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Fisher and Marten

Martes pennanti and *Martes americana*

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NOMENCLATURE

FISHER

COMMON NAMES. Fisher, wejack, fisher cat, black cat, Pennant's marten, marten, pekan; only fisher is used commonly today, and locally fisher cat in some places in New England; the name fisher may have come from early immigrants, who noted the fisher's similarity to the dark European polecat (*Mustela putorius*), names for which included fitchet, fitche, and fitchew (Brander and Books 1973)
SCIENTIFIC NAME. *Martes pennanti*
SUBSPECIES. *M. p. pennanti, M. p. pacifica,* and *M. p. columbiana.* Hagmeier (1959) concluded that none of the subspecies is separable on the basis of pelage or skull characteristics, and questioned the classification. As have most authors since Hagmeier, we ignore subspecies taxonomy except when discussing certain conservation issues, which are often organized around designated subspecies rather than around detailed ranges.

MARTEN

COMMON NAMES. Marten, American marten, and pine marten are the only names commonly used today; Marten cat, American sable, Canadian sable, saple, and Hudson Bay sable have been used in the past and appear in old literature
SCIENTIFIC NAME. *Martes americana*
SUBSPECIES. The subspecies have been divided into *americana* and *caurina* subspecies groups (Hagmeier 1961). The *americana* group includes *M. a. americana, M. a. brumalis, M. a. atrata, M. a. abieticola, M. a. actuosa, M. a. kenaiensis,* and *M. a. abietinoides.* The *caurina* group includes *M. a. caurina, M. a. humboldtensis, M. a. vancouverensis, M. a. nesophila, M. a. vulpina, M. a. origenes,* and *M. a. sierrae.* Although Hagmeier concluded that the subspecies differed too little to warrant continued recognition, Carr and Hicks (1997) argued from mitochondrial DNA data that the *americana* and *caurina* groups constitute two separate species, *M. americana* and *M. caurina,* as originally described by Merriam (1890). The groups intergrade morphologically and genetically, indicating hybridization (Wright 1953; Stone 2000), and although the groups differ in mitochondrial DNA genotypes by six nucleotide substitutions, no two specimens within a group differ by more than two substitutions. Thus, Carr and Hicks (1997) concluded that the putative *M. americana* and *M. caurina* differ to a similar degree as do the Eurasian pine marten, *M. martes,* and the sable, *M. zibellina.* From mitochondrial and nuclear DNA, Stone (2000) concluded that the *americana* and *caurina* groups have descended from a single colonization of North America and not two colonizations as previously hypothesized, and are indeed more closely related than are the Eurasian pine marten and sable. Whether the groups of American martens will be determined to be distinct species is not yet known, and Hagmeier (1961) and Anderson (1970) suggested that the American marten, Eurasian pine marten, sable, and Japanese marten, *M. melampus,* are conspecific. Because evidence is not yet compelling, we shall treat the *caurina* group as *M. americana* and consider the entire *M. americana* to be a good species. As with fishers, we ignore subspecies taxonomy except when discussing certain conservation issues.

DISTRIBUTION

The genus *Martes* is circumboreal in distribution, with extensions into southern (*M. gwatkinsii*) and southeast Asia as far as 7°S latitude (*M. flavigula*; Anderson 1970). The fisher (subgenus *Pekania*) is endemic to the New World and restricted to mesic coniferous forest of the boreal zone and its southern peninsular extensions (Hagmeier 1956; Gibilisco 1994). The boreal forest martens, comprising four sibling species (*M. martes, M. zibellina, M. melampus, M. americana*), are distributed parapatrically or allopatrically across the boreal zone from Ireland eastward across Eurasia to North America as far east as Newfoundland Island (Buskirk 1994). The American marten (Fig. 29.1) is distributed similarly to the fisher (Fig. 29.2) in the southern parts of its range, but is found farther north, to the northern limit of trees, than the fisher. In the Rocky Mountains, the range of the marten extends much farther south (to New Mexico) than does that of the fisher (to Montana and Idaho). In the Pacific states, both species occur as far south as the southern Sierra Nevada.

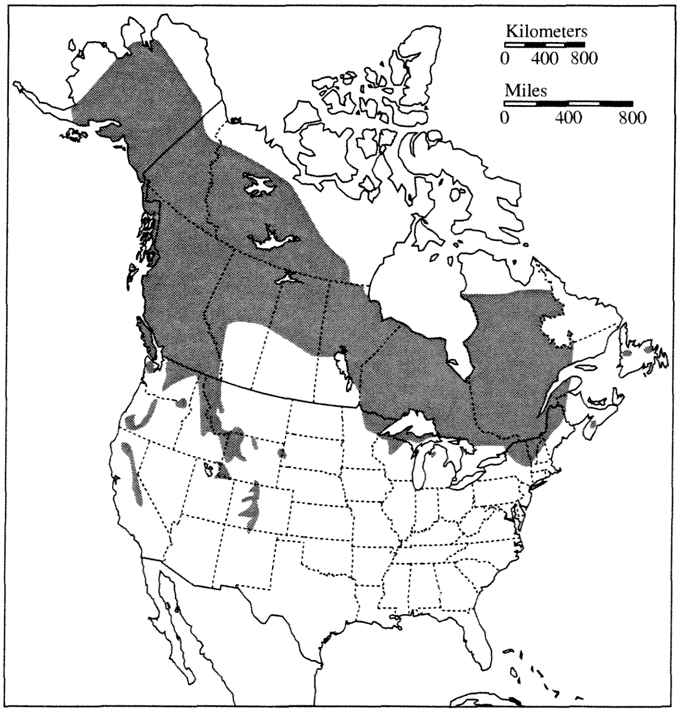

FIGURE 29.1. Distribution of the marten (*Martes americana*).

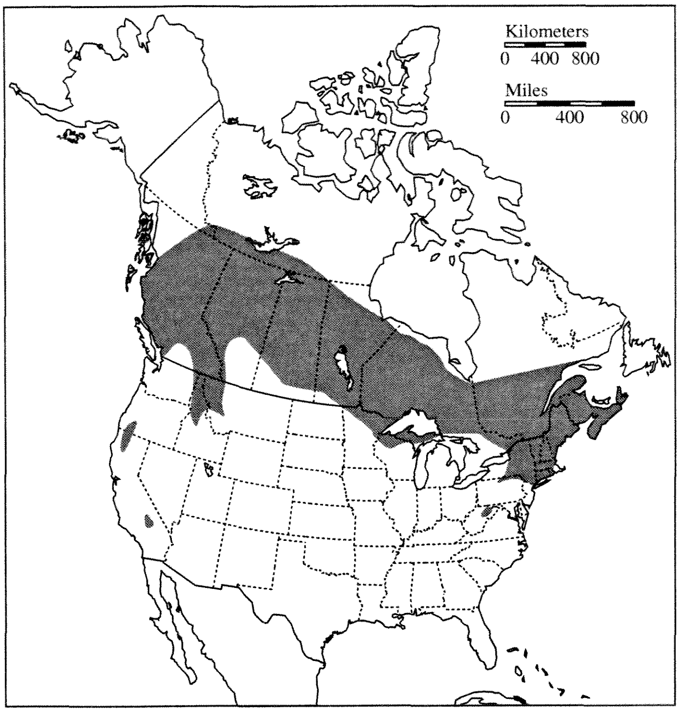

FIGURE 29.2. Distribution of the fisher (*Martes pennanti*).

Distributional changes during historical times, comprising regional extirpations, natural colonization and recolonization, and translocations, summarized by Berg (1982), Powell (1993), and Strickland et al. (1982a, 1982b), have affected the fisher more than the American marten. For the fisher, major distributional changes from presettlement times include losses from much of its previous range in the Pacific states (Gibilisco 1994; Zielinski et al. 1995), including apparently complete extirpation from Washington and northern Oregon. The fisher has undergone a slight range expansion to northwestern British Columbia and southeastern Alaska, losses from central Alberta and Saskatchewan, and losses from the southern Great Lakes and Ohio Valley regions (Gibilisco 1994). Parts of Quebec and Labrador also appear to have dropped from the fisher's range during the historical period. During the last two decades of the twentieth century, the fisher expanded its range southward into southern New England (Gibilisco 1994).

Salient changes in the distribution of the American marten since European settlement include loss of much of its range in the coast ranges of California and Oregon (Zielinski et al. 2001). The entire range of *M. a. humboldtensis* is nearly vacant and may be represented by only one small population. The geographic range in the Rocky Mountains is approximately as in presettlement times, with possible losses from some isolated areas (Gibilisco 1994). The marten is absent from much of its presettlement range in southern Manitoba, the southern Great Lakes region, the upper Ohio Valley, and southern New England. The range of the marten, however, has expanded southward into the latter area and into the north-central states since approximately 1980 (Buskirk and Ruggiero 1994). Martens have been introduced to several islands of the Alexander Archepelago of southeast Alaska (MacDonald and Cook 1996) and reintroduced to Nova Scotia and the Black Hills of South Dakota. The species is now extirpated on Prince Edward Island and very restricted in distribution on Cape Breton Island and Newfoundland (Buskirk and Ruggiero 1994).

DESCRIPTION

Fishers and martens are medium-sized carnivores with a general weasel shape but lacking the extreme elongation of the weasels. They have well-furred bodies and full tails. Their tails constitute about one third of total body length. Their faces are triangular, with muzzles less pointed than those of foxes. The fisher's ears are wide and rounded, whereas the marten's ears are pointed. Males are considerably larger than females in both species.

Fishers and martens are digitigrade with five toes on each large, well-furred paw. Claws are sharp, curved, and semiretractable but not sheathed.

Size and Weight. The fisher is the largest member of the genus *Martes*. Adult males generally weigh 3.5–5.5 kg, though larger males are not uncommon in parts of the species' range, and an exceptional male weighed over 9 kg (Blanchard 1964). Females generally weigh 2.0–2.5 kg. Males are also longer than females; total length is 90–120 cm versus 75–95 cm (Powell 1993). Although martens vary considerably in size across their range (Hagmeier 1961), they are nowhere as large as fishers. Like fishers, male martens are larger than females; males generally weigh 0.6–1.0 kg, but can be up to 1.4 kg, whereas females generally weigh 0.4–0.7 kg, but can be up to 1 kg (Buskirk and McDonald 1989). Males generally are 50–70 cm in total length, whereas females are 45–60 cm.

Juvenile martens reach adult length, but not weight, by 3 months of age, whereas fishers reach adult length, but not weight, at about 6 months of age. By 7 months, the epiphyses of female fishers long bones have ossified, indicating they have reached full size, but males do not reach this stage until 10 months of age (Dagg et al. 1975).

Pelage. On both species, the fur on the body and head is lighter in color than on the tail, legs, and shoulders. Fishers have dark-brown bodies with black legs and tails; their heads have a gold or silver, hoary appearance created by tricolored guard hairs (Coulter 1966). Many fishers have irregular white or cream patches on their chests or groins; the chest patches never become so large as to resemble a chin or throat patch. The pelage color of martens varies more across the specie's range than does that of fishers. Martens may have light-brown to dark brown to gold bodies with dark-brown tails and legs. They have irregular, often large patches of cream to gold on their chins and throats. The color of these patches varies with season, and tends to be darkest in autumn.

Skeletal Morphology. Fishers and martens have generalized skeletons capable of a wide variety of movements and locomotion, including running on the ground, running along tree limbs, and climbing trees (Leach 1977a, 1977b; Leach and de Kleer 1978; Holmes 1980). Members of both species can rotate their hind feet, allowing them to descend trees head first. The scapulae of fishers each have enlarged postscapular fossae, which probably accommodate large muscles used in climbing trees (Powell 1993).

Skull and Dentition. Skulls of male fishers generally are 110–130 mm long, whereas those of females are 95–105 mm long. Skull width for males is 62–84 mm, whereas that for females is 52–61 mm (Peterson 1966). For martens, skulls generally are 80–95 and 69–80 mm in length and 46–53 and 38–46 mm in width for males and females, respectively. The dental formula for both species is I 3/3, C 1/1, P 4/4, M 1/2. Among mustelids, only fishers, martens, and wolverines *Gulo gulo*) have four upper and lower premolars. Fishers' skulls (Fig. 29.3) can be distinguished from those of wolverines by their generally shorter length (<130 mm) and from those of martens (Fig. 29.4) by their longer length (>95 mm). In addition, fisher and marten skulls arch less than do wolverine skulls. Skulls of fully adult male fishers have a large sagittal crest that usually exceeds 1 cm in height and is an exceptional feature of the skull (Figs. 29.5 and 29.6). Skulls of small female fishers can be distinguished from those of large male martens by the exposed lateral root of the fourth upper premolar (Anderson 1970), which is diagnostic for fisher skulls in general. Skulls of martens can be distinguished from those of minks (*Mustela vison*) and skunks (*Mephitis mephitis, Spilogale* spp.) by having four premolars and from minks by their larger size and taller cranium.

Scent Glands. Fishers and American martens mark with several scents. Urine and feces are presumed to be scent marks (Buskirk 1994) because fishers and martens often place them on stumps or other prominent

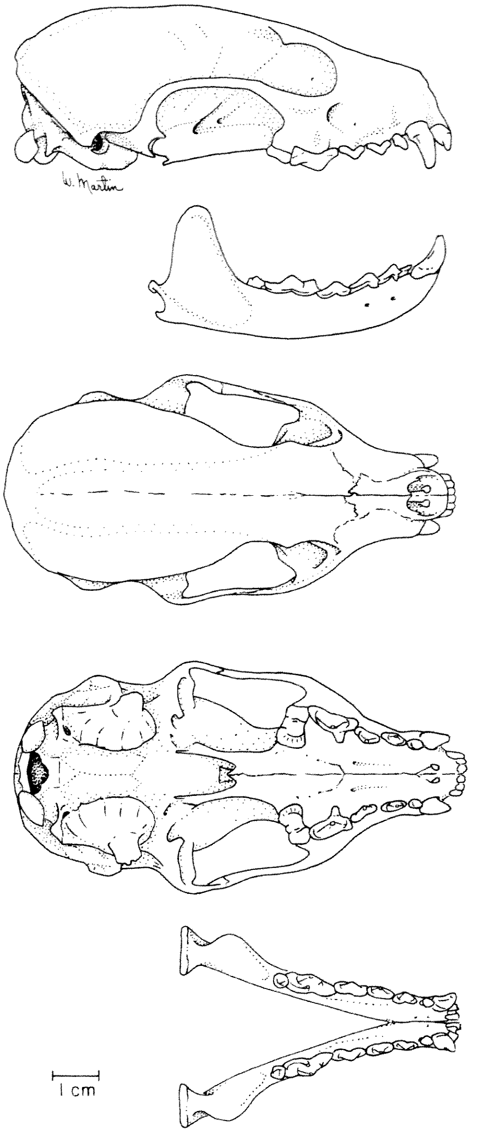

FIGURE 29.3. Skull of the fisher (*Martes pennanti*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

structures. In addition, both species have abdominal glands (Hall 1926), plantar glands (Buskirk et al. 1986; Powell 1982), and anal sacs, the latter typical of most fissipede carnivores. The scents from the latter are not as perceptible by humans as are those of other mustelids (Buskirk 1994). Plantar glands in male and female fishers undergo a large annual cycle in size (Frost et al. 1997), peaking in size at the time of mating. Ecological and behavioral consequences of scent marking are poorly known.

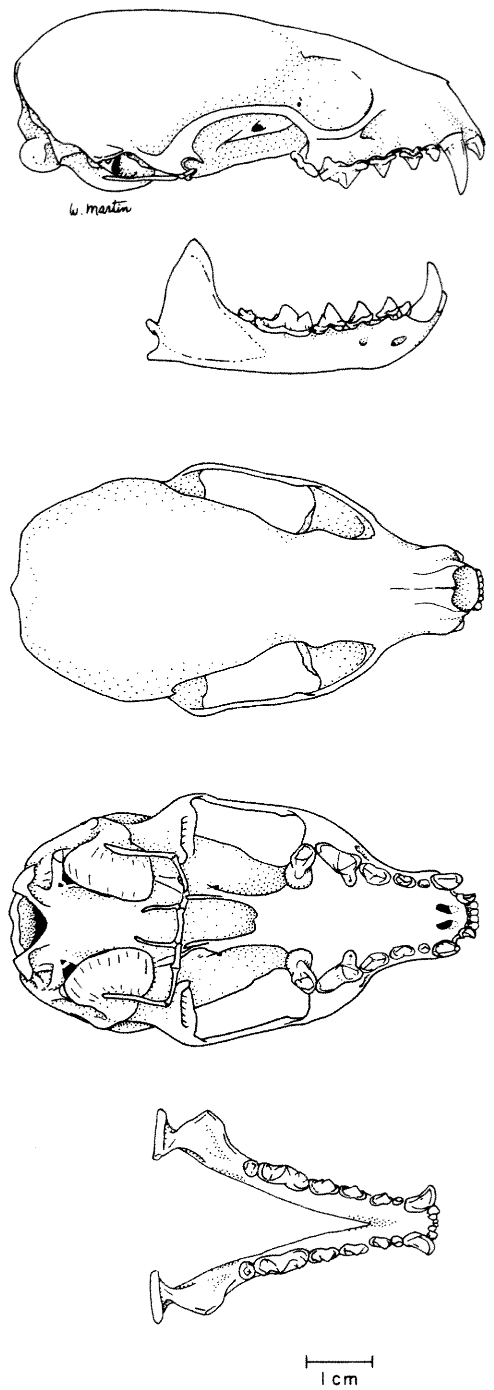

FIGURE 29.4. Skull of the marten (*Martes americana*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

Body Composition and Fat Deposits. Body composition and fat depots have been described for martens in Alaska, Ontario, and Wyoming, and in relation to sex, age, season, and habitat (Buskirk and Harlow 1989; Cobb 2000), but fat depots of fishers are less well described (Leonard 1980). Martens and fishers are very lean for their body size, with only 2.4–4.6% of the body mass of martens as extractable lipid. Fat depots are located as in other carnivores (i.e., omental, perirenal), but only exceptionally do fat animals exhibit obvious subcutaneous fat. Absolute and relative dry mass of the omental and perirenal fat are the best indicators of percentage body fat for both species (Leonard 1980; Cobb 2000) and account for up to 65% of the pooled variation in total body fat for both sexes of martens (Cobb 2000). The effect of age on body fat differs between sexes in martens (Cobb 2000), but body fat does not vary over winter (Buskirk and Harlow 1989). Body fat of martens in Ontario varies with habitat. Animals living in boreal (conifer-dominated) forests have more fat than those from "mixed forests" having a strong broad-leaved tree component (Cobb 2000). For fishers in Manitoba, body fat is directly related to the abundance of snowshoe hares (*Lepus americanus*) in their diet (Leonard 1980). Protein constitutes about 17.5% and water about 70% of the bodies of martens, values similar to those of other lean mammals. Leanness is usually seen as an adaptation to highly athletic movement styles, including foraging in small spaces beneath the snow. Although protein serves as an important secondary

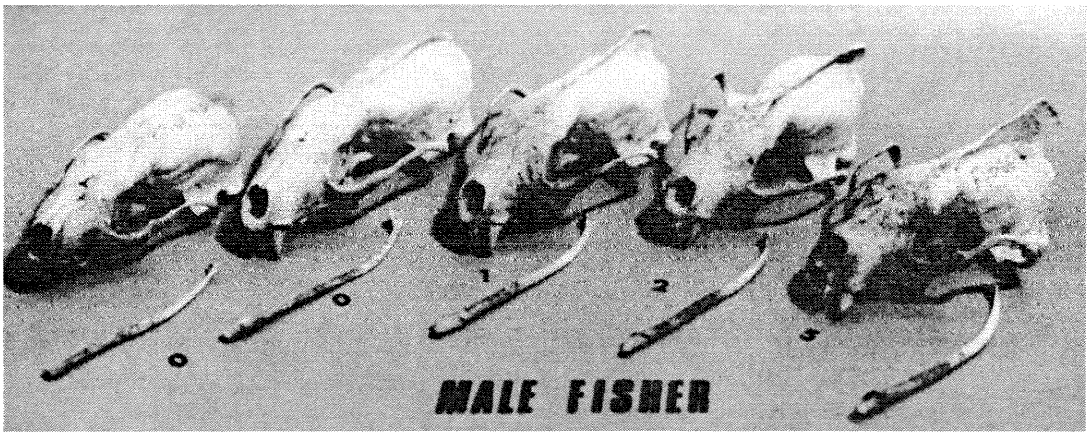

FIGURE 29.5. Skulls and bacula of male fishers (*Martes pennanti*), showing variation with age. Note the development of the sagittal crest and baculum and the fusion of the sutures with age. Numerals denote age estimated from cementum annuli. The juvenile at the extreme left was captured in November; the one adjacent was captured in February. Contrast the skull of the adult male at the extreme right with the drawing of the skull of a juvenile female in Fig. 29.3.

energy store to fat (Harlow and Buskirk 1991), martens have limited fasting endurance. They must balance their energy budgets over brief periods and must gear their activity and foraging to balance short-term energy budgets.

AGE ESTIMATION AND SEX DETERMINATION

Poole et al. (1994) reviewed methods of determining sex and estimating age of fishers and martens for protected populations and populations that are trapped for fur. Arthur et al. (1992) reviewed use of cementum annuli to estimate ages of fishers.

Cementum analysis is the only technique that provides an estimate of the ages of adult animals (Poole et al. 1994). Livetrapped animals can be aged if a tooth is extracted under anesthetic. A first premolar is usually extracted, with probably no functional effect on the animal. Canine teeth are often used to estimate age of animals trapped for fur. Age estimates made by different technicians or using different teeth agree 80–95% of the time (Poole et al. 1994), but disagreements highlight that uncontrollable factors affect these estimates. This technique often underestimates ages of very old animals (Arthur et al. 1992; Poole et al. 1994).

Radiographs of canine teeth, which show an open or closed pulp cavity, correctly distinguish juveniles from adults over 90% of the time (Poole et al. 1994). Estimating the length of the sagittal crest from coalescence of the temporal muscles on carcasses of martens trapped for fur allowed Poole et al. (1994) to distinguish juvenile from adult martens trapped in Alaska and the Northwest Territories, but many adult females from Ontario were incorrectly classed as juveniles. A number of measurements taken from teeth and skulls correctly identify sex of fishers and martens when skulls only are available. Length and width of lower canines distinguish the sexes of fishers 100% of the time, and skull length and zygomatic width distinguish the sexes with 98–100% accuracy. Upper or lower canine root width, lower canine root length, skull length, and zygomatic width distinguish the sexes of martens 92–100% of the time (Poole et al. 1994).

REPRODUCTION

Anatomy. Ovaries in both species are completely encapsulated by a bursa and the uterus has two horns with a common corpus uteri, allowing migration of blastocysts between the horns (Strickland et al. 1982a, 1982b). Males have bacula (Fig. 29.5). Testes increase in size and weight before the breeding season, which occurs in late March through early May for fishers and July and August for martens.

Reproductive Cycle and Delayed Implantation. Both sexes of both species reach sexual maturity by 1 year of age, but effective breeding may not occur before 2 years of age. One-year-old male fishers produce sperm, but their bacula have not reached adult size and shape (Coulter 1966; Wright and Coulter 1967; Frost et al. 1997). When bred, 1-year old males fail to produce offspring (Douglas 1943). Female fishers generally breed for the first time when 1 year old (Wright and Coulter

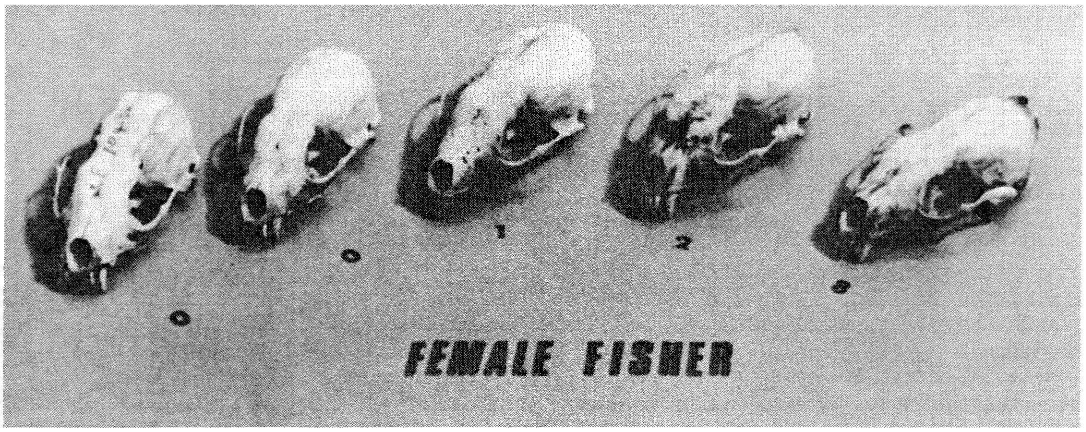

FIGURE 29.6. Skulls of female fishers (*Martes pennanti*), showing variation with age. Note the sutures and minimal development of the sagittal crest. The juvenile at the extreme left was captured in November; the one adjacent was captured in February.

1967; Strickland et al. 1982a). Literature concerning age of maturity for martens is confusing, in part because early researchers had difficulty estimating the ages of martens (Strickland et al. 1982b). Although most early literature reported that martens did not breed before 2 years of age, Strickland et al. (1982b) reported that 80% of 18- to 20-month-old female martens trapped in southern Ontario had corpora lutea, indicating pregnancy.

Female fishers and martens both give birth in late March or April (Fig. 29.7). Female fishers then enter estrus and breed approximately 7–10 days later (Hall 1942; Asdell 1946; Eadie and Hamilton 1958; Coulter 1966; Wright and Coulter 1967; Strickland 1982a). Female martens enter estrus in July or August (Strickland et al. 1982b). Ovulation in many *Mustela* and *Martes* species is induced by copulation, and shape and size of the baculum may be critical for proper stimulation of the vagina (Mead 1994). Cherepak and Connor (1992), however, recovered an unfertilized ovum in August from the reproductive tract of a female fisher who had not bred. As Ewer (1973) noted, induced ovulation may be a matter of degree, and vaginal stimulation during copulation may induce ovulation in females who might have ovulated spontaneously at a later date without breeding.

Both martens and fishers delay implantation. A fertilized zygote develops to a blastocycst and then becomes inactive in the uterus, its metabolic rate falls, and cell division ceases (Ewer 1973). The blastocyst remains dormant until late winter, when change in day length induces implantation and active gestation (Enders and Pearson 1943; Frost et al. 1997). Consequently, adult female fishers are pregnant nearly all year, except for 7–10 days following parturition. Adult female martens are pregnant for 7–8 months. Active gestation is approximately 50 days (<10 days before to delay, 40 days postimplantation) in fishers (Frost et al. 1997). Active gestation for martens may be somewhat shorter. Jonkel and Weckwerth (1963) reported that the postimplantation period for martens was 27–28 days, but their ability to detect implantation time was limited. The postimplantation period for Eurasian pine martens is 30–35 days (Mead 1994).

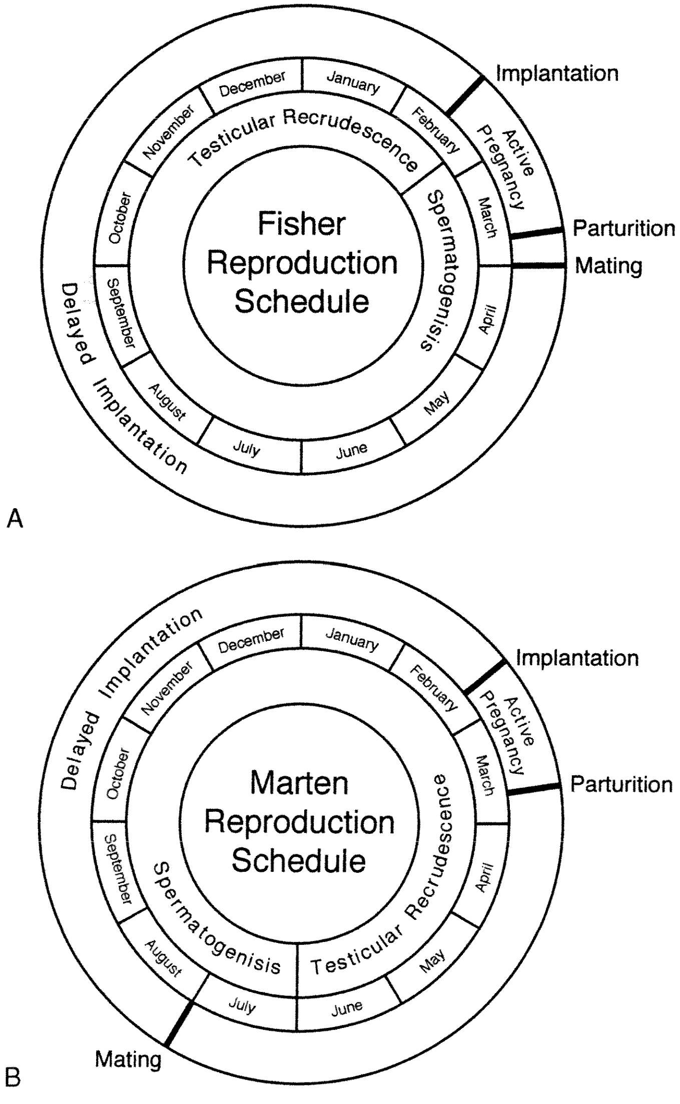

FIGURE 29.7. Reproduction schedules of (A) fishers (*Martes pennanti*) and (B) martens (*Martes americana*). SOURCE: Figure drawn by C. B. Powell.

Changes in soft body parts signal reproductive condition. Plantar glands on the hind feet of female fishers increase in size from <10 cm^2 in December to >10 cm^2 in January, remain enlarged through May, and then regress to <10 cm^2 again by June (Frost et al. 1997). For female fishers who produce offspring in a given year, nipples begin to enlarge in February–March, reach a peak in size in August–September, then decrease in size through November (Frost et al. 1999). Width times height of anterior nipples is an index of nipple size that differs significantly between breeding and nonbreeding females (Frost et al. 1999).

In male fishers, concentrations of testosterone begin to rise in December in adults and in January in juveniles, followed by an increase in testicular size, which becomes maximum in March in adults and April in juveniles (Frost et al. 1997). Production of sperm is maximal in March–May for both age classes. Concentration of testosterone begins to decrease in April and testes are fully regressed by June. Plantar glands on the hind feet of male fishers begin to increase in size from <15 cm^2 in December to >30 cm^2 in May, then regress rapidly by June (Frost et al. 1997).

Breeding Behavior. Male fishers and martens are undoubtedly polygynous and females may well be both polyandrous and selective. Large sexual dimorphism in body size, as found in martens and fishers, is strongly correlated with polygynous mating patterns in mammals (Kleiman 1977). Courtship of fishers is similar to that of other mustelines and may be prolonged and vigorous (Hodgson 1937; Laberee 1941; Enders and Enders 1963; Heidt et al. 1968; C. Kline and M. Don Carlos, Minnesota Zoological Society, unpublished records). Copulations resulting in pregnancy have been reported to last from 20 min to 7 hr (Hodgson 1937; Laberee 1941; C. Kline and M. Don Carlos, Minnesota Zoological Society, unpublished records). Such long copulations are not needed to induce ovulation, yet when copulation is interupted after 5–12 min in ferrets (*Mustela furo*) and minks (*M. vison*), no fertilization occurs (Mead 1994).

Parturition and Litter Size. Parturition dates for fishers occur from late February through early May, but most litters are born in March through early April (Hodgson 1937; Laberee 1941; Hall 1942; Douglas 1943; Hamilton and Cook 1955; Coulter 1966; Wright and Coulter 1967; Leonard 1980; Paragi 1990; Frost and Krohn 1994; Frost et al. 1997; reviewed by Powell 1993). Recorded parturition dates for martens show less variation than do those for fishers (reviewed by Strickland and Douglas 1987) and range from mid-March through the end of April. C. Kline and M. Don Carlos (Minnesota Zoological Society, unpublished records) recorded parturition and breeding dates for three captive-bred litters of fishers at the Minnesota Zoo. One female bred on 16 April 1989, gave birth on 31 March 1990, and bred again on 7–9 April 1990. Another female bred on 22 April 1990, gave birth on 2 April 1991, and bred again on 11–12 April. This second female gave birth again on 10 April 1992. The consistency of the parturition and breeding dates for these females suggests that individual females may implant around the same date each year and consequently give birth and breed at consistent times. This pattern, in turn, suggests that the variability of parturition dates reported in the literature stems from variation among females for implantation dates and not variation from year to year by individual females.

Reported litter sizes for fishers range from one to six and the means for all studies are between two and three inclusive (reviewed by Powell

1993; also Frost and Krohn 1994; Frost et al. 1997), whereas reported litter sizes for martens range from one to five (reviewed by Strickland and Douglas 1987). Mean numbers of corpora lutea for fishers ranged from 2.7 to 3.9 across several studies (reviewed by Powell 1993). Strickland and Douglas (1987) reported a mean of 3.5 for 880 female martens studied in Ontario between 1973 and 1985. Reported mean numbers of implanted blastocysts, implanted embryos, placental scars, and litter sizes show a slightly decreasing pattern in fishers, indicating small loss of young in utero through pregnancy (Powell 1993).

Pregnancy rates for fishers and martens are generally calculated as the proportion of adult females whose ovaries contain corpora lutea in carcasses turned in by trappers (Shea et al. 1985; Douglas and Strickland 1987; Crowley et al. 1990). Although placental scars should, in theory, document birth and litter sizes more accurately then corpora lutea, Frost et al. (1999) showed that placental scars sometimes fail to identify reproduction by female fishers. Four of 13 female fishers who produced young in their study did not have identifiable placental scars.

Corpora lutea generally indicate ovulation rates of 95% or more for fishers (Shea et al. 1985; Douglas and Strickland 1987; Crowley et al. 1990), but Arthur and Krohn (1991) and Paragi (1990) reported a denning rate of about 65% for the fishers they studied in Maine. Strickland and Douglas (1987) reported a pregnancy rate of 87% (90% if 1½-year-old females are excluded) for martens in Ontario. Strickland and Douglas (1987) also found greater variation in annual pregnancy rates for martens than for fishers. They attributed the variation in pregnancy rates to be food-related in martens, but did not speculate on why martens show greater variation than fishers. In the southern Sierra Nevada of California, 50–60% of 26 female fishers captured in spring were lactating each year from 1994 through 1996 (Truex et al. 1998). Further north in California, Truex et al. (1998) found greater variation in lactation rates for a smaller sample of fishers (18 over 2 years).

Bull and Heater (1995, 2001) documented 13 reproductive efforts by martens in Oregon. Of these, 4 females weaned at least one kit, 8 females failed to raise any kits, and the outcome for 1 female was unknown.

DEVELOPMENT

Martens and fishers, similar to other mustelines, are altricial and are born completely helpless with their eyes and ears closed (Hodgson 1937; Coulter 1966; LaBarge et al. 1990). They are partially covered with fine hair.

Development of fishers has been documented better than that of martens. Fishers remain helpless for weeks following birth and do not begin to crawl until ≥3 weeks old (Hodgson 1937; Coulter 1966; Powell 1993). By 3 months, they climb well (Grinnell et al. 1937; Powell 1993). Somewhere between 6 and 8 weeks, kits open their eyes (Hodgson 1937; Coulter 1966; LaBarge et al. 1990; Powell 1993). Deciduous teeth begin to erupt when kits are about 6 weeks old and canines erupt by 7–9 weeks (Coulter 1966; LaBarge et al. 1990; Powell 1993).

By 2 weeks of age, fisher kits are covered with light silver-gray fur (LaBarge et al. 1990). Around 3–4 weeks of age, they begin to change to a chocolate-brown color. By 10–12 weeks, most kits are completely chocolate-brown. From this age on, the tricolored guard hairs characteristically found on the head, neck, and shoulders of adults can be seen, but with a restricted distribution. Thus, through the summer and the early autumn, young fishers are the same general color as adults, but are more uniform in color.

Fishers weigh well under 50 g at birth, reach about 500 g by 40–50 days, and thereafter begin to exhibit sexual dimorphism in size. By late summer or early fall, they approach adult size and sexual dimorphism is pronounced (Powell 1993). Martens reach adult body weight around 3 months of age (Markley and Bassett 1942).

Fisher kits are completely dependent on milk until they are 8–10 weeks old (Coulter 1966; LaBarge 1990; Powell 1993). A litter raised by its mother in captivity was weaned by her at approximately 4 months of age (Coulter 1966).

When about 7½ weeks old, fisher kits may begin shaking pieces of bedding or other objects in play (Powell 1993), and kits 3 months old may play with prey before eating (Coulter 1966). At about 4 months, they may attack the head and neck region of small prey. Young American martens are able to kill prey proficiently by 2½ months of age (Remington 1952), a considerably younger age than fishers. Marten and fisher mothers tend to spend extensive time with their kits during the days shortly after birth and then spend progressively less time, in shorter periods, with them (Leonard 1980; Henry et al. 1997), although not all females show this pattern (Paragi 1990).

Intraspecific aggression in captive fisher kits appears when they are around 3 months old and kits are intolerant of each other by 5½ months (Hodgson 1937; Powell 1993). A mother fisher observed by Coulter (1966) became increasingly hostile toward her two kits beginning late in their fourth month. At age 5½ months, one kit was killed and the other injured by the mother. Wild kits followed by Paragi (1990) using radiotelemetry remained in their mothers' territories into the winter. The kits, now juveniles, tended to avoid areas used most by their mothers. By age 1 year, juveniles have established their own home ranges.

ECOLOGY

Population Dynamics. Unharvested populations of fishers and martens exhibit marked fluctuations in size, sometimes in excess of an order of magnitude, in response to fluctuations in prey populations (Powell 1994a). Weckwerth and Hawley (1962) and Thompson and Colgan (1987) reported fourfold and sixfold changes in population densities of martens. Where fishers and martens prey heavily on snowshoe hares, their populations fluctuate in response to the roughly 10-year cycle in hare density (Bulmer 1974, 1975). Fryxell et al. (1999) suggested that a harvested population of martens in southern Ontario was relatively stable because the martens switch to alternate prey as prey populations change. Nonetheless, Fryxell et al. (1999) reported that the rate of increase for their marten population changed significantly with abundances of major prey. Douglas and Strickland (1987) questioned whether many fisher populations fluctuate in response to snowshoe hare cycles.

Age structures of natural fisher and marten populations change with population density and therefore are never stable (Powell 1994a). When prey populations increase, the juvenile cohort constitutes a larger than average proportion of a population, and when prey populations decline, older cohorts predominate (Strickland and Douglas 1987; Thompson and Colgan 1987). When prey populations remain low for extended periods, young animals again make up a larger proportion of a population because old animals finally die and total population size decreases. Age structure of harvested populations differs from that of unharvested populations because few individuals reach old ages in harvested populations, especially males (Douglas and Strickland 1987; Strickland and Douglas 1987).

Density, Spatial Organization, and Home Range. Original estimates of densities of fishers came from tracking studies (deVos 1952; Hamilton and Cook 1955; Coulter 1966) and yielded densities as high as 1 fisher/2.6 km^2. Recent research using live-trapping and radiotelemetry have yielded consistently lower estimates of density (Table 29.1). Douglas and Strickland (1987) estimated preharvest densities in southern Ontario were about 1 fisher/6.5 km^2, whereas estimates from live-trapping data have ranged from 1 fisher/2.6 km^2 to 1 fisher/20 km^2, depending on habitat and season.

Because martens are smaller than fishers, their densities tend to be considerably higher than those of fishers. Francis and Stephenson (1972) estimated a density of about 1.5 martens/km^2 in southern Ontario. Soutiere (1979) estimated a similar density for a population in relatively undisturbed forest in Maine, but only 0.4/km^2 in commercially clearcut forests. Archibald and Jessup (1984) estimated similar densities for martens in Yukon Territory in both fall and winter.

Home range sizes for fishers and martens vary across their ranges, probably depending on densities of prey (Powell 1994a). Buskirk and

TABLE 29.1. Recent density estimates for fishers and martens in North America

Place	Density		Technique	Source
	Animals/km^2	km^2/Animal		
Fisher				
Ontario	0.15	6.5	Harvest returns	Douglas and Strickland 1987
New Hampshire	0.11	8.9–9.2	Livetrapping	Kelly 1977
New Hampshire (suitable habitat)	0.13–0.26	3.9–7.5	Livetrapping	Kelly 1977
Maine (summer)	0.09–0.34	2.8–10.5	Livetrapping	Arthur et al. 1989
Maine (winter)	0.05–0.12	8.3–20.0	Livetrapping	Arthur et al. 1989
Maine (suitable habitat)	0.09–0.38	2.6–11.7	Livetrapping	Coulter 1966
Upper Peninsula Michigan	0.08	12–13	Trapper survey	Peterson et al. 1977
Upper Peninsula Michigan	0.08	12–13	Livetrapping	Powell 1977
California	0.31	3.2	Livetrapping	Buck et al. 1983
Marten				
Yukon Territory (fall)	0.6	1.7	Livetrapping	Archibald and Jessup 1984
Yukon Territory (winter)	0.4	2.5	Livetrapping	Archibald and Jessup 1984
Southern Ontario	1.5	0.67	Livetrapping	Francis and Stephenson 1972
Maine (undisturbed forest)	1.2	0.83	Livetrapping	Soutiere 1979
Maine (disturbed forest)	0.4	2.5	Livetrapping	Soutiere 1979

NOTE: References to "suitable habitat" refer to authors's evaluations of habitat.

McDonald (1989) found no geographic pattern to the variation in home range sizes for martens, but Thompson and Colgan (1987) found that home range sizes of martens were smaller when prey density was high. From 17 studies, Powell (1994a) calculated a mean home range size of 8.1 km^2 for male martens and 2.3 km^2 for females. Means for individual studies ranged from 2.0 ± 2.6 km^2 (± *SD*) for males ($n = 5$) and 0.6 km^2 for females ($n = 1$) in Montana (Burnett 1981) to 27 and 17 km^2 ($n = 1$ for each sex) in Newfoundland (Bateman 1986; Bissonette et al. 1988). From six studies, Powell (1994a) calculated a mean home range size of 38 km^2 for male fishers and 15 km^2 for females. Means for individual studies ranged from 19 ± 17 km^2 (± *SD*) for adult males ($n = 3$) and 15 ± 5 km^2 for females ($n = 5$) in New Hampshire (Kelly 1977) to 79 ± 35 km^2 for males ($n = 6$) and 32 ± 23 km^2 for females ($n = 4$) in Idaho (Jones 1991).

Fishers and martens exhibit intrasexual territoriality consistently (Powell 1994a). Intrasexual territoriality allows the home ranges of a male and a female to overlap, although the animals may compete for limiting resources in their area of overlap. For all mustelids, and for fishers specifically, Powell (1979a, 1993) found that intrasexual territoriality, large sexual dimorphism in body size, elongate shape, and high degree of carnivory are correlated. Intrasexual territoriality may be possible in fishers and martens because their large sexual dimorphism in body size might allow members of the two sexes to have different diets. This hypothesis, however, is unsupported (Coulter 1966; Clem 1977; Powell 1979a, 1993; Holmes and Powell 1994). Spacing behavior of a species often varies across its range and through time, and such variation has been documented for fishers and martens (reviewed by Powell 1994a). Powell (1994a) proposed that intrasexual territoriality is part of a continuum, from transiency through exclusive territories to intrasexual territories to extensive home range overlap, that depends on the distribution and availability of limiting resources. For mustelids, he proposed that patchy distribution of prey and temporary resource depression of prey availability for foraging predators allow two individuals to overlap territories with minor cost. Females gain no benefit from this overlap, but males minimize their chances of reproductive failure. Thus, intrasexual territoriality is imposed on females by males, who are larger than, and dominant to, females.

Habitat. In the broadest sense, fishers and American martens occupy mesic, conifer-dominated forests with abundant physical structure near the ground. Both species avoid areas lacking overhead cover (Buskirk and Powell 1994). Sometimes, talus or boulders, subterranean lava tubes, or shrubs provide suitable overhead structure in otherwise open areas. How dependent martens and fishers are on late-successional forests with their associated physical complexity is a matter of considerable debate. In western North America, the need for old growth forest is fairly clear. Xeric forest types are subject to episodic fire, which removes woody structure near the ground, whereas mesic types burn less often and retain woody structures near the ground (Thomas et al. 1988). Here, fishers are closely associated with riparian areas, and martens consistently select mesic, late-successional stands. By contrast, in the temperate East, a stronger deciduous component is typical of late seres, spruce budworm outbreaks occur fairly often, and old-growth conditions are less typical of old stands, particularly in black spruce *Picea mariana*). Also in the East, balsam fir (*Abies balsamifera*) can produce complex structure near the ground after only a few decades of succession. In addition, snowshoe hares, which are more important prey for martens in the East than the West, associate with early deciduous seres in the East (Potvin et al. 2000).

Exceptions to these patterns provide insight into important aspects of habitat for martens. For example, martens use young conifer forests regenerating from clearcuts on Vancouver Island, but seek large stumps that predate the cutting for resting sites (Baker 1992). Thus, the part of the early-successional forest that is actually used by martens is a remnant of the old-growth forest and not an element related to cutting. Fishers and martens need physical structure near the ground in winter for access to subnivean spaces in which to forage and to rest (Buskirk and Ruggiero 1994).

Most studies of habitat selection have been conducted at the scale of the stand or microsite and have found that fishers prefer sites dominated by mid- to late-successional stands of conifers, although they will use partially or entirely deciduous stands. Riparian stands dominated by Douglas fir (*Pseudotsuga menziesii*) are important to fishers in the West. Martens use stands dominated by conifers, but use those with a greater deciduous component in the East than the West. In the West, stand types preferred by martens are moist-site associations like Pacific silver fir (*Abies amabilis*)–western hemlock (*Tsuga heterophylla*), Engelmann spruce (*Picea engelmannii*)–subalpine fir (*Abies lasiocarpa*), and white spruce (*Picea glauca*)–black spruce (reviewed by Buskirk and Ruggiero 1994). In the East, balsam fir and black spruce tend to be preferred. Although Chapin et al. (1997) found little selection by martens for coniferous overstory among stands in Maine, Cobb (2000) found that martens in conifer habitats in Ontario had more fat than martens living in mixed-hardwood habitats.

In Maine, marten populations declined precipitously when timber harvest led to >60% of the forest in early-successional stages, and they selected home ranges with <40% early-successional forest (Chapin et al. 1998; Payer 1999). Partial harvesting of timber reduces habitat quality, in part through reduction of prey and possibly through increased risk of predation (Fuller 1999), and industrial forest management may reduce carrying capacity for martens by half (Payer 1999). Hargis and Bissonette (1997) and Hargis et al. (1999) found similar responses of martens to habitat fragmentation in the intermountain West. In addition, natural and trapping mortalities are both lower in areas not logged (Thompson 1994).

Powell (1994b) considered landscape-scale selection by fishers, and found that, at a coarse scale, fishers selected for pine and lowland conifer habitat. For resting sites, however, fishers were more selective of local cover types, strongly preferring lowland conifer. Kelly (1977), Arthur et al. (1989), and Jones and Garton (1994) all found similar results. Carroll et al. (1999) and Kelly (1977) both found that habitat selection by fishers appears to be dominated by factors acting at the home range scale and above. Weir and Harestad (1997), however, found no landscape-level trends in habitat selection by fishers. For martens, Chapin et al. (1998) in Maine, Hargis et al. (1999) in Utah, and Potvin et al. (2000) in Quebec examined selection at landscape scales. All three studies found a fairly consistent upper limit to the amount of openings in the forest (including clear-cutting and natural openings) tolerated by martens: 25–30% of a marten's home range. Potvin et al. (2000) showed a strong, negative, linear relationship ($r = -0.78$) between the size of the core area of the home range of martens and the proportion of it that was uncut forest. Wisz (1999) found that the areas of mountain ranges and their distances from either the main Rocky Mountains or the nearest other isolated mountain range predicted well the distribution of martens in insular mountain ranges of Montana. Also, nonforested habitats below the elevational limit of trees were effective barriers to travel by martens, with as little as 6.5 km of nonforest habitat precluding colonization of suitable habitat (Wisz 1999). For areas of continuous forest, Minta et al. (1999) hypothesized that martens are most selective at the finest scales (scale of foraging and resting sites) and coarsest scales (population selection of landscape types), but relatively less selective at intermediate scales (patch and home range).

For fishers, seasonal differences in habitat use are not well documented, but Kelly (1977) and Arthur et al. (1989) noted potentially less habitat selection in summer than in winter. Fishers avoid habitats with deep, soft snow because of their heavy foot loadings (Powell and Zielinski 1994; Krohn et al. 1995, 1997). Seasonally, martens show their strongest habitat specialization in winter (reviewed by Buskirk and Ruggiero 1994), when habitat specialization is most closely tied to structurally complex forests. In summer, martens venture into more diverse cover types, including alpine areas above elevational treeline in western mountains (Streeter and Braun 1968), but all studies that have examined seasonal use of nonforested areas by martens have shown less use in winter (Koehler and Hornocker 1977; Soutiere 1979; Spencer et al. 1983). In alpine areas in summer, boulders fill the need of martens for overhead structure. Within seasons, martens vary their habitat selection depending on weather. Buskirk et al. (1989) and Wilbert et al. (2000) showed that, during winter, martens associated more closely with coniferous forest with old-growth characteristics during cold periods than at other times. This pattern of use likely provides martens with warm microsites in severe weather.

Young martens (<1 year old) use a broader range of habitats than do older individuals (Burnett 1981; Buskirk et al. 1989). Older animals tend to use more physically complex forest types than juveniles. Whether inexperienced martens are less selective or are excluded from the best habitats by territory-holding adults is not clear.

Foraging, resting, and Denning. Habitat use has also been studied in relation to specific behaviors. For fishers, Powell (1994b) showed that habitat selection for resting sites was stronger than for foraging, and that resting sites tended to be in closed habitats. For martens, a gradient in the strength of habitat selection has been proposed (Burnett 1981; Schumacher 1999): foraging (weakest selection), resting, maternal denning (females with older kits), and natal denning (females with young kits, strongest selection). For members of both species, this gradient of selection tends to place the most structurally complex stands at the preferred end of the scale. In the West, the most structurally complex stands are old growth coniferous forest.

Natal dens are used by mothers and neonatal young, and typically are in cavities in very large logs, snags, or live trees (Ruggiero et al. 1998; Schumacher 1999). Maternal dens are used by mothers and older, but still dependent young, and tend to be in less-specialized structures, more like resting sites (Ruggiero et al. 1998). Nearly all dens used to raise young fishers have been high in hollow trees. Thirty-eight natal dens used by fishers outfitted with transmitter collars by Leonard (1980), Arthur (1987), Paragi (1990), and Truex et al. (1998) were in large trees and 1 (in Montana) was in a hollow log (Roy 1991). Fifty-six natal and maternal dens of fishers found by Powell et al. (1997a) were also in large trees. In northern studies, over half the natal dens were in aspens *Populus* spp.). Powell et al. (1997a) found that choice of habitat for natal and maternal dens did not differ from that of the landscape, but female fishers did choose large trees. Female fishers will use one to three dens to raise a litter and these are also invariably in large trees (Paragi 1990; Powell et al. 1997a; Truex et al. 1998). The natal den observed by Leonard (1980) was approximately 7 m high in a hollow, living quaking aspen (*P. tremuloides*) and had two entrances: an entrance too small for the mother to use at the bottom of the hollow and a larger hole approximately 10 m above the ground from which the mother descended to her kits. The nest area was on flat, rough wood with no nesting material and was extremely neat after the kits left, with no sign that fishers had been raised there.

Energetics. For martens, energy is believed to be a currency closely linked to fitness in winter (Wilbert et al. 2000), and several aspects of their life history contribute to limitation of energy used. They have very limited body-fat reserves (Buskirk and Harlow 1989; Cobb 2000), have limited fasting endurance (Harlow and Buskirk 1991), and have very large home ranges (Buskirk and McDonald 1989). The lower critical temperature (T_{lc}) for animals at rest in winter is 16°C (Buskirk et al. 1988), which is well above virtually all winter temperatures experienced by martens. This high T_{lc} is due to small body size and to only moderately efficient fur, and leads to high mass-specific heat loss while resting (Buskirk et al. 1988). To reduce this heat loss, martens enter shallow torpor daily in winter (Buskirk et al. 1988). In addition, heat generated by martens while foraging should lower T_{lc}, as it does for weasels (Sandell 1989), and may put martens in thermal neutrality. In winter, martens thermoregulate behaviorally (Buskirk et al. 1989; Taylor and Buskirk 1994), alternating among positions relative to the snow surface and among forest types to minimize thermal losses while resting. Martens are thought to maximize foraging efficiency in winter by investigating sites where coarse woody debris penetrates the snow surface, providing olfactory information about prey and access to subnivean spaces.

Powell (1979b, 1981) modeled energy budgets of fishers, estimated parameter values using captive fishers trained to run on a treadmill while connected to an oxygen analyzer, and tested the model using field data. The fishers he studied in Michigan's Upper Peninsula appeared to be on a positive energy budget preying predominantly on snowshoe hares and porcupines (*Erethizon dorsatum*) and scavenging dead white-tailed deer (*Odocoileus virginianus*). Patterns of sexual dimorphism in that fisher population were consistent with Moors's (1974) hypothesis that females are small to minimize energy expenditure for maintenance during reproduction, whereas sexual selection selects for large males. In addition, daily energy expenditure of a female with kits is predicted to exceed that of a large male (Powell and Leonard 1983), but lifetime energy expenditure is more equal. Thus, large sexual dimorphism may equalize lifetime reproductive costs for males and females.

BEHAVIOR

The time that an animal spends active and the timing of that activity are influenced by proximate environmental events, such as a recent meal and weather, but the animal's endogenous circadian pacemaker favors activity at times of day (i.e., night, day, dawn, and dusk) that are favored by natural selection (Daan and Aschoff 1982; Zielinski 2000). Martens have been estimated to be active as little as 16% of the day in the winter to 60% in the summer (Thompson and Colgan 1994). Powell (1979b, 1981) estimated that fishers are active about 30% of the day in winter. The marten's patterns of activity vary with the activity budgets of its dominant prey, which vary seasonally and geographically (Hauptman 1979; Zielinski et al. 1983; Zielinski 2000). Consequently, martens are diurnal in winter and crepuscular in summer (More 1978), or largely diurnal in summer and nocturnal in winter (Zielinski et al. 1983), or diurnal in summer (Martin 1987), or arythmic in summer and diurnal in winter (Thompson and Colgan 1994). Fishers are characterized as generally crepuscular, though their activity patterns are variable (Kelly 1977; Powell 1979b, 1981; Johnson 1984; Arthur and Krohn 1991). Activity in male fishers increases during the mating season (Arthur and Krohn 1991). Activity of females is least during pregnancy and increases with the age of their kits (Leonard 1980).

FOOD HABITS

Foods. Diets of martens and fishers are similar in that both eat primarily rodents, lagomorphs, birds, and sometimes insects, fruits, and carrion when available (Martin 1994). Individual studies reveal diverse diets, suggesting that these mammals are opportunistic predators influenced by local abundance and availability of potential prey (Ben-David et al. 1997; Powell and Zielinski 1994; Powell et al. 1997b). This flexibility explains why diets are more diverse in summer than in winter (Buskirk and Ruggierro 1994; Martin 1994; Powell and Zielinski 1994) and in southern and eastern than in northern and western regions (Zielinski et al. 1983, 1999; Buskirk and MacDonald 1984; Martin 1994). Although members of both species eat a large variety of foods, only a few items dominate and the abundance of these items in particular may directly affect the abundance of martens (Weckwerth and Hawley 1962) and fishers (Powell 1993).

Voles (*Clethrionomys* spp., *Microtus* spp., and *Phenacomys* spp.) are the dominant prey of martens across their geographic range (Buskirk and Ruggierro 1994; Martin 1994). Because food preferences can be determined only by comparing what is available with what is consumed, few studies can distinguish foods that are consumed from those that are actually preferred. *Microtus* spp., however, appear to be preferred prey because, unlike red-backed voles (*Clethrionomys* spp.), deer mice (*Peromyscus* spp.) and shrews (*Sorex* spp., *Blarina* spp.), *Microtus* are consumed in a proportion greater than that of their availability (Weckwerth and Hawley 1962; Buskirk and MacDonald 1984). Prevalence of microtines in the diet may increase with latitude; voles constitute the greatest proportion of the diet of martens in Alaska and the Yukon (Douglas et al. 1983; Buskirk and MacDonald 1984).

Ben-David et al. (1997) suggested that preference for small mammals as prey appears to increase when they are least abundant. Thompson and Colgan (1990) and Poole and Graf (1996), in contrast, believed that martens primarily forage for large prey (e.g., snowshoe hares) and that they capture small mammals proficiently, but incidentally. Other researchers have found that large prey constitute more of the winter than the summer diet (Zielinski et al. 1983; Thompson 1986), but this pattern may be a product of prey availability rather than preference. Fluctuations in the commercial harvest of marten pelts were correlated with the snowshoe hare cycle until around 1920 (Bulmer 1974, 1975). Martens have important ecological relationships with red squirrels (*Tamiasciurus hudsonicus*) and Douglas's squirrels (*T. douglasii*) (Buskirk 1984; Corn and Raphael 1992; Sherburne and Bissonnette 1993) and in some studies these species constitute a significant part of the diet (Martin 1994). In coastal areas, fish and birds appear to substitute for small mammal prey (Nagorsen et al. 1989, 1991).

Fishers eat snowshoe hares and porcupines in most places where the diet has been studied (Powell 1993; Martin 1994). The fisher–porcupine predator–prey system has been the subject of considerable study (reviewed by Powell 1993) and the importance of porcupines as prey for fishers is reflected in the evolution of unique hunting and killing behaviors (Powell and Brander 1977; Powell 1978). That snowshoe hares are important prey is suggested by the correlation between the number of commercially harvested fisher pelts and the 10-year cycle of hare abundance (Bulmer 1974, 1975). Where snowshoe hares and porcupines are uncommon, the diets of fishers become more diverse and can include significant quantities of other mammals, reptiles, insects, and fungi (Zielinski et al. 1999). Small mammals are frequent components of the fisher's diet, but, unlike the diet of the marten, voles are not always dominant in this category (Martin 1994). Diets of fishers are consistent with optimal diet choices (Powell 1993).

Larger size of fishers generally makes more prey species potentially available to them, thus their diets are usually more diverse than those of martens (Martin 1994). Males of both species also appear to have a greater range of prey sizes available to them (Martin 1994; Poole and Graf 1996), but despite suggestions to the contrary (Rosenzweig 1966), no consistent differences in the diet exist between the sexes in either species (Thompson and Colgan 1990; Powell 1993) nor does evidence exist for morphological change induced by resource partitioning (Holmes and Powell 1994). Diversity of the diets of both species decreases when large prey (e.g., snowshoe hares) are consumed, which typically occurs in the winter (Buskirk and Ruggiero 1994; Martin 1994) and in northern portions of the ranges (Nagorsen et al. 1989).

Both species eat fruits and disperse seeds (Martin 1994; Hickey et al. 1999). Fruits of shrubs and trees can constitute as much as 30% of the summer diet (Stevens 1968), and two California studies reported evidence for the consumption by fishers of the fruiting bodies of false truffles (*Rhizopogon* spp.) (Grenfell and Fasenfest 1979; Zielinski et al. 1999). Davison (1975) could not induce captive fishers to eat fruit, which suggests that they do so only as a last resort. Martens and fishers scavenge carrion readily (e.g., Powell 1979b, 1981; Martin 1994; Ben-David et al. 1997) and are easily lured to traps, track plates, or camera stations using meat as bait (Strickland and Douglas 1987; Zielinski and Kucera 1995).

Foraging. Martens and fishers are active year-round, have a demanding metabolism (Davison et al. 1978; Buskirk et al. 1988; Powell 1993; Harlow 1994), and, especially martens, store very little energy as fat (Buskirk and Harlow 1989). Thus, selection is strong for efficient foraging behavior, particularly in winter. Both species use a variety of hunting methods to maximize rates of prey capture. They respond to variation in forest patch structure, physical structure near the ground, prey abundance, and probably prey behaviors (Buskirk and Powell 1994). They search for prey where prey are abundant and available (More 1978; Powell 1981; Spencer et al. 1983; Buskirk and MacDonald 1984; Arthur et al. 1989), but it is not clear whether they search for prey that are easy to catch or instead search habitats in which prey are vulnerable to capture (Buskirk and Powell 1994). Both species climb and move through tree canopies proficiently, but forage predominantly on the ground (Clark and Campbell 1976; Powell 1980; Raine 1981; Zielinski et al. 1983). During winter, martens, more than fishers, forage beneath the snow for small mammals. Unlike weasels, however, martens and fishers are too large to pursue microtine rodents in their burrows. Subnivean access points used by martens are frequently associated with the middens of red squirrels (Sherburne and Bissonette 1993). Fishers rarely forage under the snow, undoubtedly because their large body size makes travel through snow and in subnivean spaces difficult (Raine 1983; Krohn et al. 1995).

Fishers and martens appear to share two types of foraging: area-restricted search and directional search. The former is used opportunistically to surprise prey in temporary refuges and is characterized by "zigzag" search typical of the mustelines (Powell 1978). The latter is used by martens to investigate tree squirrel activity centers (Corn and Raphael 1992; Sherburne and Bissonette 1993) and by fishers to investigate snowshoe hare habitat (Powell 1978, 1993). Both species minimize the amount of time spent foraging in forest openings (Buskirk and Powell 1994; Buskirk and Ruggierro 1994; Powell and Zielinski 1994). Martens and fishers do not generally pursue prey long distances (Powell 1993), although Raine (1981) documented two instances of a fisher chasing a snowshoe hare over 1 km. Neither fishers nor martens use the "mouse pounce" hunting behavior that is so successful for canids (Buskirk and Powell 1994). Instead, evidence from following tracks in snow indicates that prey are surprised in refuges, sometimes after being tracked in the snow, and are captured only if they are overtaken quickly. Martens use a variety of additional techniques, including ambush, excavation, and hunting perches (Spencer and Zielinski 1983).

MORTALITY

Fishers in captivity have lived longer than 10 years (Bronx Zoo, New York, unpublished records), and Arthur et al. (1992) livetrapped a wild fisher estimated to be 10½ years old. Other studies have found no fishers older than 7 years (Weckwerth and Wright 1968; Kelly 1977).

Natural causes of mortality for fishers and martens are poorly known. Fishers exhibit a low incidence of disease, although enough fishers have been livetrapped to document sarcoptic mange (O'Meara et al. 1960; Coulter 1966), Aleutian disease, leptospirosis, toxoplasmosis, and trichinosis (Douglas and Strickland 1987). Fishers also exhibit low levels of parasitism (Hamilton and Cook 1955), and those animals with parasites have low infestation (Coulter 1966). Fourteen genera of nematodes, two of cestodes, two of trematodes, and a protozoan have been documented in fishers (Powell 1993). Fishers in Ontario carried detectable levels of DDT, chlordane, dieldrin, mirex, and polychlorinated biphenyls (Douglas and Strickland 1987). Five genera of fleas were collected from martens in California, and 4 of 18 individual martens were positive for plague antibodies (Zielinski 1984). Helminth parasites are common, at least in western populations of martens (Holmes 1963; Hoberg et al. 1990; Foreyt and Lagerquist 1993).

Little evidence exists that healthy fishers are subject to predation by other predators, though occasional mortality from other predators has been noted (Buck et al. 1983; Douglas and Strickland 1987; Krohn et al. 1994). Roy (1991), however, reported that a reintroduction of fishers to the Cabinet Mountains of Montana was hindered by predation on fishers by predators they had not experienced in their original range, including mountain lion (*Puma concolor*), coyote (*Canis latrans*), wolverine (*Gulo gulo*), golden eagle (*Aquila chrysaetos*), and lynx (*Lynx canadensis*).

Martens may be more subject to predation than fishers. Eight of 15 martens studied by Hodgman et al. (1997) that died in an area without trapping were killed by mammalian and avian predators. Similarly, 22 of 35 martens studied by Bull and Heater (1995, 2001) in Oregon died, and 18 of these were killed by bobcats (*Lynx rufus*), raptors, and other martens. Bull and Heater also found that the probability of survival of martens >9 months old was 0.56 for 1 year, 0.38 for 2 years, 0.22 for 3 years, and 0.16 for 4 years, which yields an average survival of approximately 0.65 per year over 4 years.

MANAGEMENT AND CONSERVATION

Conservation of fishers and martens has two areas of emphasis: (1) concern about populations that are vulnerable to extirpation and (2) interest in the sustainable harvest of animals from healthy populations for their fur. The particular emphasis depends on the size of the population and the historical use of, and current interest in, fur as a commodity in a particular region. In some instances, the status of a species can change from rare and protected to abundant and commercially harvested over a relatively short period (e.g., fisher: Coulter 1966; Kohn et al. 1993; Powell 1993). These recoveries occur when animals recolonize improved habitat, as in the northeastern and midwestern United States, where fishers have responded to successional change (Balser and Longley 1966; Brander and Books 1973; Powell 1993), and as a result of reintroductions of animals into favorable habitat in unoccupied portions of their range (Powell 1993; Slough 1994). Martens are trapped for their fur in all but a few states and provinces in the United States and Canada, whereas fishers are protected throughout most of the western states (but not provinces) and legally trapped throughout Canada and the midwestern and eastern United States (Ruggiero et al. 1994; Ray 2000). In the past, management of fishers included using them to control porcupine populations to reduce timber damage (Powell 1993).

Protected Populations. When populations become protected from trapping for fur, important information about their distribution and demography is no longer available. A number of nonlethal approaches, such as track plates and camera stations, have substituted for trapping as a means of determining the status of martens and fishers (e.g., Raphael 1994; Zielinski and Kucera 1995; Foran et al. 1997). These methods have been used to map the current distribution in regions where commercial trapping no longer occurs (e.g. Kucera et al. 1995; Zielinski et al. 1995) and to produce habitat models (Carroll et al. 1999) that can be used to assess and monitor change in habitat suitability over time.

The concept of a metapopulation of populations (Levins 1968; Wright 1978; Harrison and Taylor 1997) linked by occasional dispersal may be especially applicable to conservation of fishers and martens in the fragmented habitat in the western United States. The discontinous pattern of habitat for fishers in the West (e.g., Weir and Harestad 1997; Carroll et al. 1999) and the pattern of marten occurrence across western mountain ranges (Wisz 1999) are examples of this phenomenon operating at very large spatial and temporal scales. On a smaller scale, evidence suggests that martens abandon, or fail to colonize, home range-sized landscapes with less than about 60% mature forest cover (Bissonette et al. 1997; Chapin et al. 1998; Hargis et al. 1999; Payer 1999; Potvin et al. 2000). This reinforces earlier studies showing that martens avoid regenerating clearcuts for several decades (Campbell 1979; Thompson and Harestad 1994). Fishers demonstrate a similar avoidance of clearcut areas, especially in the West (Harris et al. 1982; Buck et al. 1994), and are associated with unfragmented forest (Rosenberg and Raphael 1986; Carroll et al. 1999). Martens may exhibit the greatest selection of habitat at the smallest (microhabitat) and the largest (landscape) scales (Minta et al. 1999), which suggests that managers should provide adequate densities of snags, large trees, and logs and also be conscious of the arrangement, composition, and connectivity of blocks of habitat (Bissonette et al. 1989). Conservation of marten and fisher populations at risk will require planning to protect large blocks of mature forest and the connections between them (Bissonette and Broekhuizen 1995).

The following subspecies are attracting conservation concern due either to their small population sizes or to their vulnerability to human activities: *M. a. humboldtensis* in northwestern California (Zielinski et al. 2001), *M. a. atrata* in Newfoundland (Burnett et al. 1989), *M. a. americana* in eastern Canada (Thompson 1991), and *M. p. pacifica* in the western United States (Powell and Zielinski 1994; Zielinski et al. 1995). *M. a. humboldtensis* was exploited heavily in the early 1900s (Twining and Hensley 1947) and occurs in a region where much of the original redwood forest has been harvested and is managed by private timber companies under short-rotation harvests (Thornburgh et al. 2000; Zielinski et al. 2001). *M. a. atrata* and *M. a. americana* in eastern Canada have suffered from timber harvest and trapping, and *M. a. atrata* is also frequently killed in snares set for snowshoe hares in Newfoundland. *M. p. pacifica* has been extirpated from most of Washington and Oregon (Aubry and Houston 1992; Drew et al. 2003; Stinson and Lewis 1998) and from the northern Sierra Nevada (Zielinski et al. 1995), presumably because of the historical effect of trapping and the widespread effects of clearcut timber harvest. Reintroductions of fishers into apparently suitable habitats in the western United States have not resulted in the success achieved in the eastern United States (Irvine et al. 1964; Roy 1991; Hienemeyer 1993; Powell 1993; Aubry and Lewis 2003).

Trapped Populations. Trapping of martens and fishers is controlled differently in the jurisdictions across the species's ranges using various combinations of limiting the number of licensed trappers, varying the time and length of trapping seasons, and setting quotas. Trapping may be limited to November and December, when pelts are prime. Such timing of trapping also targets young animals and may remove many animals that would die of natural causes later in the winter (Strickland et al. 1982a, 1982b; Krohn et al. 1994; Strickland 1994).

Fishers and martens are easily overharvested, even in a short, early trapping season, especially when trapping intensity is heavy. Such overharvesting led, at least in part, to the reductions of the ranges of both fishers and martens through the early 1900s. Where trapping is heavy, limiting the number of licensed trappers and setting quotas is necessary (Strickland et al. 1982a, 1982b).

Determining when trapping restrictions are necessary is not easy. Strickland (1994) reported that ratios of juveniles to adult females, juveniles to adults, and females to males had been used successfully to estimate the percentage of the populations being harvested. The first two ratios decrease and the third increases as greater percentages of populations are harvested. One must establish these relationships, however, before this approach can be used to regulate harvest, and some populations appear not to maintain stable relationships (Fortin and Cantin 1994). Fryxell et al. (2001) used age distribution in the harvest to back-calculate minimum number of martens alive in previous years and thereby set harvest quotas. Ratios of juveniles to adults and age distributions depend on reproduction in the preceding spring and survival of juveniles, both of which depend on prey abundance. Prey abundance varies by orders of magnitude from year to year for fishers and martens (reviewed by Powell 1993, 1994a), varies with changes in habitat quality, and affects sex ratio of martens (Payer 1999).

Recent research indicates that habitat quality interacts with trapping and that habitat quality must be considered whenever fishers and martens are trapped, especially martens. Extensive timber harvest leads to reduced marten populations and may reduce carrying capacity by half (Fuller 1999; Payer 1999). In addition, trapping mortality appears to be additive to natural mortality in industrial forests (Payer 1999). Responses of martens to habitat change and to forest fragmentation may not be linear (Hargis and Bissonette 1997). Consequently, managers must be alert to and avoid habitat and mortality thresholds when establishing trapping quotas. In some forests, even very low levels of trapping may limit marten (Schneider 1997) and fisher (Powell 1979c) populations.

A proposal by deVos (1951) to manage fisher and marten populations using refuges has received considerable discussion (Archibald and Jessup 1984; Thompson and Colgan 1987; Buskirk 1993) and the strategy has been proposed for managing martens in areas where management is highly contended (e.g., Tongass National Forest; USDA. Forest Service 1993). Refuges of appropriate size can function to maintain viable populations of martens and fishers from which juveniles disperse, thereby providing colonizers for refuges with low populations and supplementing trapped populations between refuges (Archibald and Jessup 1984; Thompson and Colgan 1987; Hodgman et al. 1994). If refuges are established, however, but populations not monitored, managers may assume that populations are stable within refuges when they are not and that animals can travel between refuges when they cannot (Buskirk 1993; Hodgman et al. 1997). Sizes of refuges, habitat quality, variability among and within refuges, and genetic variability of the target species affect the source–sink dynamics (Pulliam 1988) of a refuge system of management and must be considered in any such management plan for fishers and martens. In areas with high road densities and high trapping pressure, a refuge system alone probably will not suffice (Hodgman et al. 1997).

RESEARCH NEEDS

As is the case with most mammals discussed in this volume, martens and fishers have much to gain from research that (1) builds on inductions, deductions, and solidly grounded hunches resulting from field research and (2) tests ecological, genetic, developmental, and evolutionary theory on martens and fishers, which inevitably differ from the animals used to develop the theory and from the animals usually used to test it. Intriguing theory relative to martens and fishers deals with the relationship between habitat and fitness, especially related to multiple habitat scales (microhabitat, home range, landscape, region).

Some of the most compelling new knowledge about carnivore ecology involves competitive interactions. Competition, particularly interference competition, appears to affect carnivore communities in powerful ways, yet the ways in which martens and fishers participate in these interactions is poorly understood. In addition, carnivores may have powerful top-down effects on communities and ecosystems, effects that may even affect primary production through trophic cascades.

Management agencies are particularly interested in understanding habitat requirements of martens and fishers. Specifically, region-specific responses of martens and fishers and their prey to novel patterns of landscape alteration, timber harvest, and fire management must be learned. Understanding how martens and fishers view habitat from the framework of source–sink theory may fundamentally alter our understanding of how martens and fishers coexist with managed forests.

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