapping sessions. We captured 13 passive integrated transponder–tagged juveniles between 15 September and 8 January during their birth year. We failed to capture 1 juvenile female during her birth year but captured her as a 1 year old on 28 January within her mother’s home range. We captured 9 of the 14 juveniles within their home range (dispersal distances of 3.6 and 18.0 km). The mean maximum distance between a natal den and the most distant location recorded for juvenile fishers (including those that died during dispersal or were lost from contact) was 6.7 km (range = 2.1–20.1 km) for females and 8.1 km (range = 5.9–10.3 km) for males.

### Discussion

Forest-resource extraction and other human activities are believed to threaten the long-term persistence of fisher populations throughout their range (Proulx et al. 2004; Weir et al. 2012). An understanding of parturition dates could prove useful if the need to develop seasonal management restrictions becomes necessary. Parturition dates reported for fishers in the Pacific states range from the last 2 weeks in March through the 1st week in April, with a mean litter size of 1.8 (range = 1–3—Aubry and Raley 2002; Truex et al. 1998). In the northeastern United States, parturition dates for fishers are slightly earlier (3 March–1 April), with a mean litter size of 2.4 (range = 1–4—Paragi et al. 1994; York 1996). Our average estimate of parturition of 22 March (range = 9 March–7 April) with an average litter size of 1.9 (range = 1–3) was similar to these findings.

Our estimate of the proportion of monitored females that exhibited denning behavior (87%) was higher than estimates presented for other areas within the Pacific states (range = 50–69%—Aubry and Raley 2006; Reno et al. 2008; Truex et al. 1998; Weir and Corbould 2008) and eastern North America (range = 45–65%—Arthur and Krohn 1991; Paragi et al. 1994; York 1996). We suspect that the higher denning rates in Hoopa compared to other Pacific coastal populations could be a function of higher quality habitat at Hoopa, more accurate age
determination, population age structure of study populations, or a combination of these factors. Estimated denning rates presented by Truex et al. (1998), Aubry and Raley (2006), and Reno et al. (2008) were based on age estimates determined by subjective assessments of body and dentition condition. We speculate that if these researchers classified juveniles as potential breeders they would have underestimated denning rates of breeding-age females. In addition, the age structure of the population at the time of each study could have influenced observed denning and weaning rates. Populations weighted heavily to younger animals, such as harvested populations in eastern North America (Brown et al. 2006; York 1996), would be expected to have lower denning and weaning rates because we found older females are generally more reproductively successful than younger females.

Not all reproductive efforts in our study area were successful. Although 87% of the adult females we monitored exhibited denning behavior, only 65% weaned at least 1 kit. Similarly, Aubry and Raley (2006) reported that, on average each year, 44% of females monitored successfully weaned ≥1 kit, although 59% exhibited denning behavior. Additionally, similar to Reno et al. (2008), we found annual weaning rates of female fishers to vary widely (range = 0.33–0.92; Table 1). These results demonstrate that evidence of reproduction does not necessarily reflect successful weaning of kit(s) or recruitment and multiple years of monitoring are required to capture the range of variation in female fisher reproduction. Furthermore, younger adult female fishers are less likely than older females to den and successfully wean kits. Conservation strategies that increase female survival rates (e.g., females reaching ≥5 years of age on average) might be instrumental in efforts to increase populations of fishers. Managers should conserve patches of existing mature forest, maintain larger numbers and a diversity of structural elements in project areas, and promote tree growth (e.g., appropriate crown development), damage (e.g., low-intensity surface fires), disease, and decay that recruit fisher reproductive habitat (Lofroth et al. 2010; Weir et al. 2012).

Female fishers in Hoopa typically used more than 1 den structure during the den season, moving from 18 to 1,728 m between successive structures. Despite this distance, dens used within a season were located within a small, concentrated area of each adult female’s home range. This concentrated use could be related to availability or spatial distribution of den and rest structures with favorable microclimates, food availability within a localized area of the home range, or some other factor. This aspect of fisher spatial ecology warrants further investigation to determine its relationship to fecundity.

The unexpected female bias in our captured and radio-collared sample of kits could be due to male fishers dispersing earlier than females, prior to the start of livetrapping in early September. This hypothesis is supported by our livetrapping data. We captured a nearly equal sex ratio among marked and previously unmarked juvenile fishers during our capture efforts (22 females and 19 males). Twelve (55%) of the 22 juvenile females we captured and 2 (11%) of the 18 juvenile males we captured had been marked as kits. Our results support the theory that fishers have male-biased dispersal and female philopatry (Aubry and Raley 2006; Aubry et al. 2004; Williams et al. 2000). We suspect that the male fishers we marked as kits dispersed before we began the next trapping effort, and that some of the juveniles we captured may have immigrated onto our study area. Juvenile male fishers also may experience a disproportionate level of mortality prior to or during dispersal, which may have confounded our interpretations. Although livetrapping in late summer may have increased our chances of catching juvenile males, we avoided livetrapping during this period because of the influence of black bears (*Ursus americanus*) on trap success and concern over properly fitting radiocollars on juveniles.

Our hypothesis regarding the earlier dispersal of juvenile males was supported by subsequent livetrapping efforts. A single female kit and a single male kit were marked in the preweaning dens of different adult females on 2 May 2006 and 9 May 2008, respectively. During livetrapping efforts in their mothers’ home ranges during the following fall–winter seasons, we failed to capture either of these juveniles. However, the female was captured and radiocollared within her mother’s home range (871 m from her natal den) on 14 February 2011. Telemetry efforts demonstrated that her home range was located adjacent to, but largely outside of our study area. The male was captured on 6 November 2010, 31.6 km from his natal den on a neighboring private timberland (Green Diamond Resource Company, Korbel, California) as part of an ongoing fisher translocation effort coordinated by the California Department of Fish and Game. Future research efforts might consider repeating our methodology using global positioning systems collars on juveniles over a larger study area or neighboring study areas, while simultaneously using hair snares across a large-scale systematic grid to potentially detect juveniles marked as kits but not captured and collared. These methods would provide a more complete picture of juvenile fisher dispersal patterns, an important consideration for translocations, dispersal corridor protections, and similar conservation measures.

The dispersal distances we recorded were generally shorter than those reported in the literature. However, many of these earlier studies only reported dispersal distances of animals that were successful in leaving their mothers’ home ranges and establishing a home range some arbitrary distance from their mothers’ home ranges, which was typically based on the mean maximum distance moved by adults. In the Cascade Range of southern Oregon, Aubry and Raley (2006) reported mean female and male dispersal distances from den locations to established home-range centers of 6 km (range = 0–17 km, n = 4) and 29 km (range = 7–55 km, n = 3), respectively. In north-central British Columbia, Canada, Weir and Corbould (2008) reported mean female and male dispersal distances from den locations to established home-range centers of 16.7 km (range = 0.7–32.7 km, n = 2) and 41.3 km (n = 1). In a Massachusetts fisher population, York (1996) reported mean maximum female and male dispersal distances of 37 km (range = 12–
107 km, \( n = 19 \) and 25 km (range = 10–60 km, \( n = 10 \)), respectively. Similarly, in Maine, Arthur et al. (1993) reported mean maximum female and male dispersal distances of 14.9 km (range = 7.5–22.6 km, \( n = 2 \)) and 17.3 km (range = 10.9–23.0 km, \( n = 4 \)), respectively.

Our comparatively shorter dispersal distances might be related to a significant decline in the density of fishers in Hoopa between 1998 and 2005 (Matthews et al. 2011). Suitable habitat might have been available in close proximity to their mothers’ home ranges, resulting in comparatively short dispersal distances. We would likely have observed longer dispersal movements of males if we had collared a higher percentage of those we had marked as kits.

Because extant populations in the Pacific coastal states and provinces have not expanded into suitable, unoccupied habitat (Lofroth et al. 2010), male-biased dispersal and female philopatry have important implications for western fisher management. Fisher populations exhibiting male-biased dispersal and female philopatry are unlikely to expand unless lambda is well above 1, forcing some females to disperse greater distances (Matthysen 2005). Male fishers may disperse outside of the population boundary, and then be forced to return to find females, or they may die without having the opportunity to breed. This supports the hypothesis that fishers in this region may need to be translocated in order to reach suitable, unoccupied habitat even short distances away from the population boundaries (Lewis and Stinson 1998).

Estimates of recruitment rates are lacking for most fisher populations in western North America (Lofroth et al. 2010). In south-central British Columbia, Weir and Corbould (2008) estimated an average fall recruitment rate of 0.58 juveniles/adult female, which is double our estimate. Such estimates provide potential insights into population growth; however, they must be viewed with caution because they were derived by piecing together various information sources (e.g., denning rates of females, telemetry and livetrapping data, and anecdotal field observations) and making assumptions about age-specific survival rates (Lofroth et al. 2010). Comparing our results on recruitment with those from fisher populations in eastern North America (e.g., Paragi et al. 1994) provides limited insights into the dynamics of western populations because legal harvest of fishers in the East directly affects recruitment rates (Lofroth et al. 2010).

Estimates of female reproductive rates, recruitment, and juvenile dispersal are important elements in assessing the resilience of imperiled carnivore populations and developing effective conservation strategies (Weaver et al. 1996). Following an apparent 73% fisher population decline in Hoopa between 1998 and 2005 (Matthews et al. 2011), we found higher reproduction, higher recruitment, and lower dispersal rates than in other unharvested fisher populations. These rates demonstrate the resilience of this population. However, large home-range size, low fecundity, and limited dispersal ability make fishers sensitive to anthropogenic habitat alterations (Carroll et al. 1999; Kyle et al. 2001; Powell and Zielinski 1994). Traditional clear-cut logging practiced prior to 1990 in Hoopa and currently on commercial timberlands bordering Hoopa leaves little or no aboveground structural legacies of overstory trees or coarse woody debris (Franklin et al. 2002). Fishers are habitat specialists that rely on structural complexity to fulfill their life requirements, particularly reproduction (Lofroth et al. 2010; Weir et al. 2012). The retention of legacy structures is an important consideration for managers implementing effective forest management strategies to help ensure sufficient reproductive habitat and rates for fishers (Weir et al. 2012). Limits in fisher dispersal distances suggest managers interested in increasing or expanding existing fisher populations to suitable, unoccupied habitat even short distances away from the population boundaries may need to consider translocation (Lewis et al. 2012; Lewis and Stinson 1998).

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